REVIEW ARTICLE

First description of the male of *Psechrus jinggangensis* Wang & Yin, 2001 from China

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Abstract

The male of *Psechrus jinggangensis* Wang & Yin, 2001 is described for the first time based on many specimens from its type locality, Jinggang Mountain National Nature Reserve, Ji'an City, Jiangxi province, China. Detailed illustrations, SEM images, and distribution map are given.

Keywords

Distribution, Jiangxi Province, Jinggang Mountain National Nature Reserve, lace-sheet spiders, taxonomy

Introduction

The spider family Psechridae Simon, 1890 is one of the smallest families of spiders. Currently recorded mainly from Southeast Asia, it comprises two genera, namely *Fecenia* Simon, 1887 and *Psechrus* Thorell, 1878, and 61 species (WSC 2021). They are characterised by the medium-sized to large body and a well-developed cribellum and calamistrum. While *Fecenia* construct a pseudo-orb web with a curled-leaf re-

treat, *Psechrus* build a conspicuously large horizontal sheet-web with a funnel-shaped retreat (with a depth from 20 cm to 1.8 m) (Jocqué and Dippenaar-Schoeman 2006; Bayer 2012). *Psechrus* usually occur in shady habitats in forests, among rocky areas, soil cracks, around cave entrances at escarpments, road cuts, or ditches. To some extent, their webs can be divided into two parts, a horizontal sheet-web and a funnel-shaped web. Horizontal sheet-webs occur in both shaded and full-sun habitats, but funnel-shaped webs only occur hidden in shaded, moist habitats. *Psechrus* feed on moths, beetles, locusts, etc. Their efficient predation, high alertness, and reproductive capacity (Xu and Wang 1983) allow them to control a particularly food-rich patch of habitat, which contributes to their wide distribution in tropical Asia, including parts of China and India (WSC 2021).

The genus *Psechrus* was erected by Thorell (1878) based on the female specimens of *Tegenaria argentata* Doleschall, 1857 from Indonesia. More details of the morphological characters of this genus were not revealed until much later, in a publication by Bayer (2012). Subsequently, the genus *Psechrus* is well understood based on the characters of 46 species, divided in eight groups: the *argentatus* group, *mulu* group, *annulatus* group, *singaporensis* group, *ancoralis* group, *himalayanus* group, *sinensis* group (which includes *Psechrus jinggangensis* Wang & Yin, 2001), and the *torvus* group (Bayer 2012). Currently, it is a diverse genus with 57 species mainly distributed in tropical Asia, and more than a quarter of these (17 species) are described from China (WSC 2021). However, three species are still only known from one sex, namely *Psechrus fuscai* Bayer, 2012, *P. jinggangensis*, and *P. kenting* Yoshida, 2009. For *P. jinggangensis*, the male has not been found since this species was described two decades ago. The male is described for the first time by us.

During the past seven years, several expeditions to the Jinggang Mountain National Nature Reserve in Jiangxi province, China, have been made by the authors, and many *Psechrus* specimens were collected. The results of these expeditions suggest that either other *Psechrus* spp., or non-*Psechrus* spp., were found. These specimens have allowed us to provide herein natural history photographs, habitus illustrations, as well as SEM and genitalia images.

Materials and methods

We attempted to examine the holotype from Hunan Normal University, where it was reported and had been deposited (Wang and Yin 2001), but we were unable to find it, and it may be lost. Specimens were examined using a Zeiss Stereo Discovery V12 stereomicroscope with Zoom Microscope System. Additional details were studied using a Zeiss Axio Scope A1 compound microscope with a KUY NICE CCD camera. Both the male palps and female genitalia were detached from the spider body and observed in 80–85% ethanol. For SEM photographs, the specimens were kept under natural dry conditions, sprayed with gold with a small ion-sputtering apparatus ETD-2000, and photographed with a Zeiss EVO LS15 scanning electron microscope. The speci-

mens not sprayed with gold were stored in 80% ethanol after SEM. All specimens are deposited in Animal Specimen Museum, College of Life Science, Jinggangshan University (ASM-JGSU).

All morphological measurements were taken using a stereomicroscope (AxioVision SE64 Rel. 4.8.3) and given in millimetres. The body length of each specimen does not include the spinnerets. Leg measurements are given as total length (femur, patella, tibia, metatarsus, tarsus).

Terminology of the male and female genitalia follows Bayer (2012). The abbreviations used in the text and figures are as follows:

Body

Cde	cheliceral denticles;
OL	opisthosoma length;
OW	opisthosoma width;
PL	prosoma length;
PW	prosoma width;
TL	total length.

Eyes

ALE	anterior lateral eye;
AME	anterior median eye;
AW	anterior width;
MOA	median ocular area;
PLE	posterior lateral eye;
PME	posterior median eye;
PW	posterior width.

Male palp

| Con | conductor; |

EB	embolic base;
EBA	embolic basal apophysis;
Em	embolus;
Sco	scopula;
SD	sperm duct;
Se	serrula;
St	subtegulum;
Te	tegulum.

Epigyne

CD	copulatory duct;
CO	copulatory opening;
EF	epigynal field;
FD	fertilisation duct;
LL	lateral lobe;
MS	median septum;
SH	spermathecal head.

Legs

| Mac | macrosetae. |

Taxonomy

Family Psechridae Simon, 1890
Genus *Psechrus* Thorell, 1878

***Psechrus jinggangensis* Wang & Yin, 2001**
Figures 1–9

Psechrus jinggangensis Wang & Yin, 2001: 334, figs 11, 12; Bayer 2012: 112, fig. 61a, b.

Material examined. CHINA – Jiangxi Province • 1 ♂ (Pse-16), Ji'an City, Jinggangshan County Level City, Ciping Town, Dajing Village, Jinggang Mountain National Nature Reserve, 26°33'21.70"N, 114°07'20.08"E, 906 m, 3 Aug. 2020, Ke-ke Liu et al. leg.; 1 pre-subadult female (Pse-17), with same data as previous; 1 pre-subadult female (Pse-1), Shiliao Cave, same locality, 3 Aug. 2019, Ke-ke Liu et al. leg.; 1 ♀ (Pse-2), with same data as previous; 1 pre-subadult female (Pse-4), with same data as previous; 1 pre-subadult female (Pse-9), with same data as previous; 1 ♂ (Pse-12), same locality, 1 Nov. 2019, Zhi-wu Chen and Dan-chen Zhao leg.; 1 pre-subadult female (Pse-14), same locality, 22 Jul.2020, Ke-ke Liu et al. leg.; 1 pre-subadult female (Pse-18), same locality, 4 Jul. 2020, Ke-ke Liu et al. leg.; 1 ♀ (Pse-22), same locality, Xiaojing Village, Longtan Scenic Spot, 26°35'02.40"N, 114°08'02.4"E, 945 m, 31 May 2014, Ke-ke Liu et al. leg.; 1 ♀ (Pse-34), with same data as previous; 1 ♀ (Pse-23), same locality, 26°35'06.0"N, 114°08'06.0"E, 989 m, 1 Jun. 2014; 1 ♀ (Pse-35), with same data as previous; 1 ♀ (Pse-38), with same data as previous; 1 ♀ (Pse-40), with same data as previous; 1 ♀ (Pse-41), with same data as previous; 1 ♀ (Pse-32), same locality, 26°35'31.20"N, 114°08'13.2"E, 934 m, 2 Aug. 2014, Ke-ke Liu et al. leg.; 1 ♀ (Pse-39), with same data as previous; 1 ♀ (Pse-36), same locality, Huangyangjie Scenic Spot, 26°38'13.2"N, 114°05'02.4"E, 898 m, 3 Aug. 2014, Ke-ke Liu et al. leg.; 1 ♂, 1 pre-subadult female (Pse-25), same locality, Jingzhu Mountain, 26°29'45.60"N, 114°04'44.4"E, 1146 m, 20 Dec. 2015, Ke-ke Liu et al. leg.; 1 pre-subadult female (Pse-46), with same data as previous; 1 ♂ (Pse-26), Luofu Town, Changguling Forest Farm, 26°50'38.4"N, 114°14'09.6"E, 602 m, 29 May 2017, Ke-ke Liu et al. leg.

Diagnosis. The male of this species resembles both *Psechrus changminae* Zhang et al., 2016 (see Feng et al. 2016: 181, fig. 2b–d) and *P. clavis* Bayer, 2012 (see Bayer 2012: 121, fig. 66a–c) in having a membranous conductor with a triangular tip and the presence of five small denticles between cheliceral teeth (three in *P. changminae*). It can be separated by a more elongated tegulum along the cymbial alveolus axis (relatively expanded in *P. changminae* and *P. clavis*), an embolic base with a moderate constriction and a small apophysis (a strong constriction and a long embolic basal apophysis in *P. changminae*; an indistinct constriction and without embolic basal apophysis in *P. clavis*), and the embolus extending along the retrolateral part of the base (sub-centraxonial in *P. changminae*; sub-retrolateral in *P. clavis*). The female resembles those of *P. changminae* (see Feng et al. 2016: 181, fig. 2f, g) and *P. tingpingensis* Yin et al., 1985 (see Yin et al. 1985: 23, fig. 3C, D) in having an epigynal septum with a narrow anterior and a broad posterior part in the small globose spermathecae, but differs by the copulatory ducts separated by 1/10 of the anterior width of septum (more than 1/2 in *P. changminae*, closely touching in *P. tingpingensis*) and without a strong medial folded part (clearly present in *P. changminae* and *P. tingpingensis*), and the ratio > 1 between spermathecal head length and the spermathecal diameter (<1 in *P. changminae*; = 1 in *P. tingpingensis*) (Fig. 4C, D).

Description. Male. *Habitus* as in Figure 1A, B. Total length 13.57. Prosoma (Fig. 1A) length 6.32, width 4.72, densely covered white feathery scales. Eye (Fig. 1A) sizes and interdistances: AME 0.23; ALE 0.31; PME 0.37; PLE 0.39; AME–AME 0.18; AME–ALE 0.12; PME–PME 0.29; ALE–ALE 0.91; PME–PLE 0.28; PLE–
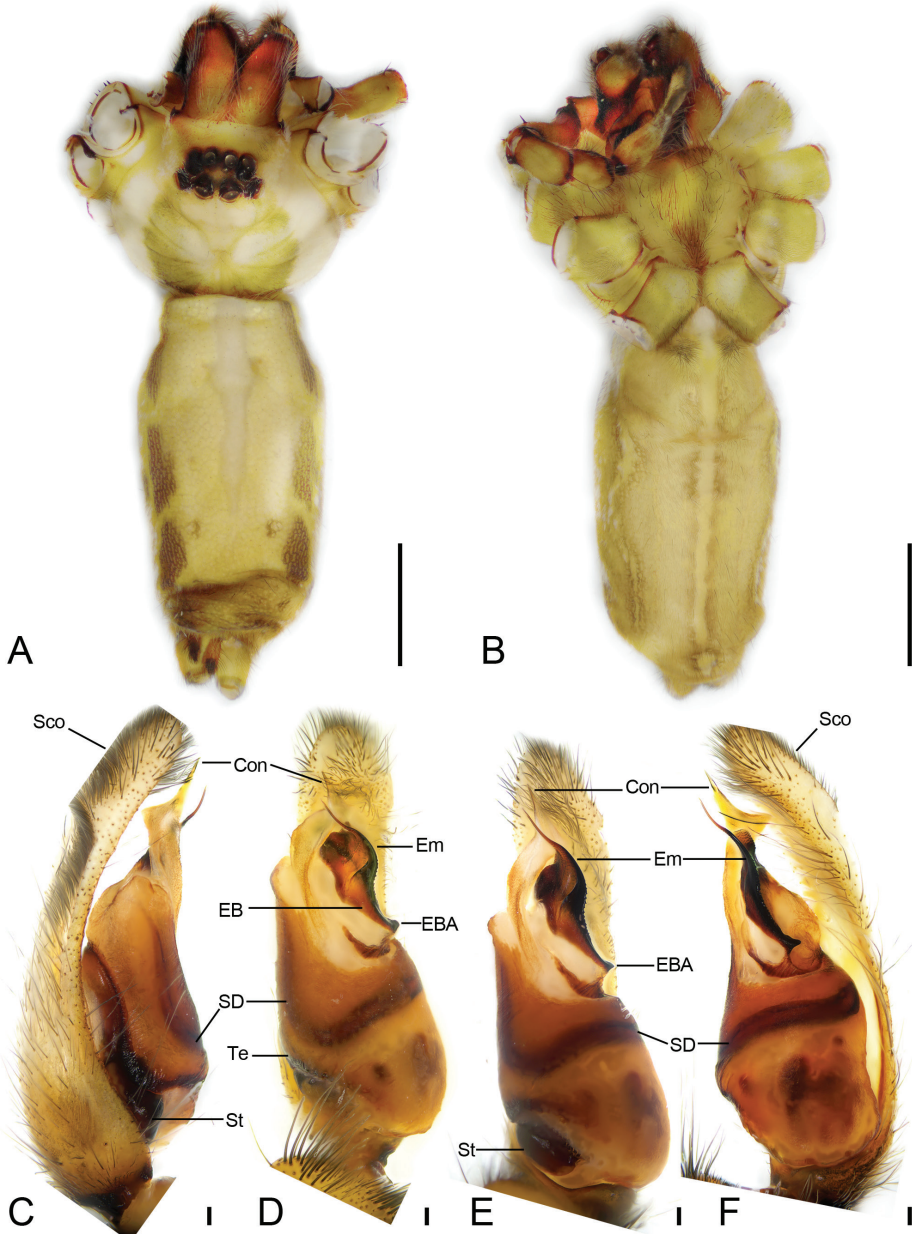
Figure 1. *Psechrus jinggangensis*, male (Pse-16) **A** habitus, dorsal view **B** same, ventral view **C** left palp, prolateral view **D** same, ventral view, slightly prolateral **E** same, ventral view **F** same, retrolateral view. Scale bars: 0.25 mm (**A, B**), 0.1 mm (**C–F**). Abbreviations: Con – conductor, EB – embolic base, EBA – embolic basal apophysis, Em – embolus, Sco – scopula, SD – sperm duct, St – subtegulum, Te – tegulum.

PLE 1.58; ALE–PLE 0.29; AME–PME 0.48; AME–PLE 0.71. MOA: 0.99 long; 0.71 front width, 1.04 back width. Chelicerae (Fig. 1C, D) covered by dense setae, with three promarginal teeth and four retromarginal teeth and including five small denti-
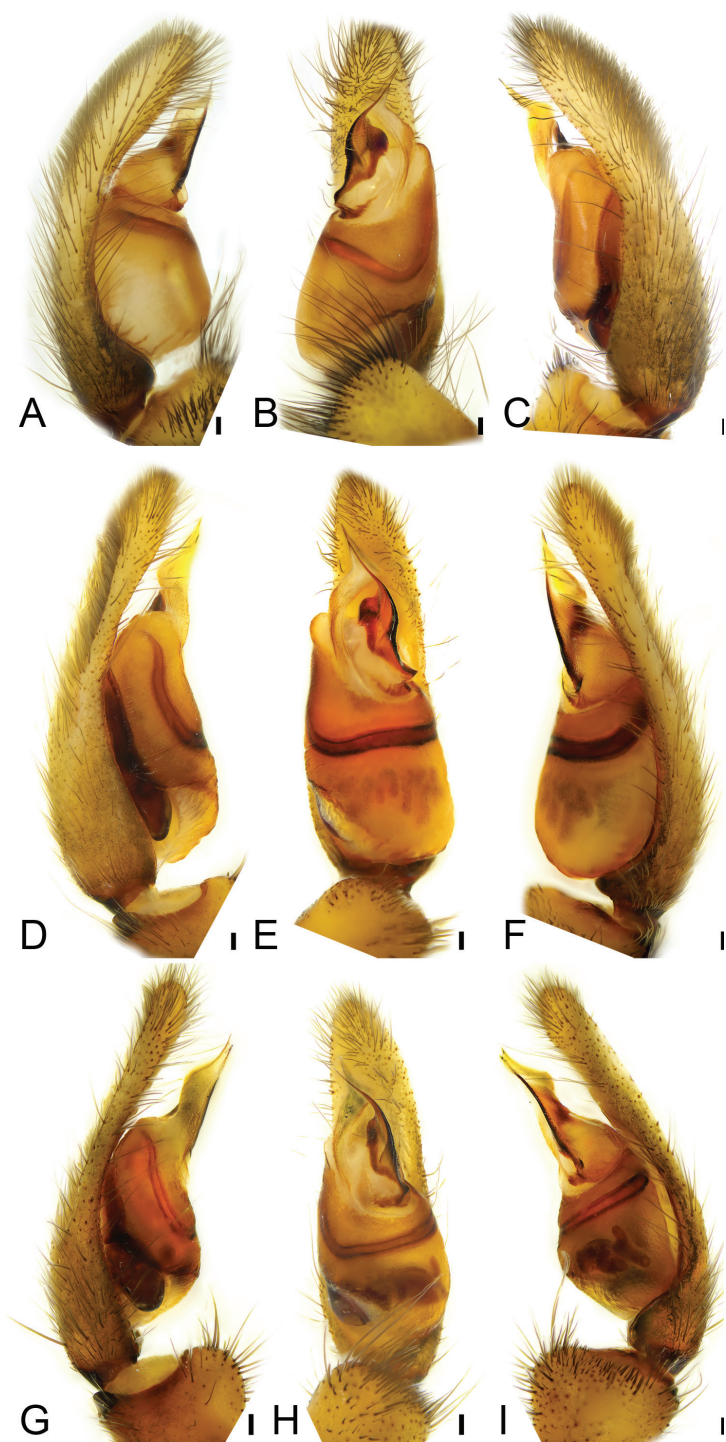
Figure 2. *Psechrus jinggangensis*, males. **A** right palp (Pse-12), prolateral view **B** same, ventral view **C** same, retrolateral view **D** left palp (Pse-25), prolateral view **E** same, ventral view **F** same, retrolateral view **G** left palp (Pse-26), prolateral view **H** same, ventral view **I** same, retrolateral view. Scale bars: 0.25 mm.
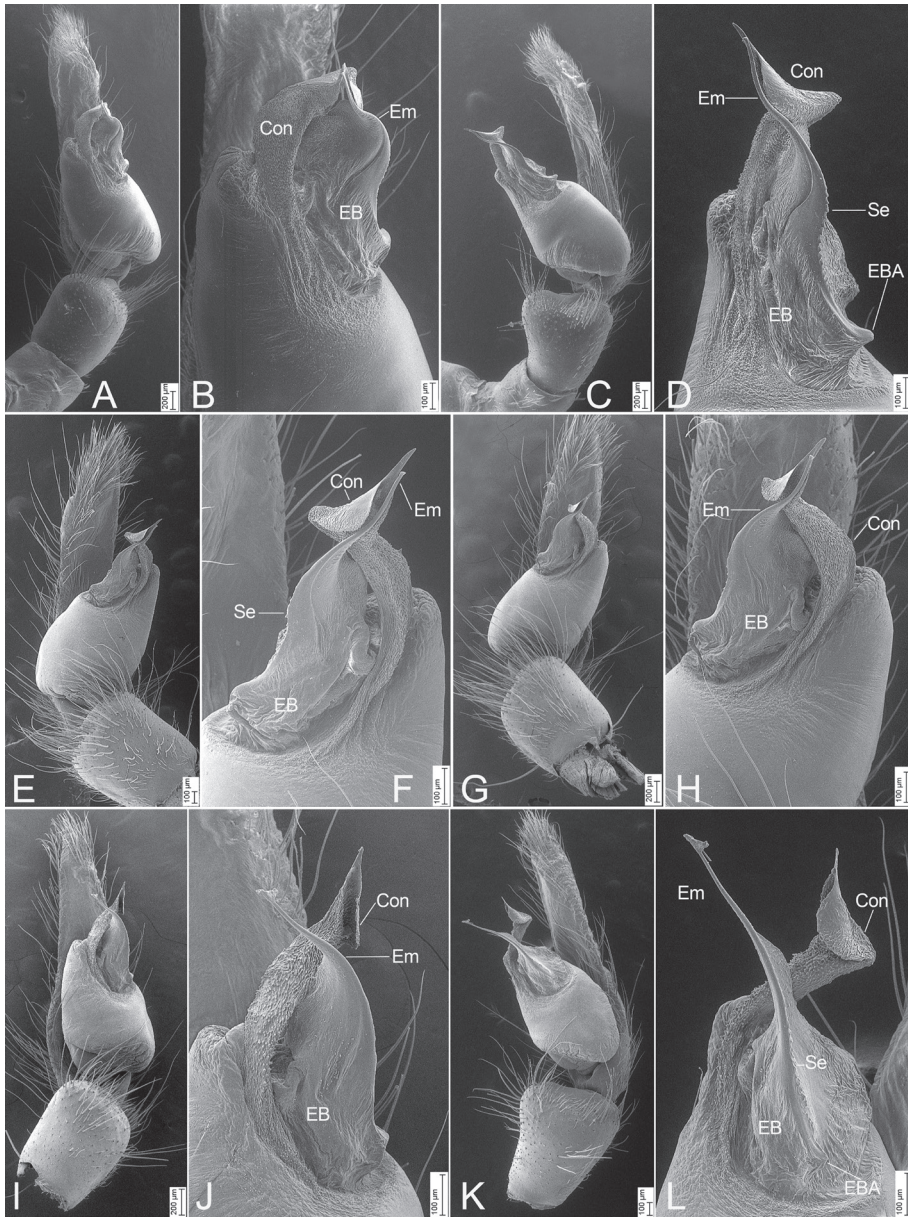
Figure 3. *Pschrus jinggangensis*, SEMs of males **A** left palp (Pse-16), ventral view, strongly prolateral **B** same, detail of conductor, embolic base and embolus, ventral view, strongly prolateral **C** same, retrolateral view, strongly ventral **D** same, detail of conductor, embolic base, embolic basal apophysis and embolus, retrolateral view, strongly ventral **E** right palp (Pse-12), prolateral view strongly ventral **F** same, detail of conductor, embolic base, embolic basal apophysis and embolus, prolateral view, strongly ventral **G** same, ventral view **H** same, detail of conductor, embolic base and embolus, ventral view **I** left palp (Pse-26), prolateral view, strongly ventral **J** same, detail of conductor, embolic base and embolus, prolateral view, strongly ventral **K** same, ventral view ventral view **L** same, detail of conductor, embolic base, embolic basal apophysis and embolus, retrolateral view, slightly retrolateral. Abbreviations: Con – conductor, EB – embolic base, EBA – embolic basal apophysis, Em – embolus, Se – serrula.
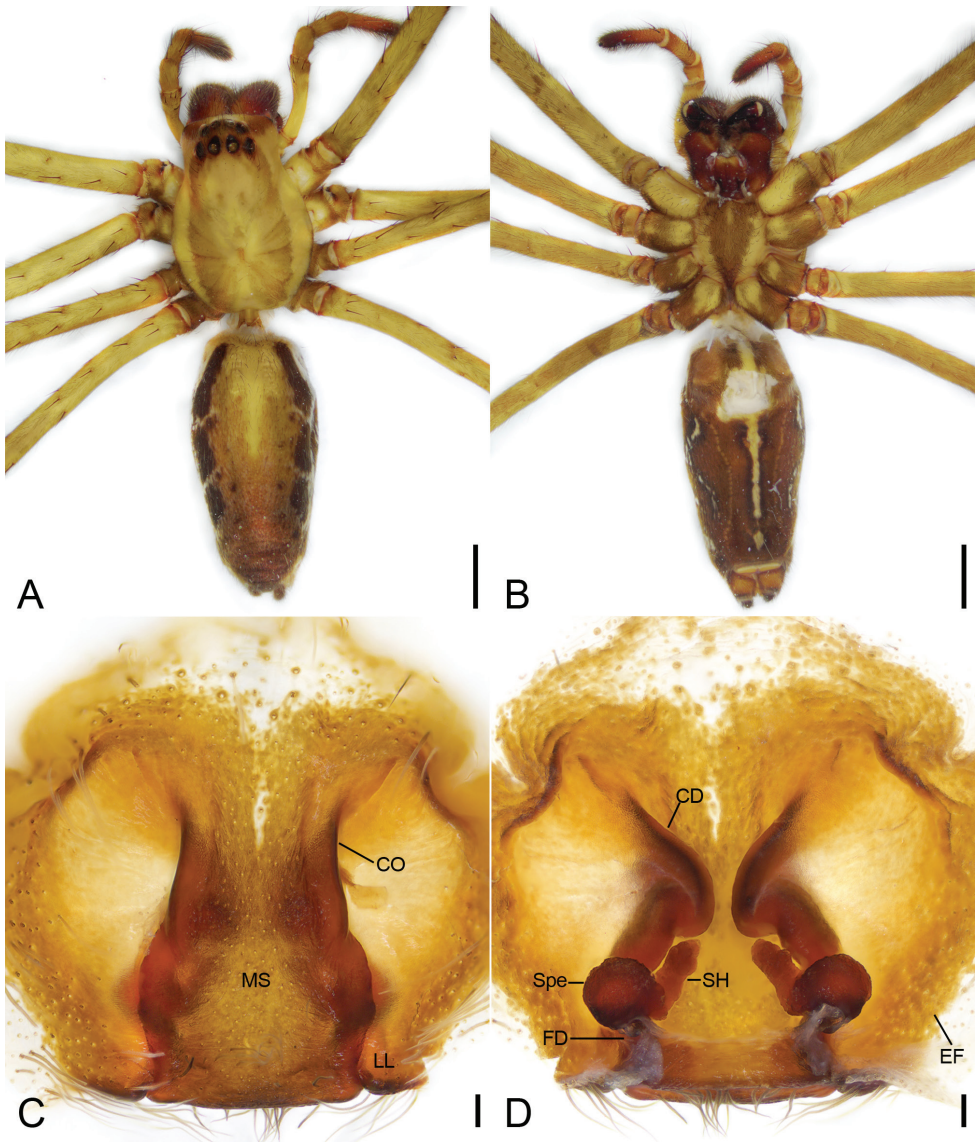
Figure 4. *Psechrus jinggangensis*, female (Pse-34) **A** habitus, dorsal view **B** same, ventral view **C** epigyne, ventral view **D** same, dorsal view. Scale bars: 0.25 mm (**A, B**), 0.1 mm (**C, D**). Abbreviations: CD – copulatory duct, CO – copulatory opening, EF – epigynal field, FD – fertilisation duct, MS – median septum, LL – lateral lobe, SH – spermathecal head, Spe – spermatheca.

cles between teeth. Endites (Fig. 1B), > 2× wider than their length, ectally with many long setae, median part clearly with a constriction. Labium (Fig. 1B) tongue-shaped, anteriorly with a row of strong setae, anterior margin procurved, subposterior part with a strong constriction. Sternum (Fig. 1B) oval, covered with dense setae, lateral margins with intercoxal extensions between coxae I and II, II and III, III and IV, poste-

Table 1. The variability in the number of small denticles between cheliceral teeth, body sizes (in mm), eye sizes, eye interdistances (in mm), and leg length (in mm) of *Psechrus jinggangensis*, males and females.

	Male (*n* = 4)	Female (*n* = 7)
CDe	4–7	6–9 (*n* = 8)
TL	9.67–13.57	13.16–20.82
PL	4.77–6.32	5.68–9.44
PW	3.72–4.72	4.57–6.41
OL	5.21–7.48	7.96–12.27
OW	2.23–3.74	4.05–7.45
AME	0.23–0.33	0.34–1.32
ALE	0.31–0.4	0.42–0.55
PME	0.35–0.41	0.43–0.55
PLE	0.35–0.45	0.42–0.59
AME-AME	0.11–0.18	0.18–0.24
AME-ALE	0.04–0.12	0.06–0.16
PME-PME	0.17–0.29	0.3–0.38
PME-PLE	0.26–0.28	0.38–0.54
AME-PME	0.39–0.48	0.56–0.69
AME-PLE	0.57–0.71	0.77–1.07
ALE-ALE	0.78–0.91	1.02–1.32
PLE-PLE	1.46–1.58	1.75–2.36
ALE-PLE	0.27–0.36	0.42–0.58
MOA L	0.94–1.17	1.18–1.59
MOA AW	0.67–0.75	0.79–1.06
MOA PW	0.88–1.04	1.15–1.41
Leg I	45.82–56.3 (*n* = 3)	37.66–49.76
Leg II	35.7–43.2	27.4–40.86
Leg III	22.75–29.26	21.84–40.75
Leg IV	35.71–43.56	28.78–39.55

riorly prolonged. Leg measurements: I 56.3 (14.73, 1.77, 16.09, 16.79, 6.92); II 43.2 (12.05, 1.95, 11.91, 12.59, 4.7); III 29.26 (8.72, 1.53, 7.28, 8.04, 3.69); IV 43.56 (11.98, 1.75, 11.56, 12.92, 5.35). Leg formula 1423. Opisthosoma length 7.46, width 3.69, hardened, with abundant short setae and feathery scales.

Colouration and pattern. Prosoma, anteriorly with a brown, procurved stripe along AER, lateral margins with an arched light stripe, from PER to posteromedial part with an oval dark area, subposteriorly with four paired radial striae around fovea. Chelicerae, endites, and labium red-brown. Sternum, medially with a clear coniform brown stripe from anterior margin extending to posteromedial part. Legs from yellow to brown. Opisthosoma, dorsum from yellow to greyish black, medially with light longitudinal cardiac stripe, lateral margins with three pairs of dark-brown stripes and white stripes, with the former separated by the latter; venter with a medial, longitudinal, yellow stripe from posterior part of pedicel extending to anterior area of cribellum, and two lines of shallow depressions from bilateral part of epigastric groove extending to sub-posterior part of opisthosoma.

Palp **(Figs 1C–F, 2A–I, 3A–D).** Palpal cymbium dorsally with very dense scopula, covering almost 1/2 of cymbium. Tegulum more than 2× longer than wide, with a clear
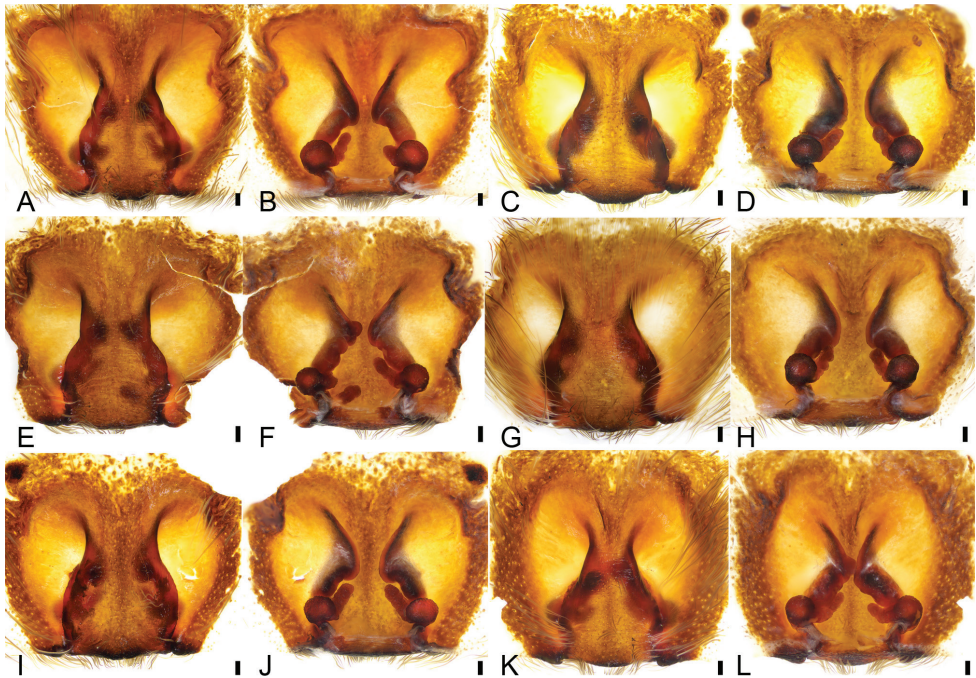
Figure 5. *Psechrus jinggangensis*, females **A** epigyne (Pse-35), ventral view **B** same, dorsal view **C** epigyne (Pse-36), ventral view **D** same, dorsal view **E** epigyne (Pse-37), ventral view **F** same, dorsal view **G** epigyne (Pse-23), ventral view **H** same, dorsal view **I** epigyne (Pse-32), ventral view **J** same, dorsal view **K** epigyne (Pse-33), ventral view **L** same, dorsal view. Scale bars: 0.1 mm.

constriction in subapical part, near the embolic base. Subtegulum strongly sclerotized, subtegular length less than tegular length in prolateral view, slightly less than posterior tegular width in ventral view. Sperm duct with V-shaped posterior part or absent in ventral view. Conductor membranous, with very dense denticles on the rough surface, slightly longer than embolus, arising from submedial part of tegulum, slightly curved retrolaterally and then pointing at the cymbial apex forming a triangular apex, with a groove on its tip. Embolic base broad, strongly sclerotized, with a small apophysis pointing retrolaterally. Embolus spine-like, extending from the subapical part of tegulum to cymbial subapex, retrolateral part strongly sclerotized, with a single row of serrula.

Female. *Habitus* as in Figure 4A, B. As in male, except as noted. Total length 18.89. Prosoma (Fig. 4A) length 8.11, width 5.55. Eye sizes and interdistances (Fig. 4A): AME 0.4; ALE 0.43; PME 0.45; PLE 0.43; AME–AME 0.23; AME–ALE 0.11; PME–PME 0.32; ALE–ALE 1.12; PME–PLE 0.54; PLE–PLE 2.07; ALE–PLE 0.58; AME–PME 0.67; AME–PLE 0.98. MOA: 1.41 long; 0.95 front width, 1.22 back width. Chelicerae (Fig. 4A, B) with six small denticles between teeth. Leg (Fig. 4A, B) measurements: I 49.43 (13.88, 2.72, 14.42, 12.82, 5.59); II 39.82 (11.65, 2.64, 10.81, 9.75, 4.97); III 27.51 (8.75, 2.02, 6.74, 6.41, 3.59); IV 39.55 (11.63, 2.77, 9.98, 10.23, 4.94). Leg formula 1243. Opisthosoma length 10.07, width 5.16.
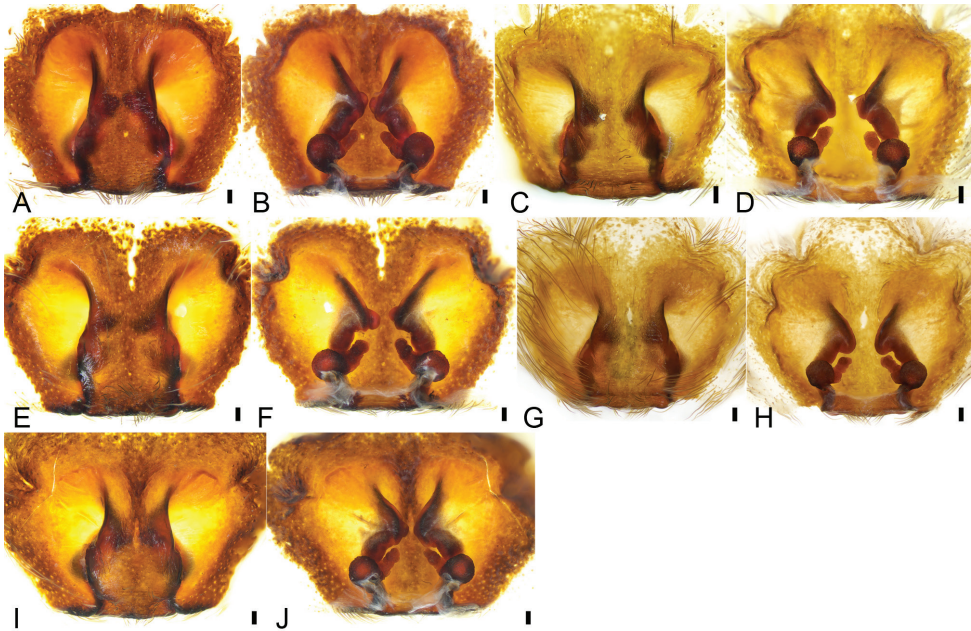
Figure 6. *Psechrus jinggangensis*, females **A** epigyne (Pse-40), ventral view **B** same, dorsal view **C** epigyne (Pse-38), ventral view **D** same, dorsal view **E** epigyne (Pse-39), ventral view **F** same, dorsal view **G** epigyne (Pse-22), ventral view **H** same, dorsal view **I** epigyne (Pse-41), ventral view **J** same, dorsal view. Scale bars: 0.1 mm.

Colouration and pattern. Darker than male. Coxae and trochanters I–IV with clear, dark, yellow–brown stripe.

Epigynum (Figs 4C, D, 7A, B). Median septum, lateral margins strongly sclerotized, anterior part covered the copulatory openings, anterior width slightly less than 1/2 of maximum epigynal width, subposterior width almost as long as 1/2 of maximum epigynal width, posterior part with a clear constriction. Copulatory openings large, converging to median. Lateral lobe with a slightly sclerotized posterior margin. Copulatory ducts, anterior part bugle-shaped, medial part S-shaped, spiralling backwards and extending posterolaterally, posterior part tube-shaped, connecting with the spermathecae. Spermathecae globose, medially connecting with spermathecal heads, separated by < 2× spermathecal diameter. Spermathecal heads with many pores on surface, relatively long, extending forward from mesial part of spermathecae to the turn of copulatory duct. Fertilisation duct relatively broad, medially located at the spermathecae.

Habitat and biology. Specimens occurred near both sides of a ditch and at the entrance areas of caves. They were usually collected by hand or by sweeping in microhabitats which included as stones, soil cracks, and plant roots. These spiders usually hang upside down on lace-sheet webs or rests on tube-shaped entrances of its web. At a slightest disturbance, they run back to their retreat with extreme speed, or they fall to the ground to feign death. This species is not easy to catch by hand and with tools.
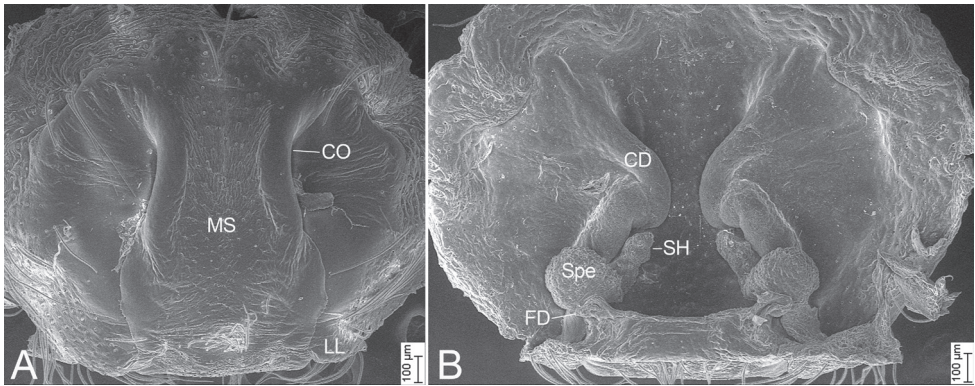
Figure 7. *Psechrus jinggangensis*, SEMs of females **A** epigyne (Pse-34), ventral view **B** same, dorsal view. Abbreviations: CD – copulatory duct, CO – copulatory opening, FD – fertilisation duct, MS – median septum, LL – lateral lobe, SH – spermathecal head, Spe – spermatheca.
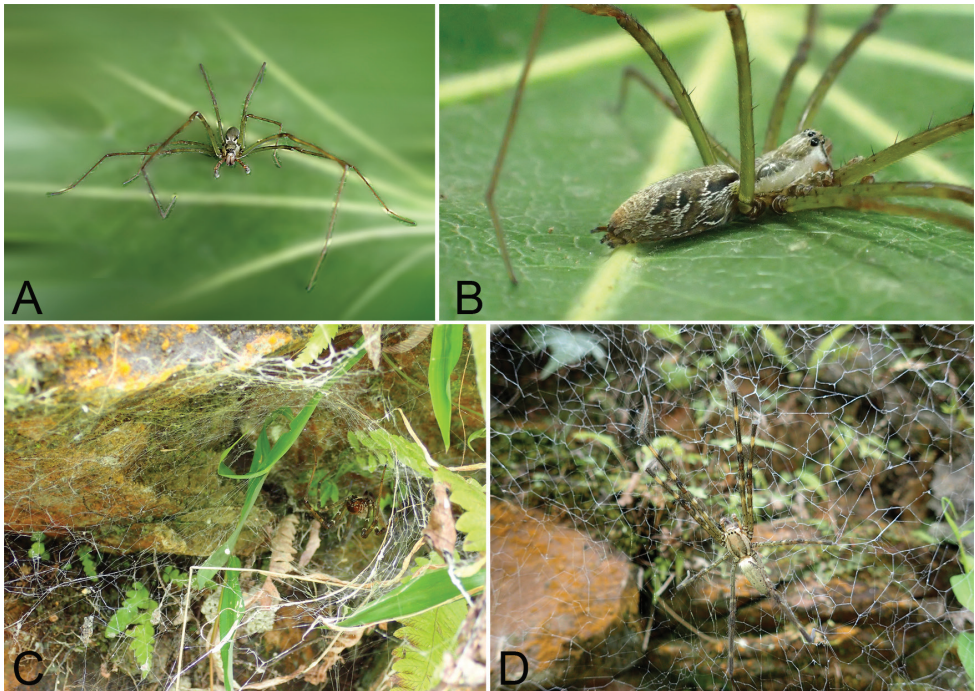
Figure 8. Photographs of living specimens of *Psechrus jinggangensis* from Jinggang Mountain National Nature Reserve. **A, B** male **C, D** female.

Distribution. Known only from Jiangxi Province, China (Fig. 9). This species is widely distributed in Jinggang Mountain National Nature Reserve in Jiangxi Province, where the nature reserve abuts Yanling County in Hunan Province.

Variability. Four males and 20 females were collected by us from Jinggang Mountain National Nature Reserve. Our detailed study of these specimens reveals that they

Figure 9. Distribution of *Psechrus jinggangensis* in China.

differ in the number of denticles present between the cheliceral teeth, as well as in their body sizes, eye sizes, eye interdistances, and leg length (Table 1). Variability was also observed in the male palp (Figs 1C–F, 2, 3) and the epigynal field (Figs 4C, D, 5–7), such as dense scopula covering from 1/2 to 2/3 of cymbium (almost 1/2 (Pse-12 and Pse-16), > 1/2 (Pse-25), > 2/3 (Pse-26)), embolic basal apophysis from indistinct (Pse-12) to distinct (Pse-16, Pse-25, and Pse-26), anterior part of embolic base from unexpanded (Pse-26) to expanded (Pse-16, Pse-12 and Pse-25), anterior part of female epigynal septum from narrow (Pse-33) to relatively broad (Pse-34, Pse-35, Pse-36, Pse-

37, Pse-23, and Pse-32), each copulatory duct from touching (Pse-33) to clearly separated (others) and with (Pse-34, Pse-35, Pse-37, Pse-23, Pse-32 and Pse-33) or without a strong turn (Pse-36), and spermathecal heads extending to the turn of copulatory ducts (Pse-34, Pse-23, and Pse-32) or not (Pse-35, Pse-37, and Pse-33). The variability observed in above may be the result of environmental factors, such as temperature, food, elevation, or habitat. Those specimens collected from stones usually had larger body sizes than specimens from other microhabitats.

Discussion

Although we have not provided evidence such as microscopic examination of the female holotype or DNA analyses to certify the specimens are conspecific with the female holotype of *Psechrus jinggangensis*, the male specimens were inferred as conspecific with the female holotype of this species based on a variety of reasons discussed below. Firstly, many specimens were collected several times at the type locality in the past seven years and their genitalia are consistent with the descriptions by Wang and Yin (2001) and Bayer (2012), although with variability within the species. Secondly, many living female specimens were close to the males when observed at their natural habitat of Jinggang Mountain National Nature Reserve; however, their copulation was observed only once, on a female lace-sheet web. In addition, the females and males are widely distributed in this area and relatively easily collected by using hand and sweeping methods during their mating period.

Acknowledgements

References

Bayer S (2012) The lace-sheet-weavers-a long story (Araneae: Psechridae: Psechrus). Zootaxa 3379: 1–170. https://doi.org/10.11646/zootaxa.3379.1.1

Doleschall L (1857) Bijdrage tot de kennis der Arachniden van den Indischen Archipel. Natuurkundig Tijdschrift voor Nederlandsch-Indie 13: 339–434. https://doi.org/10.5962/bhl.title.66068

Jocqué R, Dippenaar-Schoeman AS (2006) Spider Families of the World. Musée Royal de l'Afrique Central Tervuren, 336 pp.

Thorell T (1878) Studi sui ragni Malesi e Papuani. II. Ragni di Amboina raccolti Prof. O. Beccari. Annali del Museo Civico di Storia Naturale di Genova 13: 1–317. https://doi.org/10.1086/272171

Wang XP, Yin CM (2001) A review of the Chinese Psechridae (Araneae). Journal of Arachnology 29: 330–344. https://doi.org/10.1636/0161-8202(2001)029[0330:AROTCP]2.0.CO;2

World Spider Catalog (2021) World Spider Catalog. Natural History Museum Bern. Version 22.0. https://wsc.nmbe.ch/ [accessed 12 April 2021]

Yin CM, Peng XJ, Yan HM, Bao YH, Xu X, Tang G, Zhou QS, Liu P (2012) Fauna Hunan: Araneae in Hunan, China. Hunan Science and Technology Press, Changsha, 1590 pp.

Zhang ZS, Wang LY (2017) Chinese Spiders Illustrated. Chongqing University Press, Chongqing, 954 pp.

Megarthrus of China. Part 4. The *M. hemipterus* complex (Coleoptera, Staphylinidae, Proteininae), with description of a new species from Yunnan Province

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Abstract

The members of the *Megarthrus hemipterus* species complex occurring in China, i.e., *M. dentipes* Bernhauer, *M. flavolimbatus* Cameron and *M. hemipterus* (Illiger), are diagnosed, and a new species attributed to this informal group, *M. panda* **sp. nov.**, is described from Yunnan Province. All species are diagnosed and illustrated, and their distribution in mainland China is mapped. The limit of the *M. hemipterus* species complex is refined morphologically.

Keywords

Endemism, *Megarthrus depressus* supergroup, morphology, taxonomy

Introduction

This paper is the fourth of our series aiming at the taxonomic treatment of the fauna of *Megarthrus* Curtis, 1929 of mainland China, which consists at present of twelve species (Liu and Cuccodoro 2020a, b; Zhang et al. 2021).

Here, we deal with the members of the *M. hemipterus* species complex, i.e., *M. dentipes* Bernhauer, 1938, *M. flavolimbatus* Cameron, 1924, and *M. hemipterus* (Illiger, 1794), which form a subset of the speciose and predominantly Palaearctic, Nearctic and African *M. depressus* supergroup (Cuccodoro and Löbl 1997; Cuccodoro 2003, 2011). We also describe a new species from Yunnan Province in China, which we place in the *M. hemipterus* complex along with a refinement of the delimitation of the latter. These four species are diagnosed and illustrated, and their distribution in mainland China is mapped. A key to the Chinese species of the *M. depressus* supergroup will be provided only after the more than ten still undescribed Chinese species of this lineage will be treated.

Materials and methods

The material treated in this study is deposited in the following collections:

cAss   Volker Assing private collection (Hannover, Germany).
cPüt   Andreas Pütz private collection (Eisenhüttenstadt, Germany).
cSch   Michael Schülke collection (Museum für Naturkunde Berlin, Germany).
FMNH   Field Museum of Natural History, Chicago.
MHNG   Muséum d'histoire naturelle, Geneva, Switzerland.
NHMB   Naturhistorisches Museum, Basel, Switzerland.
NMPC   National Museum of Natural History, Prague, Czech Republic.
SWUC   Institute of Entomology, College of Plant Protection, Southwest University, Chongqing, China.

For detailed examination, specimens were relaxed in water prior dissection. Dissected body parts were dehydrated in isopropanol (genitalia after clearing in aqueous 0.1 N solution of potassium hydroxide) and mounted in Canada Balsam on acetate slides. Drawings were made by using a drawing tube mounted on a compound microscope. The habitus images were taken using a Leica DFC425 camera in conjunction with a Leica M205–C compound microscope. Images of morphological structures were made using a Canon G9 camera mounted on a Zeiss Axioscope 50 microscope. Zerene Stacker (version 1.04) was used for image stacking. All images were modified and grouped in Adobe Photoshop CS5 Extended (version 12.0). The distribution map was captured from Google Earth.

Abdominal sternites and tergites are counted from the first morphological segment and quoted in Roman numbers (i.e., last visible tergite = tergite VIII).

Taxonomy

The species treated below all share the following features typical of the *M. depressus* supergroup (Cuccodoro 2011): antennal pubescence markedly denser on antennomeres

5–11 than on antennomeres 1–4; metaventral setae shorter than proventral setae; abdominal sternites each bearing two posteromedial macrosetae; maxillary palpus with palpomere 3 about 1.5 times as long as palpomere 2; occipital ridge indistinct; antennomere 11 ovoid; pronotal hypomerom lacking marked ridge; male protarsomere 1 with adventral patch of modified tenent setae.

In addition they also share following characters: dorsal pubescence fairly uniform, slightly sparser on elytra than on pronotum and abdomen; pubescence on frons converging, with medial setae directed posteriad; anterior margin of frons slightly carinate, evenly convex in dorsal view; eyes hemispherical, with highest point above level of vertex; temples forming small sharp angle right behind eyes, and posteriorly abruptly narrowed, almost flat and fairly smooth; scape piriform, moderately compressed, about twice longer than wide; pronotum moderately deplanate, moderately convex in frontal view, and weakly convex in lateral view; lateral pronotal margins slightly raised on entire length, in dorsal view gently subangled at middle and strongly subangled subbasally, forming obsolete laterobasal inscision; medial groove well-marked on entire length; elytron slightly expanded posterior to humeral angle, shallowly depressed along lateral margin; lateral margin slightly carinate and denticulate, fairly straight or gently arcuate on posterior three-quarters in both dorsal and lateral views; male mesofemur longer than metafemur; male metatibia about as long as mesotibia; male abdominal sternite VIII similar to that in Fig. 32, lacking hyaline medial disc; hemitergites IX similar to that in Fig. 39, with lateral lobe moderately developed; aedeagus symmetrical, with dorsal valve elongate extended anteriorly beyond level of apex of parameres; base of parameres projecting posteriorly above ventral wall, forming marked cavity; female abdominal tergite VIII in lateral view with lateral margin fairly straight to apex acutely angled, not forming medioapical projection; female abdominal sternite VIII similar to that in Fig. 40, with posterior margin broadly arcuate; valvifers not meeting each other dorsally; gonocoxal plate compressed dorsoventrally, almost twice broader in dorsal view than in lateral view, lacking medioventral and mediodorsal ridges.

In order to keep the text more concise these characters will not be repeated in their respective descriptions.

Megarthrus dentipes Bernhauer, 1938
Figs 1–3, 10, 13, 16, 41

Megarthrus dentipes Bernhauer, 1938: 17; Cuccodoro and Löbl 1997: 1364 (detailed redescription).

Diagnosis. For detailed morphology see Cuccodoro and Löbl (1997). Combined length of head, pronotum, and elytra 1.6–2.0 mm; maximal pronotal width = 0.8–1.1 mm. Body (Figs 1–3) predominantly chestnut brown, with pronotum slightly paler along lateral edges, frons slightly paler than vertex, and legs slightly paler than elytra. Anterior frontal margin slightly carinate, evenly convex in dorsal view.
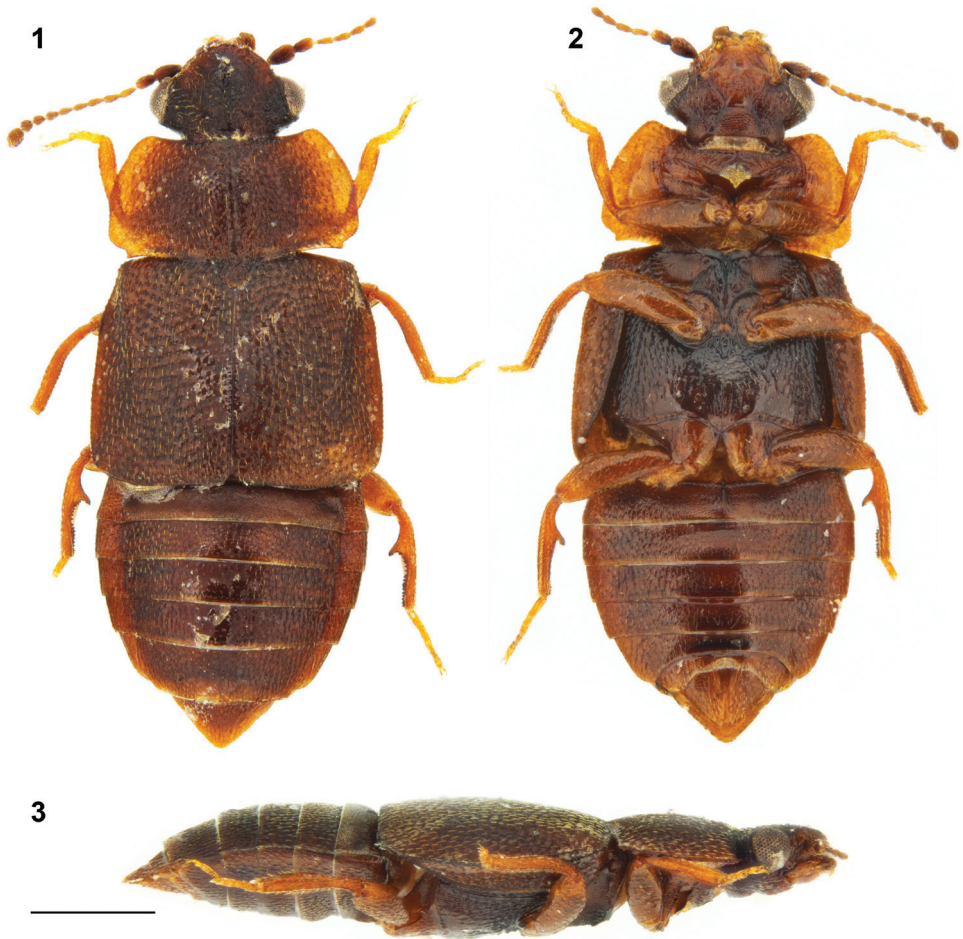
Figures 1–3. *Megarthrus dentipes* Bernhauer: habitus, male: dorsal **1** ventral **2** and lateral **3** views. Scale bar: 0.5 mm.

Male. Protibia slightly arcuate and evenly expanding from base to apex; adventral side broadly depressed transversely. Mesotrochanter with about a dozen of peg-like setae arranged in two rows. Mesofemur slightly arcuate and swollen. Mesotibia slightly arcuate, bearing peg-like setae arranged in rows. Metatrochanter and metafemur slightly swollen; posterior margin of metatrochanter evenly arcuate; inner margin of metafemur fairly straight in ventral view, forming sharp ridge on entire length. Metatibia swollen, at middle forming conspicuous tooth-like process projecting above flattened apical portion of metatibia; peg-like setae grouped as dense field on apical third, and extending in fairly continuous row to apex of distal side of tooth-like process; proximal side of tooth-like process convex, with at most 2 peg-like setae. Aedeagus (Figs 10, 13) with ventral wall slightly narrowed at base and evenly narrowed to blunt right-angled apex in ventral view, and with ventral outline slightly sinuate to apex slightly recurved ventrally in lateral view.

Female. Gonocoxal plate with lateral portions of dorsobasal margin concave to middle portion subangled, markedly projecting anterad. Dorsal part of genitalia (Fig. 16) with evenly thick semi-circular sclerite.

Comparisons and diagnostic notes. *Megarthrus dentipes* resembles in most characters of *M. flavolimbatus* and *M. hemipterus*. These species can be distinguished by the shape of the anterior frontal margin (i.e., evenly arcuate in *M. dentipes* and *M. hemipterus*, while more convex at middle than laterally in *M. flavolimbatus*) and the coloration (i.e., head fairly concolor with pronotum, and legs paler than elytra in *M. dentipes* and *M. flavolimbatus*, instead of markedly darker than the pronotum, and legs concolorous with the elytra in *M. hemipterus*). The males also differ by the shape and vestiture of the metatibial tooth-like process (i.e, its proximal side is flattened in *M. hemipterus* instead of convex in *M. dentipes* and *M. flavolimbatus*, and bearing peg-like setae on its distal side in a fairly continuous row to the apex in *M. dentipes*, while discontinuoulsy in *M. flavolimbatus* and *M. hemipterus*). The shape of the apical portion of the aedeagus ventral wall is diagnostic (i.e., subangulate in *M. dentipes* (Fig. 10), angulate in *M. flavolimbatus* (Fig. 11), and mucronate in *M. hemipterus* (Fig. 12)), as well as that of the medial portion of the dorsobasal margin of the gonocoxal plate (i.e., truncate and projecting anterad in *M. flavolimbatus*, subangled and projecting anterad in *M. dentipes*, and mucronate in *M. hemipterus*).

Material examined. (78 specimens): **China: Fujian Prov.:** Guadun, "Kuatun, Fukien, Tschung Sen [sic], 5.iv.1946, leg J. Klapperich", 1 ♂ in NHMW; 10 km E Yong'an, 25°58'N, 117°27'E, 31.v.2008, 700 m, leg. J. Tuma, 2 ♀ in NHMW; Fenshui Guan, 27.9N, 117.85E, 7.v.2005, 1700 m, leg. J. Tuma, 10 ♂ and 13 ♀ in NHMW, MHNG & ZMUC; 2km SE Xinqian, 27.05N, 117.1E, 10.v.2005, 1700 m, leg. J. Tuma, 4 ♂ and 6 ♀ in NHMW & MHNG; Ziyungdongshan, NW slopes, 25°46'N, 117°20'E, 25.iv.2006, 900–1000 m, leg. J. Tuma, 1 ♂ and 3 ♀ in NHMW; **Guangdong Prov.:** Nanling National Nature Reserve, Dadongshan, 24°54.7'N, 112°43.1'E, 770 m, 20–21.iv. 2013, leg. J. Hájek 6 J. Růžička, 1 ♂ in NHMP; **Hubei Prov.:** Mulu Shan, Jiugongshan forest park, 29.4N 114.6E, up to 1000 m, 3.v–18.vi.2002, leg. J. Tuma, 2 ♂ and 4 ♀ in NHMW; **Hunan Prov.:** Shunhuangshan forest park, 26°22–23'N, 111°00–01'E, 20.vi.2013, 1300–1600 m, leg. Jatua, 5 ♂ and 4 ♀ in NHMW & MHNG; **Jiangxi Prov.:** Jinggangshan Mts, Xiangzhou (forested valley S of the village), 26°35.5'N, 114°16.0'E, 374 m, (steam valley), 26.iv.2011, leg. Fikáček and Hájek, Jia and Song, [MF08] cut and decaying tops of bamboo trunks at the side of a trail in the secondary forest and among the fields, 1 ♂ and 2 ♀ in NHMP; Jinggangshan Mts, Songmuping, 26°34.7'N, 114°04.3'E, 1280 m, (stream valley), 27.iv.2011, leg. Fikáček, Hájek, Jia and Song [MF10] cut and decaying tops of bamboo trunks in a sparse bamboo bush, 7 ♂ and 6 ♀ in NHMP, MHNG & ZMUC; Jinggangshan Mts, Huyagta, 26°29.9'N, 114°07.3'E, 1490 m, 28.iv.2011, leg. Fikáček, Hájek, Kubeček, Jia, Song and Zhao, [MF12] cut and decaying tops of bamboo trunks in a sparse secondary bamboo forest, 2 ♂ and 2 ♀ in NHMP; **Zhejiang Prov.:** Baima Shan, 28°37'N, 119°09'E, 7–17.vi.2008, 1270–1520 m, leg. J. Tuma, 1 ♂ and 1 ♀ in NHMW.

Distribution and natural history. Till now *M. dentipes* was known only from the Chinese Provinces of Jiangsu and Zhejiang (Cuccodoro and Löbl 1997: 1364). The new materials examined indicate that the species occurs in Zhejiang Province also at Baima Shan, as well as in several other localities of Hubei, Fujian, Jiangxi, and Guangdong Provinces (Fig. 41), where it was collected at elevations ranging from 374 to 1700 m a. s. l., mainly in rotten bamboo trunks and decaying cut tops of bamboo trunks.

Megarthrus flavolimbatus Cameron, 1924
Figs 4–6, 11, 14, 17, 41

Megarthrus flavolimbatus Cameron, 1924: 164; Cuccodoro 2003: 377 (detailed rede-
    scription, the first record for China); Cuccodoro 2011: 38 (photograph of dorsal
   habitus, Taiwanese records in China).

Diagnosis. For detailed morphology see Cuccodoro (2003). Combined length of head, pronotum, and elytra 1.6–1.9 mm; maximal pronotal width = 0.9–1.1 mm. Body (Figs 4–6) predominantly chestnut brown, with pronotum slightly paler along lateral edges, frons slightly paler than vertex, and legs slightly paler than elytra. Anteri-or frontal margin slightly carinate, more convex at middle than laterally in dorsal view.

Male. Protibia fairly straight and evenly expanding from base to apex; adventral side shallowly depressed transversely. Mesotrochanter with about a dozen peg-like setae ar-ranged in two rows. Mesofemur fairly straight and slightly swollen. Mesotibia subangulate, bearing peg-like setae arranged in one row. Metatrochanter and metafemur slightly swol-len; posterior margin of metatrochanter evenly arcuate; inner margin of metafemur fairly straight in ventral view, forming sharp ridge on entire length. Metatibia swollen, at middle forming conspicuous tooth-like process projecting above flattened apical portion of metat-ibia; metatibial peg-like setae grouped as a dense field on apical third, discontinuously with 1 peg-like seta to at most 7 peg-like setae on distal side of tooth-like process; proximal side of tooth-like process convex, with at most 1 peg-like seta. Aedeagus (Figs 11, 14) with ventral wall slightly narrowed at base and evenly narrowed to acutely angled apex in ventral view, and with ventral outline fairly straight to slightly recurved apex in lateral view.

Female. Gonocoxal plate with lateral portions of dorsobasal margin with oblique to middle portion truncate, markedly projecting anterad. Dorsal part of genitalia (Fig. 17) with evenly thick semi-circular sclerite.

Comparisons and diagnostic notes. See above under *M. dentipes*.

Material examined. (92 specimens): **China: Fujian Prov.:** N of Wutongyang, 26°03'N, 117°38'E, 12.v.2010, 1000–1700 m, leg. J. Tuma, 25 ♂ and 9 ♀ in MHNG, NHMW & ZMUC; **Hunan Prov.:** Shunhuangshan Forest Park, 26°24'N, 111°01'E, 22.v.2013, 700–1200 m, leg. Jatua, 6 ♂ and 7 ♀ in MHNG & NHMW; **Shaanxi Prov.:** Qin Ling Shan, river valley 40 km S Xian, highway km 50, 33.55N, 108.49E, 1200 m, 31.viii.1995, leg. D. W. Wrase, river bank, 1 ♂ in cSch; **Sichuan Prov.:** Qingcheng Shan, NW Chengdu, 650–700 m, 30°53'57"N, 103°32'23"E, 3–4.vi.1997, leg. M.

4 **5**

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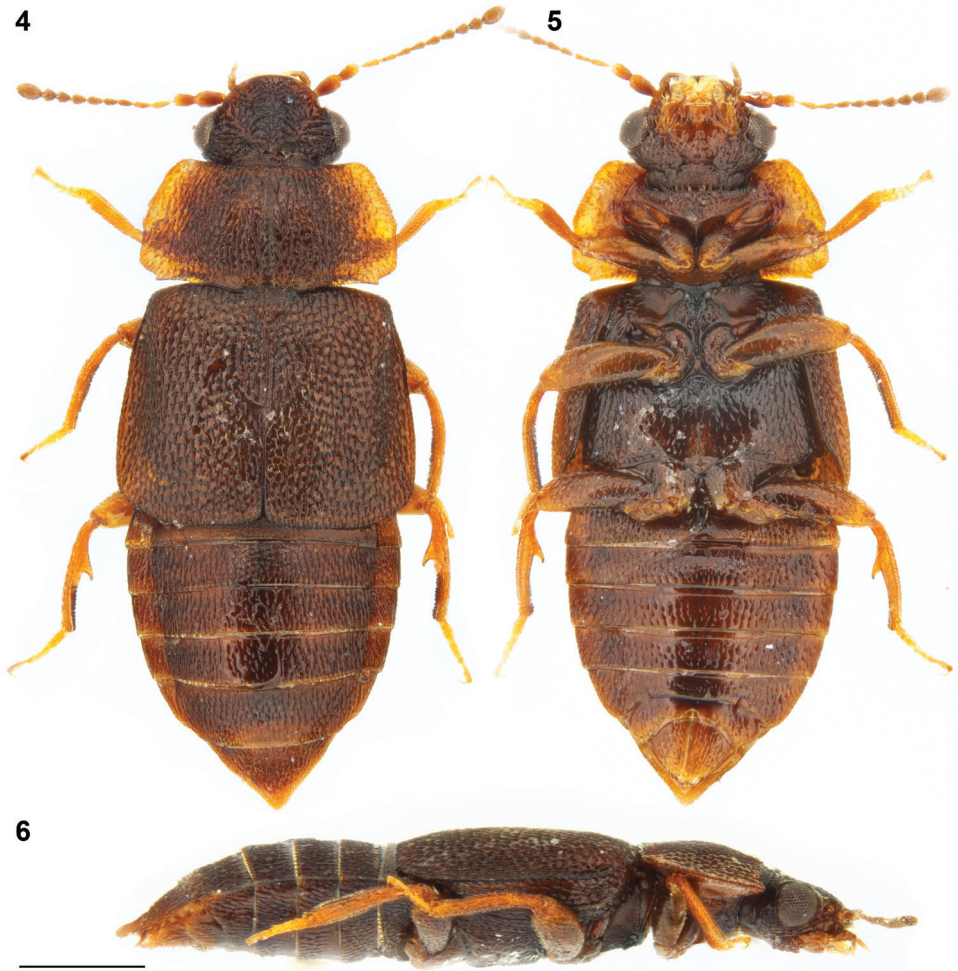
Figures 4–6. *Megarthrus flavolimbatus* Cameron: habitus, male: dorsal **4** ventral **5** and lateral **6** views. Scale bar: 0.5 mm.

Schülke (17), 1 ♂ and 2 ♀ in cSch; Qingcheng Shan, 65 km NW Chengdu, 8 km W Taiping, 35.53N, 103.33 E, 800–1000m, 18.v./3–4.vi.1997, leg. A. Pütz, 2 ♂ and 2 ♀ in cPüt & MHNG; Emei Shan, 29°33'04"N, 103°21'19"E, 25.vi.2011, 1729 m, leg. V. Grebennikov (sift 05) 2 ♂ and 1 ♀ in MHNG; Emei Shan, 29°36'06"N, 103°20'06"E, 27.vi–.5.vii.2009, 1800–2400 m, leg. V. Grebennikov (siftings 11–17) 2 ♂ and 1 ♀ in MHNG; Ya'an Pref., Shimian Co. Xiaoxiang Ling, 11 km S Shimian, side-valley above Nanya Cun near Caluo, 1250 m, 7. VII.1999, leg. A. Pütz, 1 ♀ in cPüt; **Yunnan Prov.:** Baoshan Pref., Gaoligong Shan, E pass, 36 km SE Tengchong, 24°49'32"N, 98°46'06"E, 2200 m, 31.v.2007, leg. A. Pütz, [CH07–13] deciduous forest, litter, wood, fungi sifted, 2 ♂ in cPüt; Baoshan Pref., Gaoligong Shan, 36 km SE Tengchong, 24°51'22"N, 98°45'36"E, 2100–2200 m, 31.v.2007, leg. A. Pütz [CH07–14], deciduous forest, litter,

wood, fungi, sifted, 1 ♂ in cPüt; Baoshan Pref., mountain range 14 km E Tengchong, 25°00'28"N, 98°38'07"E, 1850 m, 1.vi.2007, leg. A. Pütz [CH07–16] second, mixed forest, litter sifted, 1 ♂ in cPüt; Baoshan Pref., mountain range 25 km S Tengchong, 24°48'28"N, 98°32'03"E, 1900 m, 2.vi.2007, leg. A. Pütz [CH07–17], dev. primary deciduous forest, litter, fungi, sifted, 1 ♀ in cPüt; Ruili, 4.ii.1993, G. de Rougemont, 2 ♂ and 2 ♀ in MHNG & SCNU; Xishuangbanna, 22.i.1993, G. de Rougemont, 2 ♂ and 3 ♀ in MHNG; Kunming, 9.x.1985, G. de Rougemont, 1 ♀ in MHNG; Kunming, x.1986, G. de Rougemont, 1 ♂ in MHNG; Baoshan Pref., Gaoligong Shan, E pass, 36 km SE Tengchong, 2200 m, 24°49'32"N, 98°46'06"E, 4.vi.2007, leg. M. Schülke [CH07–13], deciduous forest, litter, wood, fungi, sifted, 4 ♂ and 1 ♀ in cSch; Xishan Mts, 24.57N 102.38E, 2300 m, 27.vi.1993, leg. V. Kubáň, 1 ♂ in NHMB; NE Kunming, 25°08'40"N, 102°53'48"E, 2290 m, 11. VIII. 2014, leg. V. Assing [5] mixed forest, sifted, 1 ♂ in cAss; NE Kunming, Xiaobailong Forest Park, 24°55'43"N, 103°05'27"E, 2110 m, 10.viii.2014, leg. M. Schülke [CH14–03], secondary pine forest margin, litter, sifted, 3 ♀ in cSch; Dali Bai Aut. Pref., Wuliang Shan, 9km SW Weishan, 25°10'15.5"N, 100°14'21.8"E, 2480 m, 14.ix.2009, leg. M. Schülke [CH09–51], scrub with (oak, alder, pine) litter and mushrooms, sifted, 2 ♀ in cSch; Baoshan Pref. Mountain range 25 km S Tengchong, 24°48'28"N, 98°32'03"E, 1900 m, 2.vi.2007, leg. M. Schülke, [CH07–17], dev. primary deciduous forest, litter, fungi, sifted, 1 ♀ in cSch; Gaoligong Shan, Pass SW Baoshan, 4–8.vi.2006, leg. Jeniš, 1 ♀ in cAss.

Distribution and natural history. *Megarthrus flavolimbatus* is the most widespread member of the genus in the Oriental Realm, with records ranging from North India (Himachal Pradesh and West Bengal) to Yunnan Province and Taiwan in China (Cuccodoro 2003, 2011); here, we report it for the first time also from Fujian, Hunan, Shaanxi and Sichuan Provinces in China (Fig. 41). It was found at elevations ranging from 250 to 3375 m a. s. l. in Taiwan (Cuccodoro 2011), and its altitudinal range appears quite wide also in mainland China (i.e., from 1000 to 1700 m a. s. l. in Fujian, from 7000 to 1200 m a. s. l. in Hunan, from 1850 to 2480 m a. s. l. in Yunnan, from 650 to 2400 m a. s. l. in Sichuan, and at 1200 m a. s. l. in Shaanxi). The species occurs in various types of forests (evergreen broadleaved, deciduous broadleaved, mixed coniferous and evergreen broadleaved, and coniferous forests) as well as in orchards, where it was collected mainly from sifted samples of moist decaying debris of vegetation (leaf litter, humus, rotting wood) with fungi, and occasionally even from chicken excrement (Cuccodoro 2011).

Megarthrus hemipterus (Illiger, 1794)
Figs 7–9, 12, 15, 18, 41

Silpha hemiptera Illiger, 1794: 597; Cuccodoro 1996: 485 (new synonymy, Japanese records); Cuccodoro and Löbl 1997 (synonymic framework, detailed redescription, general distribution, the first record for China); Cuccodoro et al. 2011 (synonymic framework, photograph of dorsal habitus, records in Korea).

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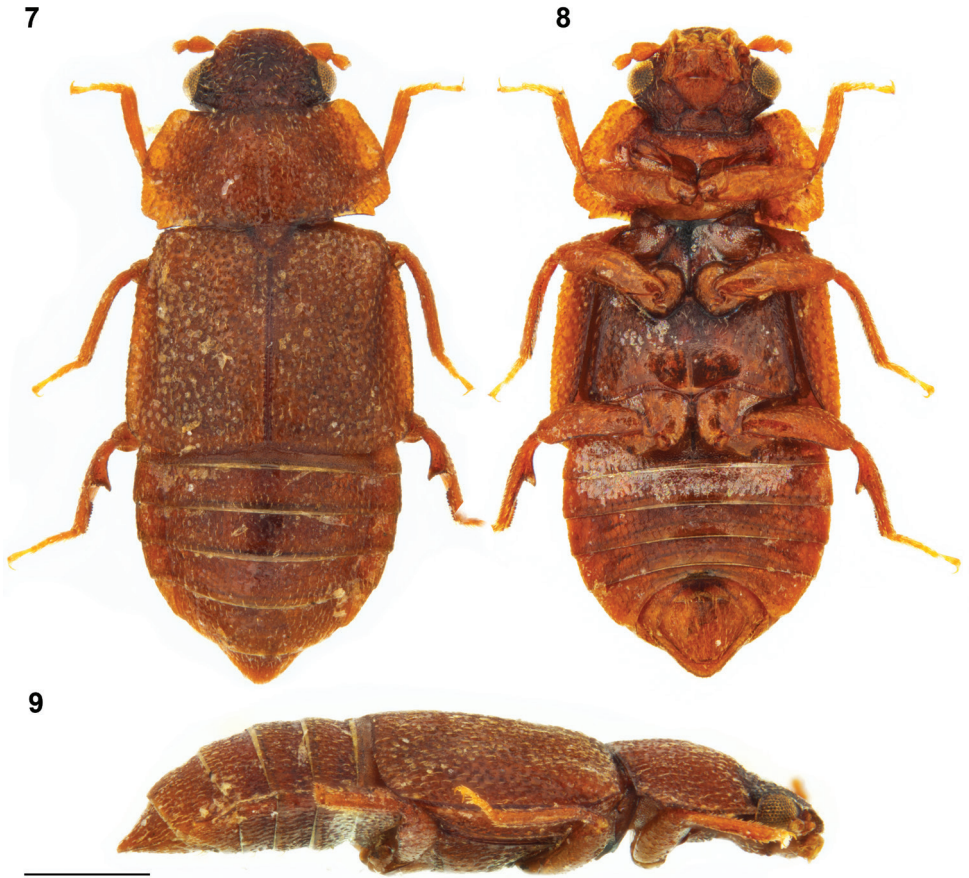
Figures 7–9. *Megarthrus hemipterus* (Illiger): habitus, male: dorsal **7** ventral **8** and lateral **9** views. Scale bar: 0.5 mm.

Diagnosis. For detailed morphology see Cuccodoro and Löbl (1997). Combined length of head, pronotum, and elytra 1.6–1.9 mm; maximal pronotal width = 0.9–1.1 mm. Body and appendages (Figs 7–9) rust brown; head markedly darker with frons slightly paler than vertex. Anterior frontal margin slightly carinate, evenly convex in dorsal view.

Male. Protibia fairly straight and slightly enlarged toward apex, evenly, with adventral side markedly depressed transversely at middle. Mesotrochanter with about a dozen of peg-like setae arranged in two rows. Mesofemur slightly arcuate and slightly swollen. Mesotibia subangulate, bearing peg-like setae arranged in one row. Metatrochanter and metafemur slightly swollen; posterior margin of metatrochanter evenly arcuate; inner margin of metafemur slightly concave in ventral view, forming sharp ridge on entire length. Metatibia swollen, at middle forming conspicuous tooth-like process projecting above flattened apical portion of metatibia; metatibial peg-like setae arranged in 1–2 rows on apical third, the latter group of 15–20, discontinuously
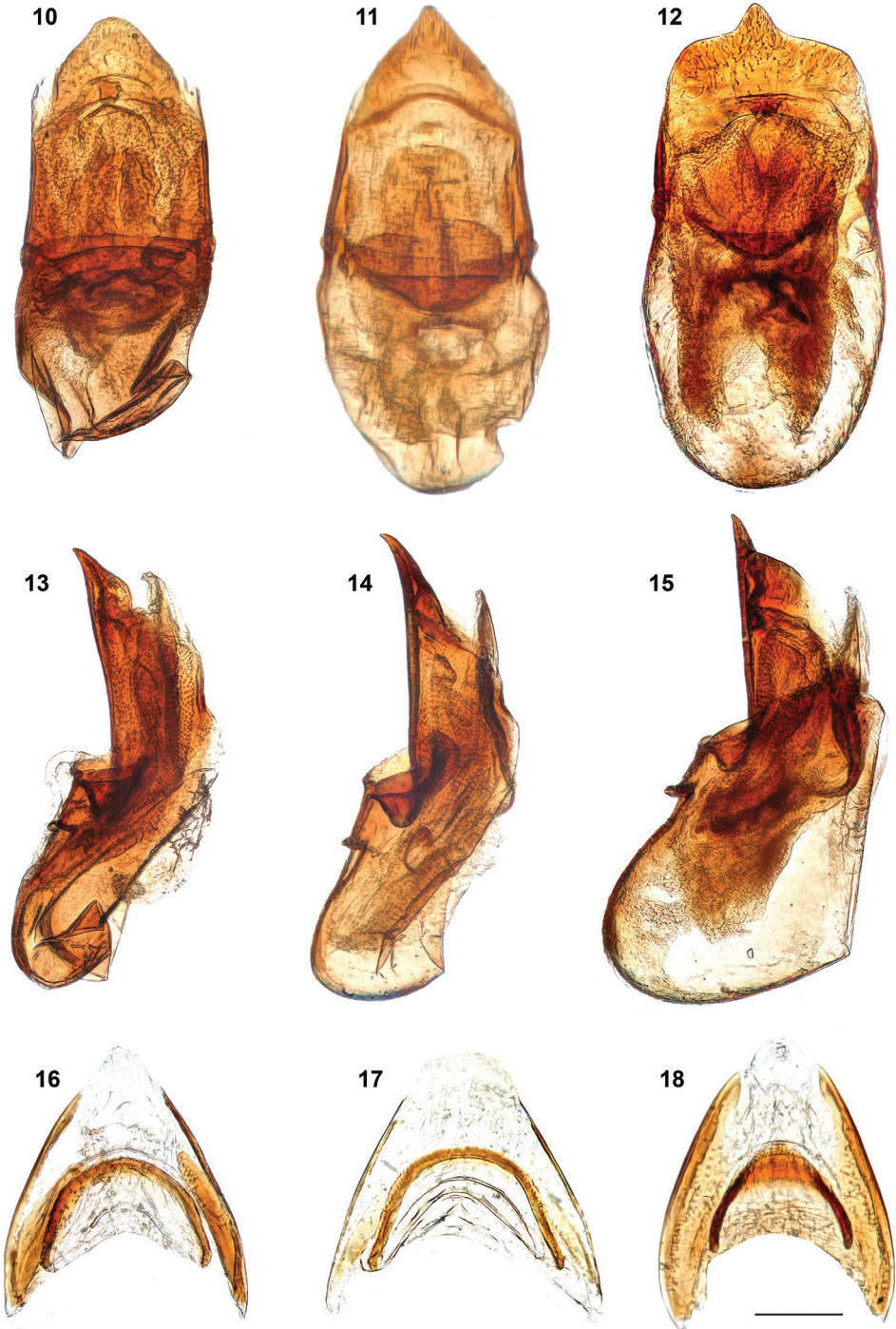
Figures 10–18. *Megarthrus dentipes* Bernhauer (**10, 13, 16**) *M. flavolimbatus* Cameron (**11, 14, 17**) *M. hemipterus* (Illiger) (**12, 15, 18**) ᴍale: aedeagus in ventral (**10–12**) and lateral (**13–15**) views female: genital segments, dorsal part (**16–18**) in ventral view. Scale bars: 0.1 mm.

with more than 12 peg-like setae arranged in two rows on distal side of tooth-like process; proximal side of tooth-like process broad and flat, bearing 4–10 scattered peg-like setae. Aedeagus (Figs 12, 15) with ventral wall not narrowed at base and gradually narrowed to mucronate apex in ventral view, with ventral fairly straight to apex in lateral view.

Female. Gonocoxal plate with lateral portions of dorsobasal margin straight to middle portion forming small blunt process slightly projecting anterad. Dorsal part of genitalia with arcuate sclerite wider at middle (Fig. 18).

Comparisons and diagnostic notes. See above under *M. dentipes.*

Material examined. (4 specimens): **China: Beijing:** ca 1400 m, Dongling Mts, Xiaolongmen, Liu Lang Yu, 39.97 N, 115.43 E, 15.vi.2001, leg. J. Cooter & P. Hlavá, mixed woodland litter, 1 ♀ in MHNG; **Heilongjiang Prov.:** "Süd-Mandshurei Chi-Kuan Shan, leg K. Rost", 2 ♂ and 1 ♀ in FMNH.

Distribution and natural history. *Megarthrus hemipterus* is the most widespread member of the genus, with records ranging from the United Kingdom in the West to China, South Korea, Japan, and Far East Russia in the East (Cuccodoro 1996; Cuccodoro and Löbl 1997; Cuccodoro et al. 2011). It occurs in a wide range of microhabitats (carrion, fungi, leaf litter, and various types of decaying organic matter); in South Korea it was abundantly collected from fresh and rotten fungi. The first record for China without precise locality data (Cuccodoro and Löbl 1997) refers to the three specimens cited here from Chi-Kuan Shan from the Max Bernhauer's collection, housed in the FMNH. The species, which occurs on most land masses surrounding the Sea of Japan, seems to reach its southern limit of extension in China in the Western Hills (Fig. 41), where it was collected in mid-April at 1400 m a. s. l. from mixed woodland litter on Mount Dongling (Beijing).

Megarthrus panda sp. nov.
http://zoobank.org/536B7DD8-8691-4D7F-84AC-3BA210384AE1
Figs 19–40

Type material. *Holotype* (♂): **China: Yunnan Prov.:** Jizu Shan 25.58N 100.21E, 2500–2700 m, 6–10.vii.1994, leg. V. Kubáň, in NHMB. *Paratypes* (20): Same data as holotype, 1 ♂ and 1 ♀ in NHMB, 1 ♂ and 1 ♀ in MHNG; **China: Yunnan Prov.:** NE Kunming, 25°08'35"N, 102°53'49"E, 2320 m, 13.viii.2014, leg. M. Schülke [CH14–06], mixed forest with alder, oak and pine, litter and mushrooms, sifted, 2 ♂ and 3 ♀ in cSch, 1 ♂ and 1 ♀ in MHNG & 1 ♂ and 1 ♀ in SWUC; NE Kunming, 25°08'40" N, 102°53'48"E, 2290 m, 11.viii.2014, leg. M. Schülke [CH14–05], mixed deciduous forest with scattered pine trees, litter and mushrooms sifted, 1 ♂ in cSch; Dali Aut. Pref. Máo Jiao Shan, E pass, 58 km NE Dali, 25°56'41"N, 100°40'05"E, 2525 m, 4.ix.2009, leg. M. Schülke [CH 09–26] secondary mixed forest, litter, moss & mushrooms, sifted, 1 ♂ and 4 ♀ in cSch & 1 ♀ in MHNG.
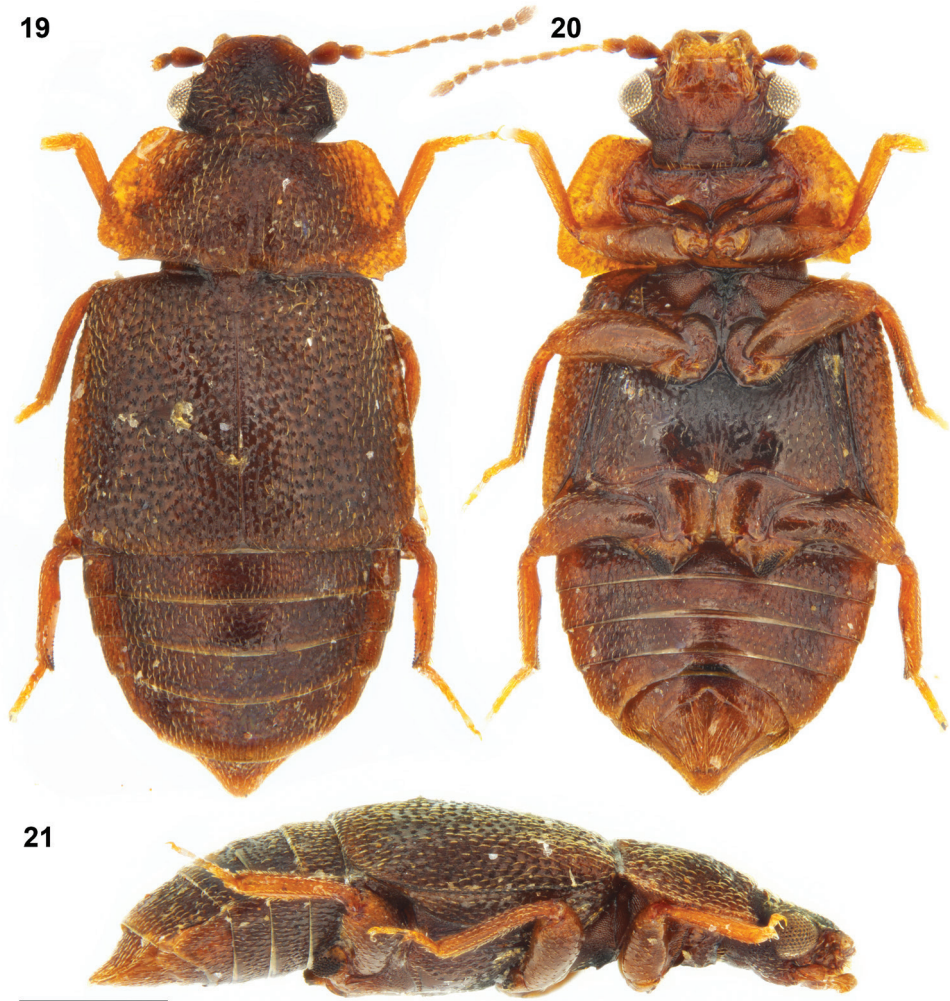
Figures 19–21. *Megarthrus panda* sp. nov.: habitus, male: dorsal **19** ventral **20**, and lateral **21** views. Scale bar: 0.5 mm.

Description. Combined length of head, pronotum and elytra = 1.7–2.1 mm; maximal pronotal width = 0.9–1.3 mm. Body (Figs 19–21) predominantly chestnut brown, with pronotum usually slightly paler, frons slightly paler than vertex, and legs slightly paler than elytra. Anterior frontal margin slightly carinate, evenly convex in dorsal view. Antenna as in Fig. 36. Prothorax as in Figs 22, 23.

Male. Protibia fairly straight and evenly expanding from base to apex; adventral side flattened. Mesotrochanter (Fig. 28) with about twenty peg-like setae grouped as a field. Mesofemur (Fig. 28) slightly arcuate and slightly swollen. Mesotibia (Fig. 27) subangulate, bearing peg-like setae arranged in two rows. Metatrochanter and metafemur (Fig. 29) markedly swollen; posterior margin of metatrochanter broadly rectan-
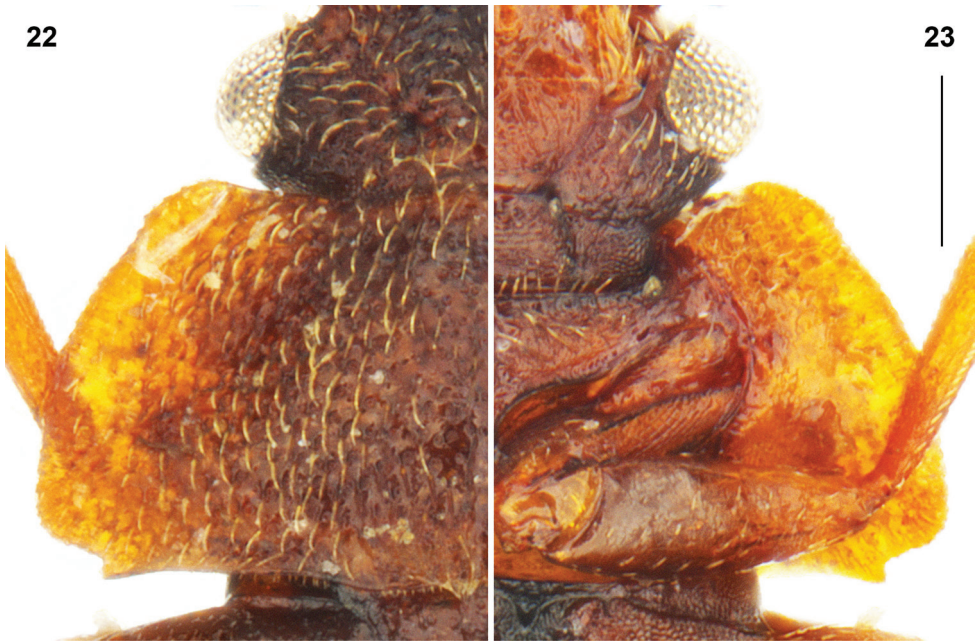
Figures 22–23. *Megarthrus panda* sp. nov., prothorax in dorsal **22** and ventral **23** views. Scale bar: 0.2 mm.

gular; posterior margin of metafemur concave in ventral view, forming sharp ridge on half length. Metatibia (Fig. 26) swollen, with adventral side flattened and broadly emarginated on apical two-thirds; metatibial peg-like setae grouped as a field on apical quarter with additional peg-like setae arranged in scattered row bordering each side of emargination. Abdominal tergite VIII as in Figs 30, 31; abdominal sternite VIII in Fig. 32; hemitergites IX as in Fig. 39. Aedeagus (Figs 24, 25) with ventral wall strongly narrowed at apical third in ventral view, with ventral outline markedly sinuate to slender apex strongly recurved ventrally in lateral view.

  Female. Abdominal tergite VIII as in Figs 37, 38. Valvifers as in Figs 34, 35. Gonocoxal plate (Figs 34, 35) with lateral portions of dorsobasal margin oblique to median portion truncate, markedly projecting anterad. Dorsal part of genitalia (Fig. 33) with arcuate sclerite slightly wider at middle.

  Comparisons and diagnostic notes. *Megarthrus dentipes*, *M. flavolimbatus*, *M.hemipterus* and *M. panda* sp. nov. are the only members of the genus to have the anterior frontal margin carinate, the antennae bearing short and dense pubescence only on antennomeres 5–11, hemispherical eyes with the highest point above level of the vertex, the lateral sides of pronotum and elytra slightly deplanate, the prohypomera without a marked ridge, and the pubescence on abdominal tergites parallel. Within these species *M. panda* sp. nov. can be easily distinguished by the shape posterior legs of the males (Figs 26, 29). Its genitalia are also diagnostic, notably in the male by the aedeagal ventral wall strongly sinuate in lateral view (Fig. 25), and in the female by the arcuate dorsal genital sclerite slightly wider at middle in combination with the dor-
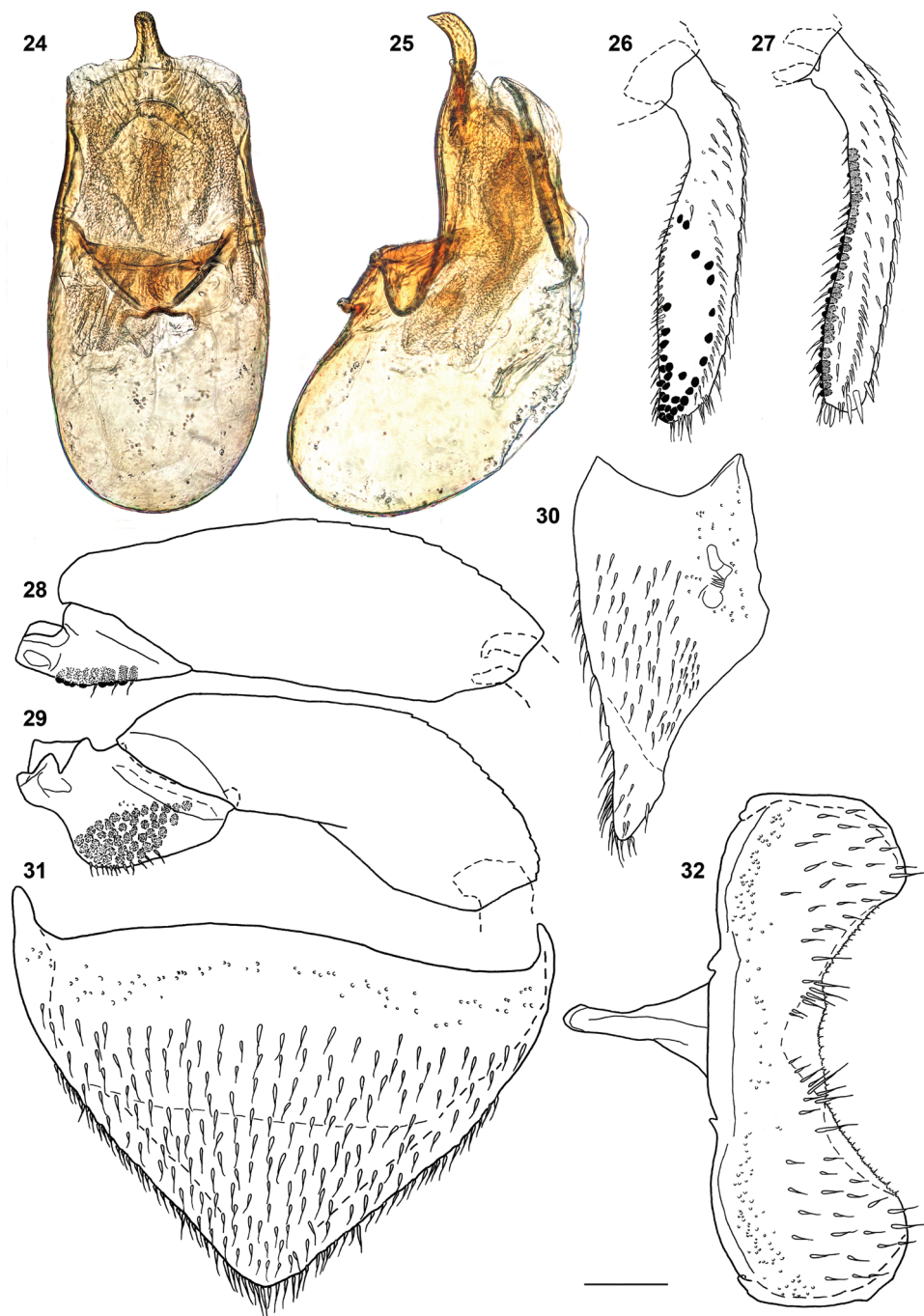
Figures 24–32. *Megarthrus panda* sp. nov., aedeagus in ventral **24** and lateral **25** views; metatibiae **26** mesotibiae **27** mesotrochanter and mesofemur **28** metatrochanter and metafemur **29** tergite VIII in lateral **30** and ventral **31** views sternite VIII in ventral view **32**. Scale bar: 0.1 mm.
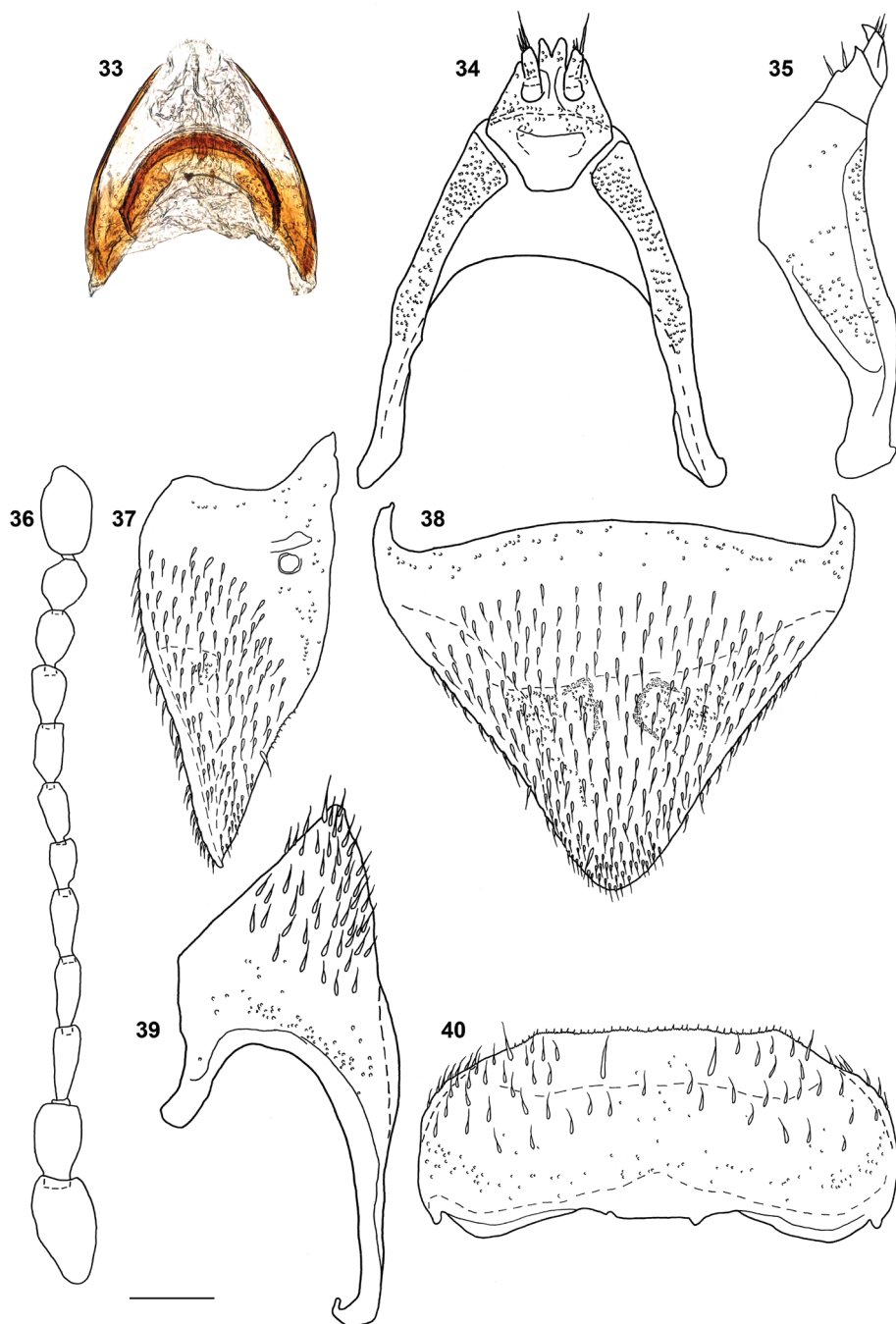
Figures 33–40. *Megarthrus panda* sp. nov., female genital segments, dorsal part in ventral view **33** and ventral part in dorsal **34** and lateral **35** views antenna **36** female tergite VIII in lateral **37** and dorsal **38** views male left hemitergite IX **39** female sternite VIII in ventral view **40**. Scale bar: 0.1 mm.
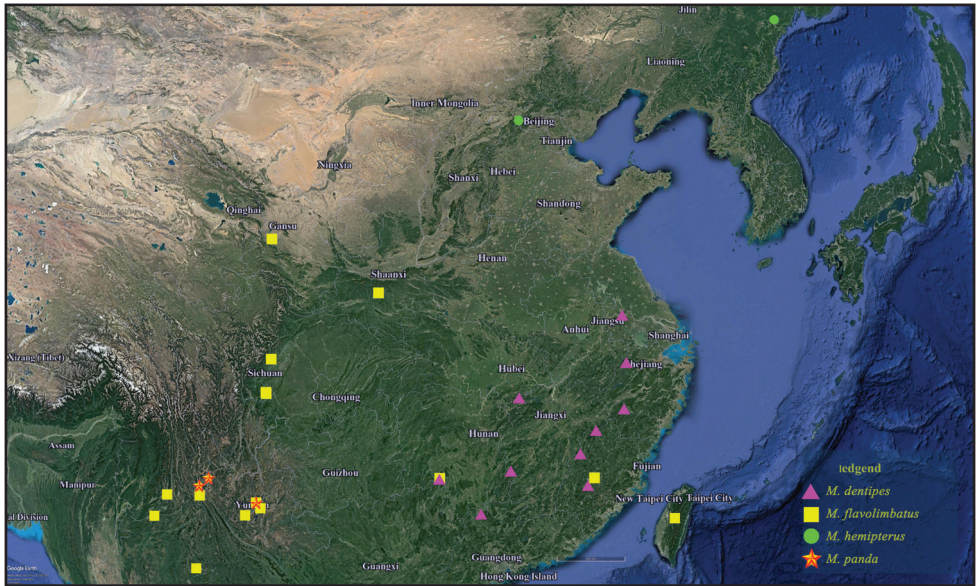
Figure 41. Distribution map in China of *Megarthrus dentipes* Bernhauer, *M. flavolimbatus* Cameron, *M. hemipterus* (Illiger) and *Megarthrus panda* sp. nov. Scale bar: 300 km.

sobasal margin of the gonocoxal plate evenly narrowed to its truncate median portion projecting anterad (Fig. 34).

Distribution and natural history. The species is endemic to Yunnan Province (Fig. 41), where it was found at elevations ranging from 2290 to 2700 m a. s. l. from July to September by sifting leaf litter with mushrooms in mixed deciduous forests with alder, oak and pine.

Etymology. *Megarthrus panda* sp. nov. shares the main body color and the forested mountains of Yunnan Province with its eponymous mammal the small panda, *Ailurus fulgens* Cuvier, 1825. Noun in apposition.

Discussion

Cuccodoro (2011) grouped *M. dentipes*, *M. flavolimbatus* and *M. hemipterus* in the informal *M. hemipterus* complex defined as a subset of species of the *M. depressus* super-group sharing strongly resembling male genitalia and metatibiae, and the female abdominal tergite VIII not forming a medioapical projection. In light of this new species, we refine the delimitation of this lineage as the members of the *M. depressus* supergroup (see Cuccodoro 2011: 89) possessing: 1) hemispherical eyes with highest point above level of vertex, 2) the dorsal valve of the aedeagus elongate, extended anteriorly beyond the apex of parameres, 3) the base of parameres projecting posteriorly above ventral

wall, forming a cavity, and 4) the apex of the female abdominal tergite VIII acutely angled in lateral view, not forming a medioapical projection.

Among the four members of the *M. hemipterus* complex, i.e., *M. dentipes*, *M. flavolimbatus*, *M. hemipterus* and *M. panda* sp. nov., the male sexual dimorphism shows trends towards 1) moderate enlargement of the protibia with presence of a transverse adventral depression, 2) conspicuous enlargement of the metafemur and metatrochanter, and 3) presence of conspicuous tooth-like metatibial process. However, the precise phylogenetic relationships between these species have not been investigated.

The *M. hemipterus* complex includes both the most widespread *Megarthrus* species in the Palaearctic (*M. hemipterus*) and Oriental (*M. flavolimbatus*) realms, with its four constitutive members occurring in China. This country is also the only to host all species of this lineage, suggesting this area might have been its center of origin.

Acknowledgements

References

Bernhauer M (1938) Zur Staphylinidenfauna von China u. Japan. (9. Beitrag). Entomologisches Nachrichtenblatt 12: 17–39.

Cameron M (1924) New species of Staphylinidae from India. Transactions of the Royal Entomological Society of London, 160–198. https://doi.org/10.1111/j.1365-2311.1924.tb03357.x

Cuccodoro G (1996) Revision of the Japanese rove-beetles of the genus *Megarthrus* (Coleoptera, Staphylinidae, Proteininae). Revue suisse de Zoologie 103(2): 475–524. https://doi.org/10.5962/bhl.part.79957

Cuccodoro G (2003) A revision of *Megarthrus* Curtis of India, Nepal and Sri Lanka (Coleoptera, Staphylinidae, Proteininae). In: Cuccodoro G, Leschen RAB (Eds) Systematics of Coleoptera: Papers celebrating the retirement of Ivan Löbl. Memoirs on Entomology, International, Gainesville (Vol. 17), 359–455.

Cuccodoro G (2011) *Megarthrus* of Taiwan, with notes on phylogenetic relationships within the genus (Coleoptera: Staphylinidae: Proteininae). Studies and reports, taxonomical Series 7(1–2): 25–92.

Cuccodoro G, Löbl I (1997) Revision of the Palaearctic rove-beetles of the genus *Megarthrus* Curtis (Coleoptera: Staphylinidae: Proteininae). Journal of Natural History 31: 1347–1415. https://doi.org/10.1080/00222939700770761

Cuccodoro G, Kim HM, Ahn KJ (2011) *Megarthrus* of Korea, with description of a new species (Coleoptera: Staphylinidae: Proteininae). The Canadian Entomologist 143: 317–331. https://doi.org/10.4039/n11-004

Illiger JKW (1794) Beschreibung einiger neuen Käferarten aus der Sammlung des Herrn Professors Hellwig in Braunschweig, Neuestes Magazin für die Liebhaber der Entomologie. herausgegeben von D. H. Schneider 1(5): 593–620.

Liu ZP, Cuccodoro G (2020a) *Megarthrus* of China. Part 1. Description of a new species resembling *M. antennalis* Cameron, 1941 (Coleoptera: Staphylinidae: Proteininae). Zootaxa 4750(2): 269–276. https://doi.org/10.11646/zootaxa.4750.2.10

Liu ZP, Cuccodoro G (2020b) *Megarthrus* of China. Part 2. *Megarthrus basicornis* Fauvel, 1904 with description of a new species from Mount Emei (Coleoptera: Staphylinidae: Proteininae). Zootaxa 4895(1): 124–134. https://doi.org/10.11646/zootaxa.4895.1.7

Zhang S, Cuccodoro G, Chen L, Liu ZP (2021) *Megarthrus* of China. Part 3. About the occurrence of *Megarthrus nitidulus* Kraatz, 1857 in China, with description of a new species, and notes on teratology and phoretic acari in the genus (Coleoptera: Staphylinidae: Proteininae). Zootaxa 4920(4): 554–564. https://doi.org/10.11646/zootaxa.4920.4.6

RESEARCH ARTICLE

Five new species of the leaf-beetle genus *Monolepta* Chevrolat (Coleoptera, Chrysomelidae, Galerucinae) from China

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Abstract

In this study, five new species of the leaf-beetle genus *Monolepta* Chevrolat, 1836 (Coleoptera, Chrysomelidae, Galerucinae) are described from China: *M. albipunctata* **sp. nov.**, *M. alticola* **sp. nov.**, *M. bivittata* **sp. nov.**, *M. mengsongensis* **sp. nov.**, and *M. rubripennis* **sp. nov.** A key and catalogue to the 68 Chinese species of *Monolepta* with the second and third antennomeres of equal length are given as well as photographs of the habitus and aedeagus of the new species and type habitus images of 37 known species.

Keywords

Coleoptera, Chrysomelidae, Galerucinae, Monoleptites, *Monolepta*, new species

Introduction

With 708 species and six subspecies distributed worldwide (Nie et al. 2017), the leaf-beetle genus *Monolepta* is one of the largest genera in Galerucinae (Coleoptera, Chrysomelidae). There are 342 species distributed in the Oriental region, which is

almost half the species in this genus. Several new Chinese species have been described since revision (Gressitt and Kimoto 1963) and 73 species have been recorded, 71 in the Oriental region and two in the Palaearctic region (Yang et al. 2015).

During sorting of specimens in the Institute of Zoology, Academy of Sciences, five new species were found and are described here. In addition, photographs of the habitus, external parts and aedeagus of the new species and habitus of known species (in Suppl. material 1) are also given together with a key to the Chinese species.

Material and methods

The specimens were examined with an Olympus SZ61 microscope.

Dissections

The abdomen was taken from the specimens, then transferred to a vial containing 5% NaOH solution and heated in boiled water around 5–7 minutes. The abdomen with aedeagus was washed in distilled water 3 or 4 times, transferred into a cavity slide using fine forceps and the aedeagus was separated by hooked minute-pin dissecting needles.

Photographs

Habitus images were taken using a Canon 5DSR digital camera, equipped with a lens EF 75–300 mm f/4–5.6 linking a Nikon CFI Plan Apochromat Lambda 4× or 2× objective lens. Illumination was by flash, and each photo was taken by a macro slide system.

Aedeagus images were taken using a Nikon D610 digital camera, linking a Zeiss V microscope, with 5× and 10× objective lens. A cable shutter release was used to prevent the camera from shaking. The number of images taken was depending on the size of the aedeagus.

To get full depth of focus, all images were stacked with HELICON FOCUS 6 (http://www.heliconsoft.com/heliconsoft-products/helicon-focus/) and the resulting output, edited with Adobe Photoshop CC (https://www.photoshop.com/).

Labels

The label data is translated into English from the original Chinese.

Type depository

Type specimens of the five new species are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**IZAS**).

Biology

The life cycle of most species of *Monolepta* is little known, but in China the life cycle of *M. signata* (Olivier, 1808) (= *M. hieroglyphica* (Motschulsky, 1858)) has been recorded in detail. It has one generation each year and overwinters as eggs, hatching in May. Its larvae live underground for about a month, feeding on grass roots. The mature larvae pupate in the soil after 7–10 days of emergence. Adults normally appear in July and survive until October (Research Group of Leaf Beetle 1979). Some species of this genus are important agriculture pests, for example *M. signata*, which is a widely distributed pest in Asia and causes serious damage to plants (such as *Arachis hypogaea*, *Gossypium* sp., *Pyracantha crenulate*, *Rubus* sp., *Salix* sp., *Viburnum* sp., *Zea mays*) in China, Nepal, and Bangladesh (Neupane et al. 2006; Zhang 2012), while *M. australis* Jacoby, 1882 is harmful to peanut crops in Queensland, Australia (Turner 1980).

Taxonomy

Genus *Monolepta* Chevrolat

Monolepta Chevrolat 1836: 383. Type species: *Crioceris bioculata* Fabricius, 1781, by subsequent designation (Chevrolat 1845: 5).
Damais Jacoby 1903: 118. Type species: *Damais humeralis* Jacoby, 1903, by monotypy. Synonymized by Maulik (1936: 373).
Aemulaphthona Scherer 1969: 89. Type species: *Aemulaphthona ochracea* (Weise, 1922), by monotypy. Synonymized by Konstantinov (2002: 210).
Chimporia Laboissière 1931: 413. Type species: *Chimporia monardi* Laboissière, 1931, by monotypy. Synonymized by Wagner (2007: 84).

Distribution. Palaearctic, Oriental, Australian, Afrotropical, Neotropical region.
Diagnosis. Body length: 1.9–9.5 mm. Antennae longer than half or even equal to the body, segments 2 and 3 almost equal in length, segment 4 equal to or longer than sum of segments 2 and 3. Width of pronotum longer than length; anterior margin slightly depressed, basal margin protruding and lateral margins slightly protruding; basal margin and lateral margins with frame; anterior and posterior angle thickened, each angle with a seta-pore; disc convex, generally depressed on both sides. Scutellum triangular, smooth, and impunctate. Elytra broader than pronotum, humeral angle obvious; epipleuron broad before basal 1/3, then strongly narrowed and disappearing at beginning of apex. Anterior coxal cavities open or closed, each tibia with a spine in apex, spine of hind tibiae longest, 1st segment of hind tarsi longer than remaining segments combined; claws appendiculate. Last sternite of male with trilobate concavities, female normal, without any concavities (Gressitt and Kimoto 1963).
Remarks. Since its description, several genera have been synonymized with *Monolepta*. Of these, Maulik (1936) synonymized *Damais* Jacoby, 1903 based on the

length of the 1ˢᵗ segment of the hind tarsi which is longer than the remaining combined segments in *D. humeralis* Jacoby, 1903, the type species. Konstantinov (2002) synonymized *Aemulaphthona* Scherer, 1969, originally placed in Alticini, based on several characters of the type species *Aemulaphthona ochracea* (Weise, 1922), such as the flat head in lateral view, absence of a supraorbital sulcus, and metafemur without a metafemoral spring. Wagner (2007) synonymized *Chimporia* Laboissière 1931 based on the similarity of the aedeagus. Also, based on characters of the anterior coxae and the second antennomere, and morphology of aedeagus, many new genera were described for species previously included in *Monolepta*, such as *Afromaculepta* Wagner, 2000, *Afromegalepta* Wagner, 2001, *Afrocandezea* Wagner, 2002, *Afronaumannia* Wagner, 2005, *Monoleptoides* Wagner, 2011, *Neobarombiella* Wagner, 2012, *Orthoneolepta* Hazmi & Wagner, 2013, *Paraneolepta* Hazmi & Wagner, 2013, *Bicolorizea* Wagner, 2015, and *Doeberllepta* Wagner, 2017.

The ratio of antennomeres 2 and 3 is of great importance for the identification in *Monolepta* and related genera. The length of 2 to 3 in the type species, *M. bioculata*, is 0.83–1.00 (Wagner 2007). Sometimes antennomere 2 is slightly shorter than 3, as in *M. jeanneli* (0.78–0.87), or on the contrary, antennomere 2 is slightly longer than 3, as in *M. usambarica* (1.00–1.20; Wagner 2000). In general, the ratio of antennomeres 2 and 3 is 0.80–1.20.

There are also some similar genera in the Oriental region. In *Arcastes*, the lack of pronotal depressions and the significantly enlarged antennomeres 3–8 distinguishes it from other genera, as does the ratio of antennomeres 2 and 3, which is 0.5–0.57; thus, it is easily recognized from *Monolepta* (Hazmi and Wagner 2010a). *Rubrarcastes* has the similarly enlarged antennomeres of *Arcastes*, but the ratio of antennomeres 2 and 3 is 0.43–0.57 (Hazmi and Wagner 2010b). In the Oriental region, the relatively large body and the transverse depression on the pronotum distinguish *Paraneolepta*; antennomeres 4–6 are significantly widened in *Orthoneolepta*, which is different from that of *Monolepta*. In *Ochralea* Clark, 1865 the relatively large body (7.75–14.40 mm) and the deeply incised median lobe of aedeagus are characteristic (Hazmi and Wagner 2010c). The ratio of antennomeres of *Neolepta* is 0.75–0.80, *Paraneolepta* is 0.75–0.86, and *Orthoneolepta* 0.60–1.00. *Neolepta* is usually with widened median antennomeres. However, these three similar genera have a tansverse depression on pronotum, which is not present in *Monolepta*.

Eleven similar genera are distributed in China. In *Atrachya* Dejean, 1837, antennomere 3 is much longer than 2, and the tectum is deeply incised and with strong apical hooks (Lee 2020). In *Sermyloides* Jacoby, 1884, there is a strong frontal depression in males and a usually modified antennomere 3. In *Ochralea* Clark, 1865 antennomeres 2 and 3 are almost equal in length. In *Shaira* Maulik, 1936, the elytra is very short, and so this genus can be easily distinguished. In *Pseudosepharia* Laboissière, 1936, the epipleuron is very broad and 1/3 times as wide as the elytron. In *Paleosepharia* Laboissière, 1936, the epipleuron is gradually narrowed from its base to its apex, and there is sexual dimorphism (Lee 2018). In *Macrima* Baly, 1878, there is a frontal depression in males. *Trichosepharia* Laboissière, 1936 has the basal part of the median lobe incised and the

tectum enlarged at its apex. In *Chinochya* Lee, 2020, tasomere 1 is swollen in males, and there are two types of endophallic spiculae. *Tsouchya* Lee, 2020, has antennomere 2 much shorter than 3, and there are two types of endophallic spiculae. In *Neochya* Lee, 2020 antonnomeres 2 and 3 are almost the same length, but the coxal cavities are widely open and there is only one pair of endophallic spiculae.

The species included in *Monolepta* generally have two types of antennae: either with segments 2 and 3 equal in length or with segment 3 longer than 2. Most species of the former group have a similar type of aedeagus; these include: *M. babai* Kimoto, 1996; *M. bicavipennis* Chen, 1942; *M. kwangtunga* Gressitt & Kimoto, 1963; *M. mordelloides* Chen, 1942; *M. parvezi* Aslam, 1968, and *M. subflavipennis* Kimoto, 1989. Since the redescription of the type species by Wagner (2007), "true" *Monolepta* can be distinguished by the similar lengths of antennomeres 2 and 3, the abruptly narrowed epipleuron after the basal 1/3, and the aedeagus type. Although, the closed anterior coxal cavities of *Monolepta* were the main character to identify the genus in the past, Wagner (1999, 2007) redescribed anterior coxal cavities of the type species and showed them to be open. So, these structures are rather variable, with some closed or almost closed and others completely open.

Although 73 species of *Monolepta* are known from China, little recent detailed work on the genus has so far been published, and some species with the second and third antennomeres of unequal length and different types of aedeagus may need to be transferred to other genera in the future, for example *M. yaosanica* Chen, 1942 and *M. postfasciata* Gressitt & Kimoto, 1963. The following key is restricted to those 68 species which have antennomeres 2 and 3 of equal length.

Key to the species of Chinese *Monolepta*

Note: the key only includes species with the second and the third antennomeres approximately equal in length (see generic Remarks).

1	Elytra with depressions	**2**
–	Elytra without depressions	**3**
2	Elytra yellow, with three transverse black bands (Suppl. material 1: Fig. S6).	***M. cavipennis* Baly, 1878**
–	Elytra orange red, with two kidney-shaped depressions, one before middle suture, another outside of middle suture (Suppl. material 1: Fig. S37)	***M. quadricavata* Chen, 1976**
3	Elytra entirely red	**4**
–	Elytra yellowish brown, reddish brown or black	**5**
4	Pronotum black, elytra red (Fig. 29)	***M. rubripennis* sp. nov.**
–	Pronotum orange red, elytra with a pale-yellow dot near apex (Suppl. material 1: Fig. S11)	***M. eunicia* Maulik, 1936**
5	Elytra black	**6**
–	Elytra yellowish brown, reddish brown or partially black	**16**

6   Head yellow (Suppl. material 1: Fig. S51) ....***M. yaosanica* Chen, 1942**
–   Head black or partial black...7
7   Head partially black **8**
–   Head black, body wide oval (Suppl. material 1: Fig. S43) ....
        ....***M. semenovi* Ogloblin, 1936**
8   Head partially black **9**
–   Head yellow, yellowish brown or reddish brown..**12**
9   Pronotum dark brown **10**
–   Pronotum yellowish brown or reddish brown **11**
10   Abdomen yellowish brown...............................***M. asahinai* Chûjô, 1962**
–   Abdomen black (Suppl. material 1: Fig. S14) ....***M. horni* Chûjô, 1938**
11   Head black, frontal area dark yellowish brown (Suppl. material 1: Fig. S9) ...
        ....***M. epistomalis* Laboissière, 1934**
–   Head yellowish brown (Fig. 22).......................................***M. alticola* sp. nov.**
12   Abdomen yellowish brown **13**
–   Abdomen black or dark brown **14**
13   Scutellum yellowish brown (Suppl. material 1: Fig. S41) ....
        ....***M. schereri* Gressitt & Kimoto, 1963**
–   Scutellum black ....***M. longicornis* (Jacoby, 1890)**
14   Legs black (Suppl. material 1: Fig. S10).......***M. erythrocephala* (Baly, 1878)**
–   Legs reddish brown **15**
15   Antennae yellowish brown, segments 9–11 darker (Suppl. material 1:
        Fig. S32) ....***M. ovatula* Chen, 1942**
–   Antennae black, basal 4–5 segments yellowish brown......................................
        ....***M. chinkinyui* Kimoto, 1996**
16   Elytra yellow or reddish brown, without any bands **17**
–   Elytra with yellow or with black bands **39**
17   Head black or partially black...**18**
–   Head not black **20**
18   Occiput reddish brown (Suppl. material 1: Fig. S27)......................................
        ....***M. meridionalis* Gressitt & Kimoto, 1963**
–   Occiput black or head entirely black...**19**
19   Pronotum yellow; punctures of head stronger than that of elytra (Suppl.
        material 1: Fig. S50)..***M. xanthodera* Chen, 1942**
–   Pronotum red; punctures of head finer than that of elytra (Suppl. material 1:
        Fig. S5)...***M. capitata* Chen, 1942**
20   Abdomen black..**21**
–   Abdomen not black..**22**
21   Apex of elytra truncate (Suppl. material 1: Fig. S48)...***M. subrubra* Chen, 1942**
–   Apex of elytra rounded..................................***M. mandibularis* Chûjô, 1962**
22   Body usually small, less than 8 mm..**23**
–   Body very large, 9.5 mm.................................***M. severini* (Jacoby, 1896)**

23   Body length less than 2.5 mm...**24**
–   Body length more than 3.0 mm **26**
24   Elytral punctures arranged in irregular longitudinal rows (Suppl. material 1:
          Fig. S29) ....*M. minutissima* **Chen, 1942**
–   Elytral punctures not arranged in rows **25**
25   Pronotum punctures larger than elytral ones; punctures of elytra not com-
          bined (Suppl. material 1: Fig. S28)...........................*M. minor* **Chûjô, 1938**
–   Pronotum punctures finer than elytral ones; some punctures of elytra com-
          bined (Suppl. material 1: Fig. S4)..
          ....*M. brittoni* **Gressitt & Kimoto, 1963**
26   Antennae black, yellowish, or reddish brown..**27**
–   Antennae yellowish or reddish brown, except basal 3 segments black............
          ....*M. indochinensis* **Medvedev, 1999**
27   Antennae black **28**
–   Antennae yellowish brown or reddish brown **31**
28   General color reddish brown..**29**
–   General color yellowish brown...**30**
29   Elytra with strong punctures; abdomen without long hairs............................
          ....*M. annamita* **Laboissière, 1935**
–   Elytra with fine punctures; abdomen with long hairs.....................................
          ....*M. meihuai* **Lee, Tian & Staines, 2010**
30   Apex of aedeagus constricted dorsally (Suppl. material 1: Fig. S38)..............
          ....*M. rufofulva* **Chûjô, 1938**
–   Apex of aedeagus expanded dorsally, constricted near apex ....
          ....*M. nakanei* **Kimoto, 1969**
31   Antennomere 4 longer than or equal to the sum of 2 and 3.........................**32**
–   Antennomere 4 shorter than the sum of 2 and 3 (Suppl. material 1:
          Fig. S18) ....*M. lauta* **Gressitt & Kimoto, 1963**
32   Pronotum yellowish brown, lateral margins black (Suppl. material 1:
          Fig. S31) .... *M. ongi* **Lee & Staines, 2010**
–   Pronotum yellowish brown, without any color margin.................................**33**
33   Antennomere 3 as long as 2 ....**34**
–   Antennomere 3 1.3 times as long as 2 (Suppl. material 1: Fig. S33) ....
          ....*M. pallidula* **(Baly, 1874)**
34   Body length less than 3.5 mm..**35**
–   Body length more than 5.5 mm (Suppl. material 1: Fig. S7) ....
          ....*M. cheni* **Beenen, 2008**
35   Ventral side of mesothorax yellow or brown...**36**
–   Ventral side of mesothorax black .... *M. hongkongensis* **Kimoto, 1967**
36   Ventral side of mesothorax yellow **37**
–   Ventral side of mesothorax brown (Suppl. material 1: Fig. S3) ....
          ....*M. arundinariae* **Gressitt & Kimoto, 1963**

37 Space between elytral punctures equals to or larger than diameter of punctures **38**
– Space between elytral punctures less than diameter of punctures (Suppl. material 1: Fig. S34) ....***M. palliparva* Gressitt & Kimoto, 1963**
38 Space between punctures equals to diameter of punctures (Suppl. material 1: Figs S15, S16)..............................***M. hupehensis* Gressitt & Kimoto, 1963**
– Space between punctures 3 times as diameter of punctures (Suppl. material 1: Fig. S1) ....***M. aglaonemae* Gressitt & Kimoto, 1963**
39 The apical area of elytra mostly black...**40**
– The apical area of elytra not black...**44**
40 Head partially black or not black..**41**
– Head black ....***M. bacboensis* Medvdev, 2012**
41 Head partially black **42**
– Head not black **43**
42 Vertex black, basal 2/3 of elytra reddish brown..
.... ***M. yama* Gressitt & Kimoto, 1965**
– Frontal area black, basal 2/3 of elytra yellowish brown (Suppl. material 1: Fig. S42) ....***M. selmani* Gressitt & Kimoto, 1963**
43 Ventral surface of mesothorax and metathorax black, basal 1/2 of elytra reddish brown, apical 1/2 black (Suppl. material 1: Fig. S39) ....
.... ***M. sasajii* Kimoto, 1969**
– Ventral surface of mesothorax and metathorax yellowish brown, basal 3/5 of elytra yellowish brown, apical 1/2 dark brown (Suppl. material 1: Fig. S47)......................................***M. subapicalis* Gressitt & Kimoto, 1963**
44 Elytra with colorful border...**45**
– Elytra with black markings **51**
45 Ventral side of mesothorax yellowish brown...**46**
– Ventral side of mesothorax black (Suppl. material 1: Fig. S49) ....
.... ***M. wilcoxi* Gressitt & Kimoto, 1965**
46 Lateral margin of pronotum has the same color as pronotum....................**47**
– Lateral margin of pronotum black ....***M. takizawai* Kimoto, 1996**
47 Antennae reching more than 2/3 of elytra..48
– Antennae reaching middle of elytra...................***M. weigeli* Medvedev, 2012**
48 Antennae almost as long as body..**49**
– Antennae not reaching apical 2/3 of elytra **50**
49 Elytra yellowish brown, 4/5 lateral margin of elytra black (Suppl. material 1: Fig. S17) ....***M. kuroheri* Kimoto, 1966**
– Elytra yellowish brown, 2/5 lateral margin of elytra black (Suppl. material 1: Fig. S40) ....***M. sauteri* Chûjô, 1935**
50 Ventral surface of mesothorax and metathorax black (Suppl. material 1: Fig. S2)...***M. alnivora* Chen, 1976**
– Ventral surface of metathorax black, mesothorax yellow (Suppl. material 1: Fig. S13) ....***M. gracilipes* Chûjô, 1938**

51   Elytra with black stripes or bands..**52**
–   Elytra with black or yellowish-brown spots **58**
52   Pronotum reddish brown..**53**
–   Pronotum yellowish brown, each elytron with a semicircle spot in the middle, apex with a black parentheses-shaped marking (Suppl. material 1: Fig. S35) .... ***M. parenthetica* Gressitt & Kimoto, 1963**
53   Elytra black, with two pale spots in basal and apical area; or apex not black, with yellow spots in basal part (Suppl. material 1: Fig. S46).......................
        .... ***M. signata* (Olivier, 1808)**
–   Elytron without above characters **54**
54   Pronotum reddish brown..**55**
–   Pronotum yellowish brown **62**
55   Elytra without two black transverse bands...**56**
–   Elytra with two black transverse bands (Fig. 8) ....***M. bivittata* sp. nov.**
56   Elytra with a black thin longitudinal band (Suppl. material 1: Fig. S44) ....
        ....***M. sexlineata* Chûjô, 1938**
–   Elytra bands not longitudinal...**57**
57   Apex and base of elytra with a black band, middle yellow (Suppl. material 1: Fig. S30)..***M. occifluvis* Gressitt & Kimoto, 1963**
–   Basal 1/6 of elytra and apical 1/6 with black bands, middle with transverse brown and yellow bands (Suppl. material 1: Fig. S53)..................................
        .... ***M. zonalis* Gressitt & Kimoto, 1963**
58   Elytra with a small spot near base, a slightly larger spot after middle (Suppl. material 1: Fig. S23, S24) .... ***M. longitarsoides* Chûjô, 1938**
–   Elytra with more than two black spots or with yellow or brown bands......**59**
59   Elytra with black spots between humeral angle and middle suture (Suppl. material 1: Fig. S45) ....***M. shaowuensis* Gressitt & Kimoto, 1963**
–   Elytra with yellow or brown bands..**60**
60   Abdomen not black **61**
–   Abdomen black; basal 2/3 of elytra black, with a yellow spot ....
        ....***M. quadriguttata* (Motschulsky, 1860)**
61   Basal part of elytra red, turn black gradually to apex, with a rounded spot in middle (Suppl. material 1: Fig. S25)..
        ....***M. lunata* Gressitt & Kimoto, 1963**
–   Middle part of elytra with a "T" shape black stripes (Suppl. material 1: Fig. S36) ....***M. postfasciata* Gressitt & Kimoto, 1963**
62   Abdomen black..................................***M. discalis* Gressitt & Kimoto, 1963**
–   Abdomen yellowish brown or reddish brown **63**
63   Antennae as long as body (Fig. 15) ....***M. mengsongensis* sp. nov.**
–   Antennae not reaching apical 2/3 of elytra...**64**
64   Antennae not reaching to half length of body **65**
–   Antennae reaching more than half length of body.................................**66**

65 Tibiae and tarsi yellowish brown (Suppl. material 1: Fig. S26) ....
.... *M. maana* **Gressitt & Kimoto, 1963**
– Fore-legs yellowish brown, apex of tibiae and tarsi dark brown; coxae to fe-
murs of meso and meta-legs yellow, tibiae and tarsi dark brown (Suppl. mate-
rial 1: Figs S19, S20).. *M. leechi* **Jacoby, 1890**
66 Elytra without any transverse bands..**67**
– Elytra dark brown with a transverse yellow band (Suppl. material 1:
Figs S21, S22)...*M. liui* **Gressitt & Kimoto, 1963**
67 Elytra yellowish brown with wide dark brown frame (Suppl. material 1:
Fig. S12) .... *M. flavovittata* **Chen, 1942**
– Elytra black with a yellow dot in the middle (Suppl. material 1: Fig. S52) ....
....*M. yunnanica* **Gressitt & Kimoto, 1963**

Description of new species

Monolepta albipunctata **sp. nov.**
http://zoobank.org/C2EB97A0-B103-4666-8451-1082316A27C3
Figs 1–10

Type material. *Holotype*: CHINA • ♂; Guangxi, Jinxiu, Luoxiang; 400 m; 14-V-
1999; Xing-ke Yang leg. (IZAS). *Paratypes*: CHINA • 1♂; same data as holotype •
1♀; Guangxi, Jinxiu, Luoxiang; 450 m; 30-VI-2000; Jun Chen leg. • 2♀♀; Guangxi,
Jinxiu, Luoxiang; 400 m; 15-V-1999; Da-jun Liu leg. (all IZAS).

Description. Length: 5.5–6.6 mm, width 2.7–3.7 mm. Holotype: length 6.6 mm,
width 3.4 mm.

Head, pronotum, prothorax, scutellum, ventral side of mesothorax and metatho-
rax, abdomen, and legs orange; clypeus and mouthparts black; antennae black except
1st segment paler; tibiae slightly dark orange, tarsi black; basal area of elytra orange,
middle to apical area black with an oval white spot.

Vertex slightly convex, with transverse wrinkles, punctures obvious, space between
punctures almost equal to diameter of punctures, each puncture with a seta; frontal
tubercle obvious, not deeply divided by ecdysial suture, triangular, glabrous and with
several large punctures near frontal area; antennae longer than half of body, 1st segment
arc-shaped, length ratio of 2nd and 3rd segment 19: 18; length ratio of 4th and the com-
bination of 2nd and 3rd 2: 1.

Pronotum transverse, pronotum around 1.6 times as broad as long; disc slightly
convex, glabrous, shallowly depressed on each side, surface with irregular strong and
fine punctures, each puncture with short seta.

Scutellum triangular, smooth and impunctate.

Elytra about 1.5 times as long as broad, basal part wider than pronotum; hu-
meral angle obvious; two types of punctures in elytra: space between large punctures
about 3 times as wide as diameter of puncture, small punctures irregularly distrib-
uted; epipleuron strongly narrowed after basal 1/3 and disappearing at the beginning
of apex.
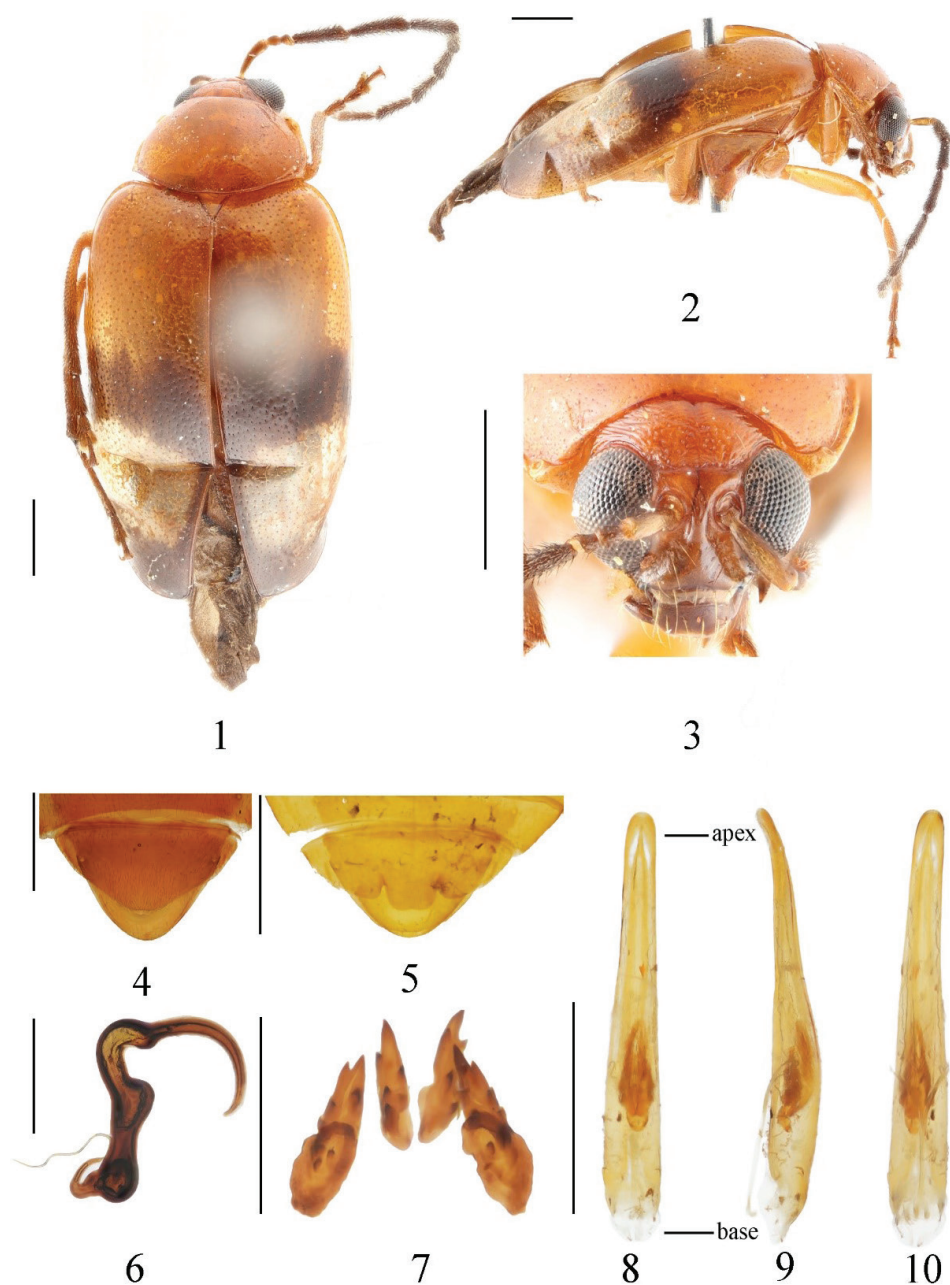
Figures 1–10. *Monolepta albipunctata* sp. nov. (holotype) **1** dorsal view **2** lateral view **3** frontal view **4** ventral view of 5th ventrite, female **5** ditto, male **6** spermatheca **7** bursa sclerites **8** aedeagus, dorsal view **9** ditto, lateral view **10** ditto, ventral view. Scale bars: 1 mm (**1–5, 8–10**); 0.5 mm (**6, 7**).

Ventral surface of mesothorax and metathorax covered with long setae. 1st segment of hind tarsi 1.9 times as long as remaining segments combined. Anterior coxal cavities open.

Male. Last ventrite of male with trilobite concavities. The median apical lobe of the last sternite around twice as broad as long (Fig. 5). Aedeagus very slender, almost parallel-sided from base to middle, suddenly narrowed before 1/2 part, rounded at apex, slightly curved towards ventral side (Fig. 9). Tectum extends almost to apex of aedeagus (Fig. 8).

Female. Last ventrite of female with very slight concavities. Spermathecal cornu slender, curved almost vertical, middle part short, curved, nodulus middle narrow. Ventral part of bursa sclerites slender, slightly undulate at outer side, dorsal pair slender, pointed at apex.

Etymology. The specific epithet *albipunctatus*, *-a*, *-um* (meaning 'white-spotted') is a New Latin adjective formed from the Latin adjective *albus*, *-a*, *-um* ('white') and the New Latin adjective *punctatus*, *-a*, *-um* ('punctate', 'marked by spots or punctures'); it refers to the large white spots on the elytra of this species.

Distribution. China: Guangxi.

Diagnosis. This species is similar to *M. postfasciata* Gressitt & Kimoto, 1963, but the latter has a smaller body with an obvious T-shaped black spot on each elytron, whereas *M. albipunctata* sp. nov. has a larger body with two separate large, white, round spots on each elytron.

Monolepta alticola sp. nov.

http://zoobank.org/FE2246D1-7C30-42C5-9D58-2137498E3545
Figs 11–20

Type material. *Holotype*: CHINA • ♂; Yunnan, Zhongdian, Gezan; 3000 m; 3-VIII-2003 (IZAS). *Paratypes*: CHINA • 1♂; Yunnan, Zhongdian, Gezan; 3000 m; 3-VIII-2003 • 2♀♀; Yunnan, Lunan, Shilin; 1700 m; 9-VII-1956; Kryzhanovskiy leg. (IZAS).

Description. Length: 2.5–3.5 mm, width: 1.5–2.0 mm. Holotype: length 3.5 mm, width 2.0 mm.

Vertex orange, frons yellow, mouthparts dark brown; antennae dark brown except segments 1–3 brown; dorsal and ventral side of prothorax, coxae of front legs, femora yellow; scutellum, elytra, ventral side of mesothorax, metathorax, middle and hind legs dark brown; tibiae and tarsi of front legs pale brown, apex of middle and hind legs pale yellow.

Vertex convex, punctures sparsely and irregularly distributed; frontal tubercle developed; antennae longer than half of body, 1st segment arc-shaped, length ratio of 2nd and 3rd segment 16: 15, length ratio of 4th segment and the combination of 2nd and 3rd 45: 31.

Pronotum transverse, around 1.6 times as broad as long; disc slightly convex, shallowly depressed on each side, punctures unapparent, sparsely distributed; space between punctures wider than diameter of punctures.

Scutellum triangular, smooth and impunctate. The elytron about 1.6 times as long as broad; basal part wider than pronotum, humeral angle obvious; punctures on
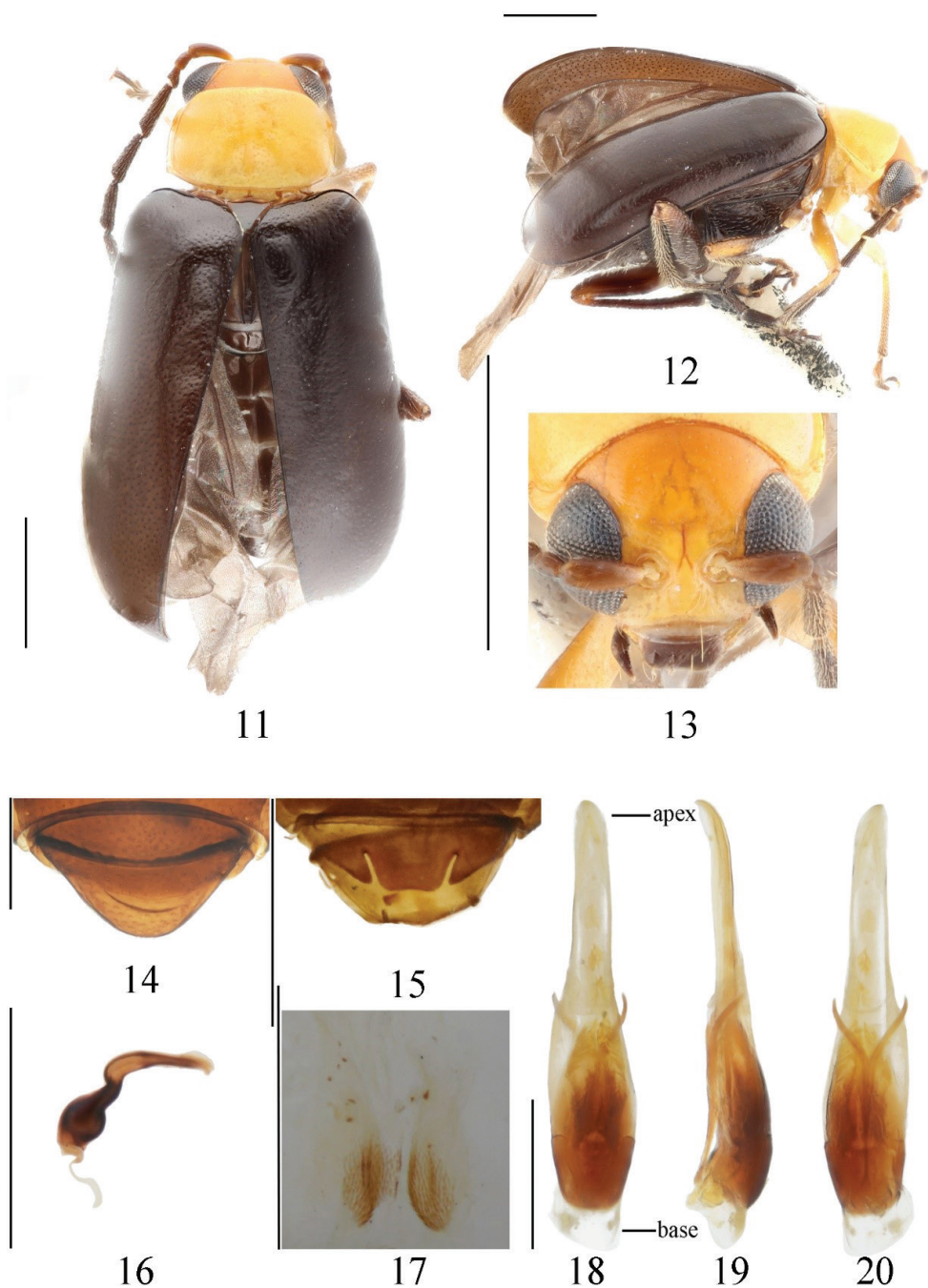
Figures 11–20. *Monolepta alticola* sp. nov. (holotype) **11** dorsal view **12** lateral view **13** frontal view **14** ventral view of 5th ventrite, female **15** ditto, male **16** spermatheca **17** bursa sclerites **18** aedeagus, dorsal view **19** ditto, lateral view **20** ditto, ventral view. Scale bars: 1 mm (**11–15, 18–20**); 0.5 mm (**16, 17**).

elytra irregularly distributed, space between punctures about 3 times as diameter of punctures. Epipleuron strongly narrowed after basal 1/3 and disappearing at beginning of apex.

Ventral surface of mesothorax, metathorax, and abdomen covered with long hairs.

Width and length ratio of median apical lobe 1.1 (apex part width to length), 2.2 (basal part width to length) (Fig. 15). 1st segment of hind tarsi about 1.7 times as long as remaining segments combined.

Male. Aedeagus slender, ratio of length and width around 5; greatest width in basal 1/3, and suddenly narrowed from basal 1/2 and parallel sided; apex slightly cuspidate. Tectum extends almost to the apex of aedeagus, cuspidate apically (Fig. 18).

Female. Last ventrite of female normal, male with trilobite concavities. Spermathecal cornu slender, apex slightly pointed, middle part short, curved, nodulus nearly spherical, large.

Etymology. The specific epithet *alticola*, *altus* (meaning 'living in high altitude') is a Latin adjective and the Latin *col*, ('lives'); it refers to the high-altitude habitat of this species.

Distribution. China: Yunnan.

Diagnosis. This species is similar to *M. schereri* Gressitt & Kimoto, 1963 and *M. epistomalis* Laboissière, 1935. The main differences are the following: the ventral side of the meso- and meta-thorax and the abdomen of *M. schereri* are yellowish brown, whereas these are dark brown in *M. alticola* sp. nov. *M. epistomalis* has a dark-brown head and a yellowish-brown abdomen, whereas *M. alticola* sp. nov. has a yellow head and a black abdomen, and with the aedeagus tapering towards its apex.

Monolepta bivittata sp. nov.

http://zoobank.org/B9A59187-352B-4171-8B08-B49BB8A1061D
Figs 21–27

Type material. *Holotype*: China • ♂; Zhejiang, Taishun, Wuyanling Nature Reserve station by light; 800 m; 1-VIII-2005; Liu Ye leg. (IZAS). *Paratypes*: China • 3♂♂; Zhejiang, Taishun, Wuyanling Nature Reserve station, at light; 800 m; 1-VIII-2005; Liu Ye leg. (IZAS).

Description. Length: 3.0–3.6 mm, width: 1.5–1.7 mm. *Holotype*: length 3.6 mm, width 1.7 mm.

Head, dorsal and ventral side of prothorax, and legs yellowish brown; mouthparts, scutellum, ventral side of mesothorax and metathorax black; antennae black, except segments 1–3 yellowish brown; elytra and abdomen pale yellow, basal and postmedian area of elytra with transverse black stripe.

Vertex convex, with sparsely distributed punctures; frontal tubercle developed, trapezoid, glabrous and without punctures; antennae reach half of body, 1st segment arc-shaped, length ratio of segment 2nd and 3rd 15: 16, length ratio of 4th and combination of 2nd and 3rd 34: 31.
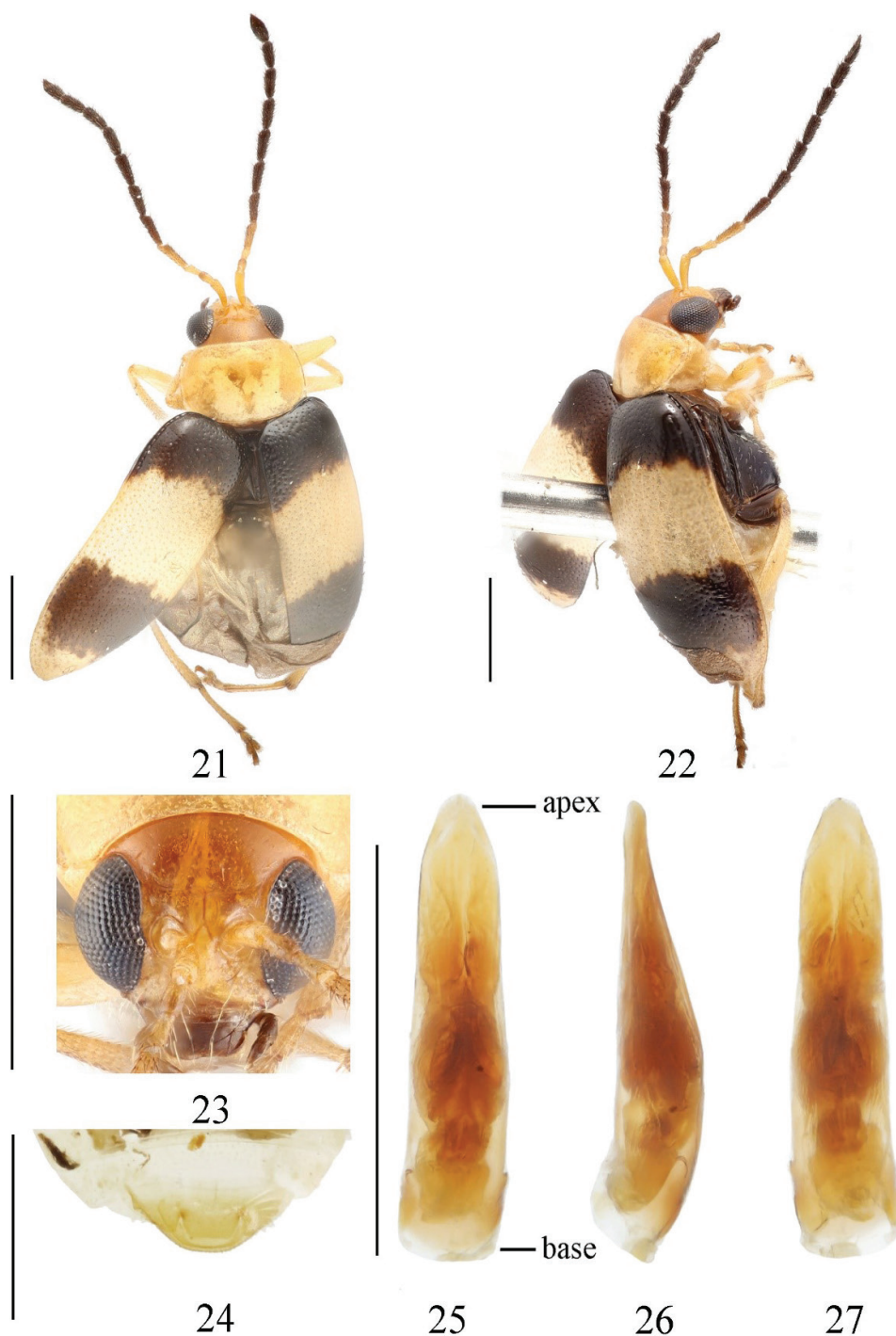
Figures 21–27. *Monolepta bivittata* sp. nov. (holotype) **21** dorsal view **22** lateral view **23** frontal view **24** ventral view of 5th ventrite, male **25** aedeagus, dorsal view **26** ditto, lateral view **27** ditto, ventral view. Scale bars: 1 mm.

Pronotum about 1.5 times as broad as long; disc slightly convex, shallowly depressed on each side, punctures unapparent and sparsely distributed.

Scutellum triangular, smooth and impunctate. Elytron about 1.5 times as long as broad; basal part wider than pronotum, humeral angle obvious; punctures evenly distributed, space between punctures is about 2 times as diameter of puncture, each puncture with seta; epipleuron strongly narrowed after basal 1/3, disappearring at beginning of apex. Ventral side of mesothorax, metathorax and abdomen covered with long hairs.

Male. Last ventrite of male with trilobite concavities. Width and length ratio of median apical lobe 1.4 (apex width to length), 1.5 (basal width to length) (Fig. 24). Aedeagus: ratio of length to width around 4:3; gradually and slightly tapering from base to near apex then abruptly constricted in distal 1/5 in lateral view; apex rounded and slightly pointed (Figs 25, 27). Tectum broad, long, reaching to apex of aedeagus (Fig. 25).

Etymology. The specific epithet *bivittatus*, *-a*, *-um* (meaning 'bivittate', 'having two bands or stripes or vittae') is a New Latin adjective formed from the Latin prefix *bi-* (a shortened form of *bis*, 'twice') and the Latin adjective *vittatus*, *-a*, *-um* ('banded'); it refers to the two transverse black stripes on the elytra of this species, a character which distinguishes this species from all other species in the genus.

Distribution. China: Zhejiang.

Diagnosis. This species is similar to *M. leechi* Jacoby, 1890, *M. maana* Gressitt & Kimoto, 1963, and *M. liui* Gressitt & Kimoto, 1963. The main differences are the following: the abdomen of *M. leechi* is black and the apex of the aedeagus is sharp, whereas the abdomen of *M. bivittata* sp. nov. is pale yellow and the apex of the aedeagus is blunt. The space between the punctures on the elytra of *M. maana* is equal to the diameter of the punctures, whereas in *M. bivittata* sp. nov., it is about twice the diameter of the punctures. The mid- and hind-legs of *M. liui* are dark brown, whereas the legs of *M. bivittata* sp. nov. are yellowish brown.

Monolepta mengsongensis sp. nov.
http://zoobank.org/BCF69DF0-2A5A-49AC-BB27-36D0D561EC9D
Figs 28–34

Type material. *Holotype*: China • ♂; Yunnan, Menglong, Banna, Mengsong; 1600 m; 27-IV-1958; Shu-yong Wang leg. (IZAS). *Paratype*: China • 1♂; Yunnan, Menglong, Banna, Mengsong; 1600 m; 27-IV-1958; Shu-yong Wang leg. (IZAS).

Description. Length: 5.5–6.5 mm, width 3–3.5 mm. *Holotype*: length 6.5 mm, width 3.5 mm.

Head, dorsal and ventral side of prothorax, mesothorax, metathorax, and femora orange; mouthparts darker; antennae dark brown, 1st segment pale; scutellum, tibiae, and tarsi black; a wide, transverse, pale, yellowish-brown stripe after middle part of elytra, which reaches middle sutures but not to lateral margins.
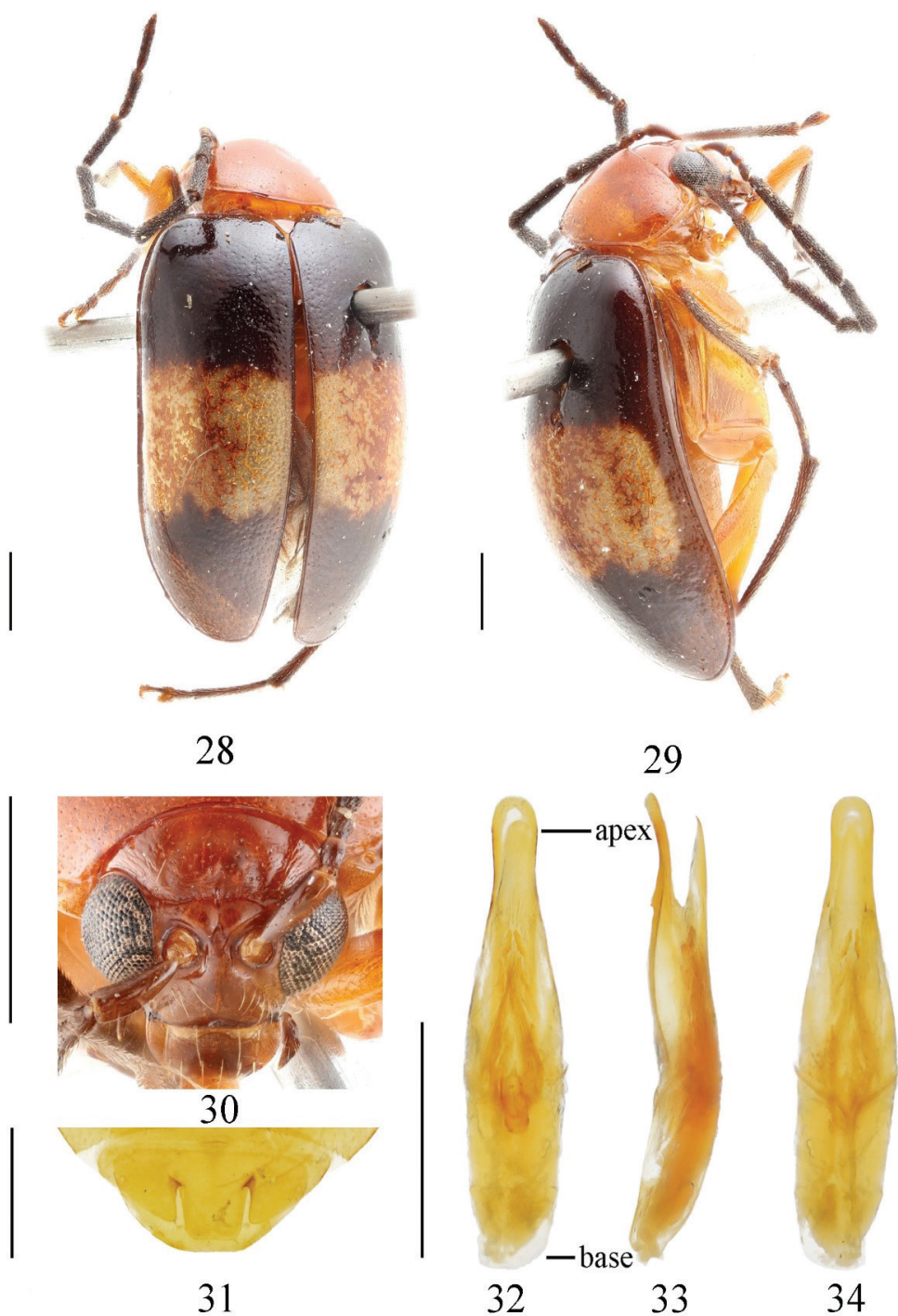
Figures 28–34. *Monolepta mengsongensis* sp. nov. (holotype) **28** dorsal view **29** lateral view **30** frontal view **31** ventral surface of 5th ventrite, male **32** aedeagus, dorsal view **33** ditto, lateral view **34** ditto, ventral view. Scale bars: 1 mm.

Vertex convex, with transverse wrinkle, punctures obvious and evenly distributed, space between punctures is about twice as diameter of punctures; frontal tubercle developed, deeply divided by ecdysial suture, not reaching compound eye, triangular, glabrous and with a few punctures; antennae reach apex of elytra, 1st segment arc-shaped, 2nd antennomere equal to 3rd, 4th segment longer than sum of 2nd and 3rd.

Pronotum about 1.5 times as broad as long; disc slightly convex, shallowly depressed on each side; punctures obvious, densely and irregularly distributed, space between punctures wider than diameter of punctures.

Scutellum triangular, smooth and impunctate. Elytron nearly 1.6 times as long as broad; basal part broader than pronotum, humeral angle obvious; punctures evenly distributed, space between punctures about 2–3 times diameter of punctures. Epipleura strongly narrowed after basal 1/3 and disappearing at beginning of apex. Ventral side of mesothorax, metathorax and abdomen covered with long hairs.

Male. Last ventrite of male with trilobite concavities. Width and length ratio of median apical lobe 0.76 (apex width to length), 1.3 (basal width to length) (Fig. 31). Aedeagus almost straight, parallel sided in apical 1/5, slightly widened in the middle part, narrowed after 1/3 of apex, rounded at apex, slightly curved towards ventral side (Fig. 33). Tectum not reaching apex of aedeagus, apex rounded (Fig. 32). 1st segment of hind tarsi about 1.5 times as long as remaining segments combined.

Etymology. This species is named after its type locality at Mengsong.

Distribution. China: Yunnan.

Diagnosis. This species resembles *M. leechi*, *M. liui*, and *M. lunata*, but the length of the antennae reaches half of the body in *M. leechi* and *M. liui*, whereas in this species the length of the antennae reaches the apex of elytra. *M.lunata* has a rounded spot on the elytra, but in the new species there is a transverse band. This species has a transverse stripe on each elytron and its antennae reach the apex of the elytra, which can easily distinguish it from other species of *Monolepta* with transverse stripes.

Monolepta rubripennis sp. nov.
http://zoobank.org/9B3D7F14-3838-450E-959E-1274765678C5
Figs 35–44

Type material. *Holotype*: China • ♂; Sichuan, Mount Emei, Baoguo temple; 550–750 m; 2-VI-1957; Ke-ren Huang leg. (IZAS). *Paratypes*: China • 2♀♀; Hunan, Guiding, Sidu, Xinlong village; 12-VII-2008; Hong-bin Liang leg. • 1♂; Fujian, Chongan, Xing village, Sangang; 740 m; 4-VI-1960; Yong Zuo leg. • 1♀; Sichuan, Mount Emei, Baoguo temple; 550–750 m; Ke-ren Huang leg.; 2-VI-1957 • 1♀; Mount Emei; 28-II-1955; Ke-ren Huang leg. • 1♀; Sichuan, Mount Emei, Baoguo temple; 550–750 m; 29-V-1957; Zong-yuan Wang leg. (all IZAS).

Description. Length: 4.5–5.5 mm, width 2.2–3.0 mm. **Holotype**: length 5.5 mm, width 2.8 mm.

Head, pronotum, prothorax, and legs black; scutellum, elytra, mesothorax, metathorax, and abdomen orange to reddish brown. Basal 1/2 of hind femur orange.
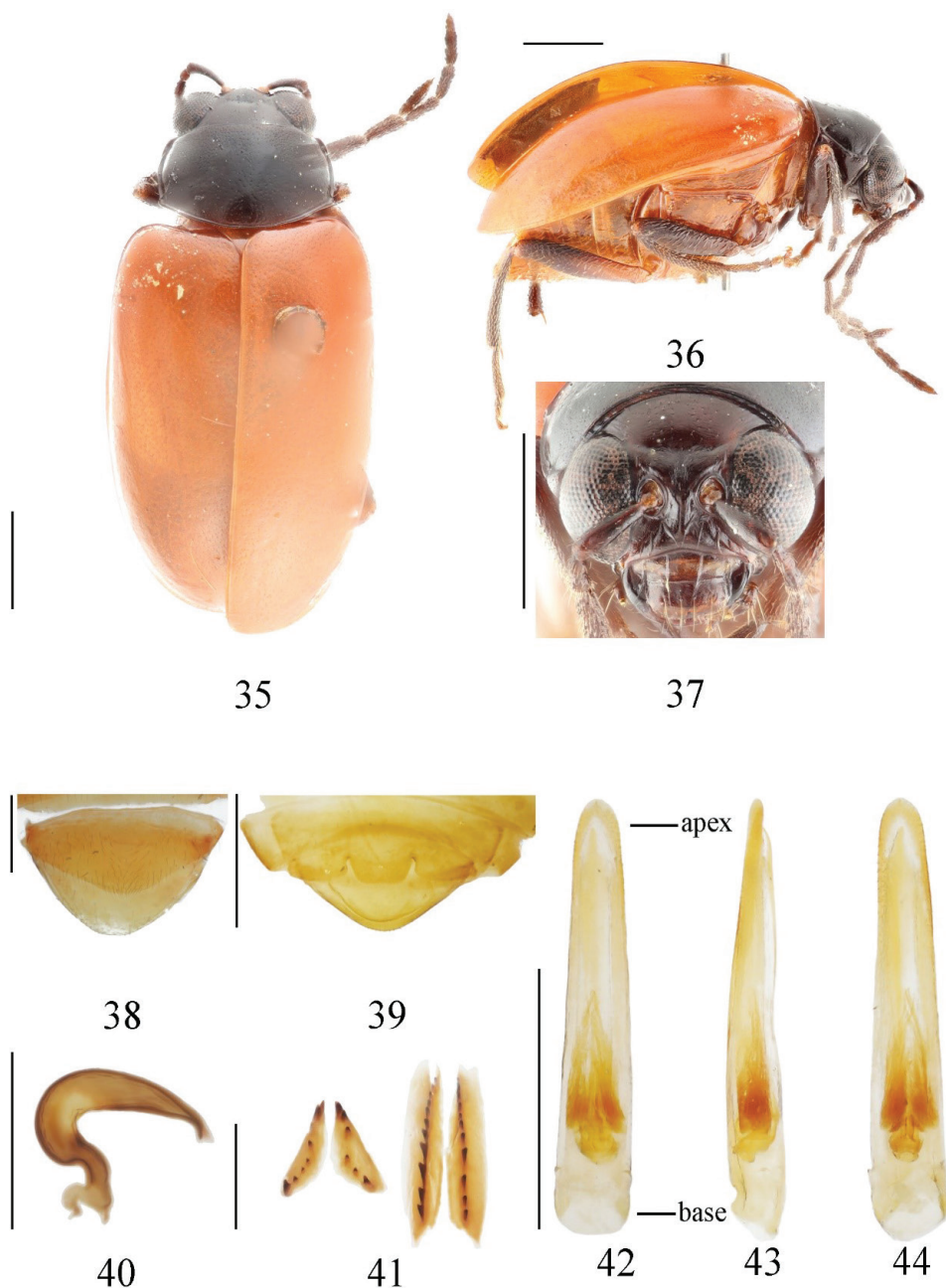
Figures 35–44. *Monolepta rubripennis* sp. nov. (holotype) **35** dorsal view **36** lateral view **37** frontal view **38** ventral view of 5th ventrite, female **39** ditto, male **40** spermatheca **41** bursa sclerites **42** aedeagus, dorsal view **43** ditto, lateral view **44** ditto, ventral view. Scale bars: 1 mm (**35–39, 42–44**); 0.5 mm (**40, 41**).

Vertex slightly convex with transverse wrinkle visible only laterally, punctures sparsely and irregularly distributed; frontal tubercle developed, deeply divided by ecdydial suture, triangular, not very glabrous and with many wrinkles on; antennae

reach half of the body, 1st segment arc-shaped, length ratio of segment 2nd and 3rd 19:21, length ratio of 4th and the combination of 2nd and 3rd 23:18.

The pronotum is about 1.7 times as broad as long; disc slightly convex, shallowly depressed on each side; surface with irregular strong punctures, densely distributed near anterior margin, sparsely near basal margin. Anterior coxal cavities open.

Scutellum triangular, smooth and impunctate. Elytra is about 1.4 times as long as broad; basal part wider than pronotum, humeral angle obvious; punctures on elytra evenly distributed, with very short seta, space between punctures about 2–4 times as diameter of punctures; epipleuron strongly narrowed after basal 1/3 and disappearing at the beginning of apex. Ventral side of mesothorax, metathorax and abdomen glabrous, covered with longhairs.

The width and length ratio of median apical lobe is 1.2 (apex width to length), 2.3 (basal width to length) (Fig. 39). The 1st segment of hind tarsi is about 1.5 times as long as remainder combined.

Male. Last ventrite of male with trilobite concavities. Aedeagus very slender and evenly narrowing from base to apex, apex rounded with a small cuspidate process. Tectum not reaching the apex of aedeagus, acute angle apex and curved towards ventral side (Fig. 43).

Female. Last ventrite of female normal. Spermathecal cornu curved strongly, middle part short, curved, very slender, nodulus small, nearly spherical. Ventral part of bursa sclerites fusiform, dorsal pair triangular, pointed at apex.

Etymology. The specific epithet *rubripennis*, *rubripenne* (meaning 'having red feathers or wings') is a New Latin adjective formed from the Latin adjective *ruber*, *rubra*, *-um* ('red') and the Latin noun *penna*, *-ae* ('feather', 'wing'); it refers to the red elytra of this species.

Distribution. China: Hunan, Fujian, Sichuan.

Diagnosis. This species is similar to *M. rufipennis* Jacoby, 1899 and *M. langbianica* Kimoto, 1989. The main differences are the following: *M. rubripennis* sp. nov. has. an orange abdomen and black antennae, whereas *M. rufipennis* has a black abdomen and yellow antennae, and *M. langbianica* has yellowish-brown antennae and a yellowish-brown abdomen.

Acknowledgements

References

Bolz H, Wagner T (2012) *Neobarombiella*, a diverse, newly described genus of Afrotropical Galerucinae (Coleoptera, Chrysomelidae). Zootaxa 3463: 1–112. https://doi.org/10.11646/zootaxa.3463.1.1

Chen SH (1942) Galerucinae nauveaux de la faune chinoise. Notes Ent Chinoise Shanghai 9: 9–67.

Chen SH, Yu PY, Wang SY, Jiang SQ (1976) New leaf beetles from west China. Acta Entomologica Sinica 19: 205–224.

Chevrolat LAA (1837) *Monolepta*. In: Dejean PFMA (Ed.) Catalogues des Coléopterès de la collection de M. LeComte Dejean. Troisième édition, revue, corrigée et augmentée, livraison. Méquignon-Marvis Père et Fils, Paris. Vol. 5, 385–503.

Chevrolat LAA (1845) Galérucites. In: D'Orbigny C (Ed.) Dictionaire Universel d'Histoire Naturelle 6. Paris, 4–6.

Gressitt JL, Kimoto S (1963) The Chrysomelidae (Coleopt.) of China and Korea. Part II. Pacific Insects Monograph 1B: 301–1026.

Hasenkamp R, Wagner T (2000) Revision of *Afromaculepta* gen. n., a monophyletic group of Afrotropical galerucine leaf beetles (Coleoptera: Chrysomelidae). Insect Systematics & Evolution 31: 3–26. https://doi.org/10.1163/187631200X00282

Hazmi IR, Wagner T (2010a) Revision of *Arcastes* Baly, 1865 from the Oriental Region (Coleoptera, Chrysomelidae, Galerucinae). ZooKeys 42: 79–99. https://doi.org/10.3897/zookeys.42.336

Hazmi IR, Wagner T (2010b) *Rubrarcastes* gen. nov., a new group of Oriental galerucine leaf beetles (Coleoptera: Chrysomelidae, Galerucinae). Entomologische Zeitschrift 120(2): 85–88.

Hazmi IR, Wagner T (2010c) Revalidation and revision of *Ochralea* Clark, 1865 (Coleoptera: Chrysomelidae: Galerucinae) from the Oriental Region. Zootaxa 2530: 47–59. https://doi.org/10.11646/zootaxa.2530.1.5

Hazmi IR, Wagner T (2013) Revision of *Neolepta* Jacoby, 1884 and related Galerucines from the Oriental region, including descriptions of two new genera (Coleoptera: Chrysomelidae: Galerucinae). Raffles Bulletin of Zoology 61: 73–95.

Heunemann LO, Dalstein V, Schulze M, Wagner T (2015) *Bicolorizea* gen. nov. from tropical Africa (Coleoptera: Chrysomelidae, Galerucinae). Entomologische Zeitschrift 125(4): 235–246.

Jacoby M (1890) Descriptions of new species of Phytophagous Coleoptera received by Mr. J. H. Leech, from Chang-yang, China. Entomologist 23: 84–217.

Jacoby M (1899) Descriptions of the new species of phytophagous Coleoptera obtained by Dr Dohrn in Sumatra. Entomologische Zeitung 40: 259–320.

Jacoby M (1903) Descriptions of the new genera and species of phytophagous Coleoptera obtained by Mr H. L. Andrewes and Mr T. R. D. Bell at the Nilgiri Hills and Kanara. Annales de la Société Entomologique de Belgique 47: 80–128.

Kimoto S (1989) Chrysomelidae (Coleoptera) of Thailand, Cambodia, Laos and Vietnam. 4. Galerucinae. Esakia 27: 1–241.

Kimoto S (2001) The Chrysomelidae (Insecta: Coleoptera) collected by the Kyushu University Scientific Expedition to the Nepal Himalaya in 1971 and 1972. Bulletin of the Kitakyushu Museum of Natural History 20: 17–80.

Konstantinov AS, Lingafelter SW (2002) Revision of the Oriental species of *Aphothona* Chevrolat (Coleoptera: Chrysomelidae). Entomological Society of Washington, Washington DC, 345 pp.

Laboissière V (1931) Galerucini (Coleoptera Chrysomelidae) d'Angola. Revue Suisse de Zoologie 38: 405–418. https://doi.org/10.5962/bhl.part.117646

Laboissière V (1935) Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas. 20. Coleoptera. 6. Galerucinae. Arkiv for Zoologi Stockholm 27A: 1–9.

Lee CF (2020) Revision of Taiwanese species of *Atrachya* Chevrolat, 1836 (Coleoptera, Chrysomelidae, Galerucinae): descriptions of three new genera, two new species, and designations of three new synonyms. ZooKeys 940: 117–159. https://doi.org/10.3897/zookeys.940.51800

Maulik S (1936) Coleoptera. Chrysomelidae (Galerucinae). In: Maulik S [Cantab MA, FZS, FRES] (Ed.) The Fauna of British India including Ceylon and Burma. Taylor and Francis, London, Vol. 4, 395–430. https://doi.org/10.5962/bhl.title.48423

Neupane FP, Sharma MD, Neupane KR (2006) Incidence of insect pests on chaoyote, *Sechium edule* (Swartz.) in Nepal. Journal of the Institute of Agriculture and Animal Science 27: 161–164. https://doi.org/10.3126/jiaas.v27i0.711

Nie R-E, Bezdek J, Yang X-K (2017) How many genera and species of Galerucinae s. str. do we know? Updated statistics (Coleoptera, Chrysomelidae). ZooKeys 720: 91–102. https://doi.org/10.3897/zookeys.720.13517

Research Group of Leaf Beetle [Division of Insect Taxonomy Institute of Zoology Academia Sinica, Plant Protection Group Institute of Agriculture of Baxia Changchiakou District, Hopei Province, Technical Station, Plant Protection Station of Xiheying People's Commune, Agricultural Bureau of Yu County, Hopei Provinge] (1979) A preliminary study on the bionomics of the galerucid beetle, *Monolepta hieroglyphica* (Motschulsky). Acta Entomologica Sinica 22: 115–117.

Scherer G (1969) Die Alticinae des indischen Subkontinentes (Coleoptera – Chrysomelidae). Pacific Insects Monograph 22: 1–251.

Schmitz J, Wagner T (2001) *Afromegalepta* gen. nov. from tropical Africa (Coleoptera: Chrysomelidae, Galerucinae). Entomologische Zeitschri 111(9): 283–286.

Turner JW (1980) Insect pests of peanuts in southern Queensland. Queensland Agricultural Journal 106: 172–176.

Wagner T (1999) An introduction to the revision of the afrotropical *Monolepta* and related taxa (Coleoptera, Chrysomelidae, Galerucinae). Courier Forschungsinstitut Senckenberg 215: 215–220.

Wagner T (2000) Revision of Afrotropical *Monolepta* Chevrolat, 1837 (Coleoptera: Chrysomelidae, Galerucinae). Part l: species with red and black coloured elytra, pronotum and head, with description of new species. Entomologische Zeitschrift Stuttgart 110(8): 226–237.

Wagner T (2007) *Monolepta* Chevrolat, 1837, the most speciose galerucine taxon: redescription of the type species *Monolepta bioculata* (Fabricius, 1781) and key to related genera from (Chrysomelidae, Coleoptera). Journal of Natural History 41: 81–100. https://doi.org/10.1080/00222930601127384

Wagner T (2011) Description of *Monoleptoides* gen. nov from the Afrotropical Region, including the revision of nine species (Coleoptera: Chrysomelidae: Galerucinae). Bonn Zoological Bulletin 60: 169–199.

Wagner T (2017) *Doeberllepta* gen. nov., a new monotypic genus for a widely distributed galerucine species from Africa (Coleoptera: Chrysomelidae: Galerucinae). Entomologische Blaetter fuer Biologie und Systematik der Kaefer 113: 245–253.

Wagner T, Scherz X (2002) *Afrocandezea* gen. nov. from tropical Africa (Coleoptera: Chrysomelidae, Galerucinae). Entomologische Zeitschrift 112: 357–362.

Yang XK, Ge SQ, Nie RE, Ruan YY, Li WZ (2015) Chinese Leaf Beetles. Science Press, Beijing, 500 pp.

Zhang C (2012) Study on the occurrence and biological characteristics of *Monolepta hireoglyphica* in corn field. MA thesis. Chinese Academy of Agricultural Sciences, Beijing, 82 pp.

Supplementary material 1

Appendix S1. *Monolepta* checklist
Authors: Qi-long Lei, Rui-e Nie, Xing-ke Yang
Data type: catalogue and habitus
Explanation note: The file contains the catalogue of Chinese *Monolepta* with third antennal segment longer than second are denoted by Wagner. Also provide the habitus of most of these species.
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Link: https://doi.org/10.3897/zookeys.1056.65335.suppl1

RESEARCH ARTICLE

Two new species of doryline ants (Hymenoptera, Formicidae) with 11-segmented antennae from India

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Abstract

Two new species of the subfamily Dorylinae Leach, 1815 namely *Parasyscia ganeshaiahi* **sp. nov.** and *Syscia indica* **sp. nov.** are described and illustrated based on the worker caste. These species were collected in the Eaglenest Wildlife Sanctuary, Arunachal Pradesh, Northeast India. Keys to *Parasyscia* of India and *Syscia* of Asia are provided based on the worker caste.

Keywords

Introduction

The subfamily Dorylinae Leach, 1815 is a monophyletic group of predatory ants, distributed in the tropical and subtropical regions of the world (Borowiec 2016). It forms the formicoid clade with the subfamilies Aneuretinae, Dolichoderinae, Ectatomminae, Formicinae, Heteroponerinae, Myrmeciinae, Myrmicinae and Pseudomyrmecinae

(Ward 2014; Borowiec et al. 2019). The formicoid clade consists of almost 90% of all extant ants (Borowiec et al. 2020). Dorylinae has 733 extant species in 27 genera. The fossil records of the subfamily include one genus and eight species (Bolton 2021). Dorylinae is known to occur on all continents except Antarctica (Borowiec 2016). In India, this subfamily has eight genera and 59 species including four subspecies (Bharti et al. 2016; Bharti et al. 2021; AntWeb 2021).

Parasyscia Emery, 1882 and Syscia Roger, 1861 are two tropical genera belonging to Dorylinae. Parasyscia is a rare ant genus described by Emery with P. piochardi Emery, 1882 from Syria as the type species. Later Forel (1892) treated Parasyscia as a subgenus of Cerapachys and Kempf (1972) synonymised it. Borowiec (2016) revived the status of Parasyscia as a valid genus while performing a generic revision of the ant subfamily Dorylinae. The members of this genus are small, cryptic, and nest in decaying logs or under rocks (Brown 1975) while P. zimmermani is the only known arboreal species (Sarnat and Economo 2012). This genus consists of 51 valid species, distributed in Afrotropical, Australasia, Indomalaya, Malagasy, Oceania and Palearctic biogeographic regions (AntWeb 2021; Bolton 2021). In India, seven species of the genus Parasyscia are recorded: Parasyscia aitkenii (Forel, 1900); P. indica (Brown, 1975); P. keralensis (Karmaly, 2012); P. browni (Bharti & Wachkoo, 2013); P. schoedli (Bharti & Akbar, 2013); P. seema (Bharti & Akbar, 2013) and P. wighti (Bharti & Akbar, 2013). Parasyscia aitkenii, reported from Meghalaya, is the only species known from Northeast India (Bharti et al. 2016) so far. The species is also reported from Goa, Haryana, Karnataka, Kerala, Punjab and West Bengal. Parasyscia browni is known from Himachal Pradesh and Uttarakhand while P. indica, P. keralensis, P. schoedli, P. seema and P. wighti are reported from Kerala (Bharti et al. 2016). All species except P. aitkenii are endemic to India. The present discovery of P. ganeshaiahi sp. nov. marks the first record of the genus Parasyscia from the state Arunachal Pradesh, Northeast India. Syscia is a rare ant genus erected by Roger (1861) in his paper on Ponera-like ants, with the Sri Lankan species S. typhla Roger, 1861 as the type species. Forel (1900) and Bingham (1903) treated Syscia as a valid genus while Wheeler (1902) and Emery (1911) considered it as a subgenus of Cerapachys Smith, 1857. Later Kempf (1972) treated Syscia as a junior synonym of Cerapachys. However, after molecular studies on Dorylinae, Borowiec (2016) recognized Syscia as a valid genus. Currently, this genus has 38 valid species (Longino and Branstetter 2021). These rare ants are usually encountered in leaf litter, rotting wood, and soil habitats (Jaitrong et al. 2020). Members of the genus Syscia are distributed in the New and Old Worlds (Borowiec 2016; AntWeb 2021). In Asia, the genus has been known from China, Japan, Sri Lanka and Thailand (AntWeb 2021). The literature record shows the presence of Syscia typhla in India as Cerapachys typhlus (Ghosh et al. 2007). However, this species was not listed in an updated checklist of the Indian ants by Bharti et al. (2016) and global ant database AntWeb (2021). Hence the present study is the first verified record of the genus Syscia from India.

We have collected a single worker specimen belonging to each of the genera Parasyscia and Syscia in the Eaglenest Wild Life Sanctuary, Arunachal Pradesh, Northeast India in 2013. Even though we have performed an extensive collection in the region
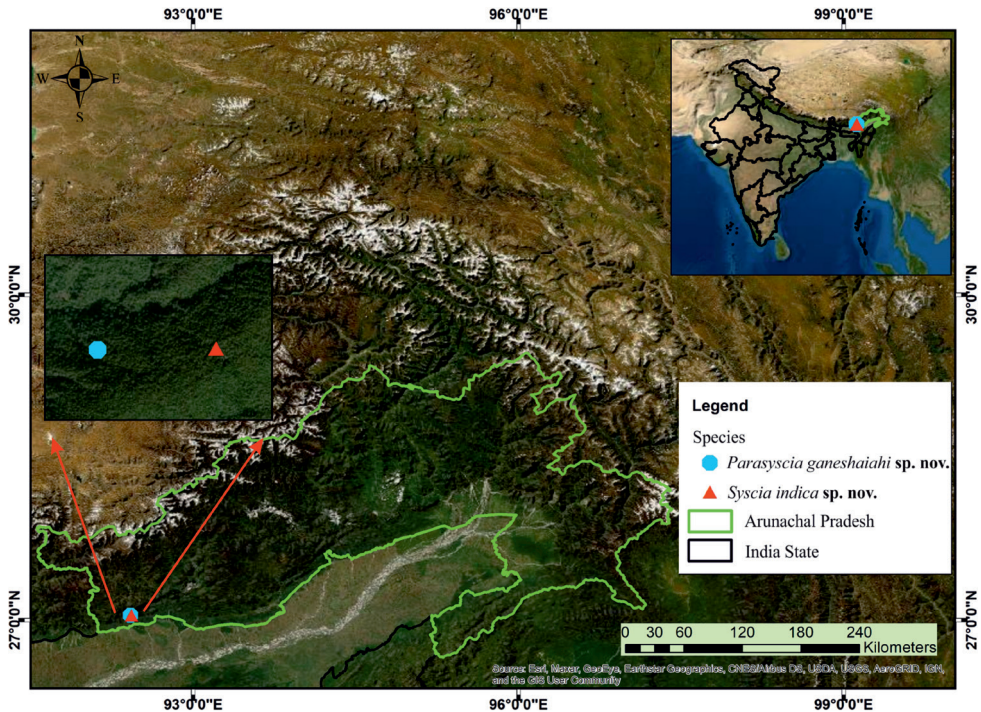
Figure 1. Map showing the type localities of *Parasyscia ganeshaiahi* sp. nov. and *Syscia indica* sp. nov. in the Eaglenest Wildlife Sanctuary, Arunachal Pradesh, Northeast India (Source: Esri, Maxar, GeoEye, Earthstar geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).

with Winkler traps, pitfall traps and hand picking, we could not find more than one specimen of the aforementioned species. This suggests that such subterranean ants are rarely encountered in the field and are therefore hard to collect. A considerable number of such rare ants are known based on a single specimen and, provided they are significantly different in morphology from closely related species, warrant new species description. Keys to all known valid species of *Parasyscia* of India and *Syscia* of Asia are also provided based on the worker caste.

Materials and methods

A worker specimen of *Parasyscia* and *Syscia* were collected in the Eaglenest Wildlife Sanctuary, West Kameng District of Arunachal Pradesh, an Indian state in the Himalayan foothills (Fig. 1). The specimens were collected from a high elevation leaf litter sample using Winkler extractors. The collected specimens were preserved in alcohol before mounting. The point mounted specimens were examined under a Zeiss SteREO Discover.V8 microscope. We compared our specimens with the images of closely similar species such as *P. piochardi* Emery, 1882, *S. chaladthanyakiji* Jaitrong, Wiwatwitaya

& Yamane, 2020 and *S. typhla* Roger, 1861. The images of *P. piochardi* were accessed on AntWeb.org (2021, CASENT0281973, photographed by Michele Esposito, California Academy of Sciences). Similarly, the type images of *S. typhla* were accessed on AntWeb.org (2021, FOCOL0804, California Academy of Sciences) while the holotype images of *S. chaladthanyakiji* were obtained from Jaitrong et al. (2020). The specimens were imaged at 200× magnification and extended focus montage images were taken using a Keyence VHX 6000 digital microscope. Artefacts and unnecessary parts of the images were removed and aligned into a plate using Adobe Photoshop CC 2019. A distribution map of the newly described species was prepared using ArcGIS 10.4.1 (ArcGIS 2021). Body measurements were taken with AxioVision 4.8 (Carl Zeiss, Germany). The holotype specimens of both species are deposited in the National Bureau of Agricultural Insect Resources (**ICAR-NBAIR**), Bangalore, India. Measurements and morphological terminology follow Jaitrong et al. (2020) and Sharaf et al. (2018).

BL	Body length: total length of body calculated by summing lengths of head, mesosoma, petiole and gaster;
HL	Head length: maximum length of head in full-face view, from transverse line spanning the anterior-most points of clypeus to that of posteriormost points of head;
HW	Head width: maximum width of head in full-face view (excluding eyes);
EL	Eye length: maximum length of eye;
TL	Tempora length: measured from posterior margin of eye to posteromedian margin of head capsule;
SL	Scape length: maximum length of antennal scape excluding condyle;
PRW	Pronotal width: maximum width of pronotum in dorsal view;
WL	Weber's length: diagonal length of mesosoma in profile, from anterior-most point of pronotal slope (excluding the neck) to posteroventral margin of propodeal lobe;
PL	Petiolar length: maximum length of petiole in lateral view (excluding helcium);
PH	Petiolar height: maximum height of petiole (including subpetiolar process);
PW	Petiolar width: maximum width of petiole in dorsal view;
PPL	Postpetiolar length: maximum length of postpetiole in lateral view (excluding helcium);
PPH	Postpetiolar height: maximum height of postpetiole in lateral view;
PPW	Postpetiolar width: maximum width of postpetiole in dorsal view;
CI	Cephalic index: HW/HL × 100;
SI	Scape index: SL/HW × 100;
EI	Eye index: EL/HW × 100;
PI1	Petiolar index 1: PL/PH × 100;
PI2	Petiolar index 2: PW/PL × 100;
PPI1	Postpetiolar index 1: PPL/PPH × 100;
PPI2	Postpetiolar index 2: PPW/PPL × 100;
WI	Waist index: PPW/PW × 100.

Results

Parasyscia Emery, 1882

Parasyscia Emery, in André, 1882c: 235. Type species: *Parasyscia piochardi*, by monotypy.
Parasyscia subgenus of *Cerapachys*: Forel 1892l: 243.
Parasyscia junior synonym of *Cerapachys*: Kempf 1972a: 76.
Parasyscia as genus: Borowiec 2016: 198.

Diagnosis. *Parasyscia* workers can be identified by the following combination of characters: 1) propodeal spiracle positioned low on the sclerite and propodeal lobes present; 2) presence of a constriction between abdominal segments III and IV; 3) petiole dorsolaterally not marginate; 4) constriction between abdominal segments IV, V, and VI not present; 5) pronotomesopleural suture fused; 6) helcium axial; 7) middle tibiae with a single pectinate spur; 8) pretarsal claws unarmed; 9) abdominal segment III anterodorsally often marginate (Borowiec 2016).

Parasyscia ganeshaiahi sp. nov.

http://zoobank.org/4E992EB2-10F9-4CCD-A1EB-45E5F9D55915
Fig. 2A–F

Material examined. *Holotype* One worker, point mounted. Original label: "India, Arunachal Pradesh, West Kameng, Eaglenest WLS, 27.0433°N, 92.4209°E, 1400m, Winkler extraction method, 14th April 2013, Aniruddha Marathe leg." [NBAIR/HYM-FOR/1721-1].

Worker description. Measurements and indices (holotype): BL 2.82; HL 0.58; HW 0.46; EL 0.05; TL 0.31; SL 0.22; PRW 0.32; WL 0.79; PL 0.21; PH 0.39; PW 0.30; PPL 0.39; PPH 0.44; PPW 0.45. Indices. CI 79; EI 11; SI 48; PI1 54; PI2 143; PPI1 89; PPI2 115; WI 150 (all measurements in mm). ***Head.*** In full-face view, rectangular, distinctly longer than broad; lateral margin weakly convex; posterior margin weakly concave (Fig. 2A). Antennae 11 segmented; scape short, when folded back fail to reach posterior margin of eyes; Antennal segment II almost as long as broad; segments III–X distinctly broader than long; apical segment (XI) swollen forming a distinct club, 2×longer than IX–X combined (Fig. 2F). Frontal carinae short, united and slightly extended behind the antennal socket. Eyes small; located slightly anterior to the mid-length of head (Fig. 2A). Mandibles triangular; masticatory margin with a row of denticles (Fig. 2F). ***Mesosoma.*** In dorsal view, elongate with almost parallel lateral sides (Fig. 2C). In profile view, dorsal outline weakly convex; promesonotal suture and metanotal groove absent (Fig. 2B). Propodeal declivity in profile view, lightly concave; declivous face with distinct carina across the top and along the lateral margins; propodeal lobe in profile view, strongly convex (Fig. 2B, C). ***Metasoma.*** Petiole in dorsal view, distinctly broader than long; anterior and lateral margin with distinct

Figure 2. *Parasyscia ganeshaiahi* sp. nov., holotype worker **A** head in full-face view **B** body in profile view **C** mesosoma in dorsal view **D** petiole and postpetiole in dorsal view **E** girdling constriction and gaster in dorsal view **F** antenna and Mandibles.

carina; anterior and posterior margins transverse (Fig. 2B, D). In profile view, petiole shorter than high with weakly convex dorsal outline. Postpetiole in dorsal view, larger than petiole; broader than long; strongly convex posterior margin (Fig. 2D). In profile view, postpetiole shorter than high; dorsal outline weakly convex (Fig. 2B). Abdomi-

nal tergite IV (first gastral tergite) in dorsal view, elongate, occupying most part of gaster; anterior margin strongly concave; lateral sides strongly convex. Base of cinctus of first gastral tergite with cross ribs (Fig. 2E). ***Sculpture.*** Body with numerous distinct foveolae with smooth interspaces. Propodeal dorsal surface medially with a distinct unsculptured area. Postpetiole with more closely-spaced foveolae. First gastral tergite anteriorly with large foveolae and posteriorly with smaller foveolae. Remaining gastral segments anteriorly smooth and posteriorly with small foveolae.

Pilosity. Body covered with erect to sub-erect hairs. Sides of head and legs with relatively shorter hairs. Apical antennal segment with abundant short decumbent hairs. *Body coloration.* Body mainly yellowish brown. Antennal segment III to X and mandibles reddish brown.

Recognition. *Parasyscia ganeshaiahi* sp. nov. is similar to the Palearctic *P. piochardi* Emery, 1882 in general appearance and 11-segmented antennae. *Parasyscia piochardi* is known from Israel, Lebanon, Syrian Arab Republic and Turkey (AntWeb 2021; Bolton 2021). *Parasyscia ganeshaiahi* is distinguished from *P. piochardi* by the following characteristics: 1) head in full-face view, rectangular with weakly convex lateral sides in *P. ganeshaiahi* (head nearly oval shaped with strongly convex lateral sides in *P. piochardi*); 2) strong sculpturing with relatively larger foveolae in *P. ganeshaiahi* (weakly sculptured with shallow, small foveolae in *P. piochardi*); 3) head in full-face view, fovea larger in size and comparatively closely spaced in *P. ganeshaiahi* (fovea smaller with distinct unsculptured area present in *P. piochardi*); 4) frontal carinae united posteriorly and extended behind in *P. ganeshaiahi* (frontal carinae not united and extended behind in *P. piochardi*); 5) mesosoma in dorsal view, with nearly straight lateral margins in *P. ganeshaiahi* (mesosoma in dorsal view, medially concave in *P. piochardi*); 6) petiole in profile view, with straight anterior slope in *P. ganeshaiahi* (weakly convex anterior margin in *P. piochardi*); 7) anterior margin of petiole in dorsal view, with a distinct carina in *P. ganeshaiahi* (carina absent in *P. piochardi*); 8) *P. ganeshaiahi* is a smaller species, HW 0.46, TL 2.82 in (*P. piochardi* is larger, HW 0.53, TL 3.40); 9) *P. ganeshaiahi* has comparatively bigger eyes in relation to head width, EI 11 (*P. piochardi* has smaller eyes in relation to the head width, EI 6).

Habitat. The type specimen was collected from the Eaglenest Wildlife Sanctuary at an elevation of 1400 m above sea level. The collection site has a canopy cover of about 90% with low light penetration. The soil had a pH of 6.83 and temperature 17°C at the time of collection. A single worker specimen was collected using a Winkler extractor from sifted leaf litter taken from 1 m², which accounted for 760 ml of leaf litter. We captured three additional ant genera (*Aphaenogaster*, *Carebara* and *Paratrechina*) in the same trap.

Distribution. Indomalaya: India (Arunachal Pradesh).

Etymology. With 2021 being the 25th anniversary of ATREE, this species is a Latin noun in the genitive case named in honour of one of its founders, Prof. K. N. Ganeshaiah, eminent ecologist and writer, who was instrumental in establishing Insect Taxonomy and Conservation Laboratory in ATREE.

Key to *Parasyscia* of India based on the worker caste

Modified after Bharti and Akbar 2013.

1   Antenna 11-segmented (Fig. 1F)............................. *P. ganeshaiahi* **sp. nov.**
–   Antenna 12-segmented **2**
2   Cephalic dorsum with rugo-reticulate sculpture...
         ....*P. browni* **(Bharti & Wachkoo, 2013)**
–   Cephalic dorsum with either small punctures or foveae.............................**3**
3   Punctures on dorsum of head relatively small, their diameter smaller than the
         average distance separating them **4**
–   Punctures on head dorsum large, foveiform, dense, their diameter as large, or
         larger than, the average distance separating them, and in most cases these are
         contiguous **5**
4   Shiny species; body sculpture reduced; eyes breaking the lateral margins of
         head; colour varies from light orange to dark red ....
         ....*P. schoedli* **(Bharti & Akbar, 2013)**
–   Dull coloured species; body sculpture prominent; eyes not breaking the lat-
         eral margins of head; colour brown to dark brown......................................
         .... *P. seema* **(Bharti & Akbar, 2013)**
5   Eyes reduced (EL < 0.1 mm)................... *P. wighti* **(Bharti & Akbar, 2013)**
–   Eyes large (EL > 0.2 mm) **6**
6   Head reddish brown or red; trunk and both nodes red; gaster black or dark
         brown; dorsal surface of mesosoma densely and finely sculptured; foveate or
         rugo reticulate.. *P. aitkenii* **(Forel, 1900)**
–   Body unicolorous, lighter brownish red; dorsal surface of mesosoma mostly
         smooth with few scattered punctures along sides.... *P. indica* **(Brown, 1975)**

Note: *Parasyscia keralensis* (Karmaly, 2012) is highly dubious and considered as a spe-
cies inquirenda (Bharti and Akbar 2013). Hence *P. keralensis* is not included in this key.

Syscia **Roger, 1861**

Syscia Roger, 1861a 19. Type species: *Syscia typhla*, by monotypy.
Syscia subgenus of *Cerapachys*: Wheeler, W.M. 1902d: 185; Emery 1902c: 24.
Syscia senior synonym of *Cysias*: Emery 1911d: 10.
Syscia junior synonym of *Cerapachys*: Kempf 1972a: 76.
Syscia as genus: Borowiec 2016: 219.

Diagnosis. Borowiec (2016) defined this genus as follows: 1) 11- or 9-segmented an-
tennae; 2) eyes small to absent; 3) body usually heavily sculptured with abundant pilos-
ity; 4) uniformly coloured body, ranges from yellow through reddish to dark brown but

never black; 5) basal segment of hind tarsus widening distally with a light patch of cuticle on the inner (flexor) side; 6) abdominal tergite IV anteriorly folding over sternite.

Syscia indica sp. nov.

http://zoobank.org/3A9C67DF-8692-40EF-A3FD-3102D10C1253

Fig. 3A–F

Material examined. *Holotype* One worker, Point mounted. Original label: "India, Arunachal Pradesh, West Kameng, Eaglenest WLS, 27.0434°N, 92.4302°E, 1600 m, Winkler extraction method, 10.IV.2013, Aniruddha Marathe leg." [NBAIR/HYM-FOR/1721-2].

Worker description. Measurements and indices (holotype): BL 3.33; HL 0.68; HW 0.50; SL 0.25; PRW 0.35; WL 0.85; PL 0.36, PH 0.31, PW 0.29, PPL 0.41, PPH 0.47, PPW 0.43. Indices: CI 74, SI 50, PI1 116, PI2 81, PPI1 87, PPI2 105, WI 148 (all measurements in mm).

Head. In full-face view, rectangular, distinctly longer than broad; lateral margin weakly convex; posterior margin weakly concave (Fig. 3A). Antennae 11-segmented, apical segment (XI) longer than IX–X combined; scape short, reaching mid-length of head when folded back. Antennal segment II almost as long as broad, segments III–X slightly broader than long (Fig. 3F). Frontal carinae short and narrow, reaching less than half of head length. Eyes and ocelli completely absent (Fig. 3A). Mandibles triangular; masticatory margin serrated, without distinct teeth (Fig. 3F). *Mesosoma.* In dorsal view, elongate with almost parallel lateral sides (Fig. 3C). In profile view, dorsal outline weakly convex; promesonotal suture and metanotal groove absent; mesopleuron demarcated from propleuron by a distinct pronotomesopleural suture; mesopleuron not clearly differentiated from metapleuron. Propodeal declivity feebly concave, encircled with a distinct thin rim (Fig. 3B). *Metasoma.* In dorsal view, petiole distinctly longer than broad; almost parallel sided (Fig. 3D). In profile view, petiole subrectangular; slightly longer than high with weakly convex dorsal outline. Subpetiolar process subrectangular; ventral outline strongly concave (Fig. 3B). Postpetiole in dorsal view, larger than petiole; slightly longer than broad (Fig. 3D). In profile view, postpetiole slightly shorter than high; dorsal outline weakly convex. Postpetiolar sternite in profile view low, ventral margin weakly convex; anteroventrally produced into a blunt angle (Fig. 3B). Abdominal tergite IV (first gastral tergite) in dorsal view, elongate with anterior margin weakly concave; lateral sides weakly convex (Fig. 3E). Base of cinctus of first gastral tergite with cross ribs (Fig. 3E). *Sculpture.* Body with numerous, relatively small, closely-spaced foveolae. Ventrolateral surface of petiole with two distinct almost parallel carinae just above the subpetiolar process. Antennal scape, outer surface of mandible and legs with fine dense micropunctures. *Pilosity.* Body covered with erect and sub-erect hairs. Dorsum of postpetiole and first gastral tergite with sparse erect hairs mixed with dense long decumbent hairs. Antennae and legs with dense short decumbent hairs. *Body coloration.* Body reddish brown. Antennae and legs yellowish brown.

Figure 3. *Syscia indica* sp. nov., holotype worker **A** head in full-face view **B** body in profile view **C** mesosoma in dorsal view **D** petiole and postpetiole in dorsal view **E** girdling constriction and gaster in dorsal view **F** antenna and Mandibles.

Recognition. *Syscia indica* sp. nov. is similar to *S. chaladthanyakiji* in general appearance and 11-segmented antennae. However, *S. indica* can be separated from *S. chaladthanyakiji* by the following characteristics: 1) weak sculpture with relatively small and closely-spaced foveolae in *S. indica* (stronger sculpturing with well-defined macropunctures in *S. chaladthanyakiji*); 2) abdominal segment IV (first gastral tergite) with large number of closely-spaced foveolae in *S. indica* (first gastral tergite with lesser number of relatively widely spaced foveolae in *S. chaladthanyakiji*); 3) remaining gastral segments with feeble foveolae in *S. indica* (remaining gastral segments anteriorly

with an unsculptured area in *S. chaladthanyakiji)*; 4) head in full-face view oval shaped with convex lateral sides and moderately concave posterior margin in *S. indica* (head in full-face view rectangular, almost parallel sides, posterior margin weakly concave in *S. chaladthanyakiji)*; 5) CI 74, SI 50 in *S. indica* (CI 80–84, SI 56–63 in *S. chaladthanyakiji)*. *Syscia indica* sp. nov. is also similar to the Sri Lankan and Chinese *S. typhla* in general appearance. However, the new species can be easily separated from *S. typhla* by the 1) presence of 11-segmented antennae (9-segmented in *S. typhla*); 2) foveolae on cephalic dorsum smaller in diameter and closely spaced in *S. indica* (foveolae comparatively larger in diameter and widely spaced in *S. typhla*); 3) posterior cephalic margin nearly transverse in *S. Indica* (posterior cephalic margin strongly concave in *S. typhla*); 4) base of cinctus of first gastral tergite with cross ribs in *S. indica* (base of cinctus of first gastral tergite without cross ribs in *S. typhla*).

Habitat. The holotype was collected from the Eaglenest Wildlife Sanctuary at an elevation of 1600 m above sea level. The region has a canopy cover of about 85% and no indications of anthropogenic disturbances. The soil had a pH of 6.85 and temperature 16°C at the time of collection. The specimen was collected using a Winkler extractor from sifted leaf litter of 1 m^2. We were able to capture one additional ant genus *Carebara* in the same trap, which consisted of 295 ml leaf litter.

Distribution. Indomalaya: India (Arunachal Pradesh).

Etymology. The specific epithet indica is a Latin singular feminine adjective in the nominative case and refers to the country where the species was collected.

Key to *Syscia* of Asia

1	Antennae 9-segmented...***S. typhla* Roger, 1861**
–	Antennae 11-segmented **2**
2	Body surface opaque with fine reticulations ....**S. humicola** (Ogata, 1983)
–	Body surface with well-defined punctures or foveolae **3**
3	Body entirely covered with deep foveae; WI 110–122................................... ....***S. reticularis* Jaitrong, Wiwatwitaya & Yamane, 2020**
–	Body with numerous punctures or foveolae; WI ≥ 130 ....**4**
4	Weak sculpture with relatively small and closely-spaced foveolae (Fig. 2); CI 74, SI 50.. ***S. indica* sp. nov.**
–	Stronger sculpturing with well-defined macropunctures; CI 80–84, SI 56–63... ....***S. chaladthanyakiji* Jaitrong, Wiwatwitaya & Yamane, 2020**

Discussion

Parasyscia and *Syscia* are rare ants belonging to the subfamily Dorylinae which were previously included in the genus *Cerapachys*. Recent phylogenetic studies have revived the status and considered them as valid genera. Here we describe two new species of

doryline ants one in each of these genera, based on the worker caste. A single worker specimen of *P. ganeshaiahi* sp. nov. and *S. indica* sp. nov. were collected using Winkler extractors in the Eaglenest Wildlife Sanctuary in Northeast India. The Eaglenest Wildlife Sanctuary has an area of 218 km^2 and the elevation ranges from 500 m to 3250 m. It has a wide range of forests starting from tropical evergreen forests in the lower elevation, to temperate broad-leaved forest in the mid-elevation to rhododendrons and conifers in the higher altitudes. The protected area lies in a region of Himalayas with exceptional biodiversity. The present discovery of two new species of doryline ants shows the importance of exploring the Eastern Himalayas especially by using non-conventional extraction methods such as Winkler traps. The Winkler extraction method is exceptionally good for collecting rarely sampled subterranean ants from the leaf litter. The discovery of *P. ganeshaiahi* sp. nov. and *S. indica* sp. nov. is an important contribution to the understanding of the Indian myrmecofauna. *Parasyscia ganeshaiahi* sp. nov. marks the first record of a *Parasyscia* species with 11-segmented antennae from India. All other seven known species of the Indian *Parasyscia* have 12-segmented antennae (Bharti and Akbar 2013). It also marks the first record of the genus *Parasyscia* from Arunachal Pradesh. Although literature records show the presence of *S. typhla* in India as *Cerapachys typhlus* (Ghosh et al. 2007), the species lacks a verified museum record. Considering data in the global ant database (AntWeb 2021) and checklist of the Indian ants (Bharti et al. 2016), the previous record of *S. typhla* in India is highly dubious and needs to be verified with specimen records. Hence, the present discovery is the first confirmed record of the genus from India. In the Indomalaya region, *Syscia* has only three known species. Though we have performed an extensive sampling across northeastern states in India using pitfall and Winkler traps, we were not able to find additional specimens of *P. ganeshaiahi* and *S. indica*. Based on the rarity and significant character differences from other known species, we can undoubtedly consider them as valid species.

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References

AntWeb (2021) AntWeb. Version 8.63.2. California Academy of Sciences. https://www.antweb.org/ [Accessed 17th February, 2021]

ArcGIS (2021) Esri Geographic Information System (version 10.4.1). http://desktop.arcgis.com [Accessed 9th July, 2021]

Bharti H, Akbar SA (2013) Taxonomic studies on the ant genus *Cerapachys* Smith (Hymenoptera, Formicidae) from India. ZooKeys 336: 79–103. https://doi.org/10.3897/zookeys.336.5719

Bharti H, Wachkoo AA (2013) *Cerapachys browni* and *Cerapachys costatus*, two new rare ant species (Hymenoptera: Formicidae) from India. Biologia 68(6): 1189–1192. https://doi.org/10.2478/s11756-013-0260-9

Bharti H, Rilta JS, Dhadwal T (2021) Two new species of *Ooceraea* (Hymenoptera, Formicidae, Dorylinae) from India with ten-segmented antennae. ZooKeys 1010: 165–183. https://doi.org/10.3897/zookeys.1010.58436

Bharti H, Guénard B, Bharti M, Economo EP (2016) An updated checklist of the ants of India with their specific distributions in Indian states (Hymenoptera, Formicidae). ZooKeys 551: 1–83. https://doi.org/10.3897/zookeys.551.6767

Bingham CT (1903) The Fauna of British India, Including Ceylon and Burma. Hymenoptera (Vol. II). Ants and Cuckoo-wasps. Taylor and Francis, London, 506 pp.

Bolton B (2021) An online catalog of the ants of the world. https://antcat.org/ [Accessed 17th February, 2021]

Borowiec ML (2016) Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). ZooKeys 608: 1–280. https://doi.org/10.3897/zookeys.608.9427

Borowiec ML, Moreau CS, Rabeling C (2020) Ants: phylogeny and classification. In: Starr CK (Ed.) Encyclopedia of Social Insects. Springer, Cham, 56–69. https://doi.org/10.1007/978-3-319-90306-4_155-1

Borowiec ML, Rabeling C, Brady SG, Fisher BL, Schultz TR, Ward PS (2019) Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. Molecular Phylogenetics and Evolution 134: 111–121. https://doi.org/10.1016/j.ympev.2019.01.024

Brown WL Jr (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. Search. Agriculture (Ithaca, New York) 5(1): 1–115.

Emery C (1882) ['1881'] [Untitled. 3e Genre. – *Parasyscia*, Emery, n. gen.]. [Pp. 235–236] In: André E (Ed.) Les fourmis [part]. 233–280; 1881–1886. Species des Hyménoptères d'Europe et d'Algérie. Tome Deuxième. Edmond André, Beaune, 919 pp. [+ 48 pp.]

Emery C (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum 118: 1–125.

Forel A (1892) Les Formicides. [concl.]. In: Grandidier A (Ed.) Histoire Physique, Naturelle, et Politique de Madagascar (Vol. XX). Histoire naturelle des Hyménoptères. Deuxième partie. Supplèment au 28e fascicule. Hachette et Cie, Paris, 229–280.

Forel A (1900) Les Formicides de l'Empire des Indes et de Ceylan. Part VII. Journal of the Bombay Natural History Society 13: 303–332.

Ghosh SN, Chattopadhyay A, Bhattacharyya DK (2007) Studies on roadside soil inhabiting ants (Hymenoptera: Formicidae) of Kolkata with reference to the effects of lead emitted through automobile exhaust. Records of the Zoological Survey of India. Occasional Paper 257: 1–149.

Jaitrong W, Wiwatwitaya D, Yamane S (2020) First record of the ant genus *Syscia* Roger, 1861 (Hymenoptera: Formicidae) from Thailand, with descriptions of two new species. Far Eastern Entomologist 411: 1–9. https://doi.org/10.25221/fee.411.1

Karmaly KA, Rabeesh TP, Sumesh S (2012) Description of new species of genus *Cerapachys* Smith (Hymenoptera: Formicidae) from Kerala, India. Journal of Entomological Research 36(2): 157–159.

Kempf WW (1972) Catálogo abreviado das formigas da região Neotropical. Studia Entomologica 15: 3–344.

Leach WE (1815) Entomology. In: Brewster D (Ed.) The Edinburgh encyclopedia (Vol. 9). William Blackwood, Edinburgh, 57–172.

Longino JT, Branstetter MG (2021) Integrating UCE phylogenomics with traditional taxonomy reveals a trove of New World *Syscia* species (Formicidae: Dorylinae). Insect Systematics and Diversity 5(2): 1–51. https://doi.org/10.1093/isd/ixab001

Roger J (1861) Die *Ponera*-artigen Ameisen (Schluss). Berliner Entomologische Zeitschrift 5: 1–54.

Sarnat EM, Economo EP (2012) The ants of Fiji. University of California Publications in Entomology 132: 1–384.

Sharaf MR, Akbar SA, Aldawood AS (2018) Review of the Arabian rare ant genus *Parasyscia* Emery, 1882 (Hymenoptera: Formicidae) with description of a new species from the Asir Mountains, Saudi Arabia. African Entomology 26(1): 215–223. https://doi.org/10.4001/003.026.0215

Smith F (1857) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A. R. Wallace. [part]. Journal and Proceedings of the Linnean Society of London. Zoology 2: 42–88. https://doi.org/10.1111/j.1096-3642.1857.tb01759.x

Ward PS (2014) The phylogeny and evolution of ants. Annual Review of Ecology, Evolution, and Systematics 45: 23–43. https://doi.org/10.1146/annurev-ecolsys-120213-091824

Wheeler WM (1902) An American *Cerapachys*, with remarks on the affinities of the Cerapachyinae. Biological Bulletin (Woods Hole) 3: 181–191. https://doi.org/10.2307/1535872

RESEARCH ARTICLE

The genus *Dettopsomyia* Lamb, 1914 (Diptera, Drosophilidae) from southern China

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Abstract

The genus *Dettopsomyia* was established by Lamb in 1914 for a single species, *De. formosa* described therein. It contains 13 known species recorded from the Old World (the Oriental, Australasian, Palearctic and Afrotropical regions). In the present paper, five new species discovered from southern China are described as members of *Dettopsomyia*: *De. acutipenis* Wang & Gao, **sp. nov.**, *De. serripenis* Wang & Gao, **sp. nov.**, *De. discontinua* Wang & Gao, **sp. nov.**, *De. camelonota* Wang, Li & Gao, **sp. nov.** and *De. paranigrovittata* Wang, Li & Gao, **sp. nov.** The new species were delimitated, based on not only morphological characters but also molecular data.

Keywords

Dettopsomyia, DNA barcoding, new species, *Styloptera*, Yunnan

Introduction

The genus *Dettopsomyia* was established by Lamb (1914) for *De. formosa* described therein as the type species. Since then, a number of species have been added as new members to this genus or transferred from other genera by some authors, bringing the total number of known species in *Dettopsomyia* to 13. Duda (1926) described two Indonesian species, *Dettopsomyia jacobsoni* and *De. acrostichalis*, and transferred *Drosophila pictipes* de Meijere,

1911 from Indonesia and the Philippines into *Dettopsomyia*, together with *Pictostyloptera preciosa* (de Meijere, 1911) from Indonesia and *Styloptera fruhstorferi* Duda, 1924 from Vietnam. Wheeler (1951) transferred the Australasian species *Drosophila nigrovittata* Malloch, 1924 to *Dettopsomyia*. In addition, four more species, *Dettopsomyia equscauda* Takada & Momma, 1975 from Malaysia, *De. philippina* Takada, 1976 from the Philippines, *De. alba* Carson & Okada in Okada (1982) from Papua New Guinea and *De. woodruffi* Takada in Takada et al. (1990) from Kenya, have been described as new members of this genus, and two other species, *Mycodrosophila bombax* Burla, 1954 from Ivory Coast and Uganda and *Styloptera repletoides* Carson & Okada, 1980 from Papua New Guinea, have been transferred to *Dettopsomyia* by Tsacas (1980) and Okada (1982), respectively. Currently, a total of 13 species is assigned to this genus and are mainly distributed in the Old World tropics, i.e., the Oriental, Australasian and Afrotropical regions (Toda 2020).

From the early days of this taxonomic history, the status of the genus *Dettopsomyia* has been argued, especially in relation to the genus *Styloptera* Duda. Duda (1924) established the genus *Styloptera* for two new species, *S. formosae* Duda, 1924 and *S. fruhstorferi* Duda, 1924, and one known species, *S. pictipes* (de Meijere, 1911), transferred from the genus *Drosophila* Fallén, and the genus *Pictostyloptera* for *Drosophila preciosa* de Meijere, 1911. But later, Duda (1926) regarded both genera *Styloptera* and *Pictostyloptera* as synonymous with *Dettopsomyia* by finding intermediate morphologies between these genera in a study of *Dettopsomyia formosa* (the type species). Wheeler and Takada (1964) resurrected the genus *Styloptera* by choosing *S. formosae* as the type species because of its distinct morphology, but leaving *De. fruhstorferi* and *De. pictipes* in *Dettopsomyia*. Then, nine new species were added to the genus *Styloptera* by Okada and Carson (1980, 1983), Okada (1982) and Bock (1982), currently resulting in a total of ten species (Toda 2020). Wheeler and Takada (1964) and Bock (1982) gave the morphological diagnoses mostly on the head/thorax (color pattern and chaetotaxy) and the wing (color pattern and venation) for *Dettopsomyia* and *Styloptera*. However, some characters listed in the diagnoses were not contradictory between these two genera, but partially overlapping between them. Okada (1982) compared the morphology of the two genera in a revisional study covering 12 *Dettopsomyia* and eight *Styloptera* species. He listed some characters common to the two genera, e.g., wing costal lappet more or less developed and black, dorsocentral setae usually in three pairs, and frons and thorax usually ornamented, indicating close relationships between them. On the other hand, he proposed 13 characters (Table 1) as being diagnostic to distinguish between these two genera, at least for a few 'representative' species of them. However, none of these characters is applicable to most of the component species of either genus (Okada 1982). Bock (1982) argued that these two genera are closely related but most of their component species are very poorly known, and proposed that a complete revision of the two genera is necessary.

As Bock (1982) pointed out, the two genera *Dettopsomyia* and *Styloptera* are still less explored, making a full-scale revision of their phylogeny and taxonomy difficult. In the present paper, we describe five new species of *Dettopsomyia* discovered from China, and briefly address the ambiguity of *Dettopsomyia* and *Styloptera* in the systematics of the subfamily Drosophilinae.

Table 1. Diagnostic characters used to distinguish between the genera *Dettopsomyia* and *Styloptera* (adapted from Okada 1982).

	Dettopsomyia		*Styloptera*
Code	**State**	**Code**	**State**
A	Eye much oblique to the body axis.	a	Eye nearly rectangular to the body axis.
B	Ocellar setae inserted inside triangle made by ocelli.	b	Ocellar setae inserted outside triangle made by ocelli.
C	Anterior reclinate orbital minute.	c	Anterior reclinate orbital >> 1/3 as long as proclinate.
D	Cheek not very broad, ~ 1/3 as broad as greatest diameter of eye.	d	Cheek very broad, ~ 2/3 as broad as greatest diameter of eye.
E	Costal lappet large.	e	Costal lappet moderate.
F	C-index < 1.0.	f	C-index > 1.0.
G	R_{2+3} strongly curved to costa apically.	g	R_{2+3} straight or merely gently curved to costa.
H	R_{4+5} and M_1 divergent distally.	h	R_{4+5} and M_1 parallel.
I	Acrostichal bristles present.	i	Acrostichal bristles absent.
J	Tibia ringed.	j	Tibia not ringed.
K	Wing spotted.	k	Wing not spotted.
L	Acrostichal setulae in 2 rows.	l	Acrostichal setulae in 4 or 6 rows.
M	C3-fringe > 1/2.	m	C3-fringe < 1/2.

Materials and methods

Specimens

Taxon sampling for morphological examination and DNA barcoding is shown in Table 2. The specimens were mostly captured by net sweeping above herbs in open forest, or at forest edge. Specimens were preserved in 70% (for morphological examination) or 100% ethanol (for DNA sequencing).

The examined specimens are deposited in the following institutes:

KIZ Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China;

SEHU Systematic Entomology, the Hokkaido University Museum, Hokkaido University, Sapporo, Japan.

Species delimitation and description

As pointed out by Okada (1982) and Bock (1982), it is difficult to definitely determine the generic assignment of the studied specimens to *Dettopsomyia* Lamb, 1914 or *Styloptera* Duda, 1924, based on morphological characters, for the present. As we address this issue in Discussion, it needs a systematic revision for these genera based on a full-scale molecular phylogenetic analysis of the subfamily Drosophilinae and ancestral state reconstruction of the morphology by character-mapping on the inferred tree. In the present study, therefore, we provisionally classify all studied specimens into *Dettopsomyia* according to the principle of priority (ICZN), since there is a possibility that the two genera are synonymized in future systematic studies. Then, they were classified into morpho-species referring to Okada's (1982) 13 characters (Table 1): the character states (referred to as CS-code in descriptions of species) for all the known and putatively new species of *Dettopsomyia* are summarized in Table 3. The morpho-species were further

Table 2. Summary of *Dettopsomyia* species and specimens examined in this study. Voucher numbers in bold indicate holotype specimens; gender of each specimen is given in parentheses, and GenBank accession numbers of *COI* sequences in brackets.

Species	Collection site	Collection date	Voucher #
De. acutipenis sp. nov.	Xishuangbanna Tropical Botanical Garden, Mengla, Xishuangbanna, Yunnan, China	19.iii.2006	#00138 (♀) [MZ645108], **#00151** (♂)
		18.iv.2007	#00380 (♀) [MZ645110], #00381 (♀) [MZ645111], #00382–386 (5♀)
		16.iv.2007	#00387–389 (3♀)
De. serripenis sp. nov.	Xishuangbanna Tropical Botanical Garden, Mengla, Xishuangbanna, Yunnan, China	19.iii.2006	**#00152** (♂), #00155 (♂), #00156 (♀) [MZ645109], #00157 (♂), #00158 (♀)
		24.iii.2006	#00153 (♂)
		25.iii.2006	#00154 (♀)
De. discontinua sp. nov.	Baihualing, Baoshan, Yunnan, China	4.viii.2012	#01139 (♂) [MZ645112], #01140 (♂) [MZ645113], #01141 (♂), #01142 (♂), #01143 (♀) [MZ645114], #01144 (♂) [MZ645115]
	From rearings of *R. decursiva* infructescences collected from Baihualing, Baoshan, Yunnan, China	23.ix.2012	#01167–169 (3♀) [MZ645117–119], #01172–174 (3♂) [MZ645120–122]
	Banpo, Yixiang, Simao, Pu'er, Yunnan, China	2.x.2012	#01584 (♂) [MZ645136], **#01585** (♂) [MZ645137]
De. camelonota sp. nov.	Banpo, Yixiang, Simao, Pu'er, Yunnan, China	25.x.2012	**#01607** (♂) [MZ645138], #01608 (♀) [MZ645139]
De. paranigrovittata sp. nov.	Baihualing, Longyang, Baoshan, Yunnan, China	3.viii.2012	**#01145** (♂) [MZ645116]
	From rearings of host infructescences collected from Baihualing, Baoshan, Yunnan, China	23.ix.2012	#01579 (♂) [MZ645131]
De. nigrovittata (Malloch, 1924)	Dinghushan Nature Reserve, Zhaoqing, Guangdong, China (by net sweeping above herbs)	13.iv.2008	#00132 (♂) [MZ645104], #00135–137 (3♀) MZ645105–107]
		23–26.iii.2009	#01582 (♀) [MZ645134], #01583 (♂) [MZ645135]
	From rearings of infructescences of *Rhaphidophora decursiva* collected from Baihualing, Baoshan, Yunnan, China	5.ix.2012	#01177 (♀) [MZ645123], #01178 (♂) [MZ645124], #01179 (♂) [MZ645125], #01180 (♀) [MZ645126], #01182–184 (3♀) [MZ645127–129]
		23.ix.2012	#01578 (♀) [MZ645130], #01580 (♂) [MZ645132], #01581 (♀) [MZ645133], #01721 (♀) [MZ645141]
	Haoping Station, Taibaishan National Nature Reserve, Shaanxi, China (by net sweeping above herbs along waterside)	16.viii.2013	#01680 [MZ645140]

examined for other external morphology and detailed structures of dissected phallic and periphallic organs by the same methods as in Li et al. (2014). For each morphospecies, at least one representative specimen was selected for mitochondrial *COI* DNA sequencing. We followed Li et al. (2014) and Yang et al. (2017) for extraction of DNA, PCR and sequencing, using Folmer et al. (1994) primer pair LCO1490 (5'- GGT-CAACAAATCATAAAGATATTGG -3') and HCO2198 (5'- TAAACTTCAGGGT-GACCAAAAATCA -3'). The sequences were edited in the SeqMan module of the DNAStar package (DNAStar Inc. 1996), and aligned in MEGA7 (Kumar et al. 2016). We performed tree- and distance-based DNA barcoding, with a neighbor-joining (NJ) tree constructed in MEGA7 with K2P distances (i.e., the Kimura 2-parameter distances) and comparison of the maximum intraspecific and the minimum interspecific p-distances. The morpho-species were then reconsidered by integrating information from the morphology and DNA barcode data.

McAlpine (1981) was followed for the morphological terminology, and Zhang and Toda (1992) for the definitions of measurements and indices.

Table 3. A character-state matrix of Okada's (1982) 13 characters for all *Dettopsomyia* species.

Species	Characters													Reference*
	1	2	3	4	5	6	7	8	9	10	11	12	13	
De. formosa Lamb, 1914	A	B	C	D	E	F	G	H	i	J	K	l	M	1)
De. jacobsoni Duda, 1926	A	B	C	D	E	F	G	H	I	J	K	L	M	1)
De. preciosa (de Meijere, 1911)	A	B	C	D	e	f	G	H	I	J	K†	L	m	1)
De. fruhstorferi (Duda, 1924)	–	–	–	–	–	f	G	–	i	J	k	–	–	1)
De. pictipes (de Meijere, 1911)	A	B	C	D	e	f	G	H	I	J	k	L	m	1)
De. repletoides (Carson & Okada, 1980)	a	b	c	d	E	f	G	H	i	J	k	L	m	1)
De. alba Carson & Okada, 1982	a	b	c	d	E	f	G	H	i	j	k	L	m	1)
De. acrostichalis Duda, 1926	–	–	–	–	–	–	G	h	I	–	k	–	–	1)
De. nigrovittata (Malloch, 1924)	a	b	c	d	E	F	G	h	i	J	k	l	M	1)
De. philippina Takada, 1976	a	b	C	d	E	f	g	h	i	J	k	l	m	1)
De. equscauda Takada & Momma, 1975	A	b	c	d	e	f	G	H	i	J	k	L	m	1)
De. bombax (Burla, 1954)	–	–	C	D	E	f	G	h	i	j	k	l	m	1)
De. woodruffi Takada, 1990	A	b	–	D	E	–	G	h	i	J	k	l	M	2)
De. acutipenis sp. nov.	A	b	?	?	e	f	G	H	i	J	k	l	M	3)
De. serripenis sp. nov.	A	b	C	D	?	?	G	H	i	J	K	?	M	3)
De. discontinua sp. nov.	A	b	C	D	?	F	G	H	i	J	K	L	M	3)
De. camelonota sp. nov.	A	B	C	D	?	F	G	h	i	J	K	?	m	3)
De. paranigrovittata sp. nov.	a	b	c	D	?	f	g	h	i	J	k	l	M	3)

The symbols "-" and "?" in the table indicate missing data and ambiguous state, respectively.
* Reference: 1) Okada (1982), 2) Takada et al. (1990), and 3) the present study.
† Revised according to de Meijere (1911: fig. 49).

Results

Species delimitation

The specimens were assigned into six morpho-species (one known and five new) of the genus *Dettopsomyia*. The alignment of the 38 barcodes spans (658 nucleotide sites in length) included 169 variable sites, among which 156 were parsimony informative. Fig. 1 shows the NJ tree built with the barcodes (GenBank accession numbers: MZ645104–MZ645141). The tree lends strong supports to the monophyly of each of the morpho-species with BP (bootstrap percentage) = 100, except *De. serripenis* sp. nov. for which only one barcode was determined. The minimum and maximum K2P distances between and within the morpho-species are shown in Table 4. All the minimum interspecific K2P distances (≥ 0.0924), except for that between *De. serripenis* sp. nov. and *De. discontinua* sp. nov. (0.0132), were substantially larger than the maximum intraspecific distances (≤0.0391). *Dettopsomyia serripenis* sp. nov. formed a highly supported clade (BP = 100) with a compact cluster (K2P ≤ 0.0048, BP = 100) of 12 barcodes of *De. discontinua* sp. nov. (Fig. 1, Table 4). However, the former is readily distinguished from the latter in the morphology of both male and female (see the morphological diagnosis defined below for *De. discontinua* sp. nov.). On the other hand, the largest intraspecific distance (0.0391) was observed within the morpho-species *De. nigrovittata* (Table 4). Although the 18 barcode sequences of this species formed a monophyletic cluster (BP = 100), they were split into two subclusters with BPs = 58 and 96 (Fig. 1). However, no significant differentiation attributable to this
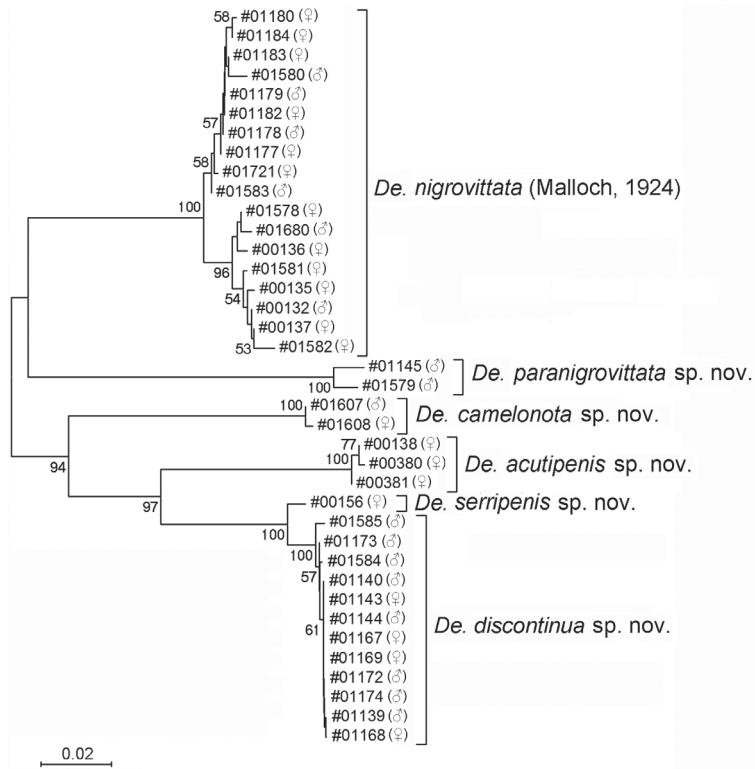
Figure 1. An un-rooted, neighbor-joining tree built with DNA barcodes (mitochondrial *COI* sequences) of six *Dettopsomyia* species. Label of each operational taxonomic unit (OTU) is given in the format of "voucher number (sex)". Node confidences (i.e., bootstrap percentages from 1000 replicates) ≥ 50% are shown.

Table 4. Minimum and maximum of intra- and interspecific K2P distances of six *Dettopsomyia* species.

Species	n^a	Intraspecific distance		Interspecific distances[b]					
		Minimum	Maximum	1	2	3	4	5	6
De. nigrovittata (Malloch, 1924)	18	0.0000	0.0391		0.1355	0.1330	0.1499	0.1380	0.1420
De. paranigrovittata sp. nov.	2	0.0152	0.0152	0.1741		0.1784	0.1946	0.1776	0.1708
De. camelonota sp. nov.	2	0.0000	0.0000	0.1621	0.1897		0.1435	0.1372	0.1320
De. acutipenis sp. nov.	3	0.0000	0.0017	0.1829	0.2069	0.1489		0.0978	0.0924
De. serripenis sp. nov.	1	n/a	n/a	0.1484	0.1780	0.1445	0.1046		0.0132
De. discontinua sp. nov.	12	0.0000	0.0048	0.1756	0.1847	0.1434	0.1035	0.0164	

[a] Number of sequences; [b] Maximum distances below diagonal, and minimum distances above diagonal.

subdivision was detected in either morphology (see Taxonomic account), habitat or geographical distribution (Table 2) between the two subclusters. We therefore regarded all these 18 specimens as of the same species (i.e., *De. nigrovittata*). Similarly, we identified two specimens of which K2P distance (0.0152) slightly exceeded the least interspecific distance (0.0132) (Table 4) as *De. paranigrovittata* sp. nov. based on the morphology.

Taxonomic account

Genus *Dettopsomyia* Lamb, 1914

Dettopsomyia Lamb, 1914: 349; Wheeler & Takada 1964: 210; Bock 1982: 42; Okada 1982: 270; Bächli et al. 2004: 119. Type species: *Dettopsomyia formosa* Lamb, 1914.

Pictostyloptera Duda, 1924: 192. Syn. Duda 1926: 61. Type species: *Drosophila preciosa* de Meijere, 1911.

Included species. *acrostichalis* Duda, 1926; *alba* Carson & Okada in Okada (1982); *bombax* (Burla, 1954); *equscauda* Takada & Momma, 1975; *formosa* Lamb, 1914; *fruhstorferi* (Duda, 1924); *jacobsoni* Duda,1926; *nigrovittata* (Malloch, 1924); *philippina* Takada, 1976; *pictipes* (de Meijere, 1911); *preciosa* (de Meijere, 1911); *repletoides* (Carson & Okada, 1980); *woodruffi* Takada in Takada et al. (1990); *acutipenis* Wang & Gao, sp. nov.; *camelonota* Wang, Li & Gao sp. nov.; *discontinua* Wang & Gao, sp. nov.; *paranigrovittata* Wang, Li & Gao, sp. nov.; and *serripenis* Wang & Gao, sp. nov.

Geographical distribution. Collection records of all the known species from the world are plotted in a map (Fig. 2) using Simplemappr (http://www.simplemappr.net/), and collection sites of the five new species plotted in a separate, online map (Fig. 3) from https://d-maps.com.
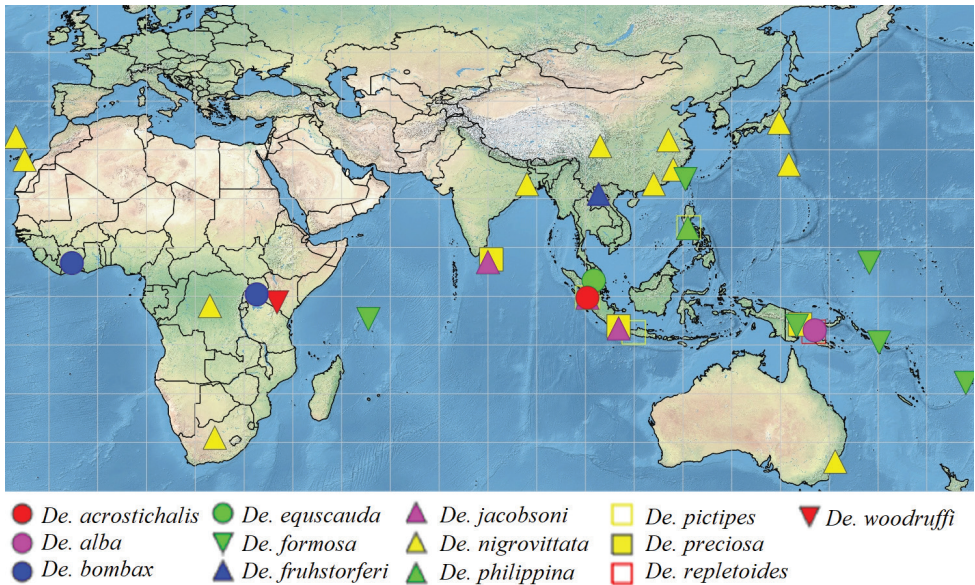
Figure 2. Geographical distribution of the known species in the genus *Dettopsomyia*.

Key to Oriental species of *Dettopsomyia*

In this key, some figures published by Lamb (1914), Duda (1924, 1926), Okada (1956, 1982), Hardy (1965), and Takada (1976) are cited.

1	Wing spotted (Figs 5C, 6C, 7C; Lamb 1914: fig. 33; Duda 1924: fig. 39; Duda 1926: fig. 3; Hardy 1965: fig. 20b).	**2**
–	Wing not spotted (Figs 4C, 8C; Duda 1924: fig. 40).	**7**
2	Acrostichal bristles present (Okada 1982: fig. 1B, C).	**3**
–	Acrostichal bristles absent (Figs 5–7B; Okada 1982: fig. 1A).	**4**
3	Wing with two black spots along costa (Duda 1924: fig. 39). .... *De. preciosa* (de Meijere)
–	Wing with four black spots along costa (Duda 1926: fig. 3). ....*De. jacobsoni* Duda
4	Wing with approximately 24 pale spots; R_{4+5} and M_1 parallel (Fig. 7C). ....*De. camelonota* Wang, Li & Gao, sp. nov.
–	Wing with 14–17 pale spots; R_{4+5} and M_1 divergent distally (Figs 5C, 6C; Lamb 1914: fig. 33; Hardy 1965: fig. 20b).	**5**
5	Ocellar setae inserted inside triangle made by ocelli (Okada 1982) fig. 1A); epandrial, ventral lobe elongated (Okada 1982: fig. 2A). ....*De. formosa* Lamb
–	Ocellar setae inserted outside triangle made by ocelli (Figs 5B, 6B); epandrial, ventral lobe short (Fig. 5F, G) or absent (Fig. 6F, G).	**6**
6	Cercus somewhat pointed but not protruded caudoventrally (Fig. 5F); surstylus with 14 or 15 prensisetae arranged in V-shape (Fig. 5F, G); marginal peg-like ovisensilla in continuous row (Fig. 5J, K) ....*De. serripenis* Wang & Gao, sp. nov.
–	Cercus caudoventrally protruded ventrad like finger (Fig. 6F); surstylus with approximately 11 prensisetae on distal margin and 9 or 10 ones on medial portion of outer surface, arranged together nearly in circle (Fig. 6F, G); row of marginal peg-like ovisensilla interrupted around subterminal, long, trichoid seta (Fig. 6J, K). ....*De. discontinua* Wang & Gao, sp. nov.
7	R_{2+3} nearly straight (Fig. 8C; Takada 1976: fig. 1c).	**8**
–	R_{2+3} more or less curved to costa apically (Fig. 4C).	**9**
8	Scutum and scutellum blackish brown to black (Fig. 8B). ....*De. paranigrovittata* Wang, Li & Gao, sp. nov.
–	Scutum and scutellum with brownish, longitudinal stripes (Takada 1976: fig. 1a). ....*De. philippina* Takada
9	Acrostichal bristles present.	**10**
–	Acrostichal bristles absent (Figs 4B, 8B).	**11**
10	R_{4+5} and M_1 divergent distally (Duda 1924: fig. 40). ... *De. pictipes* (de Meijere)
–	R_{4+5} and M_1 parallel ....*De. acrosticholis* Duda
11	C-index < 1.0 (Okada 1956: fig. 31). ....*De. nigrovittata* (Malloch)
–	C-index > 1.0 (Fig. 4A).	**12**

12   Scutum with 10 dark stripes...**De. fruhstorferi (Duda)**
–   Scutum with < 10 dark stripes (Fig. 4B), or with complex dark marks. **13**
13   Acrostichal setulae in 2 rows. ....**De. equscauda Takada & Momma**
–   Acrostichal setulae in 4 rows (Fig. 4B)..... **De. acutipenis Wang & Gao, sp. nov.**

Descriptions of species

Dettopsomyia acutipenis Wang & Gao, sp. nov.

http://zoobank.org/46AA8D2F-D9A1-43BB-A251-524BB1E60157
Figure 4

Material. *Holotype* ♂ (#00151), Yunnan: Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences, Menglun, Mengla, Xishuangbanna, ca. 570 m (21.92°N, 101.28°E), 19.iii.2006, *ex* flower of *Zinger* sp. (M.J. Toda) (KIZ). *Paratypes* China: 7♀ (#00380–386), the data same as holotype except for 18.vi.2007 (J.J. Gao); 3♀ (#00387–389), the data same as holotype except for 16.vi.2007 (J.J. Gao) (KIZ).

Diagnosis. This species differs in CS-code (Ab??efGHiJklM) from all the remaining congeneric species, except for *De. fruhstorferi* (?????fG?iJk?? according to Okada, 1982), which is, however, distinguished from the new species by the number of dark, longitudinal stripes on scutum: six in the new species, but ten in *De. fruhstorferi*.

Description. (♂, ♀). *Head* (Fig. 4A, B): Eye red, much oblique to body axis, with dense interfacetal setulae. Ocellar triangle matte black. Ocellar setae located outside triangle made by ocelli. Fronto-orbital plate anteriorly with a black spot at the base of proclinate and anterior reclinate orbital setae. Frons grayish yellow, with pale brown stripes. Face yellow; carina large, ventrally with blackish brown, T-shaped spot. Clypeus black. Gena yellowish brown, with dark stripe along ventral margin. Palpus yellow. Pedicel (2nd antennal segment) yellow, laterally with black spot; 1st flagellomere (3rd antennal segment) grayish yellow.

Thorax (Fig. 4A, B): Scutum, scutellum, and thoracic pleura yellowish brown; scutellum apically white. Scutum with six blackish brown stripes; median pair close to each other. Scutellum medially with X-shaped, dark marking posteriorly covering the bases of apical scutellar setae, laterally with dark spots at the bases of basal scutellar setae. Thoracic pleura with three blackish, longitudinal stripes. Acrostichal long setae absent; acrostichal setulae in four rows. Dorsocentral setae three pairs. Basal scutellar setae slightly divergent; apical scutellar setae cruciate.

Wing (Fig. 4C): Wing pale yellow. Veins yellowish brown. Costal lappet black, moderate in size. R$_{2+3}$ curved to costa apically; R$_{4+5}$ and M$_1$ slightly diverged from each other distally. Haltere pale yellow, ventrally with small grayish patch; stalk slightly grayish.

Legs (Fig. 4A): Legs yellow: femora and tibiae ringed.

Abdomen (Fig. 4D, E): Tergites yellow, posteriorly with narrow, blackish brown, dorsomedially interrupted bands, which bend forward laterally, and with an isolated black spot on lateral margin.
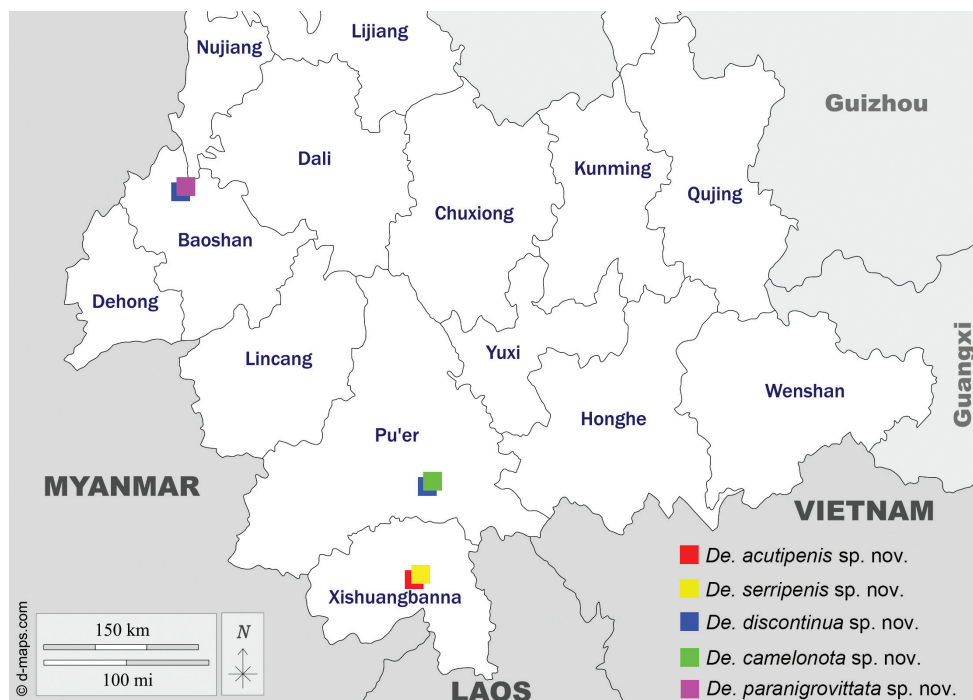
Figure 3. Geographical distribution of five newly described species in the genus *Dettopsomyia*.

Male terminalia (Fig. 4F–I): Epandrium pubescent except for anterior margin and ventral portion, with five setae per side on ventral portion and triangular, distally somewhat roundish apodeme on antero-dorsal to -sublateral margin, slightly protruded anteriad at anteroventral corner. Surstylus broadly fused to epandrium; distal margin with a row of 12 or 13 peg-like, apically pointed prensisetae, which are more loosely arranged dorsally; outer surface with six or seven long, trichoid setae on subdorsal to ventral portion; caudoventral apex with a few short, trichoid setae. Cercus oblong, wider than 1/2 length, partially fused to epandrium, caudoventrally pointed, pubescent except for anteroventral margin, with approximately 17 setae. Hypandrium somewhat triangular, with a pair of minute setae (paramedian setae?), caudomedially deeply notched and revolute along inner edges, with large patches of pubescence on the revolute parts. Aedeagus apically acute, slightly curved dorsad, basally with recurved, dorsal flap; aedeagal guide broadly fused to revolute portion of hypandrium; apodeme fused to aedeagus, rod-like, < 1/3 length of aedeagus.

Female terminalia (Fig. 4J–L): Oviscapt with single lateral and 13 or 14 marginal, apically more or less pointed, peg-like ovisensilla, and one subterminal, trichoid seta; anteroventral bridge short. Spermatheca somewhat fusiform, basally ridged; introvert ca. 1/4 height of outer capsule.
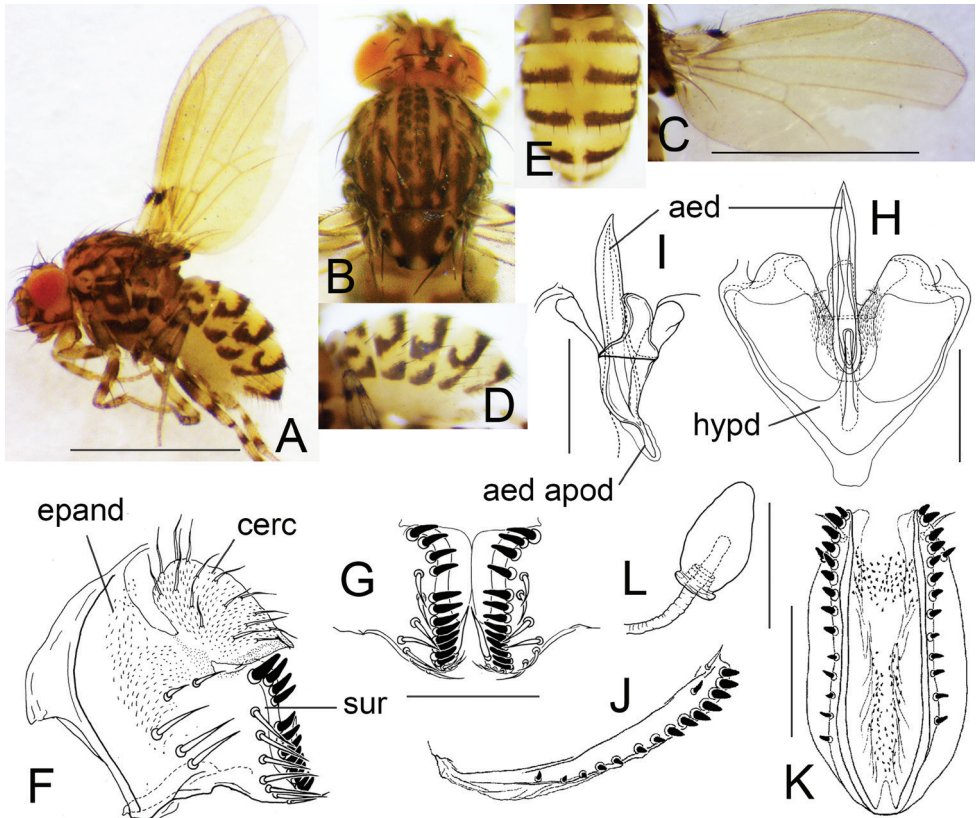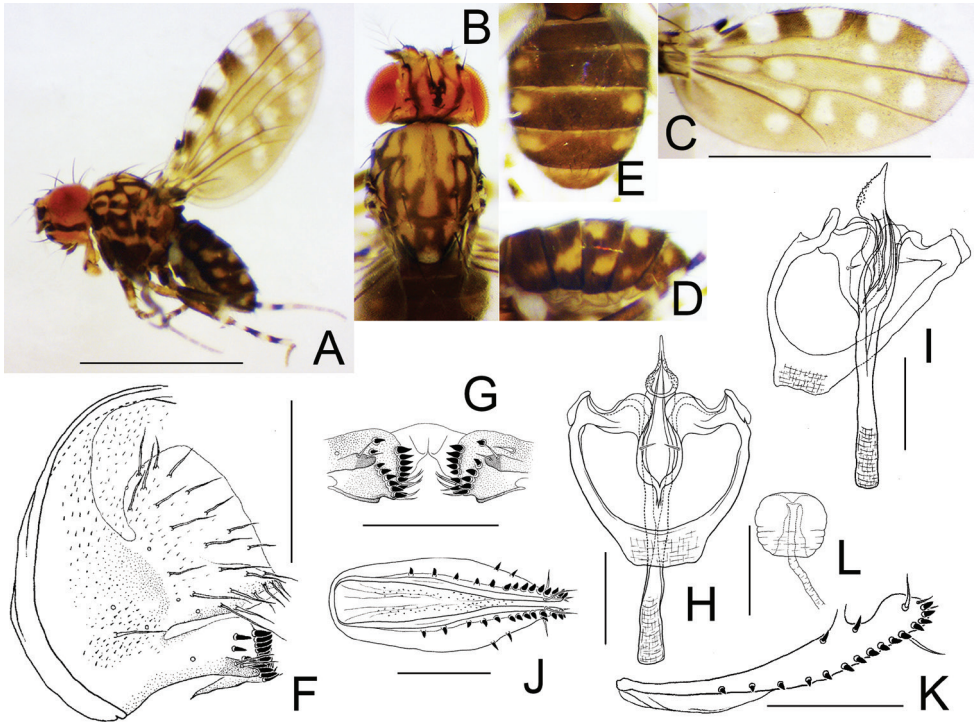
Figure 4. *Dettopsomyia acutipenis* Wang & Gao, sp. nov. (**A–I** #00151, **J–L** paratype #00380) **A** left lateral habitus **B** head and thorax (dorsal view) **C** wing (right, dorsal view) **D** abdomen (lateral view) **E** abdomen (dorsal view) **F** periphallic organs (posterolateral view) **G** surstylus **H** phallic organs (ventral view) **I** aedeagus (dorsolateral view) **J** oviscapt (lateral view) **K** oviscapt (ventral view) **L** spermatheca. Abbreviations: aed = aedeagus, aed apod = aedeagal apodeme, cerc = cercus, epand = epandrium, hypd = hypandrium, sur = surstylus. Scale bars: 1.0 mm (photograph) or 0.1 mm (line drawing).

Measurements: BL (straight distance from anterior edge of pedicel to tip of abdomen) = 1.69 mm in holotype (range in 9♀ paratypes: 1.42–2.18 mm); ThL (distance from anterior notal margin to apex of scutellum) = 0.71 (0.62–0.74) mm; WL (distance from humeral cross vein to wing apex) = 1.46 (1.40–1.60) mm; WW (maximum wing width) = 0.73 (0.67–0.86) mm.

Indices: arb (dorsal branches/ventral branches of arista) = 3/2 in holotype (range in 9♀, or less if noted, paratypes: 3–4/2), FW/HW (frontal width/head width) = 0.59 (0.57–0.61), ch/o (maximum width of gena/maximum diameter of eye) = 0.42 (0.41–0.51), prorb (proclinate orbital seta/posterior reclinate orbital seta in length) = 0.70 (0.53–0.70), rcorb (anterior reclinate orbital seta/posterior reclinate orbital seta in length) = 0.33 (0.32–0.47), vb (subvibrissal seta/vibrissa in length) = 0.44 (0.24–

0.47), dc_1l (1st dorsocentral seta/3rd dorsocentral seta in length) = 0.91 (0.88–0.95), dc_2l (2nd dorsocentral seta/3rd dorsocentral seta in length) = 0.78 (0.77–0.92), sctl (basal scutellar seta/apical scutellar seta in length) = (n/a)/(0.96–1.06), sterno (anterior katepisternal seta/posterior katepisternal seta in length) = 0.39 (0.39–0.56), orbito (distance between proclinate and posterior reclinate orbital setae/distance between inner vertical and posterior reclinate orbital setae) = 0.56 (0.40–0.61), dc_1p (distance between ipsilateral 1st and 2nd dorsocentral setae/distance between 2nd dorsocentral setae) = 0.76 (0.70–0.79), dc_2p (distance between ipsilateral 2nd and 3rd dorsocentral setae/distance between 2nd dorsocentral setae) = 0.79 (0.69–0.80), sctlp (distance between ipsilateral scutellar setae/distance between apical scutellar setae) = 0.94 (0.93–1.04), C (2nd costal section between subcostal break and R_{2+3}/3rd costal section between R_{2+3} and R_{4+5}) = 1.31 (1.17–1.51), 4c (3rd costal section between R_{2+3} and R_{4+5}/M_1 between r-m and dm-cu) = 2.29 (1.72–2.54), 4v (M_1 between dm-cu and wing margin/M_1 between r-m and dm-cu) = 3.21 (2.40–3.36), 5× (CuA_1 between dm-cu and wing margin/dm-cu between M_1 and CuA_1) = 3.82 (2.97–3.85), ac (3rd costal section between R_{2+3} and R_{4+5}/distance between distal ends of R_{4+5} and M_1) = 2.92 (2.84–3.33), M (CuA_1 between dm-cu and wing margin/M_1 between r-m and dm-cu) = 1.43 (1.10–1.48), C3F (length of heavy setation in 3rd costal section/length of 3rd costal section) = 0.53 (0.50–0.60).

Distribution. China (Yunnan).

Relationships. This species closely resembles *De. repletoides* (CS-code = abc-dEfGHiJkLm, Okada 1982) in the structures of male terminalia Carson and Okada 1980: fig. 3).

Etymology. Referring to the apically more or less acute (*acuti-*) aedeagus (*penis*).

Dettopsomyia serripenis Wang & Gao, sp. nov.
http://zoobank.org/7B6F20BB-1217-4333-9A45-F11C20F50D4A
Figure 5

Material. *Holotype*: ♂ (#00152), Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences, Menglun, Mengla, Xishuangbanna, Yunnan, China, ca. 570 m (21.92°N, 101.28°E), 19.iii.2006, *ex* Zingerberaceae flower (M.J. Toda) (KIZ). *Paratypes*: China: 1♂ (#00153), same data except for 24.iii.2006, *ex Alocasia odora*; 1♀ (#00154), same data except for 25.iii.2006; 2♂, 2♀ (#00155–158), same data except for habitat (host plant unknown) (M.J. Toda) (KIZ, SEHU).

Diagnosis. This species is characteristic in sharing the spotted wings (Fig. 5C) with three known species of *Dettopsomyia*, *De. formosa* (Lamb 1914: fig. 33; Hardy 1965: fig. 20b), *De. jacobsoni* (Duda 1926: fig. 3) and *De. preciosa* (de Meijere 1911: fig. 49; Duda 1924: fig. 39), but differs in CS-code (AbCD??GHiJK?M) from them: *De. formosa* (ABCDEFGHiJKlM), *De. jacobsoni* (ABCDEFGHIJKLM) and *De. preciosa* (ABCDefGHIJKLm) (Table 3).

Figure 5. *Dettopsomyia serripenis* Wang & Gao, sp. nov. (**A–I** #00152, **J–L** paratype #00156) **A** left lateral habitus **B** head and thorax (dorsal view) **C** wing (right, dorsal view) **D** abdomen (lateral view) **E** abdomen (dorsal view) **F** periphallic organs (posterolateral view) **G** surstylus **H** phallic organs (ventral view) **I** phallic organs (dorsolateral view) **J** oviscapt (lateral view) **K** oviscapt (ventral view) **L** spermatheca. Scale bars: 1.0 mm (photograph) or 0.1 mm (line drawing).

Description. (♂, ♀; not repeating characters common to *De. acutipenis* sp. nov.). *Head* (Fig. 5A, B): Ocellar setae located just outside triangle made by ocelli. Frons yellow, with blackish brown stripes. Face gray. First flagellomere black.

Thorax (Fig. 5A, B): Scutum, scutellum, and thoracic pleura yellow. Scutum with confluent stripes. Scutellum with somewhat H-shaped, dark marking medially and dark stripes covering bases of ipsilateral scutellar setae laterally. Acrostichal setulae in 2–4 vestigial rows. Dorsocentral setae two pairs.

Wing (Fig. 5C) grayish yellow, black to blackish brown basally, with four dark spots along anterior margin and 14 scattered, pale spots. Veins brown. R_{2+3} waved, strongly curved to costa apically; R_{4+5} and M_1 distally diverged from each other.

Legs (Fig. 5A) pale brown.

Abdomen (Fig. 5D, E): Tergites blackish brown, laterally with yellowish spots: one per side on tergite II, two per side on tergites III–VI.

Male terminalia (Fig. 5F–I): Epandrium with three setae per side laterally; ventral lobe short, narrow, apically round and sclerotized like peg, with two small setae

subapically. Surstylus with prensisetae arranged in V-shape (approximately seven on caudal margin and 6–8 in oblique row on outer surface; one or two dorsalmost on outer surface somewhat separated from others), several upward-curved setae on ventral to subventral portion of inner surface and one or two trichoid setae on outer surface near base of epandrial ventral lobe. Cercus broadly fused to epandrium, pubescent anteriorly, with approximately 28 setae; several setae along caudoventral margin shorter. Hypandrium somewhat trapezoid; apodeme anteriorly truncate, twice as wide as long. Paramere fused to hypandrium, not pubescent but with a single setula. Aedeagus distally membranous, subapically dilated and serrated on lateral margins around gonopore, apically sharply pointed; apodeme as long as aedeagus.

Female terminalia (Fig. 5J–L): Oviscapt with one trichoid and two peg-like lateral ovisensilla and 15 marginal peg-like ovisensilla more loosely arranged anteriorly; distal portion approximately 1/4 of whole length, convex on dorsal margin in lateral view. Spermathecal capsule as broad as long, finely wrinkled on basal half, with shallow apical indentation; introvert ca. 4/5 height of outer capsule.

Measurements: BL = 1.51 mm in holotype (range in 3♂ paratypes: 1.41–1.66 mm; range in 3♀ paratype: 1.53–1.80 mm); ThL = 0.57 (0.57; 0.58–0.62) mm; WL = 1.37 (1.34–1.41; 1.47–1.52) mm; WW = 0.73 (0.66–0.71; 0.71–0.74) mm.

Indices: arb = 3/2 (range in 3♂, 3♀, or less if noted, paratypes: 3 or 4/2), FW/HW = 0.60 (0.59–0.62), ch/o = 0.38 (0.33–0.47), prorb = 0.60 (0.49–0.70), rcorb = 0.20 (0.20–0.23), vb = 0.35 (0.34–0.67), dcl (anterior dorsocentral seta/posterior dorsocentral seta in length) = 0.74 (0.82–0.89), sctl = (n/a)/(1♂: 0.90), sterno = 0.71 (0.44–0.68), orbito = 0.29 (0.21–0.26), dcp (distance between ipsilateral dorsocentral setae/ distance between anterior dorsocentral setae) = 0.71 (0.65–0.81), sctlp = 1.27 (1.03), C = 1.00 (0.89–1.16), 4c = 2.51 (1.71–2.79), 4v = 2.24 (1.79–2.82), 5× = 1.90 (1.68–2.01), ac = 2.78 (2.13–3.05), M = 0.87 (0.84–1.10), C3F = 0.52 (0.54–0.69).

Distribution. China (Yunnan).

Etymology. Referring to the serrated, lateral margins of the gonopore of the aedeagus.

Dettopsomyia discontinua **Wang & Gao, sp. nov.**
http://zoobank.org/A21C488D-0012-4CB4-9485-93577A0B454E
Figure 6

Material. *Holotype*: ♂ (#01585), Banpo, Yixiang, Simao, Pu'er, Yunnan, China, ca. 1300 m (22°44'N, 101°.07'E), by net sweeping above herbs, 2.x.2012 (J.J. Gao) (KIZ). *Paratypes*: China: 1♂ (#01584), same data as holotype; 5♂, 1♀ (#01139–1144), Zaotanghe, Baihualing, Baoshan, Yunnan, ca. 1540 m (25°18'N, 98°47'E), 4.viii.2012, *ex* small mushroom (J.J. Gao); 3♀, 3♂ (#01167–1169, #01172–1174), from decaying aroid (*Rhaphidophora decursiva*) infructescences collected from Baihualing, Baoshan, Yunnan, 23.ix.2012 (J.J. Gao, Z. Fu, and J.M. Chen) (KIZ, SEHU).

Diagnosis. This species is closely related to *De. serripenis* sp. nov., forming a highly supported (BP = 100) clade with it (Fig. 1). These two species are indistin-

guishable in CS-code from each other: *De. discontinua* sp. nov. (AbCD?FGHiJKLM) and *De. serripenis* sp. nov. (AbCD??GHiJK?M). However, they can be easily distinguished from each other by the following characters: 1) cercus caudoventrally strongly sclerotized and protruded ventrad like finger (Fig. 6F) in *De. discontinua* sp. nov. (abbreviated *Dd* here), but only pointed at caudoventral corner (Fig. 5F) in *De. serripenis* sp. nov. (abbreviated *Ds*); 2) surstylus with approximately 11 prensisetae on distal margin and nine or ten ones on medial portion of outer surface, arranged together nearly in circle (Fig. 6F, G) in *Dd*, but with 14 or 15 prensisetae arranged in V-shape (Fig. 5F, G) in *Ds*; and 3) marginal peg-like ovisensilla in row interrupted around subterminal, long, trichoid seta (Fig. 6J, K) in *Dd*, but in continuous row (Fig. 5J, K) in *Ds*.

Description. (♂, ♀; not repeating characters common to *De. serripenis* sp. nov.). *Head* (Fig. 6A, B): Frons with black stripes. Gena yellow. Palpus grayish yellow.

Thorax (Fig. 6A, B): Scutum, scutellum, and thoracic pleura with color patterns similar to those of *De. serripenis* sp. nov. Acrostichal setulae in two rows. Basal scutellar setae slightly converged.

Wing (Fig. 6C): Wing maculated as in *De. serripenis* sp. nov.

Legs (Fig. 6A) pale grayish yellow.

Abdomen (Fig. 6D, E): Tergites blackish brown to black; II–V each laterally with a pale brown spot per side.

Male terminalia (Fig. 6F–I): Epandrium pubescent on mediolateral portion only, with one seta per side on mediolateral portion; ventral lobe not differentiated; apodeme narrow, somewhat triangular. Surstylus somewhat quadrate, large plate, with one trichoid seta and 10–11 prensisetae in sinuated row on outer surface and 6–8 prensisetae decreasing in size downward on caudal margin. Cercus unpubescent, with approximately 33 setae. Hypandrium somewhat hemicircular; apodeme slightly wider than long. Aedeagus subapically with a pair of triangular lateral flaps; apodeme shorter than aedeagus.

Female terminalia (Fig. 6J–L): Oviscapt with three trichoid lateral ovisensilla, 14–16 peg-like marginal ovisensilla and one subterminal, trichoid, long seta; distal portion approximately 1/3 of whole length, nearly flat on dorsal margin in lateral view.

Measurements: BL = 1.50 mm in holotype (range in 5♂ paratypes: 1.42–1.67 mm; range in 4♀ paratypes: 1.57–1.75 mm); ThL = 0.52 (0.55–0.64; 0.55–0.68) mm; WL = 1.30 (1.26–1.37; 1.36–1.58) mm; WW = 0.66 (0.62–0.70; 0.63–0.80) mm.

Indices: arb = 4 or 5/2 (range in 5♂, 4♀, or less if noted, paratypes: 4/2), FW/HW = 0.60 (0.57–0.61), ch/o = 0.38 (0.35–0.49), prorb = 0.72 (0.59–0.77), rcorb = 0.14 (0.16–0.21), vb = 0.32 (0.22–0.46), dcl = 0.74 (0.72–0.85), sctl = 0.98 (0.95–1.12), sterno = 0.73 (0.44–0.64), orbito = 0.19 (0.25–0.32), dcp = 0.65 (0.65–1.08), sctlp = 1.06 (0.95–1.14), C = 0.88 (0.90–0.96), 4c = 2.53 (2.11–2.34), 4v = 2.39 (1.93–2.30), 5× = 2.04 (1.63–2.09), ac = 3.18 (2.68–3.06), M = 0.93 (0.78–0.85), C3F = 0.58 (0.42–0.63).

Distribution. China (Yunnan).

**Etymology.** Referring to the interruptedly arranged marginal ovisensilla.
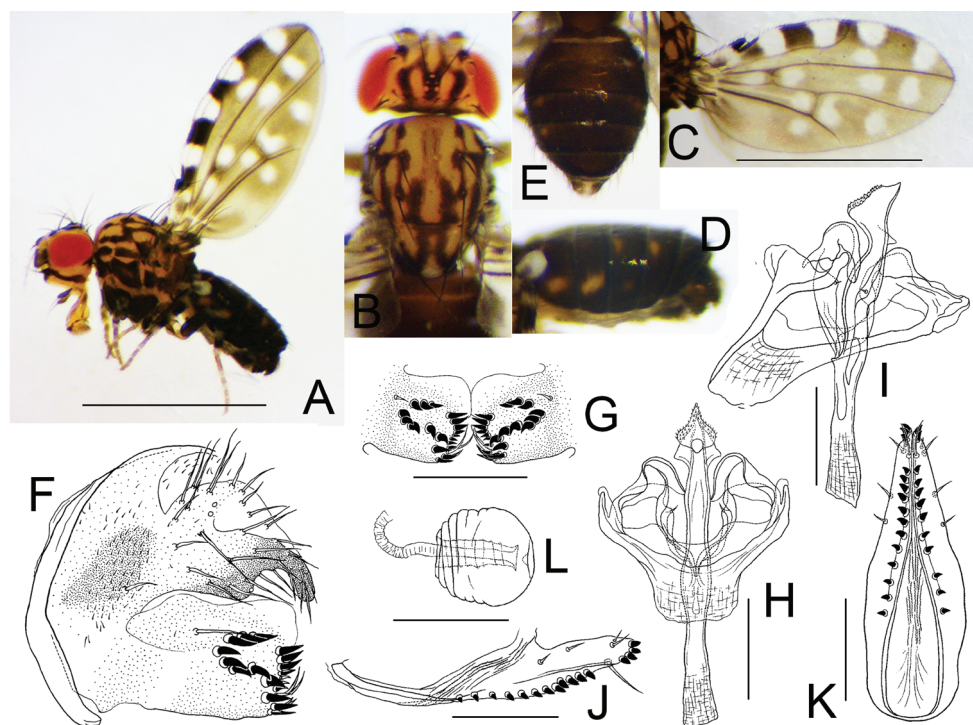
Figure 6. *Dettopsomyia discontinua* Wang & Gao, sp. nov. (**A–I** #01585, **J–L** paratype #01168) **A** left lateral habitus **B** head and thorax (dorsal view) **C** wing (right, dorsal view) **D** abdomen (lateral view) **E** abdomen (dorsal view) **F** periphallic organs (posterolateral view) **G** surstylus **H** phallic organs (ventral view) **I** phallic organs (dorsolateral view) **J** oviscapt (lateral view) **K** oviscapt (ventral view) **L** spermatheca. Scale bars: 1.0 mm (photograph) or 0.1 mm (line drawing).

Dettopsomyia camelonota Wang, Li & Gao, sp. nov.
http://zoobank.org/7BCD32DA-ABD3-47B3-AAC9-5DF315757B63
Figure 7

Material. *Holotype*: ♂ (#01607), Banpo, Yixiang, Simao, Pu'er, Yunnan, China, ca. 1300 m (22.73°N, 101.12°E), 25.x.2012 (J.J. Gao) (KIZ). *Paratype*: China: 1♀ (#01608), same data as holotype (KIZ).

　　Diagnosis. This species differs from all the remaining congeneric species in CS-code (ABCD?FGhiJK?m) (Table 3) and having the following diagnostic characters: unique, distinctly humpbacked scutum in lateral view (Fig. 7A); aedeagus characterized by large, vault-like arch (Fig. 7H, I); and large, spoon-shaped paramere densely hirsute on inner surface (Fig. 7H, I). It resembles *De. formosa*, *De. jacobsoni*, *De. serripenis* sp. nov., and *De. discontinua* sp. nov. in wing marking pattern, but can be distinguished from them by much more (approximately 24) pale spots (Fig. 7C).

　　Description. (♂, ♀; not repeating characters common to *De. acutipenis* sp. nov.). *Head* (Fig. 7A, B): Ocellar setae located just inside triangle made by ocelli. Frons with
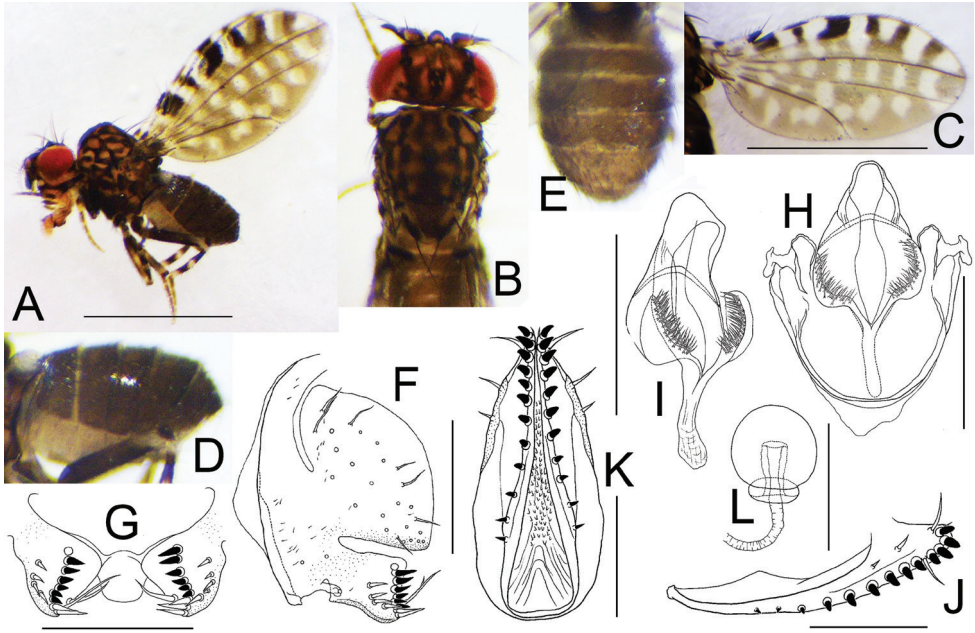
Figure 7. *Dettopsomyia camelonota* Wang, Li & Gao, sp. nov. (**A–I** #01607, **J–L** paratype #01608) **A** left lateral habitus **B** head and thorax (dorsal view) **C** wing (right, dorsal view) **D** abdomen (lateral view) **E** abdomen (dorsal view) **F** periphallic organs (posterolateral view) **G** surstylus **H** phallic organs (ventral view) **I** phallic organs (dorsolateral view) **J** oviscapt (lateral view) **K** oviscapt (ventral view) **L** spermatheca. Scale bars: 1.0 mm (photograph) or 0.1 mm (line drawing).

blackish brown stripes. Face grayish yellow to blackish brown; carina broad, dorsally strongly swollen and blackish brown, medially yellowish brown, ventrally nearly flat, black and with broad, pale yellow, traverse band. Clypeus blackish yellow. Gena pale yellow, ventrally black. Palpus gray, paddle-shaped in ventral view, with one prominent apical seta and several ventral ones. Antennal pedicel long triangular, black, laterally with yellowish patch; 1st flagellomere long, somewhat triangular, black, with pale patch on inner, dorsal margin; arista with brown dorsal and ventral branches nearly as long as whitish trunk.

Thorax (Fig. 7A, B): Scutum, scutellum, and thoracic pleura grayish yellow. Scutum with blackish brown to black, longitudinal stripes interweaved with each other. Scutellum medially with blackish brown to black patch merged with lateral black spots covering bases of ipsilateral scutellar setae. Acrostichal setulae in two vestigial rows. Dorsocentral setae three pairs; anteriormost pair distinctly shorter and thinner, located slightly anterior to transverse suture and more widely separated from each other. Basal scutellar setae divergent.

Wing (Fig. 7C): Veins brown. R_{2+3} not waved medially, strongly curved to costa apically. R_{4+5} and M_1 veins distally nearly parallel with each other.

Legs (Fig. 7A) yellow to pale brown.

Abdomen (Fig. 7D, E): Tergites blackish brown.

Male terminalia (Fig. 7F–I): Epandrium nearly completely smooth, with two setae per side on ventral portion; ventral lobe very small; somewhat triangular apodeme present on anteromedial margin. Surstylus with a row of approximately six prensisetae on distal margin, approximately four thick, short setae on submedial to ventral portion of outer surface and a few trichoid setae around caudoventral corner. Cercus broadly fused to epandrium, large, somewhat fan-shaped, caudoventrally not pointed, nearly smooth, with approximately 25 short setae. Hypandrium broad, anteriorly rounded, with triangular apodeme. Aedeagus bilobed; apodeme approximately 1/2 as long as aedeagus.

Female terminalia (Fig. 7J–L): Oviscapt with three lateral trichoid and 12 or 13 marginal, apically somewhat blunt peg-like ovisensilla. Spermathecal capsule spherical, strongly constricted near base; introvert ca. 3/5 height of outer capsule.

Measurements: BL = 1.54 mm in holotype (1♀ paratype: 1.70 mm); ThL = 0.57 (0.65) mm; WL = 1.42 (1.53) mm; WW = 0.72 (0.72) mm.

Indices: arb = 4/2 (1♀: 4/2), FW/HW = 0.65 (0.64), ch/o = 0.41 (0.48), prorb = 0.71 (n/a), rcorb = 0.18 (0.15), vb = 0.34 (0.29), dc_1l = 0.36 (0.28), dc_2l = n/a (0.72), sctl = 0.94 (0.95), sterno = n/a (0.80), orbito = 0.18 (0.21), dc_1p = 0.39 (0.32), dc_2p = 0.67 (0.62), sctlp = 1.14 (1.00), C = 0.94 (0.90), 4c = 2.75 (2.60), 4v = 3.00 (2.73), 5× = 1.85 (1.63), ac = 4.21 (4.17), M = 1.04 (0.87), C3F = 0.34 (0.50).

Distribution. China (Yunnan).

Etymology. A combination of the Greek words *camelos* and *notos*, referring to the humped, camel-like notum.

Dettopsomyia paranigrovittata Wang, Li & Gao, sp. nov.
http://zoobank.org/B1789016-279E-4E0A-8817-FE2D1F394558
Figure 8

Materials. *Holotype*: ♂ (#01145), *ex.* inflorescence of *Rh. decursiva*, Laomengzhai, Baihualing, Baoshan, Yunnan, China, ca. 1500 m (25°17'N, 98°48'E), 3.viii.2012 (J.J. Gao) (KIZ). *Paratype*: China: 1♂ (#01579), emerged (together with many adults of *De. nigrovittata*) from decaying spathes of *Rh. decursiva* collected from Laomengzhai, Baihualing, Baoshan, Yunnan (same as holotype) and cultured in laboratory, 23.ix.2012 (J.J. Gao, Z. Fu, J.M. Chen) (KIZ).

Diagnosis. This species closely resembles *De. nigrovittata* in the external morphology and male terminalia, but can be distinguished from it by the surstylus chaetotaxy: in *De. paranigrovittata* sp. nov., approximately 23 subequal, peg-like prensisetae arranged roughly in five sets on medial to distal portion of outer surface and two upward-curved, trichoid setae on subventral portion of inner surface (Fig. 8F, G); but in *De. nigrovittata*, approximately 25 more or less heteromorphic setae arranged in three rows on upper half of outer surface and two larger setae at lower tip (Okada 1956: fig. 31C, as *De. argentifrons*).

Description. (♂; not repeating characters common to *De. acutipenis* sp. nov.). **Head** (Fig. 8A, B): Eye nearly rectangular to body axis. Fronto-orbital plate yellowish brown. Frons and frontal vittae grayish brown, somewhat shining. Face grayish yellow, black at
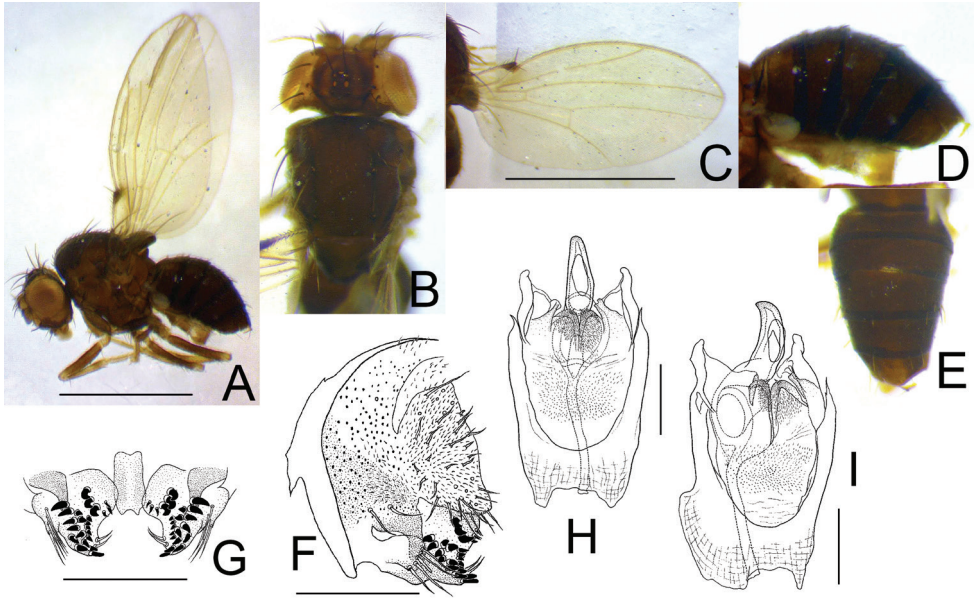
Figure 8. *Dettopsomyia paranigrovittata* Wang, Li & Gao, sp. nov. (**A–I** #01145) **A** left lateral habitus **B** head and thorax (dorsal view) **C** wing (right, dorsal view) **D** abdomen (lateral view) **E** abdomen (dorsal view) **F** periphallic organs (posterolateral view) **G** surstylus **H** phallic organs (ventral view) **I** phallic organs (ventrolateral view). Scale bars: 1.0 mm (photograph) or 0.1 mm (line drawing).

middle and lateral sides; carina grayish yellow, rather prominent. Gena blackish brown, with pale spots antero- and medio-dorsally. Palpus grayish yellow, with large black spot. Antennal pedicel grayish yellow; 1st flagellomere dark gray. Subvibrissal seta short.

Thorax (Fig. 8A, B): Scutum blackish brown to black, with four narrow, silver stripes; scutellum and thoracic pleura blackish brown. Acrostichal setulae in six rows. Dorsocentral setae two pairs. Basal scutellar setae divergent.

Wing (Fig. 8C) hyaline. Veins pale brown. R_{2+3} nearly straight; R_{4+5} and M_1 distally parallel. Haltere pale whitish to grayish yellow.

Legs (Fig. 8A) pale brown to blackish brown.

Abdomen (Fig. 8D, E): Tergites entirely black.

Male terminalia (Fig. 8F–I): Epandrium pubescent on lateral to dorsal portion, with one and two setae per side on sub-dorsal and -ventral portions, respectively; ventral lobe distally with five long, trichoid setae; apodeme on anterior margin. Surstylus somewhat triangular, large plate. Cercus broadly fused to epandrium, somewhat roundish at caudoventral corner, entirely pubescent, with approximately 36 setae. Hypandrium anteriorly slightly narrower, caudomedially notched. Paramere fused to hypandrium, densely pubescent, apically with one minute setula. Aedeagus curved ventrad proximally but dorsad distally, distally narrowing like horn in lateral view, ventro-subapically with large, oval gonopore; apodeme slightly shorter than aedeagus.

Measurements: BL = 1.69 mm in holotype (1♂ paratype: 1.52 mm); ThL = 0.68 (0.65) mm; WL = 1.50 (1.40) mm; WW = 0.74 (0.71) mm.

Indices: arb = 4/2 (1♂ paratype: 4/2), FW/HW = 0.56 (0.55), ch/o = 0.36 (0.41), prorb = 0.68 (0.73), rcorb = n/a (0.32), dcl = 0.71 (0.71), sctl = 0.83/(0.85), sterno = n/a (0.61), orbito = 0.57 (0.52), dcp = 0.80 (0.83), sctlp = 0.91 (0.92), C = 1.36 (1.23), 4c = 1.94 (2.20), 4v = 2.92 (3.15), 5× = 3.20 (2.67), ac = 4.73 (3.89), M = 1.23 (1.25), C3F = 0.60 (0.65).

Distribution. China (Yunnan).

Etymology. Referring to the close morphological affinity to *De. nigrovittata*.

Discussion

Since the early days of taxonomy for *Dettopsomyia* and *Styloptera*, these two genera have been ambiguous in their systematic positions. Until now, only few phylogenetic studies have been conducted to clarify the relationships between them. Grimaldi (1990) classified these two genera with *Jeannelopsis* Seguy, *Tambourella* Wheeler, *Mulgravea* Bock, *Sphaerogastrella* Duda, *Hypselothyrea* de Meijere, and *Liodrosophila* Duda in the *Styloptera* genus group, based on a cladistic analysis using 217 characters of 120 species. However, each genus was represented by a single species in his analysis. In Yassin's (2013) Bayesian phylogenetic tree based on DNA sequences of 70 genera of the Drosophilidae, *Styloptera* (represented by *S. formosae* only) was coupled with the subgenus *Dorsilopha* Sturtevant (represented by *Drosophila busckii* Coquillett, 1901), and *Dettopsomyia* (represented by *De. nigrovittata*) was placed into a clade containing the genera *Jeannelopsis*, *Dichaetophora* Duda, *Hirtodrosophila* Duda, *Zygothrica* Wiedemann, and *Mycodrosophila* Oldenberg. To completely solve this ambiguity in the systematics of the subfamily Drosophilidae a full-scale molecular phylogenetic analysis should be conducted with extensive taxon sampling from *Dettopsomyia*, *Styloptera* and putatively related genera and subgenera. The species diversity of *Dettopsomyia* and *Styloptera* has also been less explored: only 13 and ten species were known, respectively, before the present study. Our finding of five new *Dettopsomyia* species from southwestern China (Fig. 3) suggests that more unknown species remain to be discovered from the Oriental region. To precisely delimit the boundaries of these genera, as many species as possible need to be incorporated into the systematic study.

The natural history of *Dettopsomyia* flies is still less explored. However, our collection records suggest their florivorous nature. Adult flies of *De. acutipenis* sp. nov. and *De. serripenis* sp. nov. were collected from flowers of Zingerberaceae, *De. serripenis* sp. nov. also from inflorescences of *Alocasia odora* (Araceae), and *De. paranigrovittata* from an inflorescence of *Rhaphidophora decursiva* (Araceae). Additionally, offspring adults of *De. paranigrovittata* sp. nov., *De. discontinua* sp. nov., and *De. nigrovittata* emerged from infructescences with decayed spathe of *R. decursiva* in laboratory rearings, and Carson and Okada (1980) reported rearing *De. repletoides* (under the name of *Styloptera repletoides*) from infructescences of *Colocasia esculenta* (Araceae). Wheeler (1951) observed dipteran larvae and puparia in a rotting, bleeding part of banana plant, and adults emerged from them and were identified as *De. nigrovittata*. Thus, some species of *Dettopsomyia* use decayed plant materials as a breeding substrate.

Acknowledgements

References

Bächli G, Vilela CR, Escher SA, Saura A (2004) Drosophilidae (Diptera) of Fennoscandia and Denmark, Fauna Entomologica Scandinavica, vol. 39. Brill, Leiden, 362 pp.

Bock IR (1982) Drosphilidae of Australia V. Remaining genera and synopsis (Insecta: Diptera). Australian Journal of Zoology, Supplement series 89: 1–164. https://doi.org/10.1071/AJZS089

Carson HL, Okada T (1980) Drosophilidae associated with flowers in Papua New Guinea I. *Colocasia esculenta*. Kontyû 48: 15–29. https://dl.ndl.go.jp/info:ndljp/pid/10652398

de Meijere JCH (1911) Studien über südostasiatische Dipteren. VI. Tijdschrift voor Entomologie 54: 258–432. [pls. 18–22.]

Duda O (1924) Beitrag zur Systematic der Drosophiliden unter besonderer Berücksichtigüng der paläarktischen u. orientalischen Arten (Dipteren). Wiegmann's Archiv fur Naturgeschichte (A) 90: 172–234.

Duda O (1926) Drosophilidae (Dipt.), Fauna sumatrensis. Supplementa Entomologica 14: 42–116.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299. https://www.mbari.org/wp-content/uploads/2016/01/Folmer_94MMBB.pdf

Grimaldi DA (1990) A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bulletin of the American Museum of Natural History 197: 1–139. https://doi.org/10.1016/0006-3207(90)90116-7

Hardy DE (1965) Diptera: Cyclorrhapha II, Series Schizophora. Section Acalypteratae I. Family Drosophilidae. In: Zimmerman EC (Ed.) Insects of Hawaii. The University Press of Hawaii, Honolulu 12: 28–796.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Lamb CB (1914) Reports of the Percy Sladen Trust Expedition, Diptera, No. 15. Heteroneuridae, Ortalidae, Trypetidae, Sepsidae, Micropezidae, Drosophilidae, Geomyzidae, Milichidae. Transaction of the Linnean Society of London (second series-Zoology) 16: 307–372. https://doi.org/10.1111/j.1096-3642.1913.tb00152.x

Li NN, Toda MJ, Fu Z, Chen JM, Li SH, Gao JJ (2014) Taxonomy of the *Colocasiomyia gigantea* species group (Diptera, Drosophilidae), with descriptions of four new species from Yunnan, China. ZooKeys 406: 41–64. https://doi.org/10.3897/zookeys.406.7176

McAlpine JF (1981) Morphology and terminology: adults. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera (Vol. 1). Biosystematics Research Institute, Ottawa, 9–63.

Okada T (1956) Systematic Study of Drosophilidae and Allied Families of Japan. Gihodo Co. Ltd., Tokyo, 183 pp.

Okada T (1982) A revision of the genera *Dettopsomyia* Lamb and *Styloptera* Duda (Diptera, Drosophilidae). Kontyû 50: 270–282. https://dl.ndl.go.jp/info:ndljp/pid/10652715

Okada T, Carson HL (1980) Drosophilidae associated with flowers in Papua New Guinea II. *Alocasia* (Araceae). Pacific Insects 22: 217–236.

Okada T, Carson HL (1983) Drosophilidae from banana traps over an altitudinal transect in Papua New Guinea. I. Descriptions of new species with notes on newly recorded species. International Journal of Entomology 25: 127–141.

Takada (1976) A new species of *Dettopsomyia* (Diptera, Drosophilidae) from the Philippines. Kontyû 44:169–171.

Takada H, Woodruff RC, Thompson Jr JN (1990) Collection of Drosophilidae (Diptera) in Kenya, with description of a new species of *Dettopsomyia*. Entomological News 101: 246–255. https://www.biodiversitylibrary.org/part/40615

Toda MJ (2020) DrosWLD-Species: Taxonomic Information Database for World Species of Drosophilidae. http://bioinfo.museum.hokudai.ac.jp/db/modules/stdb/index.php?ml_lang=en [accessed 2 July 2020]

Tsacas L (1980) Family Drosophilidae. In: Crosskey RW (Ed.) Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, 673–685.

Wheeler MR (1951) *Dettopsomyia* and *Ptilomyia*: Two genera new to the United States (Diptera: Drosophilidae; Ephydridae). The Pan-Pacific Entomologist 27: 92–93. https://www.biodiversitylibrary.org/page/53432957

Wheeler MR, Takada H (1964) Diptera: Drosophilidae. Insects of Micronesia. Bernice P. Bishop Museum 14: 164–242.

Yang JH, Toda MJ, Suwito A, Hashim R, Gao JJ (2017) A new species group in the genus *Dichaetophora*, with descriptions of six new species from the Oriental region (Diptera, Drosophilidae). ZooKeys 665: 121–146. https://doi.org/10.3897/zookeys.665.11609

Yassin A (2013) Phylogenetic classification of the Drosophilidae Rondani (Diptera): the role of morphology in the postgenomic era. Systematic Entomology 38: 349–364. https://doi.org/10.1111/j.1365-3113.2012.00665.x

Zhang WX, Toda MJ (1992) A new species-subgroup of the *Drosophila immigrans* species-group, with description of two new species from China and revision of taxonomic terminology. Japanese Journal of Entomology 60: 839–850. https://dl.ndl.go.jp/info:ndljp/pid/10654425

RESEARCH ARTICLE

Composition and natural history of a snake community from the southern Cerrado, southeastern Brazil

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Abstract

The natural history of a cerrado snake community in a protected area in southeastern Brazil (Santa Bárbara Ecological Station; SBES) is described. A visual guide and an identification key are also provided to assist researchers and local people in identifying snakes in that region.

Sampling was performed through pitfall traps, time-constrained search, accidental encounters, and observations by local people for two years, which corresponded to 240 days of sampling. Among the 388 individuals found in the field, 33 snake species belonging to 21 genera of seven families were recorded. Most species were restricted or found at least once in non-forest vegetation types (campo sujo, campo cerrado, and cerrado sensu stricto) and a few were restricted to forest habitats (cerradão). Our results show that most species (1) occupy open areas; (2) present both diurnal and nocturnal activity; (3) are primarily terrestrial; (4) include lizards, mammals and/or anurans in the diet; (5) present seasonal reproductive activity; and (6) use mainly visually oriented defensive tactics. Despite its small size (3,154 ha), the SBES harbours preserved habitats and a rich and typical Cerrado snake fauna, including threatened species. Furthermore, most of the SBES snakes occur in non-forest environments (54%) and some species are sensitive to habitat disturbance.

Keywords

Introduction

The gathering of information related to natural history, what the organisms do in their respective environments, including the interactions between them (Greene 1994), contributes to the understanding of the functioning of ecosystems and, consequently, to many aspects of conservation, management, and even the appreciation of nature (Caughley 1994; Brooks and McLennan 2002; Dayton 2003). However, even though its relevance is obvious, there is still a large gap in knowledge about the ecology and behaviour of most extant taxa, even in the best-studied regions of the planet (Greene 2005). This type of information is available for only a small fraction of species, usually large or common, and relatively easily studied (Greene 1994).

Despite the high diversity of neotropical snakes (Cadle and Greene 1993; Martins and Oliveira 1998; Sawaya et al. 2008; Guedes et al. 2018; Nogueira et al. 2019), even the most basic information about their natural history is still scarce for most species (Sazima and Haddad 1992; Sawaya et al. 2008; Guedes et al. 2014). In addition, although the number of studies on snake communities from non-forest vegetation types like those of the Caatinga, Cerrado, and Pantanal has increased considerably in recent decades (e.g., Strüssmann and Sazima 1993; Sawaya et al. 2008; Rocha and Prudente 2010; Mesquita et al. 2013a; Guedes et al. 2014), much primary information about the herpetofauna of these areas is still lacking (Colli et al. 2002). In southeastern Brazil, the Cerrado have suffered an extensive loss during the 20th century, mainly due to agricultural and livestock practices. Currently, < 0.8% of the Cerrado original vegetation remains in the state of São Paulo (Kronka et al. 2005); therefore, studies should urgently be carried out in these remnant areas.

Several protected areas in the southern portion of the Cerrado include a mosaic of typical vegetation types of the biome (from grasslands to woodlands), which has contributed to maintaining a high species diversity of amphibians and reptiles within their limits (Sawaya et al. 2008; Araujo et al. 2010, 2013, 2014; Araujo and Almeida-Santos 2011). Thus, these protected areas may guarantee the persistence of populations of several species, contributing to the conservation of this rich fauna.

Herein we provide basic natural history information for a Cerrado snake community inhabiting a protected area, Santa Bárbara Ecological Station, in southeastern Brazil. The snake fauna of this area was previously studied by Araujo et al. (2010), who listed 21 species, 18 of which were found in the field and three from museum records for the Municipality of Águas de Santa Bárbara, where the reserve is located. Here we provide information for 33 species of snakes found during our study. For each species, we provide primary information on habitat and micro-habitat use, time of activity, feeding habits, reproduction, and defence. We also provide a short review of the natural history of each species based on our observations and on previously published accounts.

Materials and methods

This study was carried out at the Santa Bárbara Ecological Station (**SBES**), located in Águas de Santa Bárbara, State of São Paulo, Brazil (22°46' to 22°41'S and 49°16' to

49°10'W, elevation 600–680 m, Figure 1). SBES has a total area of 3,154 ha (Melo and Durigan 2011) and contains different Cerrado vegetation types, from open (such as campo sujo and campo cerrado) to forest (such as cerradão, a cerrado woodland, Figure 2), and some small areas with other types of forest vegetation (semi-deciduous seasonal forest, gallery forests, and pine and eucalyptus plantations), which were not the subject of this study.

It is estimated that the SBES harbours 4–9.5% of the total plant species present in the Cerrado (Meira-Neto et al. 2007). The climate is markedly seasonal, and the climate type is humid subtropical with a dry winter, type Cwa in the Köppen's classification (Peel et al. 2007). The mean temperature is 17 °C in the coldest months and 24 °C in the warmest months. Maximum temperature is 35.2 °C and minimum, 3.4 °C. Frosts occur sporadically in Autumn and Winter. The annual rainfall is 1,010 to 2,051 mm (mean 1,454.2 mm) and there are marked dry (April to September, monthly mean 70.2 mm) and wet (October to March, monthly mean 172.1 mm) seasons (data for 1995–2014 at Manduri, state of São Paulo, 20.3 km from SBES; Centro integrado de informações agrometeorológicas, 2015). Most soils in the region are classified as red latosol, but grasslands usually occur on quartzene neossol and wetfields on hydromorphic quartzene neossol; these neossols have high levels of sand and low fertility (Melo and Duringan 2011).

The samplings were performed periodically, for 10 days each month, from August 2016 to July 2018, for a total sample time of 240 days. Snakes were sampled with pitfall traps with drift fences (Greenberg et al. 1994; Cechin and Martins 2000), time-constrained searches (sensu Campbell and Christman 1982; Martins and Oliveira 1998), accidental encounters (Martins and Oliveira 1998), and assisted by the observations of local people (**OLP**; Martins and Nogueira 2012). Four main vegetation types were sampled with pitfall traps (**PT**) with drift fence: campo sujo, campo cerrado, cerrado sensu stricto, and cerradão (Figure 3). Our sampling design for pitfall traps included three sampling units per vegetation type, each sampling unit comprising two 40 m-long PT lines, located 60 m from each other, totalling 12 sampling units comprising a total of 24 lines and 96 buckets (Figure 4). Sampling units were located at least 400 m from each other. Each line had four 100 L plastic buckets connected by a 60 cm-high plastic fence, which was buried 10 cm below the soil surface and held upright by stakes. The buckets were perforated at the bottom to avoid accumulation of rainwater. A plastic plate (20 cm in diameter) and a piece of Styrofoam (20 × 20 cm) were placed in each bucket to provide moisture (plates were filled with water) and shelter for the captured animals. We also included individuals captured in four additional lines of PTs (16 buckets) located in two campo cerrado areas, which were part of a study on the effects of fire on the herpetofauna, results of which will be published elsewhere. Not all individuals recorded were collected.

Time-constrained searches (**TCS**; sensu Campbell and Christman 1982, Scott et al. 1989, Martins and Oliveira 1998) consisted of walking slowly in search of snakes in all visually accessible microenvironments. The sampling effort and the encounter rate were measured in person hours of visual search (Martins and Oliveira 1998). Sampling effort in TCS was not the same in all vegetation types. When performing TCS,
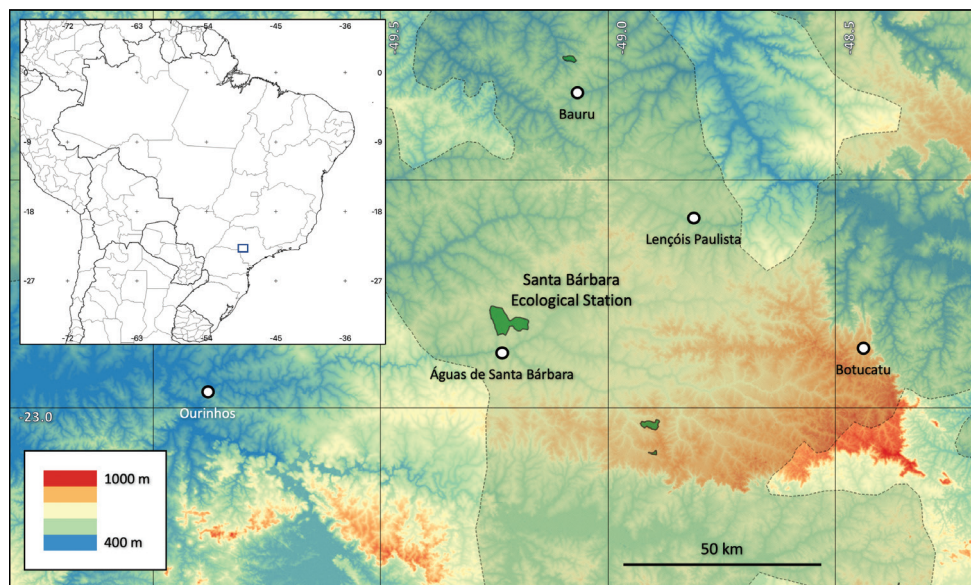
Figure 1. Topographic map of the region where the Santa Bárbara Ecological Station is located. Only the main cities of the region are shown. The Cerrado limits in this region are indicated by dashed lines. The green areas are strict conservation protected areas (PAs). Note that there are just four PAs in the Cerrado of this region.
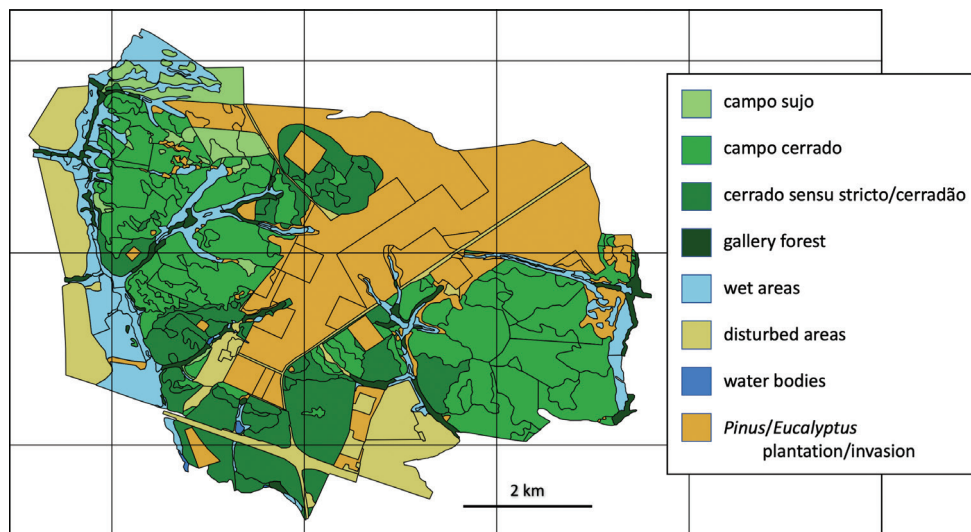

Figure 2. Land use types in the region of the Santa Bárbara Ecological Station.

we recorded the habitat (e.g., campo sujo, cerradão) and micro-habitats used by each snake (aquatic, arboreal, cryptozoic, fossorial, or terrestrial) and perch height (in case of arboreal species). To characterise micro-habitats, we used only information obtained during active searches; for individuals collected with PTs, only vegetation type (campo
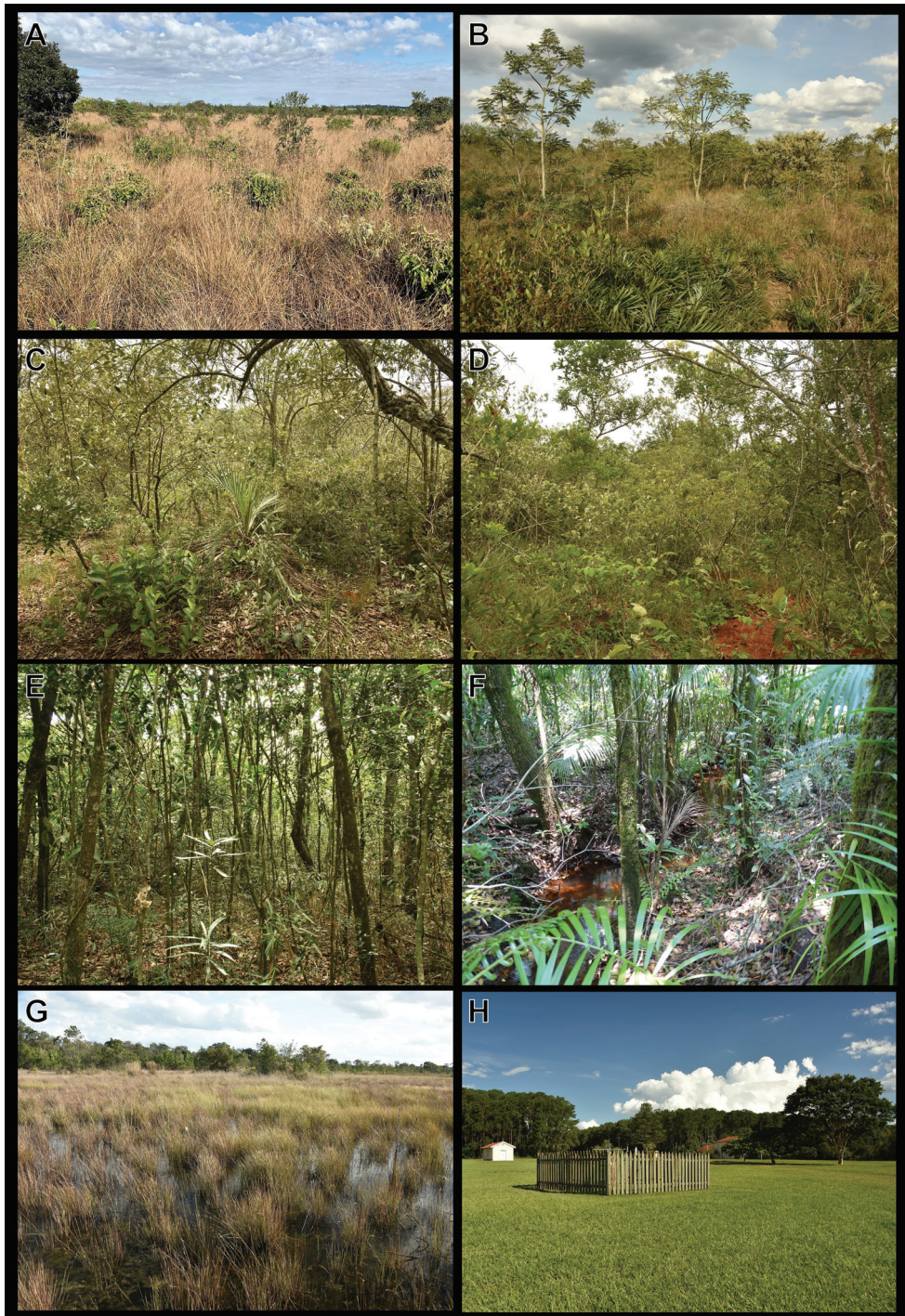
Figure 3. Natural vegetation types of Santa Bárbara Ecological Station **A** campo sujo (grassy scrubland) **B** campo cerrado (grassy scrubland with scattered trees) **C, D** cerrado sensu stricto (dense savanna) **E** cerradão (cerrado woodland) **F** gallery forest **G** wet field; and **H** disturbed area.
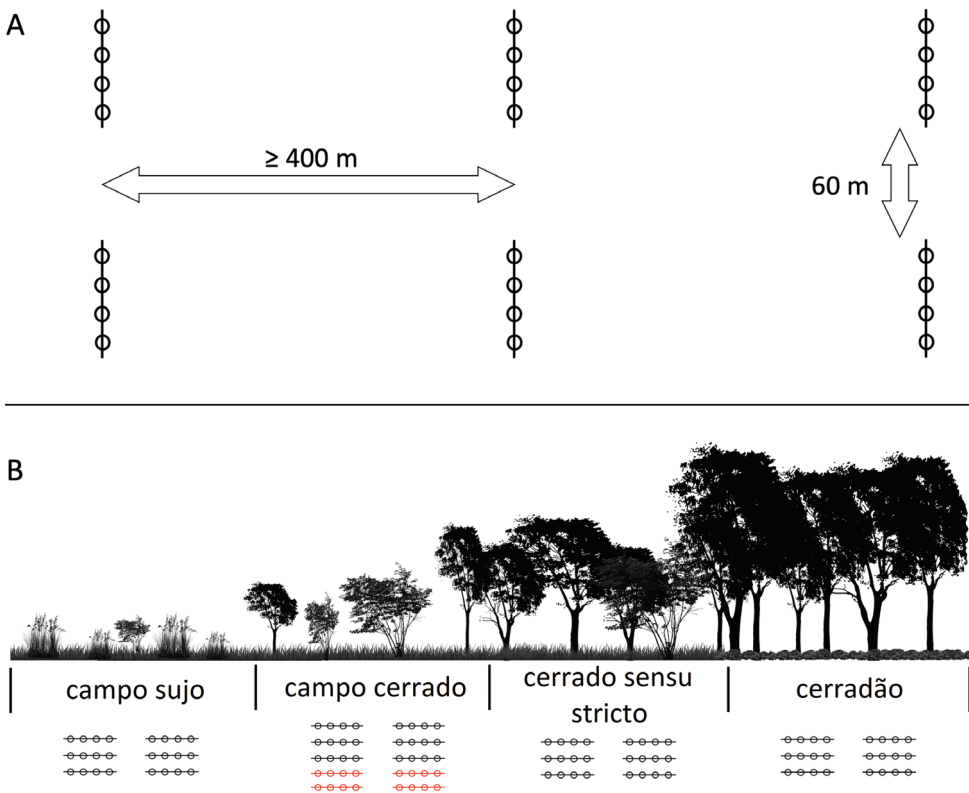
Figure 4. Schematic representation of the sampling design used in this study at the Santa Bárbara Ecological Station **A** representation of the distribution of three sampling units of pitfall traps (the sampling design in each vegetation type); each sampling unit was composed of two straight lines of drift fence (each of them 40 m long, 60 cm high), each line with four 100-L buckets 10 m apart from each other **B** representation of the sampling units used in each vegetation type; the red sampling units were fire treatments of a study on the effects of fire on the herpetofauna, results of which will be published elsewhere.

sujo, campo cerrado, cerrado sensu stricto, or cerradão) was recorded. Behavioural descriptions are based on observations made over short periods of time (ad libitum and sequence samplings; Altmann 1974). Defensive behaviours were recorded when individuals were observed in the field and when handled.

Accidental encounters (**AE**; Martins and Oliveira 1998), included all the specimens obtained by the researchers in activities other than the two-year regular sampling (August 2016–July 2018) with PTs and time-constrained searches. Accidental encounters occurred from June 2015 to December 2020 and were included in our database. OLP consisted of additional records made by people who live and/or work at the SBES, during their daily activities. When an animal was observed by these observers, they would photograph or warn researchers and we would go to the place to carry out the capture. At no time was the death of animals encouraged or requested (cf. Martins and Nogueira 2012).

The sampling efficiency of each method (AE, OLP, PT, and TCS) was evaluated through rarefaction curves of individuals with 5,000 randomisations (Sanders 1968; Gotelli and Colwell 2001), using number of individuals as a unit of sampling effort (Suppl. material 1). Dominance and Shannon diversity indices (H') were also calculated in order to simultaneously evaluate snake diversity captured by each method (Suppl. material 1). Additionally, richness estimates were made for each method, using the First Order Jackknife estimator, in order to estimate how many species could still be found with each method (Suppl. material 1). This method (Jackknife I) estimates the total richness using the number of species that occur in only one (unique) sample (Burham and Overton 1979). These analyses were performed using the program EstimateS v. 8.20 (Colwell et al. 2012).

To describe the diet of each species, collected specimens (see below) were dissected through an incision in the ventral region. Food items were identified to the lowest possible taxonomic rank using taxonomic keys, identification guides, specimens deposited in scientific collections, and help from experts. Whenever the prey came from a snake captured in a PT, this information was included, given the possibility of the snake having ingested prey that had also fallen in the trap (Cechin and Martins 2000) but which is not part of the snake's usual diet. To describe reproductive condition, we recorded the length of the largest ovarian follicle (**LOF**), the presence of egg or embryo, and the number of vitellogenic follicles (> 5 mm) per month of sampling.

The capture location of all animals sampled by the methods described above was georeferenced. In addition, all captured individuals were weighed and measured (snout-vent length; SVL). The average SVL (mean SVL) of each species was calculated based on adult individuals, which in turn were classified according to the SVL of the smallest reproductive female (containing ovarian follicles) or information from the literature. When adult individuals were not found, data from the literature were presented. New-born individuals were thus classified according to the presence of an evident umbilical scar. All captured individuals were released at the site of capture, except for voucher specimens. Owing to the importance of collecting voucher specimens for taxonomic identification and analysis of gastrointestinal and reproductive tracts to obtain useful natural history data, specimens and tissue samples were collected and preserved and these will later be deposited in the herpetological collections of the Museu de Zoologia da Universidade de São Paulo (**MZUSP**) and the Instituto Butantan (see Appendix 1). All collections were authorised by the Instituto Chico Mendes de Conservação da Biodiversidade (**ICMBio**; SISBIO permit #50658-1) and Comissão Técnico-Científica do Instituto Florestal (permit SMA #260108–011.518/2015). Specimens were euthanised by intracoelomic injection of lidocaine, fixed in 10% formaldehyde, and preserved in 70% ethanol (Foster 2012, AVMA 2020).

Besides the detailed natural history accounts for each species, we also provide a photographic guide (Figures 5–10) and an identification key to assist researchers and local people in identifying cerrado snakes from the SBES region.

Results

With a sampling effort of 240 days of fieldwork, corresponding to 23,040 bucket-days and including 1248 person-hours of time-constrained search, we found 388 individuals (146 collected specimens; see Suppl. material 1) of 33 species of snakes (21 genera, seven families) at the SBES (Figures 5–10).

General natural history patterns

Among all 33 species encountered using all described methods, approximately half of the species (18 species, 54%) used more often or were found exclusively in open (i.e., non-forest) vegetation types (campo sujo, campo cerrado or cerrado sensu stricto), while only *Boa constrictor*, *Bothrops moojeni*, *Erythrolamprus aesculapii*, *Erythrolamprus reginae*, *Phalotris mertensi*, and *Philodryas olfersi* were found most frequently (> 80% of the records for these species) in forest vegetation types (cerradão or gallery forests). Four species (*Apostolepis dimidiata*, *Crotalus durissus*, *Pseudoboa nigra*, and *Xenodon merremi*) were considered habitat generalists (based also in the literature data), using both open and forest vegetation types (Table 1). Half of the species showed both diurnal and nocturnal activity (Table 1). The most consumed prey (based on the number of species that consume the prey, even occasionally, according to this study and the literature) were: lizards (42.4% of species), followed by amphibians (39.4%) and mammals (36.4%) (Tables 1, 2). Virtually all species mainly use the terrestrial micro-habitat (Table 1).

As expected, the different lineages in the community showed some differences regarding their natural history. The snakes of the family Dipsadidae (most represented in the community) showed similar habits within tribes, where those belonging to the tribe Elapomorphini (*A. dimidiata*, *P. lativittatus*, and *P. mertensi*) used forests (although *P. lativittatus* uses primarily open areas), exhibit (at least in part) nocturnal activity (*A. dimidiata* and *P. lativittatus* are nocturnal species and although *P. mertensi* has been found thermoregulating during the day, this species probably is also primarily nocturnal) and consume elongated fossorial vertebrates (caecilians, amphisbaenians, and other snakes). Among the species of the tribe Pseudoboini (*O. guibei*, *O. rhombifer*, *P. nigra*, and *R. brazili*), except for *P. nigra*, all were found exclusively in open areas, active during the night and include primarily mammals and/or lizards in their diets (except for *R. brazili*, which is specialised in birds and their eggs). In the tribe Xenodontini, most species showed primarily daytime activity and preyed mostly on anurans, all of which are primarily terrestrial and/or cryptozoic.

The vipers of the genus *Bothrops* differed in terms of habitat use according to the respective clade within the genus (see Carrasco et al. 2011). The species of the *B. alternatus* group (*B. itapetiningae* and *B. alternatus*) strictly occupied the most open areas of the reserve (campo sujo and campo cerrado), the representative of the *B. neuwiedi* group (*B. pauloensis*) was also more frequent in open areas, although it was not as re-

Table 1. Natural history summary of snakes found at Santa Bárbara Ecological Station, based on both data from this study and literature data. ACTIVITY = daily activity (D = diurnal; N = nocturnal); DIET (AN = anuran; AM = amphisbaenian; BE = bird eggs; BI = birds; FI = fish; IN = invertebrate; LI = lizard; LE = lizard eggs; MA = mammal; MO = mollusc; SN = snake); HABITAT = habitats used in the study area (CC = campo cerrado; CS = campo sujo; CD = cerradão; DA = disturbed area; GF = gallery forest; SS = cerrado sensu stricto; WF = wet field); MICRO-HABITAT (AQ = aquatic; AR = arboreal; CR = cryptozoic; FO = fossorial; TE = terrestrial). Uppercase letters represent the main resources and habits used according to the present study and the literature, while lowercase letters denote those used only occasionally (< 20% of the records in this study and/or rarely documented in the literature). Letters in parentheses indicate data obtained only from the literature and which were not observed in the present study, while an asterisk indicates that the observation is exclusive to the present study. Predominantly fossorial habits were inferred mainly from data in the literature and snake morphology (small eyes, flat skull, fused head scales and relatively short tail; Greene 1997).

Taxon	Habitat	Micro-habitat	Activity	Diet
ANOMALEPIDIDAE				
Liotyphlops ternetzii	CC	(FO)	(N, D)	(IN)
LEPTOTYPHLOPIDAE				
Trilepida koppesi	CC, cd, CS, SS	(FO), TE	N, (d)	IN
BOIDAE				
Boa constrictor	CD, DA, gf	(AR), TE	D, (N)	BI, (li), MA
Epicrates crassus	CC, CS, CD	ar, TE	d, N	(BI), MA
COLUBRIDAE				
Chironius brazili	DA	(AR), TE	D	(AN)
Chironius quadricarinatus	SS	(AR), TE	D	(AN)
Tantilla melanocephala	CC, CS	(FO), TE	(D, N)	IN
DIPSADIDAE				
Apostolepis dimidiata	CC, CD, cs, ss	cr, (FO), TE	(N)	(AM), li*, (SN)
Atractus pantostictus	CC, CS, GF	(CR), (FO), TE	(D), N	IN, (li)
Dipsas mikanii	DA	TE	D, (N)	(MO)
Erythrolamprus aesculapii	CD, da	CR, TE	D	SN
Erythrolamprus almadensis	CS	(AQ), TE	(D)	(AN, FI)
Erythrolamprus poecilogyrus	CC, CS, DA, SS	TE	D, N	(AN)
Erythrolamprus reginae	CD	(AQ), TE	(D), (N)	AN, LI
Oxyrhopus guibei	CC, CS, da, ss, wf	TE	N	ma, LI
Oxyrhopus rhombifer	CS	TE	(N)	(MA, LI, sn)
Phalotris lativittatus	da, CC, cd, SS	(FO), TE	N	AM, SN
Phalotris mertensi	(CS), CD	(FO), te	D, (N)	(AM)
Philodryas olfersi	CD	(AR), TE	D	AN, MA
Philodryas patagoniensis	CS, (DA, SS)	TE	(D)	(AN, bi, LI, ma, sn)
Pseudoboa nigra	CS, GF	TE	N	(am), LI, (ma, sn)
Rhachidelus brazili	CS, CC, (da)	TE	N	(BE), bi
Taeniophallus occipitalis	CS, CC, SS	(CR), TE	D, N	(AN), LI
Thamnodynastes hypoconia	cs, WF	(AR), TE	N	(AN)
Xenodon merremi	CD, DA	cr, TE	D	(AN)
Xenodon nattereri	CS, CC	(FO), TE	(D)	(LI,sn), LE
ELAPIDAE				
Micrurus frontalis	CC	(FO), TE	(D, N)	(AM, LI, SN)
Micrurus lemniscatus	CC	(FO), TE	(D, N)	(AM, FI, SN)
VIPERIDAE				
Bothrops alternatus	CS, cc, da	TE	D, N	MA
Bothrops itapetiningae	CS, CC	TE	D, N	(an, bi, LI, MA)
Bothrops moojeni	cc, cd, da, GF, ss	(ar), TE	d, N	AN, MA
Bothrops pauloensis	CC, cd, cs, da	TE	d, N	an, (bi, LI, MA, sn)
Crotalus durissus	DA, cc, CD, cs, gf, ss	TE	D, N	(li), MA

Table 2. Occurrence (number of snakes which presented a given gut content) and total number of prey items consumed by snakes from Santa Bárbara Ecological Station, SP, Brazil. Asterisks indicate individuals captured in pitfall traps.

Taxon	Gut contents	Occurrence	Number of prey items
Leptotyphlopidae			
Trilepida koppesi	Isoptera	3*	12*
	insect eggs	1*	9*
	Formicidae pupae	3*	12*
Boidae			
Boa constrictor	feathers *Didelphis albiventris*	1	1
		1	1
	Guira guira	1	1
Epicrates crassus	mammal	1	1
Colubridae			
Tantilla melanocephala	Chilopoda	1; 3*	1; 3*
Dipsadidae			
Apostolepis dimidiata	Teiidae skin fragments	1*	1*
Atractus pantostictus	Oligochaeta	1; 1*	1; 1*
Erythrolamprus aesculapii	snake scale	1	1
Erythrolamprus reginae	lizard scale	1*	1*
	Physalaemus sp.	1*	1*
Oxyrhopus guibei	*Aspronema dorsivittatum*	4*	4*
	Teiidae scale	1*	1*
	Gymnophtalmidae skin fragments	1*	1*
	rodent	1	1
Phalotris lativittatus	Amphisbaenian fragments	1	1
	Trilepida koppesi scales	1*	1*
Philodryas olfersii	*Oligoryzomys nigripes*	1	1
	Scinax fuscovarius	1	1
Pseudoboa nigra	*Ameiva* sp. scales	1	1
Rhachidelus brazili	bird bones and feathers	1	1
Taeniophallus occipitalis	Teiidae fragments	1; 1*	1; 1*
Xenodon nattereri	lizard eggs	1	2
Viperidae			
Bothrops alternatus	*Clyomys laticeps*	1	1
Bothrops moojeni	*Leptodactylus* sp.	1	1
	rodent	1	1
Bothrops pauloensis	*Leptodactylus* sp.	1	1
Crotalus durissus	*Calomys tener*	1	1
	mammal	5	5

stricted to these habitats (it was found also in cerrado sensu stricto and in cerradão), whereas the representative of the *B. atrox* group (*B. moojeni*) was associated with forests (gallery forests) and wet fields. The rattlesnake, *C. durissus*, was found in all habitats.

We obtained 48 gut contents from 138 individuals (specimens dissected or live individuals that regurgitated or defecated prey remains; Table 2). Among the specimens examined, 22 females belonging to 18 species contained primary and secondary ovarian follicles. The largest number of females containing vitellogenic follicles (> 5 mm) occurred during the wet season (October–March; Table 3) and we had a higher number of records of new-borns during the dry season (April to September) (Table 3), with temporal overlapping of the different families (Anomalepididae, Leptotyphlopidae, Colubridae, Dipsadidae, and Viperidae) regarding the presence of ovarian follicles and new-borns.

Table 3. Temporal distribution of the number of ovarian follicles (F) and new-borns (NB) of different species found at Santa Bárbara Ecological Station between August 2016 and July 2018. Numbers in parentheses represent the length of the largest ovarian follicle (mm) and asterisks indicate a secondary or vitellogenic ovarian follicle (> 5 mm).

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	wet season			dry season						wet season		
Liotyphlops ternetzii							1NB					
Trilepida koppesi		19F(3.5)								15-48F(21.6)*		
Chironius brazili				21F(5.2)*								
Tantilla melanocephala								8F(3.8)	11F(6.5)*			
Apostolepis dimidiata			6F(5)	1NB								1F(24)*
Atractus pantostictus		7F(9.7)*	37F(9)*									
Dipsas mikanii							1NB					
Erythrolamprus aesculapii	5F(7.6)*											
Erythrolamprus almadensis							1NB					
Erythrolamprus reginae		6F(16.5)*										
Oxyrhopus guibei										7F(27.7)*		
Oxyrhopus rhombifer			1NB									
Phalotris lativittatus		1F(7.4)*										
Philodryas olfersii			22F(11)*									
Taeniophallus occipitalis		1NB		1NB					17F(8.7)*			
Xenodon merremii		26F(7.2)*										
Xenodon nattereri										8F(3.8)		
Bothrops alternatus								14F(13.7)*				
Bothrops itapetiningae											7F(3.9)	
Bothrops moojeni									1NB	28F(5.2)*		
Bothrops pauloensis	18F(4.5); 1NB	1NB				1NB		11F(6)*; 15F(3.6)				
Crotalus durissus					1NB	1NB		8F(4.3)				

Keys to families and species of snakes from Santa Bárbara Ecological Station, SP, Brazil

1	Ventral and dorsal scales of the same size... **Anomalepididae and Leptotyphlopidae**
–	Ventral and dorsal scales of distinct sizes **2**
2	Loreal pit present .... **Viperidae**
–	Loreal pit absent **3**
3	Proteroglyphous dentition..**Elapidae**
–	Other dentition types...**4**
4	Aglyphous dentition; cephalic scutes small, undifferentiated; > 30 dorsal scale rows ....**Boidae**
–	Solenoglyphous dentition; cephalic scutes large, with different forms; fewer than 30 dorsal scale rows..**Colubridae and Dipsadidae**

Species of the families Anomalepididae and Leptotyphlopidae

1	Ocular scale in contact with mouth...*Trilepida koppesi*
–	Ocular scale not in contact with mouth ....*Liotyphlops* **cf.** *ternetzii*

Species of the family Viperidae

1   Presence of a rattle or a button at the tip of the tail; some large plates on the dorsum of the head ....***Crotalus durissus***
–   No rattle or button at the tip of the tail; no large plates on the dorsum of the head **2**
2   Prelacunal scale fused with the second supralabial scale .... ***Bothrops moojeni***
–   Prelacunal scale not fused with the second supralabial scale...........................**3**
3   Postocular stripe inserted in the inferior region of the ocular orbit **4**
–   Postocular stripe not inserted in the inferior region of the ocular orbit ....
       ....***Bothrops pauloensis***
4   Colour pattern with trapezoidal dark marks; > 11 supralabial scales ....
       ....***Bothrops alternatus***
–   Colour pattern not as above; < 11 supralabial scales..........***Bothrops itapetiningae***

Species of the family Elapidae

1   Parietals completely black..***Micrurus frontalis***
–   Posterior portion of parietals red ....***Micrurus lemniscatus***

Species of the family Boidae

1   Supralabials in contact with eye ....***Epicrates crassus***
–   Suprelabials not in contact with eye .... ***Boa constrictor***

Species of the families Colubridae and Dipsadidae

1   Even number of dorsal scale rows..**2**
–   Odd number of dorsal scale rows **3**
2   Anterior third of the body blackish, with a yellowish vertebral stripe...***Chironius flavolineatus***
–   Anterior third of the body brown or light grey, without a vertebral stripe............
       .... ***Chironius quadricarinatus***
3   15 or fewer dorsal scale rows at midbody **4**
–   More than 15 dorsal scale rows at midbody...**11**
4   13 dorsal scale rows at midbody ....***Philodryas agassizii***
–   15 dorsal scale rows at midbody..**5**
5   A single prefrontal scale...**6**
–   A pair of prefrontal scales **7**
6   Presence of dark longitudinal stripes along the flanks; snout slightly pointed, with prominent rostral scute ....***Phalotris lativittatus***
–   No dark longitudinal stripes along the flanks; snout rounded, rostral scute not prominent...***Phalotris mertensi***

7   Internasal scutes absent ....***Apostolepis dimidiata***
–   Internasal scutes present **8**
8   Coral colour pattern of alternating black, yellow/white, and red bands ....
     ....***Erythrolamprus aesculapii***
–   Colour pattern not as above **9**
9   Black bands throughout the dorsum; dark oral and cloacal mucosae....***Dipsas mikanii***
–   Colour pattern not as above; light oral and cloacal mucosae............................**10**
10   Head brown to greyish, often with a pair of light ocelli on the parietal scutes; yellow venter; < 175 ventral scales ....***Taeniophallus* gr. *occipitalis***
–   Head black, without a pair of light ocelli on the parietal scutes; cream to whitish venter; > 175 ventral scales..***Tantilla melanocephala***
11   More than 19 dorsal scales at midbody ....***Rhachidelus brazili***
–   19 or fewer dorsal scales at midbody **12**
12   17 dorsal scales at midbody...**13**
–   19 dorsal scales at midbody...**14**
13   Venter yellow with black marks; dorsal scales with reduction in number towards cloaca (17/17/15).. ***Erythrolamprus reginae***
–   Venter uniformly cream; dorsal scales without reduction in number (17/17/17) . ...***Atractus pantostictus***
14   Anal plate entire...**15**
–   Anal plate divided **17**
15   Dorsum and flanks black with or without white areas; juveniles with a white band on the dorsum of the head and a nuchal black and dorsum rose-red; subcaudals entire ....***Pseudoboa nigra***
–   Coral colour pattern (alternated black, yellow/white, and red bands); subcaudals divided...**16**
16   Coral colour pattern in trios...***Oxyrhopus guibei***
–   Coral colour pattern not in trios ....***Oxyrhopus rhombifer***
17   Dorsal scale rows in 19/19/15 ....**18**
–   Dorsal scale rows in 19/19/17 ....**21**
18   Keeled dorsal scales ....***Thamnodynastes hypoconia***
–   Smooth dorsal scales **19**
19   Green dorsum, brown head and vertebral stripe...................***Philodryas olfersii***
–   Colour pattern not as above **20**
20   7 supralabials, third and fourth in contact with the ocular orbit.......................... ....***Philodryas patagoniensis***
–   8 supralabials, fourth and fifth in contact with the ocular orbit.......................... ....***Erythrolamprus poecilogyrus***
21   Snout pointed, with rostral scute upturned and keeled ....***Xenodon nattereri***
–   Snout round, without rostral scute upturned and keeled **22**
22   Venter orange-red from the 2/3 of the body onward; 8 supralabials, fourth and fifth in contact with the ocular orbit ....***Erythrolamprus almadensis***
–   Venter cream; 7 supralabials, third and fourth in contact with the ocular orbit ... .***Xenodon merremii***

Natural history accounts

Anomalepididae Taylor, 1939
Liotyphlops ternetzii **(Boulenger, 1896)**
Figure 5A

It is a small aglyphous species (mean SVL = 239 mm; range 93–319 mm; N = 30; França et al. 2008). It was found only in campo cerrado (N = 3), always after heavy rains. As all individuals were captured in PT, information on micro-habitat use or daily activity was not obtained. The available information indicates that the species is fossorial and both diurnal and nocturnal (França and Araújo 2006; Marques et al. 2015) and that it feeds on ants and termites (França and Araújo 2006). The largest individuals (SVL = 189 and 211 mm, respectively) were captured in January and February, respectively, and the third individual, a newborn, in June. It can lay two to seven eggs during the wet season (November–December: Achaval and Olmos 1997). A new-born was found (CRC = 90 mm) in the dry season (June) in this study. When handled, it pressed the sharp tip of the tail against the captor's hand, a behaviour also observed by Marques et al. (2015).

Leptotyphlopidae Stejneger, 1892
Trilepida koppesi **(Amaral, 1955)**
Figure 5B

It is a small aglyphous species (mean SVL = 245 mm; range 198–323 mm; mature males, SVL ≥ 198 mm, and mature females, SVL ≥ 225 mm; N = 83). This species was found more frequently in open areas, such as campo sujo (N = 51) and campo cerrado (N = 62), but also in cerrado sensu stricto (N = 21) and in cerradáo (N = 1). Almost all observations through TCS (only one through AE) of active individuals (moving) were made at night, between 07:00 and 09:00 PM (N = 14). Among eight individuals examined, four had stomach contents, three ingested termites (MRCM 290, 355, 383) and pupae of ants (MRCM 290, 328, 383) and one, insect eggs (MRCM 290). It is known to be fossorial and both diurnal and nocturnal (França and Araújo 2006; Sawaya et al. 2008) and feeds exclusively on invertebrates such as larvae and pupae of ants and occasionally adult ants, termite larvae and beetles (França and Araújo 2006, Sawaya et al. 2008). Virtually all captured individuals were found during the wet season (October to March), with the largest number of individuals being observed in October 2016 (N = 36) and the smallest in April 2017 (N = 1). Most females with ovarian follicles (LOF = 21.6 mm; MRCM 290, 292, 312, 318, 355, 381, 382, 383) were also found in October and a single female with follicles was found in February (LOF = 3.5 mm; MRCM 457). The available information indicates that it is oviparous and has relatively low fertility (5–7 eggs), with egg laying probably occurring in the middle of the wet season, starting in December (Sawaya et al. 2008). When handled, it

can press the sharp tip of the tail against the captor's hand (N = 11; MRCM 290, 308, 309, 323), as already described in the literature (Marques et al. 2015), it also produces cloacal discharge (N = 27; MRCM 290, 309, 314, 323) or bite (N = 1) (Table 4). It can also twist its body when handled (Sawaya et al. 2008).

Boidae Gray, 1825
***Boa constrictor* Linnaeus, 1758**
Figure 5C

It is a large aglyphous species (mean SVL = 1,122 mm; range 935–1,332 mm; N = 6; this study). Four individuals were found on the edge of forests or in forest areas (two occasionally on the edge of cerradão, one OLP on the edge of gallery forests, and the other OLP on a *Eucalyptus* plantation with surrounding forest) and five were captured in a disturbed area close to the SBES headquarters, also OLP. All individuals were moving on the ground during the day (between 07:00 AM and 04:00 PM). The available information indicates that the species is semi-arboreal and both diurnal and nocturnal (Martins and Oliveira 1998; Bernarde and Abe 2006; França and Araújo 2006). One adult male defecated bird feathers and another adult male (MRCM 386) regurgitated a freshly ingested marsupial (*Didelphis albiventris*). A third individual (not sexed) was observed preying on a Guira Cuckoo (*Guira guira*) on the ground, in a disturbed area near to the SBES headquarters at ca. 03:00 PM. The available information indicates that the species feeds mainly on mammals and birds and occasionally lizards (Martins and Oliveira 1998; Bernarde and Abe 2006; Marques et al. 2015). The species was observed throughout the year, but mostly during the wet season (five individuals between October and March). It has a seasonal reproductive cycle, with vitellogenesis in the summer (January–February) and it reaches sexual maturity with at least 1300 mm SVL in females and 1100 mm in males (Pizzatto and Marques 2007). Pregnancy lasts 4–6 months (Pizzatto and Marques 2007) and it can reproduce asexually by parthenogenesis (Bertona and Chiaraviglio 2003; Booth et al. 2011). When handled, it can bite (N = 2; MRCM 386), strike (N = 1), or open its mouth wide (N = 1) (Table 4), as already described in the literature (Sawaya et al. 2008; Marques et al. 2015).

***Epicrates crassus* Cope, 1862**
Figure 5D

It is a large aglyphous species (mean SVL = 893 mm; range 704–1000.5 mm; N = 4; this study). One individual was found in the campo sujo (AE), three in the campo cerrado (AE = 2, TCS = 1; MRCM 395) and one in the edge of a forest (TCS; MRCM 359). Three of them were moving during the night and one during the day. An individual was found perched on the drift fence of one of the PTs (MRCM 395). One of the specimens examined contained hair in its stomach (MRCM 359). The available

Figure 5. A *Liotyphlops ternetzii* **B** *Trilepida koppesi* **C** *Boa constrictor* **D** *Epicrates crassus* **E** *Chironius brazili* **F** *C. quadricarinatus.*

information indicates that the species is both diurnal and nocturnal, has terrestrial habits, and feeds mainly on birds and mammals (Sawaya et al. 2008; Cassimiro et al. 2010; Marques et al. 2015). All individuals were observed during the wet season, from November to March. It presents a seasonal reproductive cycle, producing 8–22 hatchlings per litter, and reaches sexual maturity with at least 970 mm SVL in females and 870 mm in males (Pizzatto and Marques 2007). When handled, it can strike, hide its head, perform tail display, or produce cloacal discharge (Sawaya et al. 2008; Marques et al. 2015; Table 4).

Table 4. Defensive tactics of snakes from the Santa Bárbara Ecological Station, SP, Brazil. BI = bite; CB = compress body while raising head; CD = cloacal discharge; DF death feigning; EM = perform erratic movements; FB = flatten body; FBL = flatten body laterally; HH = hide head; OM = open mouth; PT = press the sharp tip of the tail against the captor's hand; ST = strike; TB = twist the body; TD = tail display; TH = triangulate head; SC = S-coil; VT = vibrate tail. The numbers indicate field observations, and an "X" indicates data from the literature (Martins et al. 2008; Sawaya et al. 2008; Marques et al. 2015; Fiorillo et al. 2020a).

Species	BI	CB	CD	DF	EM	FB	FBL	HH	OM	PT	ST	TB	TD	TH	SC	VT
Liotyphlops ternetzii										X						
Trilepida koppesi	1		27							11		X				
Boa constrictor	2						1				1					
Epicrates crassus			X					X			X		X			
Chironius brazili	1						1								1	
Chironius quadricarinatus	1		X			X					1				1	
Tantilla melanocephalla			X									X				
Apostolepis dimidiata								X		1						
Atractus pantostictus			X		X					1						
Dipsas mikanii		X	X		1			X					1			
Erythrolamprus aesculapii	2	X	1		1	3		X					3			
Erythrolamprus almadensis			X													
Erythrolamprus poecilogyrus			1		X							X				
Erythrolamprus reginae			2		1	2										
Oxyrhopus guibei			1		3			X				X	1			
Oxyrhopus rhombifer			X		X	X		X				X				
Phalotris lativittatus					X				X							
Phalotris mertensi					1			X	X							
Philodryas olfersii			X					X			X				X	
Philodryas patagoniensis	X		X		X							X	X			
Pseudoboa nigra			1		X		1									
Rhachidelus brazili			1		1	1								1		
Taeniophallus occipitalis			X	X	X						1					
Thamnodynastes hypoconia	2		X		X			X			X	X		X		
Xenodon merremii		1				2	1	1			2		X	1		
Xenodon nattereri						X	X						X			
Micrurus frontalis					1	X		1					1			
Micrurus lemniscatus					1	X		1					1		1	
Bothrops alternatus						2	2				3					2
Bothrops itapetiningae			X		1		X	X			1					2
Bothrops moojeni	1		X		X		1	X			3					4
Bothrops pauloensis					1		1				16	1				12
Crotalus durissus			2		X						5					6

Colubridae (Ooppel, 1811)
Chironius brazili Hamdan & Fernandes, 2015
Figure 5E

It is a large aglyphous species (mean SVL = 893 mm; range 256–995 mm; N = 37; Hamdan and Fernandes 2015). The only individual found was observed by OLP (MRCM 482), in a disturbed area (open flooded area adjacent to a pine forest), at ca. 03:00 PM. The species occupies areas in the southern portion of the Cerrado in contact with the Atlantic Forest (Nogueira et al. 2019) and, apparently, forest habitats such as gallery forests (Hamdan and Fernandes 2015). The individual found was a fe-

male observed in April (late wet season) and had 21 ovarian follicles (LOF = 5.2 mm). When handled, the species can open the mouth wide (showing the oral mucosa), bite or raise its head, and form an S-coil with the anterior part of its body (N = 1) (Table 4).

Chironius quadricarinatus (Boie, 1827)
Figure 5F

Large aglyphous species (mean SVL = 633; range 504–808 mm; N = 108; Pinto et al. 2010). The single individual found AE (MRCM 1275), in cerrado sensu stricto, moving on the ground at 11:00 AM. The available information indicates that it is semi-arboreal and diurnal (Dixon et al. 1993, França and Araújo 2006), can occur in disturbed areas (Carvalho and Nogueira 1998) and feeds mainly on frogs (Dixon et al. 1993; França and Araújo 2006; Pinto et al. 2008). The individual found was a juvenile (SVL = 250 mm) and was sampled in April (onset of dry season). This species has a continuous reproductive cycle and fecundity varies from three to nine eggs (Dixon et al. 1993; Pinto 2006). It reaches sexual maturity with at least 514 mm SVL in females and 504 mm in males (Pinto et al. 2010). When handled, it can bite, strike, or form an S-coil with the anterior part of its body (N = 1) (Table 4). The available information indicates that it can also flatten the body laterally and produce cloacal discharge (Marques et al. 2015; Table 4).

Tantilla melanocephala (Linnaeus, 1758)
Figure 6A

It is a small opisthoglyphous species (range 181–296 mm; N = 146; Santos-Costa et al. 2006). In the SBES, it was observed only in open areas, campo sujo (AE = 1, PT = 5; MRCM 274, 291, 461, 514, 544) and campo cerrado (AE = 2, PT = 2; MRCM 345, 1298), all captured through PT. One individual was found at night under a fallen log in a wet area (AE). The available information indicates that the species is fossorial, cryptozoic, and both diurnal and nocturnal (Martins and Oliveira 1998; Martins et al. 2008; Marques et al. 2015). Among four individuals examined, all had remains of centipedes in the gut (MRCM 274, 461, 544, 1298). It is specialised in feeding on centipedes (Cunha and Nascimento 1978; Marques and Puorto 1998; Marques et al. 2015). Among the collected females, two (MRCM 274, 1298) had ovarian follicles (11 follicles and LOF = 6.5 mm, and eight follicles and LOF = 3.8 mm respectively), during the dry season (August and September). According to the literature, their different populations may present a seasonal or continuous reproduction (Marques and Puorto 1998; Santos-Costa et al. 2006). Its fecundity varies from one to three eggs (Fitch 1970; Dixon and Soini 1986; Sawaya et al. 2008); in the Amazon rain forest, males reach sexual maturity with at least 181 mm SVL and females with 189 mm (Santos-Costa et al. 2006). When handled, it can twist the body and produce cloacal discharge (Sawaya et al. 2008; Marques et al. 2015; Table 4).

Dipsadidae Bonaparte 1838
Apostolepis dimidiata (Jan, 1862)
Figure 6B

It is a medium-sized opisthoglyphous species (mean SVL = 387.8 mm; range 196–634 mm; N = 46; Sawaya et al. 2008). It was found in all vegetation types: three in campo sujo (MRCM 545, 1702), six in campo cerrado (MRCM 512, 524, 1256, 1802), one in a cerrado sensu stricto and five in a cerradão (MRCM 387, 463, 483, 541). One of the individuals was AE buried under the leaf litter during the day (MRCM 387). Sawaya et al. (2008) also found individuals mostly in open areas, although also in disturbed areas outside Itirapina Ecological Station. The available information indicates that it is predominantly nocturnal and has fossorial habits (Sawaya et al. 2008; Marques et al. 2015). Among six specimens examined, only one had stomach contents (skin fragments from a lizard of the family Teiidae; this study; MRCM 545). It feeds on amphisbaenians (Sawaya et al. 2008) and possibly on other elongate vertebrates (Marques et al. 2009). At the SBES, most individuals were observed during the wet season or late in the dry season (late September); a new-born was found in April. Among the females examined, one (collected in March) had six ovarian follicles (LOF = 5 mm; MRCM 1296) and the other (collected in December) had a follicle that was probably about to enter its uterus (24 mm; MRCM 387). When handled, the species pressed the sharp tip of the tail against the captor's hand (N = 1; MRCM 463) as already described in the literature (Marques et al. 2015; Table 4). The available information indicates that it can also hide its head (Sawaya et al. 2008).

Atractus pantostictus Fernandes & Puorto, 1993
Figure 6C

It is a small aglyphous species (mean SVL = 269 mm; range 122–420 mm; N = 10; França et al. 2008). Most of the individuals were observed in the most open areas of the SBES, in campo sujo (PT = 2; MRCM 352, 427) and campo cerrado (PT = 2; MRCM 389, 1100). However, an individual was observed (during TCS) moving among the grass at the edge of a gallery forest (MRCM 11). Only the latter individual was observed when active, during the night (07:30 PM). The available information indicates that the species is both diurnal and nocturnal (Martins et al. 2008), cryptozoic (França and Araújo 2006), and fossorial (Rocha-Barbosa and Moraes-e-Silva 2009). Among the four individuals examined, two had earthworm setae in their hindgut (MRCM 11, 427). The species is known to eat worms (Sawaya et al. 2008; Marques et al. 2009; Marques et al. 2015) and there is a record for lizard, with scales found in the hindgut (Sawaya et al. 2008). França and Araújo (2006) suggested that it is a habitat and diet specialist; however, it was found in urban areas by São Pedro and Pires (2009). All individuals were observed during the wet season, between December and March. Among the females examined, two had ovarian follicles, the first (MRCM 427)

Figure 6. A *Tantilla melanocephala* **B** *Apostolepis dimidiata* **C** *Atractus pantostictus* **D** *Dipsas mikanii* **E** *Erythrolamprus aesculapii* **F** *E. almadensis*.

having seven (LOF = 9.7 mm) in February and the second (MRCM 11), 37 (LOF = 9 mm) in March. The female reproductive cycle is seasonal (vitellogenesis between September and April and egg laying between November and April) and fecundity can vary from two to four eggs (Resende and Nascimento 2015). According to Sawaya et al. (2008), the species is more active on the surface during the wet season, mainly between October and February (mainly October). It reaches sexual maturity with at least 247 mm SVL in females and 187 mm in males (Resende and Nascimento 2015). When handled, it can press the sharp tip of the tail against the captor's hand (N = 1). The available information indicates that it can perform erratic movements or produce cloacal discharge (Marques et al. 2015; Table 4).

Dipsas mikanii Schlegel, 1837
Figure 6D

It is a medium-sized aglyphous species (mean SVL = 270 mm; range 122–465 mm; N = 36; França et al. 2008). Only two individuals were found (OLP), one of them moving during the day on turf in disturbed areas (MRCM 1288 near the SBES headquarters, and the other, MRCM 475, in a vegetable garden next to a residence). The available information indicates that it is terrestrial and primarily nocturnal (Sazima and Manzini 1995; França and Araújo 2006; Sawaya et al. 2008) and that it can be found in forest and disturbed areas (Sawaya et al. 2008). It feeds on gastropods, which, probably due to the low caloric value, are ingested in large numbers in a short period of time (Sazima and Manzini 1995; França and Araújo 2006; Barbo et al. 2011). One of the individuals (MRCM 1288) observed (in June, dry season) was a new-born. The species has a seasonal reproductive cycle (during the hottest and wettest months of the year) and clutch size varies from three to ten eggs (Pizzatto et al. 2008). There are reports of communal nests for this species (Albuquerque and Ferrarezzi 2004; Braz et al. 2008). When handled, it can compress the body while raising the head (MRCM 1288; see Fiorillo et al. 2019), triangulate the head, and perform erratic movements (MRCM 1288). It can also hide its head or produce cloacal discharge (Marques et al. 2015).

Erythrolamprus aesculapii (Linnaeus, 1758)
Figure 6E

It is a medium-sized opisthoglyphous species (mean SVL = 598 mm; range 580–615 mm; N = 3; this study). Most individuals (AE = 1, OLP = 1) were observed close to forest areas (MRCM 361 and a specimen not collected in cerradão and MRCM 252 in a transition area between a pine forest and cerradão); the fourth individual (MRCM 424) was captured (OLP) in a disturbed area near the SBES headquarters. Two individuals were observed moving during the day (between 09:00 AM and 09:30 AM; MRCM 252 and MRCM 361). The available information indicates that the species is terrestrial, cryptozoic, and diurnal (Bernarde and Abe 2006; França and Araújo 2006; Martins et al. 2008). Two specimens examined had contents in their digestive tracts: one contained hair (MRCM 424; probably secondary ingestion) in the hindgut and the other (MRCM 361), snake scales. This species feeds mainly on other snakes (Martins and Oliveira 1998; Bernarde and Abe 2006; Marques et al. 2015, Fiorillo et al. 2020a). The individuals observed were captured in both the dry and wet seasons (during the months of January, May, July, and December). One female collected in January (MRCM 424) had five ovarian follicles (LOF = 7.6 mm). The available information indicates that its fecundity varies from three to eight eggs and it has a continuous reproductive cycle, with vitellogenesis throughout the entire year; however, ovarian follicles (including eggs) are larger during the wet season (October–April; Marques 1996; Marques and Sazima 2004). It reaches sexual maturity with at least 635 mm SVL in females and 430 mm in males (Marques 1996). When handled, it can flatten its body (N = 2; MRCM 361, 424), raise the curled tail as in *Micrurus frontalis* (N = 3;

MRCM 252, 361, 424), bite (N = 2; MRCM 252, 361), produce cloacal discharge (N = 1; MRCM 252) or erratic movements (N = 1; MRCM 361) (Table 4). Furthermore, besides being a supposed mimic of elapids (e.g., *Micrurus frontalis*), this species can also hide its head (Martins et al. 2008; Marques et al. 2015) and compress its body while raising its head (Greene 1979). An envenomation by this species at the SBES (MRCM 361) was described by Menegucci et al. (2019).

Erythrolamprus almadensis **(Wagler, 1824)**
Figure 6F

It is a small aglyphous species (it can reach just longer than 500 mm SVL; Dixon 1991). The only individual observed (MRCM 1289) was captured by PT, in a campo sujo area. In addition to open habitats, it can also occur in forests and even disturbed areas (Strüssmann and Sazima 1993; Carvalho and Nogueira 1998; Bernarde and Abe 2006). It is semi-aquatic and diurnal (Bernarde and Abe 2006; França and Araújo 2006; Marques et al. 2015), and feeds primarily on amphibians (Bernarde and Abe 2010; França and Araújo 2006; Marques et al. 2015). The individual found was a newborn (SVL = 185 mm) and was captured in July (dry season). Its fecundity varies from four to ten eggs (Achaval and Olmos 1997). When handled, it can produce cloacal discharge (Marques et al. 2015; Table 4).

Erythrolamprus poecilogyrus **(Wied-Neuwied, 1825)**
Figure 7A

It is a small aglyphous species (mean SVL = 359 mm; range 275–429 mm; N = 3; this study). Three individuals were observed in open areas (campo cerrado, cerrado sensu stricto, and one in a disturbed area at the SBES headquarters; MRCM 369, 1277, and 241, respectively). One (MRCM 241) was accidentally found moving during the day (04:00 PM) and another (MRCM 369) during TCS at night (08:05 PM). The other was captured though AE. The available information indicates that the species is terrestrial and both diurnal and nocturnal (this study; França and Araújo 2006; Martins et al. 2008; Marques et al. 2015). A study carried out on the north coast of Rio Grande do Sul revealed that the species shows a bimodal activity pattern throughout most of the year (early morning and late afternoon), except in the coldest months when it is active in the hottest periods of the day (Maciel et al. 2003). The available information indicates that it feeds mainly on amphibians (Pinto and Fernandes 2004; França and Araújo 2006; Marques et al. 2015). All individuals observed in this study were captured during the wet season, between October and April. It has a continuous reproductive cycle (Maciel et al. 2003) and fecundity varies from three to 15 eggs, with births in January and February (Achaval and Olmos 1997; Pinto and Fernandes 2004; Sawaya et al. 2008). In Argentina, males reach sexual maturity with at least 211 mm SVL and females with 250 mm (Prieto et al. 2012). When handled, it can produce cloacal discharge (N = 1; MRCM 241) and can also flatten or twist its body (Martins et al. 2008; Sawaya et al. 2008; Marques et al. 2015) (Table 4).

Erythrolamprus reginae (Linnaeus, 1758)
Figure 7B

It is a medium-sized aglyphous species (mean SVL = 417 mm; range 190–597 mm; N = 19; França et al. 2008). All individuals (N = 4) were observed in the cerradão and captured by PT. As all individuals were captured in PTs, information on micro-habitat use or daily activity was not obtained. Among four specimens examined, only one (MRCM 368) had gastrointestinal contents, one anuran (*Physalaemus* sp.) in the stomach and lizard scales in the hindgut. The available information indicates that it is terrestrial and both diurnal and nocturnal (Martins and Oliveira 1998; Bernarde and Abe 2006; França and Araújo 2006) and feeds primarily on frogs, but occasionally lizards and invertebrates (Martins and Oliveira 1998; Bernarde and Abe 2006; França and Araújo 2006; Albarelli et al. 2010). The four individuals sampled were captured between September (late dry season) and March (wet season). A female collected in February (MRCM 434) had six ovarian follicles (LOF = 16.5 mm). The available information indicates that the species has a fecundity varying from three to six eggs (Duellman 1978). Martins and Oliveira (1998) suggested that births occur through-out the year in the Amazon. When handled, it can produce cloacal discharge (N = 2; MRCM 434, 1265), flatten the body (N = 2; MRCM 508, 1265), or perform erratic movements as previously described for the species (Marques et al. 2015) (Table 4).

Oxyrhopus guibei Hoge & Romano, 1978
Figure 7C

It is a medium-sized opisthoglyphous species (mean SVL = 551 mm; range 415–835 mm; N = 4; this study). The individuals were found in campo cerrado (AE = 4, PT = 3, TCS = 1; MRCM 326, 431, 1388), campo sujo (PT = 4; MRCM 325, 466, 1000, 1183), cerrado sensu stricto (PT = 2; MRCM 344, 1276), in a wet field near a campo cerrado area (AE = 1; MRCM 1216) and in disturbed areas, close to an area of cerradão (OLP = 1; MRCM 217). Three individuals were moving on the ground at night (between 07:00 PM and 08:00 PM; MRCM 326, 1216, and other individual). The available information indicates that it is terrestrial and nocturnal (França and Araújo 2006; Sawaya et al. 2008). One individual regurgitated a rodent (MRCM 217) and two (an adult and a juvenile; MRCM 1000 and 1183, respectively) caught in PT regurgitated lizards of the species *Aspronema dorsivittatum*. Among the eight other specimens examined, four (MRCM 325, 431, 466, 1183) had ingested lizards. The available information indicates that it feeds on lizards and mammals (Sazima and Haddad 1992; França and Araújo 2006; Marques et al. 2015). All observed individuals were captured between August (dry season) and April (late wet season). One female collected in October (MRCM 326) had seven ovarian follicles (LOF = 27.7 mm). This species presents a continuous reproductive cycle, with recruitment mainly in the late wet season and early dry season; males reach sexual maturity with at least 388 mm SVL and females with 632 mm (Pizzatto and Marques 2002). When handled, it can perform erratic movements (N = 3; MRCM 1000), produce cloacal discharge (N = 1),

Figure 7. A *Erythrolamprus poecilogyrus* **B** *E. reginae* **C** *Oxyrhophus guibei* **D** *O. rhombifer* **E** *Phalotris lativittatus* **F** *P. mertensi.*

and raise a curled tail as in *Micrurus frontalis* (N = 1; MRCM 1000). The available information indicates that it can also hide its head or twist the body (Sawaya et al. 2008; Marques et al. 2015) (Table 4).

Oxyrhopus rhombifer Duméril, Bibron & Duméril, 1854
Figure 7D

It is a medium-sized opisthoglyphous species (mean SVL = 447 mm; Cunha and Nascimento 1983; Gaiarsa et al. 2013), and can reach 958 mm SVL (Giraudo 2001). Only a juvenile was observed in this study, in the campo sujo (captured through PT). It is

terrestrial and nocturnal (França and Araújo 2006; Sawaya et al. 2008). The available information indicates that it feeds mainly on lizards and mammals, but occasionally on snakes (França and Araújo 2006; Gaiarsa et al. 2013). The only individual sampled was captured in March (wet season) and was a new-born. According to the literature, its fecundity varies from four to 17 eggs (Pontes and Di-Bernardo 1988; Yanosky et al. 1996; Gallardo and Scrocchi 2006; Sawaya et al. 2008; Gaiarsa et al. 2013) and it reaches sexual maturity with at least 452 mm SVL in males (Gaiarsa et al. 2013) and 442 mm in females (Cunha and Nascimento 1983). When handled, it can flatten or twist its body, hide its head, perform erratic movements, or produce cloacal discharge (Marques et al. 2015) (Table 4).

Phalotris lativittatus **Ferrarezzi, 1993**
Figure 7E

A medium-sized opisthoglyphous species (mean SVL = 758 mm; range 518–1,222 mm; N = 3; this study) found in campo cerrado (AE = 1, PT = 6; MRCM 317, 315, 406, 518, 535), cerrado sensu stricto (PT = 3; MRCM 322, 316, 1222), edge of cerradão (TCS = 1; MRCM 370), and in a disturbed area near to the SBES headquarters (OLP = 1; MRCM 200). One of the individuals was observed moving at night (MRCM 370). The available information indicates that it is fossorial and nocturnal (Sawaya et al. 2008; Marques et al. 2015). One specimen (MRCM 200) contained fragments of an amphisbaenian in the hindgut and in another, scales of the snake *T. koppesi* also in the hindgut (MRCM 406). It feeds on elongated vertebrates like amphisbaenians and snakes (this study; Braz et al. 2014; Marques et al. 2015). All individuals from this study were found during the wet season, between October and February. A female (MRCM 1222) collected in February had an ovarian follicle (7.4 mm). According to the literature, it can be found active in the wet season, from October to February, when females may be reproductive (Sawaya et al. 2008; Braz et al. 2014). It reaches sexual maturity with at least 507 mm SVL in females and 409 mm in males (Braz et al. 2014). When handled, it can press the sharp tip of the tail against the captor's hand or perform erratic movements (Marques et al. 2015) (Table 4).

Phalotris mertensi **(Hoge, 1955)**
Figure 7F

It is a large opisthoglyphous species (mean SVL = 802 mm; range 304–1262 mm; N = 50; Sawaya et al. 2008). Only a juvenile (MRCM 1296) was accidentally encountered (AE) in a cerradão area, while apparently thermoregulating in a sunspot during the day (01:00 PM). It can also use open habitats such as campo sujo and disturbed areas (Sawaya et al. 2008; Araujo et al. 2010). The available information indicates that it is fossorial and can present both diurnal and nocturnal activity (Sawaya et al. 2008). It is probably specialised in feeding on amphisbaenians and other elongated vertebrates with fossorial habits, like other elapomorphines (cf. Savitzky 1979). The only individual from this study was found in July (dry season). Its reproductive cycle is seasonal,

with secondary vitellogenesis occurring between August and February; it can present eggs in oviducts in December, indicating that copulation occurs around November (Sawaya et al. 2008). Males reach sexual maturity with a minimum of 481 mm SVL and females with 513 mm, and its fecundity varies from three to seven eggs (Sawaya et al. 2008). When handled, it can open its mouth wide (N = 1, see Fiorillo et al. 2018) and perform erratic movements (N = 1). It can also press the sharp tip of the tail against the captor's hand (Marques et al. 2015) (Table 4).

Philodryas olfersii (Lichtenstein, 1823)
Figure 8A, B

It is a large, opisthoglyphous species (mean SVL = 699 mm; range 285–1120 mm; N = 129; Sawaya et al. 2008). Two individuals (including MRCM 1255) were accidentally encountered (AE) on the same day, both active during the day in the cerradão; one of them had ingested a rodent inside one of the pitfall traps and the other was moving around in the leaf litter. A third individual (juvenile; MRCM 1304) found on the edge of a cerradão area after the end of the study contained an anuran (*Scinax fuscovarius*) in its stomach. It is semi-arboreal, diurnal (Bernarde and Abe 2006; Hartmann and Marques 2005; Martins et al. 2008), and feeds mainly on amphibians and mammals (Hartmann and Marques 2005; Marques et al. 2015). The first two individuals (the juvenile was found in August) from this study were observed in March (wet season) and one female (MRCM 1255) had 22 ovarian follicles (LOF = 11 mm). It presents a seasonal reproductive cycle, with secondary vitellogenesis occurring between January and May, and ovulation and oviposition occurring between September and January (Fowler et al. 1998; Mesquita et al. 2013b); its fecundity varies from four to 11 eggs (Achaval and Olmos 2008; Mesquita et al. 2013b). It reaches sexual maturity with approximately 490 mm SVL in males and 640 mm in females (Mesquita et al. 2013b). When handled, it can open its mouth wide, strike, form an S-coil with the anterior part of its body, or produce cloacal discharge (Martins et al. 2008; Marques et al. 2015) (Table 4).

Philodryas patagoniensis (Girard, 1858)
Figure 8C

A large, opisthoglyphous species (mean SVL = 696 mm; range 205–1120 mm; N = 140; Sawaya et al. 2008), reaching 1.315 mm SVL (López and Giraudo 2008). A single individual (MRCM 1287) was found in campo sujo, in a closed pitfall trap (PT). However, it can also be found in areas of denser vegetation such as cerrado sensu stricto (Araujo et al. 2010) and forest edges or in disturbed areas (Sawaya et al. 2008). It is terrestrial and diurnal (Di-Bernardo 1998; Hartmann and Marques 2005; Sawaya et al. 2008; Marques et al. 2015). *Philodryas patagoniensis* feeds mainly on frogs and lizards, and may occasionally prey on other snakes, birds, and mammals (Hartmann and Marques 2005; López and Giraudo 2008). The only individual (an adult male) was captured in July (dry season). It has a seasonal reproductive cycle, with secondary

vitellogenesis between August and December and ovulation between October and December (Fowler et al. 1998). Males reach sexual maturity with ca. 410 mm SVL and females with 550 mm and its fecundity varies from one to 26 eggs (Achaval and Olmos 1997; López and Giraudo 2008). When handled, it can bite, flatten or twist its body, produce cloacal discharge, or triangulate the head (Martins et al. 2008; Sawaya et al. 2008; Marques et al. 2015) (Table 4).

Pseudoboa nigra **(Duméril, Bibron & Duméril, 1854)**
Figure 8D, E

It is a large opisthoglyphous species (range 548–1261 mm; N = 110; Orofino et al. 2010), with a maximum SVL of 1261 mm (Gaiarsa et al. 2013). Two individuals were observed through TCS: one adult (MRCM 342) was observed on the edge of a gallery forest and another (a juvenile), under fallen eucalyptus trunks in campo sujo, both active at night. Under the trunks where the second individual was found, we also found two lizard species, *Aspronema dorsivittatum* and *Tropidurus itambere*. It can use forests and open areas and is able to persist in disturbed habitats (Gaiarsa et al. 2013). It is terrestrial and predominantly nocturnal (Guedes 2006; Gaiarsa et al. 2013). The individual captured at the edge of the gallery forest defecated lizard fragments. Although it feeds frequently on lizards, it can occasionally feed on other snakes, amphisbaenians, and even small mammals (Gaiarsa et al. 2013). The two individuals observed in this study were found during the wet season, in October (adult male) and November (juvenile female). Orofino et al. (2010) reported females with six to eight eggs in the oviducts in February and September. It reaches sexual maturity with ca. 560 mm SVL in females and 548 mm in males; its fecundity can vary from three to 24 eggs (Orofino et al. 2010). When handled, it can produce cloacal discharge, hide its head (MRCM 342), and can also perform erratic movements (Marques et al. 2015) (Table 4).

Rhachidelus brazili **Boulenger, 1908**
Figure 8F

It is a large, opisthoglyphous species (mean SVL = 786 mm; range 435–1200 mm; N = 6; França et al. 2008), reaching up to 1,372 mm SVL (Gaiarsa et al. 2013). One individual (IBSP89664) was observed (during TCS) in a transition between the campo sujo and a recently burned campo cerrado (very sparse vegetation), moving on the ground at night (07:40 PM). It is terrestrial and nocturnal, and appears to be a habitat generalist since it may use both open and forest habitats as well as disturbed areas (Sawaya et al. 2008; Gaiarsa et al. 2013). The captured individual defecated bird remains (bones and feathers). Most diet records for *R. brazili* are bird eggs, but it can occasionally feed on birds (this study; Gaiarsa et al. 2013). The captured individual was a sub-adult female and was found in November (wet season). It reaches sexual maturity with 984 mm SVL in females and 867 mm in males (Gaiarsa et al. 2013). When handled, the individual flattened its body, performed erratic movements, produced cloacal discharge, and triangulated its head (N = 1) (Table 4).

Figure 8. A *Philodryas olfersii* **B** *P. olfersii* (detail of the head) **C** *P. patagoniensis* **D** *Pseudoboa nigra* (adult) **E** *P. nigra* (juvenile) **F** *Rachidelus brazili.*

Taeniophallus occipitalis (Jan, 1863)
Figures 9A

A small aglyphous species (mean SVL = 269 mm; range 140–399 mm; N = 27; Sa-waya et al. 2008) reaching 453 mm SVL (this study). Nine individuals were found in non-forest vegetation types: campo sujo (PT = 1, TCS = 1; MRCM 435, 510), campo cerrado (AE = 3, PT = 1; MRCM 532, 1281, 1387), and cerrado sensu stricto (PT = 3; MRCM 523, 1294). One of them (MRCM 435) was moving on a sandy soil at night

(08:00 PM) and the other (MRCM 532) in campo cerrado at 10:20 AM. According to the literature, it is terrestrial and diurnal, and can be found within the leaf litter (Sawaya et al. 2008; Morato et al. 2011; Marques et al. 2015), and does not seem to use disturbed areas (Sawaya et al. 2008). Two specimens examined showed lizard fragments in their hindgut (MRCM 510, 532). The available information indicates that it feeds mainly on amphibians and lizards (Cechin 1999; Marques et al. 2009; 2015), but there is one record of ophiophagy (Balestrin 2008). A female (MRCM 510) collected in September (dry season) had 17 ovarian follicles (LOF = 8.7 mm). Two specimens collected in February and April (wet season) were new-borns. When handled, it can twist its body (N = 1; MRCM 435) and perform death feigning (N = 1; MRCM 1294; see Fiorillo et al. 2019). It can also flatten its body or produce cloacal discharge (Marques et al. 2015) (Table 4).

Thamnodynastes hypoconia **(Cope, 1860)**
Figure 9B, C

It is a small, opisthoglyphous species (mean SVL = 387 mm; range 364–417 mm; N = 5; this study). One individual was found near the campo sujo and the others in open flooded areas, always on the ground or in humid undergrowth, usually near water bodies with calling anurans. All individuals were moving at night and captured through TCS (between 06:30 and 9:20 PM). The available information indicates that the species is semi-arboreal and nocturnal (Martins et al. 2008; Sawaya et al. 2008; Marques et al. 2015) and that its diet is specialised in amphibians (França and Araújo 2006; Marques et al. 2015). All individuals were captured between October and March (the wet season). Published data indicate that its reproductive cycle is non-seasonal, with secondary vitellogenesis occurring between January and September, ovulation between March and November, and embryos are present in females between May and November, after which births should occur; its fecundity varies from one to 12 hatchlings (Achaval and Olmos 1997; Sawaya et al. 2008). When handled, it can bite (N = 2; MRCM 221). It can also open its mouth, flatten or twist the body, strike, produce cloacal discharge, or triangulate its head (Sawaya et al. 2008; Marques et al. 2015) (Table 4).

Xenodon merremii **(Wagler, 1824)**
Figure 9D

It is a large aglyphous species (mean SVL = 868 mm; range 845–903 mm; N = 3; this study). One individual (MRCM 319) was AE, while moving over the leaf litter in the cerradão during the day (11:15 AM), the others (MRCM 423, 495) were OLP in disturbed areas near the SBES headquarters. The available information indicates that it is terrestrial and diurnal (Vitt 1983; Sawaya et al. 2008; Marques et al. 2015), with a diet restricted to amphibians (Jordão 1997; Marques et al. 2015). The individuals were observed in October, February (wet season), and July (dry season) in this study. A female (MRCM 423) collected in February had 26 ovarian follicles (LOF = 7.2 mm). Males reach sexual maturity with at least 486 mm SVL and females with 561 mm (Piz-

zatto et al. 2008). It has a continuous reproductive cycle and fecundity varies from four to 44 eggs (Vitt 1983; Vitt and Vangilder 1983; Pizzatto et al. 2008). When handled, it can flatten its body (N = 2; MRCM 319, 495), compress the body while raising the head (N = 1; MRCM 495), strike (N = 2; MRCM 319, 495), open its mouth (N = 1; MRCM 319, 495), or triangulate or hide the head (N = 1; MRCM 495) (Table 4). The available information indicates that, in addition to being a supposed mimic of *C. durissus*, it can also raise a curled tail (Marques et al. 2015).

Xenodon nattereri (Steindachner, 1867)
Figure 9E

It is a small aglyphous species (mean SVL = 272 mm; range 135–442 mm; N = 73; Sawaya et al. 2008). One individual (MRCM 1749) was captured through AE in campo sujo and another (MRCM 517) was OLP on the ground, in an area of campo cerrado. It presents a wide distribution throughout the Cerrado and transitional zones with the Atlantic Forest (Nogueira et al. 2019). Sawaya et al. (2008) suggest that it is fossorial and terrestrial (its activity on the surface is virtually limited to the wet season) and diurnal. One individual (MRCM 517) defecated two lizard eggs. In addition to lizard eggs (this study; Sawaya et al. 2008), it can also prey on lizards (particularly from the family Gymnophthalmidae) and snakes (Sawaya et al. 2008). The female (MRCM 517) collected in October (wet season) had eight ovarian follicles (LOF = 3.8 mm). Its fecundity varies from two to ten eggs and Sawaya et al. (2008) suggest that it presents seasonal reproduction, with secondary vitellogenesis occurring between October and February. When handled, it can flatten its body, hide its head, or curl its tail (Marques et al. 2015) (Table 4).

Elapidae Boie, 1827
Micrurus frontalis (Duméril, Bibron & Duméril, 1854)
Figure 9F

It is a large proteroglyphous species (mean SVL highly variable according to the subspecies; range 500–1,425 mm; Roze 1996; Sawaya et al. 2008). The only individual (MRCM 489, a juvenile, SVL = 338 mm) found in this study was captured in a PT in campo cerrado. The available information indicates that it is terrestrial, fossorial, both nocturnal and diurnal, and apparently a habitat specialist of open habitats (Sazima and Abe 1991; França and Araújo 2006; Sawaya et al. 2008; Marques et al. 2015). It feeds on elongated vertebrates such as gymnophthalmid lizards, amphisbaenians, and other snakes, and there are reports of cannibalism (Roze 1996). The available information indicates that it is oviparous and presents a seasonal reproductive cycle, with a long period of vitellogenesis in the early wet season and mating from late wet season to the first half of the dry season (autumn) (Marques et al. 2006). When handled, the single individual performed erratic movements, raised a curled tail, showing it, and hid the head (Table 4). It can also flatten it body (Marques et al. 2015) and evert the hemipenes (Sazima and Abe 1991).
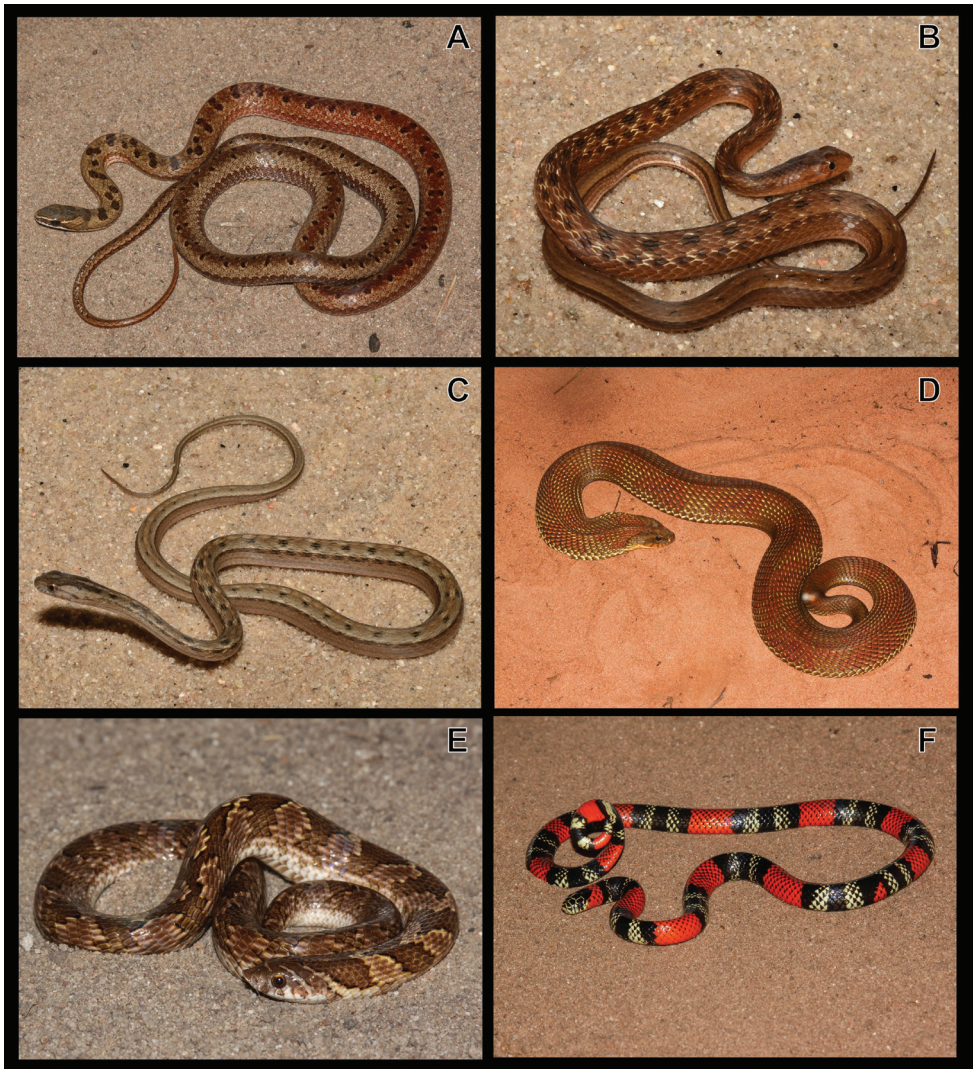
Figure 9. A *Taeniophallus occipitalis* **B** *Thamnodynastes hypoconia* (colour patterm 1) **C** *T. hypoconia* (colour patterm 2) **D** *Xenodon merremi* **E** *X. nattereri* **F** *Micrurus frontalis*.

Micrurus lemniscatus (Linnaeus, 1758)
Figure 10A

It is a large proteroglyphous species (range 500–900 mm; Roze 1996). The only individual found (MRCM 1700, a juvenile, SVL = 317 mm) in this study was captured through AE in campo cerrado. The available information indicates that it is terrestrial, fossorial, both nocturnal and diurnal (Sazima and Abe 1991; Roze 1996), and can be observed in open vegetation types, disturbed areas, and forest edge (Sazima and Abe 1991). It feeds on elongated vertebrates, such as amphisbaenians, eels (*Gymno-*

tus or *Synbranchus*), and snakes (Sazima and Abe 1991; Roze 1996). The available information indicates that it is oviparous and its reproductive cycle is probably seasonal (Marques et al. 2013). When handled, the collected individual performed erratic movements, raised and curled the tail, or hid its head under body coils. It can also bite and flatten the body (Sazima and Abe 1991) (Table 4).

Viperidae Oppel, 1811
Bothrops alternatus Duméril, Bibron & Duméril, 1854
Figure 10B

It is a large solenoglyphous species (mean SVL = 997 mm; range 930–1,070 mm; N = 4; this study), reaching 1,240 mm of CRC (Sawaya et al. 2008). Virtually all individuals were found in the most open vegetation types, such as campo sujo (AE = 7; MRCM 497) and campo cerrado (TCS = 1), and in disturbed areas near the SBES headquarters (OLP = 2). One individual was found in a recently burned campo cerrado area (with very sparse vegetation). Two adult females were found moving during the day (07:30 AM and 09:30 AM, respectively). One of them (MRCM 497, SVL = 1,000.5 mm, 660 g) regurgitated a freshly ingested rodent, *Clyomys laticeps* (body length 190 mm, 295 g). Another adult female was found foraging (coiled in ambush posture) in a recently burned area of campo cerrado at night (08:30 PM). The available information indicates that it is terrestrial, both diurnal and nocturnal (Martins et al. 2001; Sawaya et al. 2008; Marques et al. 2015; Fiorillo et al. 2020b), and is a mammal specialist (Martins et al. 2002). Most individuals were found between August (dry season) and March (wet season) and a female (MRCM 497) collected in August had 14 ovarian follicles (LOF = 13.7 mm). The reproductive cycle is seasonal, with births occurring probably between the middle and late wet season (Sawaya et al. 2008). Its fecundity varies from three to 25 young (Achaval and Olmos 1997). It reaches sexual maturity with at least 700 mm SVL in females and 440 mm in males (Nunes 2006). When handled, it can flatten the body (N = 2), strike (N = 3; MRCM 497), hide the head (N = 2; MRCM 497), or vibrate the tail (N = 2; MRCM 497) (Table 4).

Bothrops itapetiningae (Boulenger, 1907)
Figure 10C

It is a small solenoglyphous species (mean SVL = 396 mm; range 185–570 mm; N = 89; Sawaya et al. 2008). It was found only in the most open areas of the SBES, in campo sujo (AE = 3) and in a recently burned area of campo cerrado (TCS = 1; MRCM 366). One individual (MRCM 366) was found moving at night (07:35 PM) and another during the day (08:30 AM); both tried to escape by entering burrows in the ground. Two individuals were found coiled during the day (09:00 AM and 07:00 AM), one of them seemed to be foraging and the other was resting, sheltered under the lid of one of the PTs. The available information indicates it is nocturnal (occasionally diurnal) and terrestrial, specialised in open areas of the Cerrado and feeds on mammals, lizards, amphibians, birds, and centipedes (Martins et al. 2002; Sawaya et

Figure 10. A *Micrurus lemniscatus* **B** *Bothrops alternatus* **C** *B. itapetiningae* **D** *B. moojeni* **E** *B. pauloensis* **F** *Crotalus durissus.*

al. 2008; Leão et al. 2014; Marques et al. 2015; Fiorillo et al. 2020b). All individuals were found between November and March (the wet season) and one female (MRCM 366) collected in November had seven ovarian follicles (LOF = 3.9 mm). The available information indicates that it presents fecundity varying from three and 11 embryos with vitellogenic ovarian follicles occurring between January and June; births occur during the wet season (Sawaya et al. 2008; Leão et al. 2014). It reaches sexual maturity with at least 230 mm SVL in females and 340 mm in males (Leão et al. 2014). When handled, it can flatten the body (N = 1), strike (N = 1), or vibrate the tail (N = 2; MRCM 366) (Table 4). It can also open its mouth, hide its head, or produce cloacal discharge (Sawaya et al. 2008; Marques et al. 2015).

Bothrops moojeni Hoge, 1966
Figure 10D

It is a large solenoglyphous species (mean SVL = 880 mm; range 680–1,150 mm; N = 11; this study). It was generally found associated with flooded open areas and gallery forests (AE = 5, TCS = 9; MRCM 215, 338); it was also found in campo cerrado (TCS = 1; MRCM 293), cerrado sensu stricto (PT = 1) and cerradão (TCS = 1). Three individuals were found in disturbed areas (OLP = 2; MRCM 240). All individuals found in this study were active, moving, eating or in an ambush posture (tight coil and head raised at 45°), at night (between 07:30 and 11:00 PM), except for a single adult individual, OLP, moving during daytime (10:00 AM) (see also Fiorillo et al. 2020b). It is semi-arboreal and both diurnal and nocturnal (França and Araújo 2006; Sawaya et al. 2008). One individual was observed preying on a leptodactylid frog and another had rodent fragments in its faeces. The available information indicates that it presents ontogenetic changes in diet, feeding on ectothermic animals (amphibians, centipedes, lizards, and other snakes) when juvenile and on endothermic ones (mammals and birds) when adult (Brites 1992; Andrade et al. 1996; Martins et al. 2002; Nogueira et al. 2003; França and Araújo 2006; Ávila and Porfírio 2008). However, adults can occasionally prey on ectothermic vertebrates (e.g., Fiorillo et al. 2012). All individuals from this study were found between September (dry season) and March (wet season). A female (MRCM 338) collected in October (wet season) had 28 ovarian follicles (LOF = 5.2 mm) and a new-born was observed in September. Nogueira et al. (2003) suggest that their reproductive cycle is seasonal, and its fecundity varies from three to 32 young, with ovulation around July, and births probably concentrated between December and January. It reaches sexual maturity with at least 760 mm SVL in females and 590 mm in males (Nogueira et al. 2003). When handled, it can strike (N = 3; MRCM 240), hide the head (N = 1), bite (N = 1), and vibrate the tail (N = 4; MRCM 240) (Table 4). It can also open the mouth, flatten the body, or produce cloacal discharge (Sawaya et al. 2008; Marques et al. 2015).

Bothrops pauloensis Amaral, 1925
Figure 10E

It is a medium-sized solenoglyphous species (mean SVL = 611 mm; range 504–782 mm; N = 17; this study). Most individuals were found in open areas of campo sujo (AE = 6, TCS= 3; IBSP-90.262/sb0515) and campo cerrado (AE = 17, OLP = 1, PT = 1, TCS = 16; MRCM 256, 356, 425, 432, IBSP-90.262/sb0514), four in cerrado sensu stricto (AE = 2, TCS = 2; MRCM 1226), and only one (TCS) in the cerradão. Three individuals were found in disturbed areas (AE = 1, OLP = 2; MRCM 484) and four were observed OLP, without data on location or habitat (see also Fiorillo et al. 2020b). Approximately 50% of the individuals (including MRCM 484, 1024) were

found active (moving or in ambush posture) between 05:30 and 10:30 PM and four were observed moving during the day between 08:00 and 12:00 PM. Three additional individuals (including MRCM 356) were apparently found resting under bucket lids of PTs between 07:00 and 09:30 AM. It is primarily nocturnal (Valdujo et al. 2002; Campbell and Lamar 2004; Jansen 2006), terrestrial (Marques et al. 2015), and can use burrows and other cavities (e.g., termite mounds) as sites to forage and shelter (Valdujo et al. 2002; Jansen 2006; Fiorillo et al. 2020b). One individual was found under fallen *Eucalyptus* trunks and bark, near a campo sujo area, where there were also lizards of the species *A. dorsivittatum* and *T. itambere*. Among the nine specimens examined, two adults had gut contents (an anuran of the genus *Leptodactylus* in the stomach and invertebrate remains in the hindgut, respectively). The available information indicates that it feeds on mammals, lizards, amphibians, centipedes, other snakes, and birds (Martins et al. 2002; Valdujo et al. 2002). Most of the individuals found active were captured between August (dry season) and March (wet season). The examined females had 11 (LOF = 6 mm) and 15 (LOF = 3.6 mm; MRCM 256) ovarian follicles in August and 18 (LOF = 4.5 mm; MRCM 425) in January. Three new-borns were found in January, February, and June. Valdujo et al. (2002) suggested that its reproductive cycle is seasonal, with vitellogenesis apparently starting ca. March, beginning embryo development from June to October, and the end of development in December; females give birth to 4–20 hatchlings per litter. It reaches sexual maturity with at least 475 mm SVL in females and 430 mm in males (Valdujo et al. 2002). When handled, it can flatten (N = 1) or twist its body (N = 1), strike (N = 16; MRCM 256, 356, 484, 507), hide its head (N = 1), and vibrate the tail (N = 12; MRCM 256, 356, 484, 507) (Table 4).

Crotalus durissus (Linnaeus, 1758)
Figure 10F

It is a large solenoglyphous species (mean SVL = 900 mm; range 825–988 mm; N= 12; this study). The individuals were observed in all vegetation types: campo sujo (AE = 3; MRCM 421, 1218), campo cerrado (AE = 2, TCS = 2) cerrado sensu stricto (AE = 3, OLP = 2), cerradão (AE = 10, OLP = 1, TCS = 1), in a transitional area between campo sujo and campo cerrado (AE = 1, TCS = 2) in a wet field (TCS = 1), on the edge of the gallery forest (AE = 1), and in disturbed areas (near farms outside the SBES, in disturbed areas at the SBES headquarters, and in pine forests; AE = 3, OLP = 4, TCS = 1; MRCM 289, 354, 392, 421, 485, 1273) (see also Fiorillo et al. 2020b). Five individuals OLP have no information on habitat. Of the individuals observed, eight were active at night (in ambush position or moving between 07:00 and 09:30 PM) and eight were moving during the day (between 09:00 AM and 03:00 PM). The available information indicates that it presents terrestrial habits and higher activity in the first hours of the night (Tozetti and Martins 2008; Tozetti et al. 2009; Marques et al. 2015). Although it is found predominantly in open and relatively dry areas (e.g.,

Sawaya et al. 2008), it has a great ecological plasticity and can be found even inside or at the edge of forests (this study; Reinert 1992; Bastos et al. 2005; Sawaya et al. 2008; Hartmann et al. 2009). In addition, it can use disturbed habitats and urbanised areas (Almeida-Santos and Orsi 2002; Sawaya et al. 2008; São Pedro and Pires 2009). Two individuals defecated hair and bones and a new-born (MRCM 485) regurgitated a rodent. Among seven specimens examined, three (MRCM 392, 485, 1107) contained hair in their hindgut. Its diet is specialised in mammals, but it can occasionally consume lizards (Almeida-Santos and Germano 1996; Salomão et al. 2005; Sant'anna and Abe 2007). Most adult individuals were found between November and March (wet season) and new-borns in April and May (dry season), and a female (MRCM 505) collected in August (dry season) had eight ovarian follicles (LOF = 4.3 mm). According to the literature, its activity is concentrated at the end of the wet season, when copulation and combat between males occur (Almeida-Santos and Orsi 2002). It is viviparous with prolonged vitellogenesis beginning in March, pregnancy between October and January, and juvenile recruitment between January and March (Almeida-Santos and Salomão 1997; Almeida-Santos and Orsi 2002). Its fecundity varies from 21 to 31 hatchlings (Vitt 1992). It reaches sexual maturity with at least 830 mm SVL in females and 820 mm in males (Barros et al. 2012). When handled, it can strike (N = 5; MRCM 505, 1218, 1273), vibrate the tail (N = 6; MRCM 505, 1273), or perform cloacal discharge (N = 2) (Table 4). It is also known to flatten the body (Sawaya et al. 2008).

Discussion

This study has added 14 species to the previous list of snakes found at SBES (Araújo et al. 2010): *A. dimidiata*, *B. alternatus*, *B. itapetiningae*, *C. brazili*, *C. quadricarinatus*, *E. aesculapii*, *E. crassus*, *L. ternetzii*, *M. lemniscatus*, *P. lativittatus*, *P. olfersi*, *P. nigra*, *R. brazili*, and *X. merremi*. On the other hand, we failed to find two species listed by Araújo et al. (2010), *Philodryas agassizii* captured in the SBES during their study, and *Philodryas livida*, which is known only from a historical record (Instituto Butantan collection number IBSP 40953) with unclear locality data that was attributed to the Municipality of Águas de Santa Bárbara by the authors. However, there are three specimens of *P. livida* collected in the 1970s in the records of the Instituto Butantan collection, collected from the Municipality of Lençois Paulista, the centre of which is located only 44 km from the SBES. Thus, this species may have occurred at SBES in the past (see discussion on conservation below). As for *P. agassizii*, it must have gone unnoticed in our study, despite the large sampling effort. Thus, considering this study and that of Araújo et al. (2010), 35 species of snakes occur in the SBES.

Approximately half of the species of snakes found at the SBES used non-forest vegetation types almost exclusively (campo sujo, campo cerrado, and/or cerrado sensu stricto). Other studies already showed a trend of decrease in snake species richness with increasing vegetation complexity in the Cerrado (Sawaya et al. 2008; Araujo et al. 2010; Araujo and Almeida-Santos 2011; Serrano-Filho 2012). The structural dif-

ferences found between Cerrado vegetation types determine microclimatic differences at the local scale (e.g., Gianotti et al. 2013), with contrasting ranges of temperature and air humidity when the most open vegetation types (grasslands, the campos) are compared to the most closed ones (cerrado woodland, the cerradão). These different microclimates reflect differences in the solar and wind incidences between these habitats (e.g., Vitt et al. 2007; Gianotti et al. 2013) and may play a crucial role in determining snake diversity in the cerrado gradient of vegetation types, especially regarding heliophilic species.

The low proportion of species that use the arboreal strata (21%) in contrast to studies carried out in forests (e.g., Martins and Oliveira 1998; Bernarde and Abe 2006) is expected for a snake community from the Cerrado. Arboreal snakes seem to be less able to colonise non-forest formations (such as Cerrado and the southern Campos of Brazil; Cavalheri et al. 2015) due to the low availability of adequate substrates both currently and in the past (França et al. 2008; Cavalheri et al. 2015). Thus, more open vegetation types, such as those in the study area, could be working as an environmental filter (sensu Keddy 1992; Webb et al. 2002) for snake species of arboreal lineages (Cavalheri et al. 2015; Piatti et al. 2019).

The patterns of resources use described here for the snake community of SBES reflect mostly the composition of the community regarding snake lineages (Duellman 1978; Cadle and Greene 1993; Martins and Oliveira 1998; Bellini et al. 2015). In the SBES community, the closely related species were also more similar in terms of resource use as observed in other studies focusing on snake communities in the Neotropics (e.g., Duellman 1978; Martins and Oliveira 1998; Fiorillo et al. 2020a). For example, the species of the tribe Xenodontini (particularly the genera *Erythrolamprus* and *Xenodon*) are similar in terms of resource use, the same being the case for other lineages such as the tribe Pseudoboini and the families Boidae and Viperidae (see Table 1).

The most consumed prey items in the community (number of species which consumed a given prey type), based on the present study and the literature, were lizards followed by anurans and mammals. During our sampling, > 7,800 vertebrates were captured in pitfall traps, of which 64% were anurans, 16% were lizards, and 16% were small mammals. However, because of the highly seasonal rainfall in the Cerrado, frog activity is highly seasonal, with capture rates in pitfall traps increasing by orders of magnitude during the rainy season compared to the dry season (Brasileiro et al. 2005; Prado et al. 2005). Indeed, during the dry seasons (April to September) of the two years of sampling of this study, the proportion of anurans captured in PTs was 24% among vertebrates, while the capture rates of lizards and mammals were 37% each. The increased capture rates in the rainy season may reflect mostly the seasonal migrations of anurans to water bodies for breeding. On the other hand, the availability of lizards and small mammals tend to vary much less than that of amphibians. The decrease in anuran activity during the dry season may seasonally decrease the consumption rates of this item by snakes, and consequently increase that of lizards and mammals. In addition to the availability of different prey, the evolutionary history of each of the groups that make up the community also has a strong influence in relation to the prey

items consumed (see above). For instance, within dipsadids, all species of the tribe Elapomorphini in the community feed on elongate vertebrates (mainly snakes and amphisbaenians); three of the four species of the tribe Pseudoboini feed primarily on mammals and lizards; most species of the tribe Xenodontini feed primarily on anurans; and both species of the tribe Philodryadini are diet generalists (Hartmann and Marques 2005; Sawaya et al. 2008).

Most reproductive females (ovarian follicles > 5 mm) were found from late dry season to late wet season. This peak of activity during the wet season in seasonal environments has also been recorded for other Neotropical snake communities (Strüssmann and Sazima 1993; Di-Bernardo 1998; Marques 1998; Sawaya et al. 2008; Pontes et al. 2009; Fiorillo et al. 2020a). Most juveniles (61.5%) were found from the late dry season to the onset of the wet season, which is also a recurring pattern (Marques 1998; Sawaya et al. 2008; Hartmann et al. 2009). In the Atlantic Forest, Hartmann et al. (2009) found more active snakes during the rainy/warmer season (October to March) than in the dry/colder season (April to September), but they did not find a significant difference between the number of snakes (adults or juveniles) captured. On the other hand, Sawaya (2004) detected significant correlations between the numbers of snakes captured and minimum and maximum temperatures in the Cerrado. That author also suggested that the minimum temperature probably would have a stronger effect on snakes than maximum temperature, since that variable limits snake activity (Lillywhite 1987). Despite the large number of studies that indicate seasonality in the reproductive cycles of tropical snakes, almost none attempted to demonstrate quantitatively the physiological bases that mediate this synchronisation. This is largely due to problems of discrimination between the effects of climate variables, their interactions, and their effects on the abundance of prey (Oliveira and Martins 2001; Mathies 2011).

Most of the defensive tactics observed in this study were supposedly directed at visually oriented predators (80% of tactics), such as birds (especially birds of prey), probably the most important predators of Neotropical snakes, and mammals (Martins 1996; Martins and Oliveira 1998; Martins et al. 2008). Indeed, most species also have cryptic colour patterns (ca. 80% of species). Among the species that show aposematic colour patterns (*A. dimidiata*, *E. aesculapii*, *M. frontalis*, *M. lemniscatus*, *O. guibei*, and *O. rhombifer*), four have fossorial and/or cryptozoic habits (*A. dimidiata*, *E. aesculapii*, *M. frontalis*, and *M. lemniscatus*) and the others, despite being terrestrial, are predominantly nocturnal (*O. guibei* and *O. rhombifer*). The great diversity of visual defensive behaviours associated with cryptic lifestyles and colour patterns is a common pattern in Neotropical snake communities and occurs in both predominantly open environments (e.g., this study; Sawaya et al. 2008) and forests (Martins and Oliveira 1998; Martins et al. 2008; Fiorillo et al. 2020a). Another defensive behaviour frequently used by SBES snakes was cloacal discharge, which in turn seems to be frequent in most species of snakes in different types of environment (see Martins and Oliveira 1998; Marques et al. 2005; Sawaya et al. 2008; Marques et al. 2015, 2017, 2019). The sharing of potential predators may have led to the widespread convergence of defensive

tactics in snakes (Martins 1996; Martins et al. 2008), although some of these tactics are more phylogenetically conserved (e.g., the behaviour of inflating the gular region in colubrids; Martins et al. 2008).

The SBES snake fauna includes habitat specialists, sensitive to environmental disturbance, which are under different degrees of threat in the state of São Paulo. Four of these species are listed as threatened (Vulnerable, VU, or Endangered, EN) in the state of São Paulo red list (Governo do Estado de São Paulo 2018), *B. itapetiningae* (EN) *O. rhombifer* (VU), *P. agassizii* (EN) and *X. nattereri* (EN). Two species are listed as Near Threatened (NT) in the Brazilian red list (ICMBio 2018), *Phalotris lativittatus* and *B. itapetiningae*, whereas the former is listed as NT also in the IUCN red list (IUCN 2020). Additionally, *P. livida*, a species listed as VU in the three red lists cited above, is suspected to have occurred in the region of the SBES in the past (Araújo et al. 2010; see above). All these species are specialised in the open vegetation types of the Cerrado (especially the campos), are not able to persist in disturbed habitats (Sawaya et al. 2008) and seems not to be abundant in the study area. Unfortunately, one of the main conservation concerns regarding the rare fragments of cerrado in the southern portion of this biome is woody encroachment, which occurs in open vegetation types of many areas (Durigan et al. 2020). Thus, the future of the populations of the species above at SBES depends on a well-planned fire management program aiming at maintaining the open vegetation types in the long run (see recommendations in Durigan et al. 2020). It is worth noting that the local extinction of predators like snakes can lead to changes in the trophic structure of communities, consequently affecting several ecosystem functionalities (Estes et al. 2011).

Conclusions

The Cerrado is the Neotropical Ecoregion with the greatest snake species richness (N = 222), with an average of 30 to 60 species every 12,000 km^2 (1° × 1°) (Guedes et al. 2018). The SBES concentrates an important portion of this diversity in a small area (31.5 km^2). The present study adds 14 species to the previous local snake list (Araujo et al. 2010). This reflects the importance of a complement of sampling methods as used in the present study, as well as the large sampling effort (23,040 buckets-days and 1,248 person-hours of time-constrained search in addition to accidental encounters and observations made by local people during four years of fieldwork at the reserve (see a similar example in Sawaya et al. 2008). Our study also provides a large amount of primary information about the species, which can assist in both understanding the structure of snake communities and contribute to the management and conservation practices in Cerrado areas. It is important to highlight the fact that the SBES contains one of the last remaining fragments of Cerrado in the state of São Paulo (Kronka et al. 2005), which in turn harbour many typical Cerrado snakes, including threatened and near threatened species (see above). Therefore, this area is of great value for the conservation of the Cerrado snake fauna.

Acknowledgements

References

Achaval F, Olmos A (1997) Anfibios y reptiles del Uruguay. Facultad de Ciencias, Montevideo, 128 pp.

Albarelli LPP, Santos-Costa MC (2010) Feeding ecology of *Liophis reginae semilineatus* (Serpentes: Colubridae: Xenodontinae) in Eastern Amazon, Brazil. Zoologia 27: 87–91. https://doi.org/10.1590/S1984-46702010000100013

Albuquerque CE, Ferrarezzi H (2004) A case of communal nesting in the Neotropical snake *Sibynomorphus mikanii* (Serpentes, Colubridae). Phyllomedusa 3: 73–77. https://doi.org/10.11606/issn.2316-9079.v3i1p73-77

Almeida-Santos SM, Germano VJ (1996) *Crotalus durissus* (Neotropical Ratlesnake). Prey. Herpetological Review 27: e143. https://ssarherps.org/herpetological-review-pdfs/

Almeida-Santos SM, Salomão MG (1997) Long term sperm storage in the female Neotropical rattlesnake *Crotalus durissus terrificus* (Viperidae: Crotalidae). Japanese Journal of Herpetolology 17: 46–52. https://doi.org/10.5358/hsj1972.17.2_46

Almeida-Santos SM, Orsi AM (2002) Ciclo reprodutivo de *Crotalus durissus* e *Bothrops jararaca* (Serpentes Viperidae): morfologia e função dos ovidutos. Revista brasileira de reprodução animal 26: 109–112. https://ecoevo.com.br/publicacoes/pesquisadores/selma_santos/CicloreprodutCrotalusBothrops_2002.pdf

Altmann J (1974) Observational Study of Behavior: Sampling Methods. Behavior, University of Chicago 49: 227–267. https://doi.org/10.1163/156853974X00534

American Veterinary Medicine Association (2020) Guidelines for the Euthanasia of Animals. https://www.avma.org/sites/default/files/2020-01/2020-Euthanasia-Final-1-17–20.pdf

Andrade DV, Abe AS, Santos MC (1996) Is the venom related to diet and tail color during *Bothrops moojeni* ontogeny? Journal of Herpetology 30: 285–288. https://doi.org/10.2307/1565528

Ávila RW, Porfírio GEO (2008) *Bothrops moojeni* (Brazilian Lancehead). Predation. Herpetological Review 39: e467. https://ssarherps.org/herpetological-review-pdfs/

Araujo CO, Almeida-Santos SM (2011) Herpetofauna in a cerrado remnant in the state of Sao Paulo, Southeastern Brazil. Biota Neotropica 11: 47–62. https://doi.org/10.1590/S1676-06032011000300003

Araujo CO, Corrêa-Filho DT, Almeida-Santos SM (2013) Anurans of the Estação Ecológica de Santa Bárbara, a remnant of open Cerrado formations in the state of São Paulo. Biota Neotropica 13: 230–240. https://doi.org/10.1590/S1676-06032013000300026

Araujo CO, Corrêa-Filho DT, Sawaya RJ (2010) Snake assemblage of Estação Ecológica de Santa Bárbara, SP: a Cerrado remnant in Southeastern Brazil. Biota Neotropica 10: 235–245. https://doi.org/10.1590/S1676-06032010000200026

Araujo CO, Maffei F, Corrêa DT, Moya GM, Nascimento BTM, Almeida-Santos SM (2014) Lizards from Estação Ecológica de Santa Bárbara, a remnant of Cerrado in the state of São Paulo, Brazil. Check List 10: 1038–1043. https://doi.org/10.15560/10.5.1038

Balestrin RF (2008) História Natural de uma Taxocenose de Squamata e Redescrição de uma espécie de anuros no Escudo Sul-RioGrandense, Brasil. Ph.D. thesis, Rio Grande do Sul, Brazil: Pontifícia Universidade Católica do Rio Grande do Sul. http://tede2.pucrs.br/tede2/handle/tede/175

Barbo FE, Marques OAV, Sawaya RJ (2011) Diversity, natural history, and distribution of snakes in the municipality of São Paulo. South American Journal of Herpetology 6: 135–160. https://doi.org/10.2994/057.006.0301

Barros VA, Sueiro LR, Almeida-Santos SM (2012) Reproductive biology of the neotropical rattlesnake *Crotalus durissus* from northeastern Brazil: a test of phylogenetic conservatism of reproductive patterns. Herpetological Journal 22: 97–104. https://www.thebhs.org/publications/the-herpetological-journal

Bastos EGM, Araújo AFB, Silva HR (2005) Records of the rattlesnakes *Crotalus durissus terrificus* (Laurenti) (Serpentes, Viperidae) in the State of Rio de Janeiro. Revista Brasileira de Zoologia 22: 812–815. https://doi.org/10.1590/S0101-81752005000300047

Bellini GP, Giraudo AR, Arzamendia V, Etchepare EG (2015) Temperate Snake Community in South America: Is Diet Determined by Phylogeny or Ecology? PLoS ONE 10: 1–15. https://doi.org/10.1371/journal.pone.0123237

Bernarde PS, Abe AS (2006) A Snake Comunity at Espigão do Oeste, Rondônia, Southwestern Amazon, Brazil. South American Journal of Herpetology 1: 102–113. https://doi.org/10.2994/1808-9798(2006)1[102:ASCAED]2.0.CO;2

Bertona M, Chiaviglio M (2003) Reproductive Biology, Mating Aggregations, and Sexual Dimorphism of the Argentine Boa constrictor (*Boa constrictor occidentalis*). Journal of Herpetology 37: 510–516. https://doi.org/10.1670/122-02A

Booth W, Johnson DH, Moore S, Schal C, Vargo EL (2011) Evidence for viable, non-clonal but fatherless *Boa constrictor*. Biology Letters 7: 253–256. https://doi.org/10.1098/rsbl.2010.0793

Brasileiro CA, Sawaya RJ, Kiefer MC, Martins M (2005) Amphibians of an open Cerrado fragment in southeastern Brazil. Biota Neotropica 5: 93–109. https://doi.org/10.1590/S1676-06032005000300006

Braz HB, Franco FL, Almeida-Santos SM (2008) Communal egg-laying and nests-sites of the Goo-eater Snake, *Sibynomorphus mikanii* (Dipsadidae, Dipsadinae) in Southeastern

Brazil. Herpetological Bulletin 106: 26–30. https://www.thebhs.org/publications/the-herpetological-bulletin/issue-number-106-winter-2008/163-07-communal-egg-laying-and-nest-sites-of-the-goo-eater-i-sibynomorphus-mikanii-i-colubridae-dipsadinae-in-southeastern-brazil/file

Brites VLC (1992) Ofiofagia de *Bothrops moojeni* Hoge, 1966 (Ophidia, Viperidae) na natureza. In: Congresso científico da UFU. 1., Uberlândia, 251 pp.

Brooks DR, McLennan DA (2002) The Nature of Diversity: An Evolutionary Voyage of Discovery, University of Chicago Press, 676 pp. https://doi.org/10.7208/chicago/9780226922478.001.0001

Burham KP, Overton WS (1979) Robust estimation of population size when capture probabilities vary among animals. Ecology: 927–936. https://doi.org/10.2307/1936861

Cadle JE, Greene HW (1993) Phylogenetic patterns biogeography and the ecological structure of Neotropical snake assemblages. In: Ricklefs E, Schluter D (Eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, 281–293. https://www.researchgate.net/publication/266318825_Phylogenetic_patterns_biogeography_and_the_ecological_structure_of_Neotropical_snake_assemblages

Campbell HW, Christman SP (1982) Field techniques for herpetofaunal community analysis. In: Scott Jr NJ (Ed.) Herpetological Communities: a Symposium of the Society for the Study of Amphibians and Reptiles. The Herpetologist's League U.S. Fish and Wildlife Service 13: 193–200.

Campbell JA, Lamar WW (2004) The Venomous Reptiles of the Western Hemisphere (Vols. 1 and 2). Comstock (Cornell University Press), Ithaca, 962 pp.

Carrasco PA, Mattoni CI, Leynaud GC, Scrocchi GJ (2012) Morphology, phylogeny and taxonomy of South American bothropoid pitvipers (Serpentes, Viperidae). Zoologica Scripta 41: 109–124. https://doi.org/10.1111/j.1463-6409.2011.00511.x

Carvalho MA, Nogueira F (1998) Serpentes da área urbana de Cuiabá, Mato Grosso: aspectos ecológicos e acidentes ofídicos associados. Cadernos de Saúde Pública 14: 753–763. https://doi.org/10.1590/S0102-311X1998000400017

Cassimiro J, Palmuti CFS, Bertoluci J (2010) *Epicrates cenchria* (Salamanta; Rainbow Boa). Diet. Herpetological Review 41: e501. https://ssarherps.org/herpetological-review-pdfs/

Caughley G (1994) Directions in conservation biology. Journal of Animal Ecology 63: 215–244. https://doi.org/10.2307/5542

Cavalheri H, Both C, Martins M (2015) The Interplay between Environmental Filtering and Spatial Processes in Structuring Communities: The Case of Neotropical Snake Communities. PLoS ONE 10: 1–16. https://doi.org/10.1371/journal.pone.0127959

Cechin SZ (1999) História natural de uma comunidade de serpentes na região da depressão central (Santa Maria) Rio Grande do Sul, Brasil. Ph.D. thesis, Rio Grande do Sul, Brazil: Pontífica Universidade Católica do Rio Grande do Sul. http://tede2.pucrs.br/tede2/handle/tede/300

Cechin SZ, Martins M (2000) Eficiência de armadilhas de queda (pitfall traps) em amostragens de anfíbios e répteis no Brasil. Revista Brasileira de Zoologia 17: 729–740. https://doi.org/10.1590/S0101-81752000000300017

Colli GR, Bastos RP, Araujo AFB (2002) The character and dynamics of the Cerrado herpetofauna. In: Oliveira PS, Marquis RJ (Eds) The Cerrados of Brazil: Ecology and natural

history of a Neotropical Savanna. Columbia University Press, NY, 223–241. https://doi.org/10.7312/oliv12042-013

Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. Journal of Plant Ecology 5: 3–21. https://doi.org/10.1093/jpe/rtr044

Cunha OR, Nascimento FP (1978) Ofídios da Amazônia X. As cobras da região Leste do Pará. Publicações Avulsas do Museu Paraense Emílio Goeldi 31: 1–218. https://repositorio.museu-goeldi.br/handle/mgoeldi/904

Cunha OR, Nascimento FP (1983) Ofídios da Amazônia XIX. As espécies de *Oxyrhopus* Wagler, com uma subespécie nova, e *Pseudoboa* Schneider, na Amazônia Oriental e Maranhão (Ophidia: Colubridae). Boletim do Museu Paraense Emílio Goeldi 1: 1–42. https://repositorio.museu-goeldi.br/handle/mgoeldi/675

Dayton PK (2003) The importance of the natural sciences to conservation. The American Naturalist 162: 1–13. https://doi.org/10.1086/376572

Di-Bernardo M (1998) História Natural de uma comunidade de serpentes da borda oriental do planalto das Araucárias Rio Grande do Sul Brasil. Ph.D. thesis, São Paulo, Brazil: Universidade Estadual Paulista.

Dixon JR (1991) Geographic variation and taxonomy of *Liophis almadensis* (Wagler) (Serpentes: Colubridae), and description of a new species of *Liophis* from Argentina and Bolivia. Texas Journal of Science 43: 225–236.

Dixon JR, Soini P (1986) The Reptiles of the Upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee, Wisconsin, 154 pp.

Dixon JR, Wiest Jr JA, Cei JM (1993) Revision of the Neotropical Snake Genus *Chironius* Fitzinger (Serpentes Colubridae). Monografie XIII. Museo Regionale di Scienze Naturali, Torino, 279 pp.

Duellman WE (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas, 352 pp.

Ernst CH (1992) Venomous Reptiles of North America. Smithsonian Institution Press, Washington, 236 pp.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soule ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. Science 333: 301–306. https://doi.org/10.1126/science.1205106

Fiorillo BF, Nali RC, Prado CPA (2012) *Bothrops moojeni* (Brazilian Lancehead). Diet. Herpetological Review 43: e656. https://ssarherps.org/herpetological-review-pdfs/

Fiorillo BF, Rossi GN, Martins M (2019) Additional defensive behaviours of *Dipsas mikanii* (Schlegel, 1837) and *Taeniophallus occipitalis* (Jan, 1863) (Serpentes: Dipsadidae). Herpetology Notes 12: 359–362. https://www.biotaxa.org/hn/article/view/43015

Fiorillo BF, Rossi GN, Menegucci R (2018) New defensive behaviour of the false coral snake *Phalotris mertensi* (Hoge, 1955) (Serpentes: Dipsadidae). Herpetology Notes 11: 869–871. https://www.biotaxa.org/hn/article/view/39227/35441

Fiorillo BF, Silva BR, Menezes FA, Marques OAV, Martins M (2020a) Composition and Natural History of Snakes from Etá Farm region, Sete Barras, south-eastern Brazil. ZooKeys 931: 115–153. https://doi.org/10.3897/zookeys.931.46882

Fiorillo BF, Tozzetti A, Martins M (2020b) Habitat use by five species of sympatric pitvipers (*Bothrops*, *Crotalus*) in a Brazilian savannah. Herpetology Notes 13: 951–960. https://www.biotaxa.org/hn/article/view/59158

Fitch HS (1970) Reproductive cycles of lizards and snakes. Museum of Natural History Miscelaneous Publications, University of Kansas 52: 1–247.

Foster MS (2012) Preparing Reptiles as Voucher Specimens. In: McDiarmid RW, Foster MS, Guyer C, Gibbons JW, Chernoff N (Eds) Reptile Biodiversity Standard Methods for Inventory and Monitoring. Berkeley: University of California Press, 95–125.

Fowler IR, Salomão MG, Jordáo RS (1998) A description of the female reproductive cycle in four species from the neotropical colubrid snake *Philodryas* (Colubridae Xenodontinae). Snake 28: 71–78. https://www.researchgate.net/publication/282132451_A_description_of_the_female_reproductive_cycle_in_four_species_from_the_Neotropical_colubrid_snake_Philodryas_Colubridae_Xenodontinae

França FGR, Araújo AFB (2006) The Conservation Status of Snakes in Central Brazil. South American Journal of Herpetology 1: 25–36. https://doi.org/10.2994/1808-9798(2006)1[25:TCSOSI]2.0.CO;2

França FGR, Mesquita DO, Nogueira CC, Araújo AFB (2008) Phylogeny and Ecology Determine Morphological Structure in a Snake Assemblage in the Central Brazilian Cerrado. Copeia 2008: 23–38. https://doi.org/10.1643/CH-05-034

Gaiarsa MP, Alencar LRV, Martins M (2013) Natural History of Pseudoboine Snakes. Papéis Avulsos de Zoologia 53: 261–283. https://doi.org/10.1590/S0031-10492013001900001

Gallardo GA, Scrocchi GL (2006) Parametros reproductivos de ocho especies de culebras ovíparas neotropicales (Serpentes: Colubridae). Cuadernos de Herpetologia 20: 33–36. https://www.researchgate.net/publication/311666355_Parametros_reproductivos_de_ocho_especies_de_culebras_oviparas_neotropicales_Serpentes_Colubridae

Gianotti ARC, Souza MJH, Machado ELM, Pereira IM, Vieira AD, Magalhães MR (2013) Análise microclimática em duas fitofisionomias do cerrado no alto Vale do Jequitinhonha, Minas Gerais. Revista brasileira de meteorolologia 28: 246–256. https://doi.org/10.1590/S0102-77862013000300002

Gotelli N, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 2001: 379–91. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Diário Oficial (2018) Governo do estado de São Paulo. Diário Oficial. Decreto N° 63.853, 128(221): 1–10. http://www.imprensaoficial.com.br/DO/GatewayPDF.aspx?link=/2018/executivo%20secao%20i/novembro/29/pag_0001_b7b1e1ba7b93f650707cc67012e01b90.pdf

Greenberg CH, Nearby DG, Harris LD (1994) A comparison of herpetofaunal sampling effectiveness of pitfall single-ended and double-ended funnel traps used with drift fences. Journal of Herpetology 28: 319–324. https://doi.org/10.2307/1564530

Greene HW (1979) Behavioral convergence in the defensive displays of snakes. Experientia 35: 747–748. https://doi.org/10.1007/BF01968221

Greene HW (1994) Systematics and natural history foundations for understanding and conserving biodiversity. American Zoologist 34: 48–56. https://doi.org/10.1093/icb/34.1.48

Greene HW (1997) Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley, 351 pp. https://doi.org/10.1525/9780520935433

Greene HW (2005) Organisms in nature as a central focus for biology. Trends in Ecology & Evolution 20: 23–27. https://doi.org/10.1016/j.tree.2004.11.005

Guedes TB (2006) Estrutura da comunidade de serpentes de uma área de Caatinga do Nordeste Brasileiro. Master's Dissertation, Rio Grande do Norte, Brazil: Universidade Federal do Rio Grande do Norte. http://www.dominiopublico.gov.br/pesquisa/DetalheObraForm.do?select_action=&co_obra=93560

Guedes TB, Nogueira C, Marques OAV (2014) Diversity, natural history, and geographic distribution of snakes in the Caatinga, Northeastern Brazil. Zootaxa 3863: 001–093. https://doi.org/10.11646/zootaxa.3863.1.1

Guedes T, Sawaya RJ, Zizka A, Laffan S, Faurby S, Pyron RA, Bérnils RS, Jansen M, Passos P, Prudente ALC, Cisneros-Heredia DF, Braz HB, Nogueira CC, Antonelli A (2018) Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. Global Ecology and Biogeography 27: 14–21. https://doi.org/10.1111/geb.12679

Hamdan B, Fernandes DS (2015) Taxonomic revision of *Chironius flavolineatus* (Jan, 1863) with description of a new species (Serpentes: Colubridae). Zootaxa 4012: 97–119. https://doi.org/10.11646/zootaxa.4012.1.5

Hartmann PA, Marques OAV (2005) Diet and habitat use of two sympatric *Philodryas* (Colubridae) in South Brazil. Amphibia-Reptilia 26: 25–31. https://doi.org/10.1163/1568538053693251

Hartmann PA, Hartmann MT, Martins M (2009) Ecology and natural history of a snake assemblage at Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, southeastern Brazil. Biota Neotropica 9: 173–184. https://doi.org/10.1590/S1676-06032009000300018

Instituto Chico Mendes de Conservação da Biodiversidade (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. ICMBio, Brasília, 4162 pp. https://www.icmbio.gov.br/portal/images/stories/comunicacao/publicacoes/publicacoes-diversas/livro_vermelho_2018_vol1.pdf

Jansen M (2006) Primeros registros de *Bothrops pauloensis* Amaral, 1925 (Serpentes: Viperidae) en Bolivia. Kempffiana 2: 66–71. http://museonoelkempff.org/sitio/Informacion/KEMPFFIANA/Kempffiana%202(1)/66-71.pdf

Jordão RS (1997) Estudo comparativo da alimentação e da reprodução de *Waglerophis merremii* e *Xenodon neuwiedii* (Serpentes: Colubridae). Master's Dissertation, São Paulo, Brazil: Universidade de São Paulo. https://repositorio.usp.br/item/000933858

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3: 157–164. https://doi.org/10.2307/3235676

Kronka FJN, Nalon MA, Matsukuma CK (2005) Inventário florestal da vegetação natural do estado de São Paulo. Secretaria do Meio Ambiente, Instituto Florestal, São Paulo.

Leão SM, Pelegrin N, Nogueira C, Brandão RA (2014) Natural History of *Bothrops itapetiningae* Boulenger, 1907 (Serpentes: Viperidae: Crotalinae), an Endemic Species of the Brazilian Cerrado. Journal of Herpetology 48: 324–331. https://doi.org/10.1670/12-191

López MS, Giraudo AR (2008) Ecology of the Snake *Philodryas patagoniensis* (Serpentes, Colubridae) from Northeast Argentina. Journal of Herpetology 42: 474–480. https://doi.org/10.1670/07-087.1

Maciel AP, Di-Bernardo M, Hartz SM, Oliveira RB, Pontes GMF (2003) Seasonal and daily activity patterns of *Liophis poecilogyrus* (Serpentes: Colubridae) on the north coast of Rio Grande do Sul, Brazil. Amphibia-Reptilia 24: 189–200. https://doi.org/10.1163/156853803322390435

Marques OAV (1996) Biologia Reprodutiva da Cobra-coral *Erythrolamprus aesculapii* Linnaeus (Colubridae), no sudeste do Brasil. Revista brasileira de Zoologia 13: 747–753. https://doi.org/10.1590/S0101-81751996000300022

Marques OAV (1998) Composição faunística, história natural e ecologia de serpentes da Mata Atlântica, na região da estação ecológica Juréia-Itatins, São Paulo, SP. Ph.D. thesis, São Paulo, Brazil: Universidade de São Paulo. https://ecoevo.com.br/publicacoes/pesquisadores/otavio_marques/teses/tesedoutoradoserpentesmatastlantica_1998.pdf

Marques OAV, Eterovic A, Guedes TB, Sazima I (2017) Serpentes da Caatinga: guia ilustrado. Ponto A, 240 pp.

Marques OAV, Eterovic A, Nogueira C, Sazima I (2015) Serpentes do Cerrado: Guia Ilustrado. Holos, Ribeirão Preto, 248 pp.

Marques OAV, Eterovic A, Sazima I (2019) Guia Serpentes da Mata Atlântica 2 edição. Ponto A, 319 pp.

Marques OAV, Eterovic A, Strüssmann C, Sazima I (2005) Serpentes do Pantanal: guia ilustrado. Holos, Ribeirão Preto, 179 pp.

Marques OAV, Pereira DN, Barbo FE, Germano VJ, Sawaya RJ (2009) Os Répteis do Município de São Paulo: diversidade e ecologia da fauna pretérita e atual. Biota Neotropica 9: 139–150. https://doi.org/10.1590/S1676-06032009000200014

Marques OAV, Pizzatto L, Almeida-Santos SM (2013) Reproductive Strategies of New World Coral Snakes, Genus *Micrurus*. Herpetologica 69(1): 58–66. https://doi.org/10.1655/HERPETOLOGICA-D-12-00091

Marques OAV, Puorto G (1998) Feeding, reproduction and growth in the crowned snake *Tantilla melanocephala* (Colubridae), from southeastern Brazil. Amphibia-Reptilia 19: 311–318. https://doi.org/10.1163/156853898X00214

Marques OAV, Sazima I (2004) História natural dos répteis da Estação Ecológica Juréia-Itatins. In: Marques OAV, Duleba W (Eds) Estação Ecológica Juréia-Itatins. Ambiente Físico, Flora e Fauna. Editora Holos, Ribeirão Preto, 257–277.

Martins M (1996) Defensive tactics in lizards and snakes: the potential contribution of the Neotropical fauna. In: Del Claro K (Ed.) Anais do XIV Encontro Anual de Etologia. Sociedade Brasileira de Etologia, Universidade Federal de Uberlândia, 185–199.

Martins M, Araújo MS, Sawaya RJ, Nunes R (2001) Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). Journal of Zoology 254: 529–538. https://doi.org/10.1017/S0952836901001030

Martins M, Marques OAV, Sazima I (2002) Ecological and Phylogenetic Correlates of Feeding Habits in neotropical Pitvipers of Genus Bothrops. In: Schuett GW, Hoggren M, Douglas ME (Eds) Biology of the Vipers. Eagle Mountain Publishing, Utah, 22 pp.

Martins M, Marques OAV, Sazima I (2008) How to be Arboreal and Diurnal and Still Stay Alive: Microhabitat Use, Time of Activity, and Defense in Neotropical Forest Snakes. South American Journal of Herpetology 3: 58–67. https://doi.org/10.2994/1808-9798(2008)3[58:HTBAAD]2.0.CO;2

Martins M, Nogueira C (2012) Collaboration with local people for sampling reptiles. In: McDiarmid RW, Foster MS, Guyer C, Gibbons JW, Chernoff N (Orgs) Reptile Biodiversity Standard Methods for Inventory and Monitoring. University of California Press, Berkeley, 86–88.

Martins M, Oliveira ME (1998) Natural history of snakes in forests of the Manaus region Central Amazonia Brazil. Herpetological Natural History 6: 78–150. http://eco.ib.usp.br/labvert/Martins%26Oliveira-HNH-1999.pdf

Mathies T (2011) Reproductive Cycles of Tropical Snakes. In: Aldrich RD, Sever DM (Eds) Reproductive Biology and Phylogeny of Snakes. Science Publishers, Enfield, New Hampshire, 511–550. https://doi.org/10.1201/b10879-13

Menegucci RC, Bernarde PS, Monteiro WM, Ferreira-Neto P, Martins M (2019) Envenomation by an opisthoglyphous snake, *Erythrolamprus aesculapii* (Dipsadidae), in southeastern Brazil. Journal of the Brazilian Society of Tropical Medicine 52: e20190055. https://doi.org/10.1590/0037-8682-0055-2019

Meira-Neto JAA, Martins FR, Valente GE (2007) Composição florística e espectro biológico na Estação Ecológica de Santa Bárbara, Estado de São Paulo, Brasil. Revista Árvore 31: 907–922. https://doi.org/10.1590/S0100-67622007000500015

Melo ACG, Durigan G (2011) Plano de Manejo da Estação Ecológica de Santa Bárbara. Instituto Florestal, Secretaria do Meio Ambiente de São Paulo. http://www.iflorestal.sp.gov.br/Plano_de_manejo/index.asp

Mesquita PCMD, Passos DC, Borges-Nojosa DM, Cechin SZ (2013a) Ecologia e História Natural das Serpentes de uma área da Caatinga do Nordeste Brasileiro. Papéis Avulsos de Zoologia 53: 99–113. https://doi.org/10.1590/S0031-10492013000800001

Mesquita PCMD, Sá-Polidoro GL, Cechin SZ (2013b) Reproductive biology of *Philodryas olfersii* (Serpentes, Dipsadidae) in a subtropical region of Brazil. Herpetological Journal, 23: 39–44. https://www.thebhs.org/publications/the-herpetological-journal

Morato SAA, Lima AMX, Staut DCP, Faria RG, Souza-Alves JP, Gouveia SF, Scupino MRC, Gomes R, Silva MJ (2011) Amphibians and Reptiles of the Refúgio de Vida Silvestre Mata do Junco, municipality of Capela, state of Sergipe, northeastern Brazil. Check List 7: 756–762. https://doi.org/10.15560/11015

Nogueira C (2001) Ecologia histórica de *Bothrops* spp. (Serpentes: Viperidae: Crotalinae) simpátricas no Cerrado. Master's Dissertation, São Paulo, Brazil: Universidade de São Paulo.

Nogueira C, Argôlo AJS, Arzamendia V, Azevedo JÁ, Barbo FE, Bérnils RS, Bolochio BE, Borges-Martins M, Brasil-Godinho M, Braz H, Buononato MA, Cisneros-Heredia DF, Colli GR, Costa HC, Franco FL, Giraudo A, Gonzalez RC, Guedes T, Hoogmoed MS, Marques OAV, Montigelli GG, Passos P, Prudente ALC, Rivas GA, Sanchez PM, Serrano FC, Silva NJ, Strüssmann C, Vieira-Alencar JPS, Zaher H, Sawaya RJ, Martins M (2019) Atlas of Brazilian Snakes: Verified Point-Locality Maps to Mitigate the Wallacean Shortfall in a Megadiverse Snake Fauna. South American Journal of Herpetology 14: 1–274. https://doi.org/10.2994/SAJH-D-19-00120.1

Nogueira C, Sawaya RJ, Martins M (2003) Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. Journal of Herpetology 37: 653–659. https://doi.org/10.1670/120-02A

Nunes SF (2006) Dieta e biologia reprodutiva da cruzeira, *Bothrops alternatus* (Serpentes – Viperidae), na região sul do Brasil. Master's Dissertation, Rio Grande do Sul, Brazil: Universidade Federal de Santa Maria. https://repositorio.ufsm.br/handle/1/11178

Oliveira ME, Martins M (2001) When and where to find a pitviper: activity patterns and habitat use of the lancehead, *Bothrops atrox*, in central Amazonia, Brazil. Herpetological Natural History 2: 101–110. https://www.researchgate.net/publication/236897131_When_and_where_to_find_a_pitviper_activity_patterns_and_habitat_use_of_the_lance-head_Bothrops_atrox_in_Central_Amazonia_Brazil

Orofino RP, Pizzatto L, Marques OAV (2010) Reproductive Biology and Food Habits of *Pseudoboa nigra* (Serpentes: Dipsadidae) from the Brazilian Cerrado. Phyllomedusa 9: 53–61. https://doi.org/10.11606/issn.2316-9079.v9i1p53-61

Peel MC, Finlayson BL, Mcahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 5: 1633–1644. https://doi.org/10.5194/hess-11-1633-2007

Piatti L, Rosauer DF, Nogueira CC, Strüssmann C, Ferreira VL, Martins M (2019) Snake diversity in floodplains of central South America: Is flood pulse the principal driver? Acta Oecologica 97: 34–41. https://doi.org/10.1016/j.actao.2019.04.003

Pinto RR (2006) Biologia reprodutiva e dieta de *Chironius flavolineatus* (Jan, 1863) e Chironius quadricarinatus (Boie, 1827) no Brasil (Serpentes: Colubridae). Master's Dissertation, Rio de Janeiro, Brazil: Universidade Federal do Rio de Janeiro.

Pinto RR, Fernandes R (2004) Reproductive biology and diet of *Liophis poecilogyrus* (Serpentes, Colubridae) from southeastern Brazil. Phyllomedusa 3: 9–14. https://doi.org/10.11606/issn.2316-9079.v3i1p9-14

Pinto RR, Fernandes R, Marques OAV (2008) Morphology and diet of two sympatric colubrid snakes, *Chironius flavolineatus* and *Chironius quadricarinatus* (Serpentes: Colubridae). Amphibia-Reptilia 29: 149–160. https://doi.org/10.1163/156853808784125027

Pinto RR, Marques OAV, Fernandes R (2010) Reproductive biology of two sympatric colubrid snakes, *Chironius flavolineatus* and *Chironius quadricarinatus*, from the Brazilian Cerrado domain. Amphibia-Reptilia 31: 463–473. https://doi.org/10.1163/017353710X518423

Pizzatto L, Jordão R, Marques OAV (2008) Overview of Reproductive Strategies in Xenodontini (Serpentes: Colubridae: Xenodontinae) with New Data for *Xenodon neuwiedii* and *Waglerophis merremii*. Journal of Herpetology 42: 153–162. https://doi.org/10.1670/06-150R2.1

Pizzatto L, Marques OAV (2002) Reproductive biology of the false coral *Oxyrhopus guibei* (Colubridae) from Southeastern Brazil. Amphibia-Reptilia 23: 495–504. https://doi.org/10.1163/15685380260462392

Pizzatto L, Marques OAV (2007) Reproductive Ecology of Boine Snakes with Emphasis on Brazilian species and a Comparison to Pythons. South American Journal of Herpetology 2: 107–122. https://doi.org/10.2994/1808-9798(2007)2[107:REOBSW]2.0.CO;2

Pontes GMF, Di-Bernardo M (1988) Registros sobre aspectos reprodutivos de serpentes ovíparas neotropicais (Serpentes: Colubridae e Elapidae). Comunicações do Museu de Ciências e Tecnologia da PUCRS 1: 123–149.

Prado CPA, Uetanabaro M, Haddad CFB (2005) Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. Amphibia-Reptilia, Brazil 26: 211–221. https://doi.org/10.1163/1568538054253375

Prieto YA, Giraudo AR, Pez MS (2012) Diet and Sexual Dimorphism of *Liophis poecilogyrus* (Serpentes, Dipsadidae) from the Wetland Regions of Northeast Argentina. Journal of Herpetology 46: 402–406. https://doi.org/10.1670/10-228

Reinert HK (1992) Radiotelemetric field studies of pitvipers: data acquisition and analysis. In: Campbell JA, Brodie EDJR (Eds) Biology of pitvipers. Eagle Mountain Publishing, Eagle Mountain, 185–197.

Resende FC, Nascimento LB (2015) The Female Reproductive Cycle of the Neotropical Snake *Atractus pantostictus* (Fernandes and Puorto, 1993) from South-eastern Brazil. Anatomia Histologia Embryologia 44: 225–235. https://doi.org/10.1111/ahe.12132

Rocha WA, Prudente ALC (2010) The snake assemblage of Parque Nacional de Sete Cidades, State of Piauí, Brazil. South American Journal of Herpetology 5: 132–142. https://doi.org/10.2994/057.005.0207

Rocha-Barbosa O, Moraes-e-Silva RB (2009) Analysis of the microstructure of Xenodontinae snake scales associated with different habitat occupation strategies. Brazilian Journal of Biology 69: 919–923. https://doi.org/10.1590/S1519-69842009000400021

Roze JA (1996) Coral snakes of the Americas: Biology, identification and venoms. Krieger Publishing Company, Malabar, Florida, 340 pp.

Salomão MG, Santos SMA, Puorto G (2005) Activity Pattern of *Crotalus durissus* (Viperidae, Crotalinae): Feeding, Reproduction and Snakebite. Studies on Neotropical Fauna and Environment 30: 101–106. https://doi.org/10.1080/01650529509360946

Sanders H (1968) Marine benthic diversity: a comparative study. The American Naturalist, 102: 243–282. https://doi.org/10.1086/282541

Sant'Anna S, Abe A (2007) Diet of the rattlesnake *Crotalus durissus* in Southeastern Brazil (Serpentes, Viperidae). Studies on Neotropical Fauna and Environment 42: 169–174. https://doi.org/10.1080/01650520601148313

Santos-Costa MC, Prudente ALC, Di-Bernardo M (2006) Reproductive biology of *Tantilla melanocephala* (Linnaeus, 1758) (Serpentes, Colubridae) from Eastern Amazonia, Brazil. Journal of Herpetology 40: 553–556. https://doi.org/10.1670/0022-1511(2006)40[553:RBOTML]2.0.CO;2

São-Pedro VA, Pires MRS (2009) As Serpentes da Região de Ouro Branco, extremo sul da Cadeia do Espinhaço, Minas Gerais. Ceres 56: 166–171. http://www.ceres.ufv.br/ojs/index.php/ceres/article/view/3421

Savitzky AH (1979) The origin of the New World proteroglyphous snakes and its bearing on the study of the venom delivery systems in snakes. Ph.D. thesis, Kansas, United States: University of Kansas.

Sawaya RJ (2004) História natural e ecologia das serpentes de Cerrado da região de Itirapina, SP. Ph.D. thesis, Campinas, Brazil: Universidade Estadual de Campinas.

Sawaya RJ, Marques OAV, Martins M (2008) Composition and natural history of a Cerrado snake assemblage at Itirapina, São Paulo state, southeastern Brazil. Biota Neotropica 8: 129–151. https://doi.org/10.1590/S1676-06032008000200015

Sazima I, Abe AS (1991) Habits of five Brazilian snakes with coral-snake pattern including a summary of defensive tactics. Studies on Neotropical Fauna and Environment 26: 159–164. https://doi.org/10.1080/01650529109360848

Sazima I, Haddad CFB (1992) Répteis da Serra do Japi: notas sobre história natural. In: Morellato LPC (Ed.) História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil. Editora da Unicamp/FAPESP, São Paulo, 212–236.

Sazima I, Manzini PR (1995) As cobras que vivem numa reserva florestal urbana. In: Morellato PC, Leitão-Filho HF (Eds) Ecologia e Preservação de uma Floresta Tropical Urbana. Ed. Unicamp, Campinas, 78–119.

Serrano-Filho S (2012) Diversidade e distribuição dos lagartos de uma área de ecótono entre Cerrado e Mata Atlântica, no sudeste do Brasil. Ph.D. thesis, São Paulo, Brazil: Universidade Estadual Paulista. https://repositorio.unesp.br/handle/11449/87581

Strüssmann C, Sazima I (1993) The Snake Assemblage of the Pantanal at Poconé, Western Brazil: Faunal Composition and Ecological Summary. Studies on Neotropical Fauna and Environment 28: 157–168. https://doi.org/10.1080/01650529309360900

Tozetti AM, Martins M (2008) Habitat use by the South American rattlesnake (*Crotalus durissus*) in southeastern Brazil. Journal of Natural History 42: 1435–1444. https://doi.org/10.1080/00222930802007823

Tozetti AM, Vettorazzo V, Martins M (2009) Short-term movements of the South American rattlesnake (*Crotalus durissus*) in south-eastern Brazil. Herpetological Journal 19: 201–206. https://www.thebhs.org/publications/the-herpetological-journal

Valdujo PH, Nogueira C, Martins M (2002) Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian cerrado. Journal of Herpetology 36: 169–176. https://doi.org/10.1670/0022-1511(2002)036[0169:EOBNPS]2.0.CO;2

Vitt LJ (1992) Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation. In: Hamlett WC (Ed) Reproductive Biology of South American Vertebrates. Springer-Verlag, NY, 135–149. https://doi.org/10.1007/978-1-4612-2866-0_10

Vitt LJ, Colli GR, Caldwell JP, Mesquita DO, Garda AA, França FGR (2007) Detecting variation in microhabitat use in low-diversity lizard assemblages across small-scale habitat gradients. Journal of Herpetology 41: 654–663. https://doi.org/10.1670/06-279.1

Vitt LJ, Vangilder LD (1983) Ecology of snake community in the northeastern Brazil. Amphibia-Reptilia 4: 273–296. https://doi.org/10.1163/156853883X00148

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Yanosky AA, Dixon JR, Mercolli C (1996) Ecology of the snake community at el Bagual Ecological Reserve, Northeastern Argentina. Herpetological Natural History 4: 97–110.

Appendix I

Specimens examined; field number acronyms mean Marcio Roberto Costa Martins (the senior author's full name). All these specimens will be deposited in the herpetological collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Instituto Butantan

Apostolepis dimidiata (10) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1256, 1702, 1802, 387, 463, 483, 512, 524, 541, 545.

Atractus pantostictus (4) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 11, 100, 389, 427.

Boa constrictor (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 386.

Bothrops itapetiningae (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 366.

Bothrops alternatus (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 497.

Bothrops moojeni (4) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 215, 240, 293, 338.

Bothrops pauloensis (11) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, IBSP-90.262/sb0514–515, MRCM 248, 256, 356, 425, 432, 484, 507, 1024, 1226.

Chironius brazili (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 482.

Chironius quadricarinatus (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1275.

Crotalus durissus (10) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 289, 354, 392, 421, 485, 505, 1107, 1218, 1273, 1806.

Dipsas mikanii (2) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 475, 1288.

Epicrates crassus (2) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 359, 395.

Erythrolamprus aesculapii (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 252, 361, 424.

Erythrolamprus almadensis (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1289.

Erythrolamprus poecilogyrus (3) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 241, 369, 1277.

Erythrolamprus reginae (4) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 368, 434, 508, 1265.

Liotyphlops ternezii (2) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 433, 458.

Micrurus frontalis (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 489.

Micrurus lemniscatus (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1700.

Oxyrhopus guibei (12) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 217, 249, 325, 326, 344, 431, 466, 1000, 1183, 1216, 1276, 1388.

Oxyrhopus rhombifer (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, not labeled.

Phalotris lativittatus (10) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 200, 315, 316, 317, 322, 370, 406, 518, 535, 1222.

Phalotris mertensi (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1296.

Philodryas olfersii (2) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1255, 1304.

Philodryas patagoniensis (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 1287.

Pseudoboa nigra (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 342.

Rachidelus brazili (1) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, IBSP 89664.

Taeniophallus occipitalis (7) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 435, 510, 523, 532, 1281, 1294, 1387.

Tantilla melanocephala (7) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 274, 291, 345, 461, 514, 544, 1298.

Thamnodynastes hypoconia (4) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 221, 222, 339, 534.

Trilepida koppesi (24) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 290, 292, 294, 307–314, 318, 321, 323, 327, 328, 340, 355, 381–383, 457, 546, 1375.

Xenodon merremii (3) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 319, 423, 495.

Xenodon nattereri (2) – Brazil: ÁGUAS DE SANTA BÁRBARA: Estação Ecológica de Santa Bárbara, MRCM 517, 1749.

Supplementary material 1

Sampling efficiency evaluation
Authors: Bruno F. Fiorillo, Jorge Henry Maciel, Marcio Martins
Data type: Analyses
Explanation note: **Figure S1.** Rarefaction curve representing the snake species richness observed (A) and the richness estimated by the Jackknife-1 estimator (B) for all methods together, and for each method used, accidental encounters (C), observations by local people (D), pitfall traps (E), and time constrained search (F) at the Santa Bárbara Ecological Station, state of São Paulo, Brazil. **Table S1.** Snake species richness (SR), number of individuals (Ind.), number of exclusive species, estimated richness of first order Jackknife, Shannon diversity index and dominance of each method used. **Table S2.** Number of snake individuals obtained by sampling method at the Santa Bárbara Ecological Station, SP, between August 2016 and July 2018.

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RESEARCH ARTICLE

Two new species of freshwater crab of the genus *Aparapotamon* Dai & Chen, 1985 (Crustacea, Brachyura, Potamidae) from Yunnan, China

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Abstract

Two new species of freshwater crab of the genus Potamid *Aparapotamon* Dai & Chen, 1985 are described from Yunnan Province, southwest China. Morphological comparisons were made between the two new species and type materials of other 11 species of *Aparapotamon*. *Aparapotamon binchuanense* **sp. nov.** and *A. huizeense* **sp. nov.** can be separated from their congeners by the shape of the epibranchial tooth, the frontal view of the cephalothorax, the male first gonopod, and the female vulvae. The molecular analyses based on partial mitochondrial 16S rRNA gene are also included. This study brings the number of *Aparapotamon* species to 13.

Keywords

Aparapotamon, freshwater crab, new species, taxonomy, 16S rRNA

Introduction

Crabs of the family Potamidae Ortmann, 1896 (Crustacea, Decapod, Brachyura) spend their whole life history in freshwater or terrestrial environments (Yeo et al. 2008). The juvenile crabs hatch directly from large and yolky eggs, and there is no larval phase in their life history, so they are considered true freshwater crabs (Yeo et al. 2008; Daniels et al. 2015).

Due to their low fecundity and poor dispersal abilities, these crabs are easily blocked by geographical barriers, and their phylogeny often closely reflects relevant historical geological events (Shih et al. 2009, 2011; Fang et al. 2015; Ji et al. 2016; Jia et al. 2018).

Previous studies have shown that China has the world's highest number of freshwater crab species (Dai 1999; Cumberlidge et al. 2011; Shih and Ng 2011; Daniels et al. 2015; Chu et at. 2018a). Despite this substantial diversity, the rate of discovery remains high (Chu et al. 2018b; Huang et al. 2018a, b, 2020a, b; Naruse et al. 2018; Zou et al. 2018; Gao et al. 2019; Wang et al. 2019a, b, 2020a, b; Mao and Huang 2020). With the two new species described in this study, Yunnan has a total of 18 genera and 67 species, highest among all provinces in China (Chu et al. 2018a; Wang et al. 2020). Yunnan is a possible center of origin for the family Potamidae and is located in the southwest of China (Shih and Ng 2011). It is at the junction of the Asiatic Plate and the Indian Plate (Harrison et al. 1992), the geological movement remains active, the complex geographical features of this area have contributed to the rapid differentiation of crabs (Shih et al. 2009), so species of this area is richer than that in other places at the same latitude such as Guangxi Zhuang Autonomous Region and Guangdong Province (Shih and Ng 2011).

Aparapotamon was established by Dai and Chen (1985), and eleven species have been reported so far. Since all the species are from Yunnan, Sichuan, Guangxi, Hunan, Hubei, Chongqing, and Shaanxi but with only *A. gracilipedum* Chen & Chang, 1982 known from Henan Province (Dai 1999). The two new species of *Aparapotamon* collected from Yunnan Province are herein described. Morphological comparisons were made between the two new species and type materials of other eleven species of *Aparapotamon*. To analyze the phylogenetic relationship between these species and its congeners, we use the mitochondrial 16S rRNA gene for phylogenetic analysis, which has been proved to be useful in crab taxonomy (Schubart 2000; Bai et al. 2018).

Materials and methods

Specimens were collected by Han Dai from Biji Village (25°53'34"N, 100°55'30"E, alt. 1658 m), Lawu Town, Binchuan County, Dali Bai Autonomous Prefecture, Yunnan Province and Yue Huang from Zebu Village (26°30'41"N, 103°10'25"E, alt. 1954 m), Nagu Town, Huize County, Qujing City, Yunnan Province, respectively. All materials were preserved in 95% ethanol and deposited in the Department of Parasitology of the Medical College of Nanchang University, Jiangxi, China (**NCU MCP**). Carapace width and length were measured in millimeters. The abbreviation of G1 and G2 are for male first gonopod and the male second gonopod, respectively. The terminology used primarily follows that of Dai (1999) and Davie et al. (2015).

We compared two new species with type materials of other eleven species of *Aparapotamon* deposited in Chinese Academy of Sciences, Beijing, China (CAS CB). Comparative materials are as follows:

• *Aparapotamon arcuatum* Dai & Chen, 1985: Holotype, CAS CB 05091, 1♂, China, Yunnan Province, Lijiang City, Ninglang Yi Autonomous County, Daxing Town, 14 Aug 1981; NCU MCP 4032, 1♂, China, Yunnan Province, Lijiang City, Yongsheng County, Yangping Yi Autonomous Town, 6 Jul 2017.

• *Aparapotamon emineoforaminum* Dai & Chen, 1985: Holotype, CAS CB 05090, 1♂, China, Sichuan Province, Liangshan Yi Autonomous Prefecture, Mianning County, Jionglong Town, Aug 1982.

• *Aparapotamon gracilipedum* Chen & Chang, 1982: Holotype, CAS CB 05148, 1♂, China, Henan Province, Luoyang City, Luanchuan County, Chenguan Town, 20 Sep 1978.

• *Aparapotamon grahami* Rathbun, 1929: CAS CB 00142, 1♂, China, Hubei Province, Nanyang City, 1977; CAS CB 00150, 1♂, China, Shannxi Province, Ankang City, Zhenping County, 16 Jul 1978; NCU MCP 4057, 1♂, China, Chongqing City, Wulong County, Dadonghe Town, 24 Jun 2018; NCU MCP 4241, 1♂, China, Yunnan Province, Kunming City, 31 Aug 2019.

• *Aparapotamon huiliense* Dai & Chen, 1985: Holotype, CAS CB 05089, 1♂, China, Sichuan Province, Liangshan Yi Autonomous Prefecture, Huili County, 2 Jun 1982; NCU MCP 4027, 1♂, China, Yunnan Province, Lijiang City, Huaping County, Zhongxin Town, Zuofang Village, 5 Jul 2017.

• *Aparapotamon inflomanum* Dai & Chen, 1985: Holotype, CAS CB 05096, 1♂, China, Yunnan Province, Diqing Zang Autonomous Prefecture, Zhongdian County, Sanba Town, 8 Sep 1981.

• *Aparapotamon molarum* Dai & Chen, 1985: Holotype, CAS CB 05094, 1♂, China,Yunnan Province, Lijiang City, Yulong Naxi Autonomous County, Jade Dragon Snow Mountain, 28 Aug 1981.

• *Aparapotamon muliense* Dai & Chen, 1990: Holotype, CAS CB 05088, 1♂, China, Sichuan Province, Liangshan Yi Autonomous Prefecture, Muli Zang Autonomous County, Xiaojin River, 5 Dec 1984.

• *Aparapotamon protinum* Dai & Chen, 1985: Holotype, CAS CB 05093, 1♂, China, Yunnan Province, Lijiang City, Yongsheng County, Songping Town, 22 Aug 1981.

• *Aparapotamon similium* Dai & Chen, 1985: Holotype, CAS CB 05095, 1♂, China, Yunnan Province, Lijiang City, Yongsheng County, Renli Town, 22 Aug 1981; NCU MCP 4031, 1♂, China,Yunnan Province, Lijiang City, Ninglang Yi Autonomous County, Paomaping Town, 6 Jul 2017.

• *Aparapotamon tholosum* Dai & Chen, 1985: Holotype, CAS CB 05092, 1♂, China, Yunnan Province, Lijiang City, Yongsheng County, Chenguan Town, 22 Aug 1981; NCU MCP 4034, 1♂, China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Zhoucheng Town, 5 Jul 2017.

Institutional abbreviations used in the paper are as follows:

CAS CB   Chinese Academy of Sciences, Beijing, China;
NCHUZOOL   Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan;

NCU MCP	Department of Parasitology of the Medical College of Nanchang University, Jiangxi, China;
NNU	College of Life Sciences, Nanjing Normal University, Nanjing, China;
SYSBM	Sun Yat-sen Museum of Biology, Sun Yat-Sen University, Guangzhou, China;
ZRC	Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

The pereiopod muscle tissue was extracted from specimens of the new species with a DP1902 Tissue Kit (BioTeKe Inc. Beijing). Partial mitochondrial 16S rRNA gene sequences were obtained by PCR amplification with the primers 1471 (5'-CCTGTTTAN-CAAAAACAT-3') and 1472 (5'-AGATAGAAACCAACCTGG-3') (Shih et al. 2004). The parameters of the PCR were as follows: denaturation for 50 s at 94 °C, annealing for 40 s at 52 °C, extension for 1 min at 72 °C (33 cycles) and extension for 10 min at 72 °C. The PCR products were examined on an ABI 3730 automatic sequencer to sequence.

For molecular analysis, 30 partial sequences of 16S rRNA gene were used to construct BI and ML phylogenetic trees, including those of 27 species in 22 genera of potamids (Table 1). Sequences were aligned using MAFFT vers.7.355 (Nakamura et al. 2018) based on the G-INS-I method and the conserved regions were selected with

Table 1. Specimens used in the phylogenetic analysis.

Species	Museum catalogue no.	Locality	GenBank no.	Reference
Aparapotamon grahami	ZRC	Yunnan, China	AB428489	Shih et al. 2009
Cryptopotamon anacoluthon Kemp, 1918	NCHUZOOL 13122	Hong Kong	AB428453	Shih et al. 2009
Daipotamon minos Ng & Trontelj, 1996	ZRC	Guizhou, China	LC198524	Huang et al. 2017b
Diyutamon cereum Huang, Shih & Ng, 2017	SYSBM	Guizhou, China	LC198520	Huang et al. 2017b
Mediapotamon leishanense Dai, 1995	SYSBM001094	Guizhou, China	LC155164	Shih et al. 2016
Minpotamon nasicum Dai & Chen, 1979	NCHUZOOL 13121	Fujian, China	AB428450	Shih et al. 2009
Nanhaipotamon hongkongense Shen, 1940	ZRC	Hong Kong, China	AB212869	Shih et al. 2005
Parapotamon spinescens Calman, 1905	NCU MCP	Yunnan, China	AB428467	Shih et al. 2009
Pararanguna semilunatum Dai & Chen, 1985	ZRC	Yunnan, China	AB428490	Shih et al. 2009
Potamiscus yongshengense Dai & Chen, 1985	NNU150951	Yunnan, China	KY963597	Chu et al. 2017
Socotrapotamon nojidensis Apel & Brandis, 2000	ZRC 2000.2232	Socotra, Yemen	AB428493	Shih et al. 2009
Tenuipotamon huaningense Dai & Bo, 1994	CAS CB05175	Yunnan, China	AB428491	Shih et al. 2009
Trichopotamon daliense Dai & Chen, 1985	NCHUZOOL 13130	Yunnan, China	AB428492	Shih et al. 2009
Yarepotamon fossor Huang, 2018	SYSBM 001417	Guangxi, China	MG709238	Huang 2018
Artopotamon latopeos Chu, Wang & Sun, 2018	NNU 170502	Yunnan, China	MH045061	Chu et al. 2018b
Arquatopotamon jizushanense Chu, Zhou & Sun, 2017	NNU 160506 (holotype)	Yunnan, China	KY963596	Chu et al. 2017
Semicirculara lincangensis Chu, Wang & Sun, 2018	NNU 1605	Yunnan, China	MH045059	Chu et al. 2018b
Tenuilapotamon latilum Chen, 1980	ZRC	Hubei, China	AB428468	Shih et al. 2009
Sinopotamon davidi Rathbun, 1904	CAS CB	Shaanxi, China	LC155132	Shih et al. 2016
Tiwaripotamon xiurenense Dai & Naiyanetr, 1994	CAS CB	Guangxi, China	LC198522	Huang et al. 2017b
Cantopotamon zhuhaiense Huang, Ahyong & Shih, 2017	SYSBM 001439	Guangdong, China	LC342045	Huang et al. 2017a
Qianguimon splendidum Huang, 2018	SYSBM 001598	Guangxi, China	MG709241	Huang 2018
Artopotamon compressum	NCU MCP 4033	Yunnan, China	MN594116	This study
Aparapotamon huiliense	NCU MCP 4027	Yunnan, China	MN594113	This study
Aparapotamon huiliense	NCU MCP 4031	Yunnan, China	MN594118	This study
Aparapotamon similium	NCU MCP 4035	Yunnan, China	MN594114	This study
Aparapotamon binchuanense sp. nov.	NCU MCP 1707	Yunnan, China	MN943639	This study
Aparapotamon binchuanense sp. nov.	NCU MCP 1707	Yunnan, China	MN594120	This study
Aparapotamon huizeense sp. nov.	NCU MCP 1798	Yunnan, China	MN594121	This study
Aparapotamon huizeense sp. nov.	NCU MCP 1798	Yunnan, China	MN594122	This study

Gblocks 0.91b (Castresana 2000). The best-fitting model for Bayesian Inference (BI) analysis was determined by MrModeltest ver. 2.3 (Nylander 2004), selected by the Akaike information criterion (AIC). The obtained model was GTR+I+G. MrBayes 3.2.6 (Ronquist et al. 2012) was employed to perform BI analysis, and four Monte Carlo Markov Chains of 2,000,000 generations were run with sampling every 1,000 generations. The first 500,000 generations were discarded as burn-in. The best evolutionary model for Maximum Likelihood (ML) analysis was HKY+G, determined by MEGA X (Kumar et al. 2018) based on the Bayesian information criterion (BIC). A ML tree was built based on 1000 bootstrap replicates in MEGA X (Kumar et al. 2018). The pairwise distance based on the K2P (Kimura 2-Parameter) model was calculated by MEGA X (Kumar et al. 2018).

Results

Systematics

Family Potamidae Ortmann, 1896

***Aparapotamon* Dai & Chen, 1985**

Type species. *Aparapotamon grahami* Dai & Chen, 1985

***Aparapotamon binchuanense* sp. nov.**
http://zoobank.org/05703d3e-5f19-4587-9494-c1afb7df8327
Figures 1–4

Material examined. *Holotype*: NCU MCP 170701, 1♂ (17.1 × 13.6 mm), China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Lawu Town, 25°53'34"N, 100°55'30"E, alt. 1658 m, 10 Aug 2010, Han Dai leg. *Paratypes*: NCU MCP 170702, NCU MCP 170704, NCU MCP 170705, 3♂♂ (15.7 × 13.1 mm, 15.6 × 12.5 mm, 14.3 × 11.6 mm) and NCU MCP 170703, NCU MCP 170706, NCU MCP 170707, 3♀♀ (21.4 × 17.1 mm, 20.8 × 16.8 mm, 19.0 × 15.6 mm), same data as holotype.

Diagnosis. Carapace trapezoidal, regions defined. External orbital angle triangular, postorbital cristae convex, postfrontal lobe prominent. Cervical groove indistinct, H-shaped groove conspicuous. Epibranchial tooth blunt, anterolateral margin lined with numerous granules. Third maxilliped exopod without flagellum. Adult male and female chelipeds slightly unequal. Ambulatory legs relatively slender. Male sterno-pleonal cavity deep, median longitudinal groove between sternites 7/8 long. Male pleon narrow triangular, telson triangular. Vulva small, ovate, located close to each other at anterior part of sternites 6, posterior margin not convex. G1 slender, distal end tapering, distinctly bent. G2 basal segment ovate, tip of terminal segment laterally flattened.
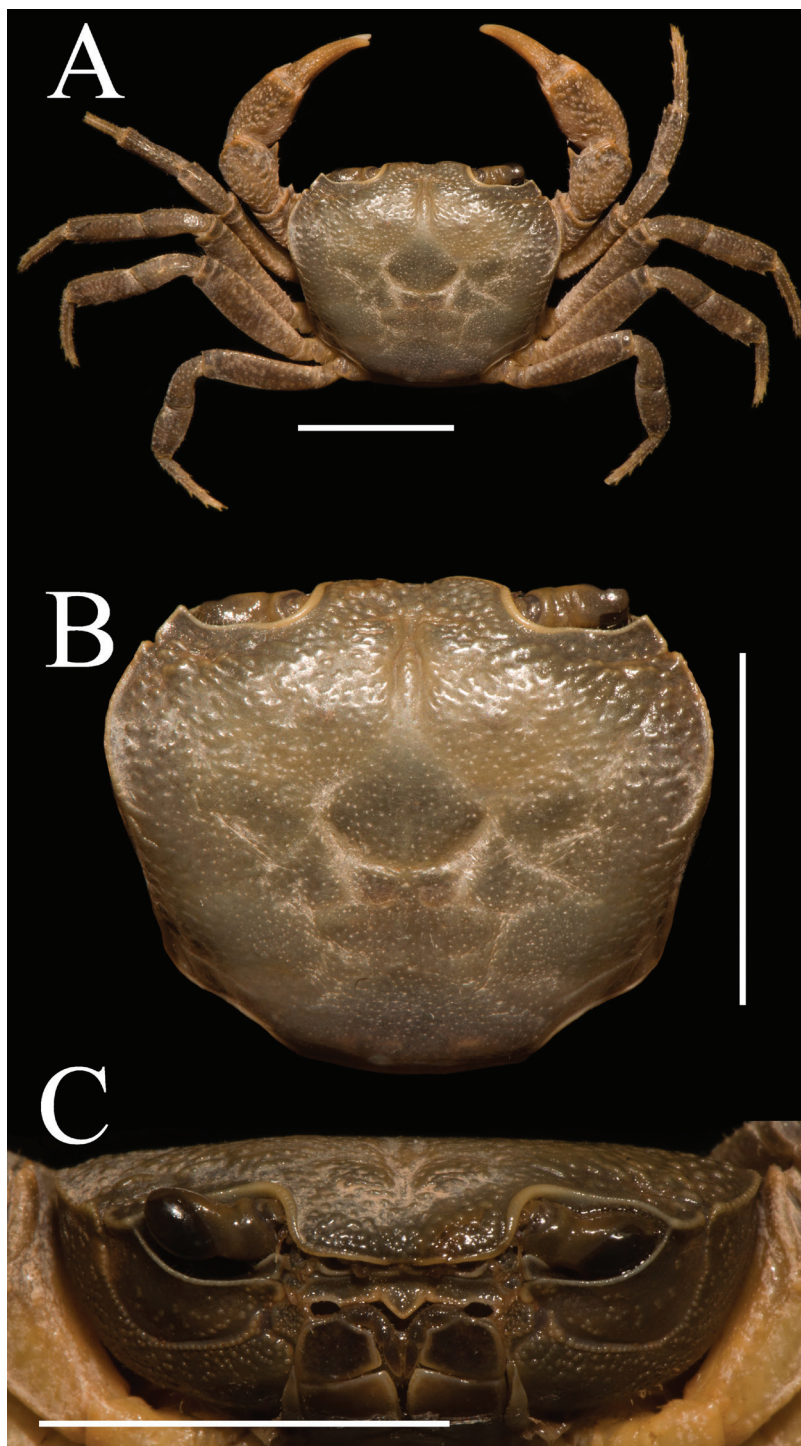
Figure 1. *Aparapotamon binchuanense* sp. nov. Holotype male (17.1 × 13.6 mm) (NCU MCP 170701). **A** overall habitus **B** dorsal view of carapace **C** frontal view of the cephalothorax. Scale bars: 1 cm.
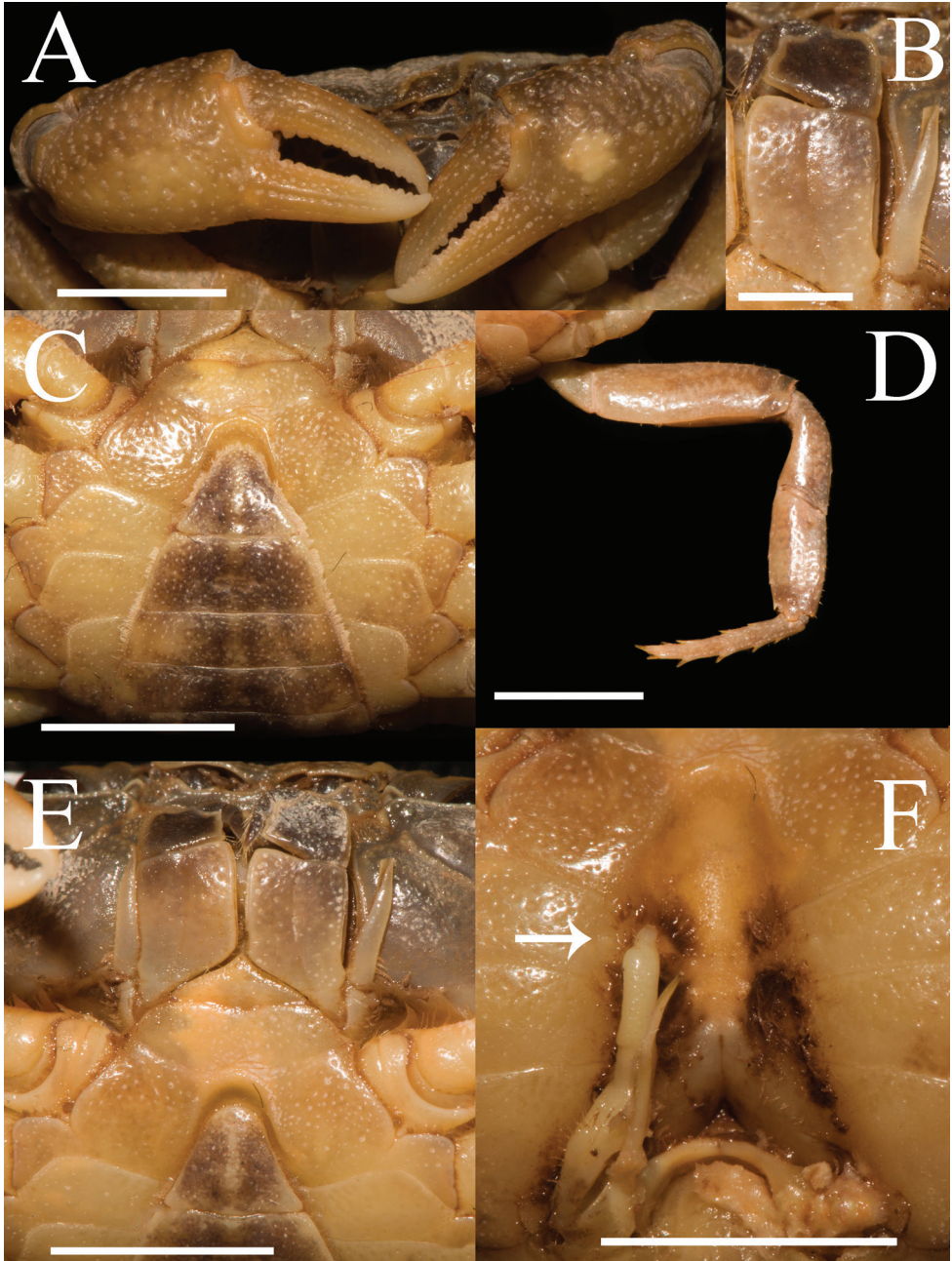
Figure 2. *Aparapotamon binchuanense* sp. nov. Holotype male (17.1 × 13.6 mm) (NCU MCP 170701). **A** outer view of chelipeds **B** left third maxilliped **C** ventral view of anterior thoracic sternum and pleon **D** right fourth ambulatory leg **E** ventral view of anterior thoracic sternum and third maxilliped **F** ventral view of sterno-pleonal cavity with right G1 in situ; arrow indicates pleonal locking tubercle. Scale bars: 2 mm (**B**); 5 mm (**A, C–F**).
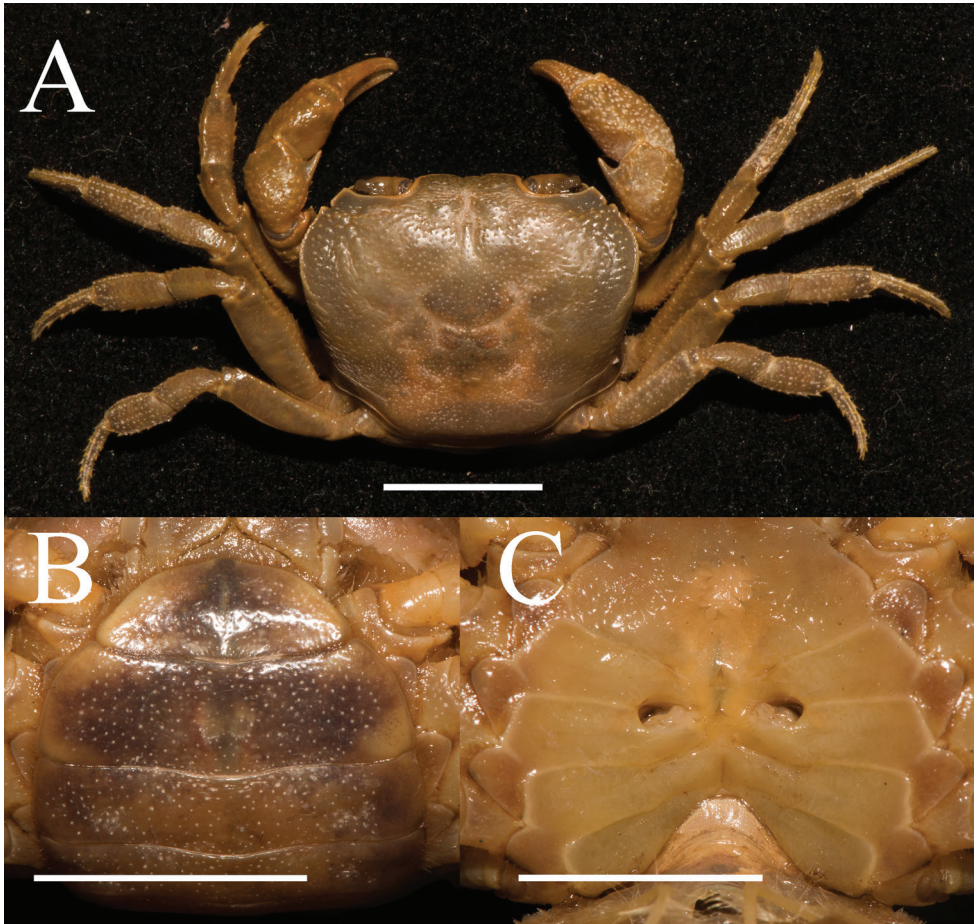
Figure 3. *Aparapotamon binchuanense* sp. nov. Paratype female (21.4 × 17.1 mm) (NCU MCP 170703) **A** overall habitus **B** ventral view of pleon **C** vulvae. Scale bars: 1 cm.

Description. Carapace width 1.25 × length (n = 7), regions defined; dorsal surface slightly convex (Figs 1A, B, 3A). External orbital angle triangular, separated from anterolateral margin by conspicuous notch (Figs 1A, C, 3A). Postorbital cristae gently convex, continuous to epibranchial tooth; postfrontal lobe prominent, separated medially by inverted Y-shaped groove (Figs 1A, B, 3A). Cervical groove indistinct; H-shaped gastro-cardiac groove distinct (Figs 1A, B, 3A). Epibranchial tooth blunt, rounded; anterolateral margin cristae, curved inward posteriorly, lined with approximately 15–17 fused granules; posterolateral surface slightly smooth, with some inconspicuous oblique striae, converging towards posterior carapace margin (Figs 1A, B, 3A). Orbits and eyes large; supraorbital margin ridged, infraorbital margin cristate, minutely granulated (Fig. 1C). Pterygostomial and sub-hepatic regions covered with dense round granules, sub-orbital region with sparse granules (Fig. 1C).
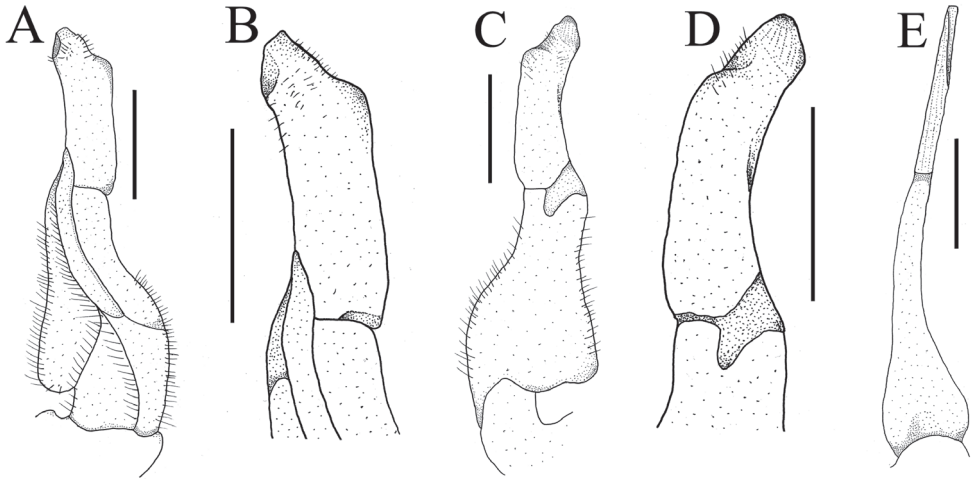
Figure 4. *Aparapotamon binchuanense* sp. nov. Holotype male (17.1 × 13.6 mm) (NCU MCP 170701) **A** ventral view of left G1 **B** ventral view of terminal segment of left G1 **C** dorsal view of left G1 **D** dorsal view of terminal segment of left G1 **E** ventral view of left G2. Scale bars: 1 mm.

Epistome posterior margin median lobe equilateral triangular, lateral margin with small projection (Fig. 1C).

Third maxilliped exopod without flagellum, claviform, reaching proximal 1/3 of merus lateral margin (Figs 1C, 2B, E). Ischium about 1.3 times as long as broad, rectangular, with distinct longitudinal median sulcus (Fig. 2B, E). Merus about 1.4 times as broad as long, subquadrate, median slightly depressed (Figs 1C, 2B, E).

Chelipeds slightly unequal in both adult male and female, right cheliped larger (Fig. 2A). Palm of larger cheliped length 1.4 × height (n = 7); dactylus 0.7 × palm length (n = 7); dactylus as long as pollex (Figs 1A, 2A, 3A). Merus outer surface punctate; carpus surface covered with several prominent granules and sharp spine at inner-distal angle (Figs 1A, 3A). Occlusal margins of fingers of adult male with numerous sparse round blunt teeth, with narrow gap when fingers closed (Fig. 2A). Ambulatory legs very slender; second ambulatory legs longest; fourth ambulatory leg propodus 2.1 × as long as broad (n = 7), shorter than dactylus, which accompanied with several thorn-like spines (n = 7) (Figs 1A, 2D).

Male thoracic sternum punctate, formed by tidy depression; sternites 1–4 broad, sternites 1/2 completely continuous; suture 2/3 complete, transverse; suture 3/4 visible, mesially reaching distolateral part of sterno-pleonal cavity (Fig. 2E). Male sterno-pleonal cavity deep; median longitudinal groove between sternites 7/8 long; male pleonal locking tubercle inconspicuous, positioned medially on sternite 5 (Fig. 2F, arrow). Male pleon narrow triangular (Fig. 2C); telson triangular, apex rounded, width 1.3 × length in males (n = 4), 1.8 × in females (n = 3); somite 6 trapezoidal, width 2.5 × length in males (n = 4), 3.3 × in females (n = 3) (Figs 2C, 3B). Vulvae small, ovate, located close to each other at anterior part of sternites 6, pushing mesial portions of

sutures 5/6 forward, deeper laterally, posterior margin not convex, the sternal vulvar cover triangular, positioned mesially (Fig. 3C).

G1 slender; terminal segment claviform, distal end tapering, distinctly bent, inner margin arc-shaped, outer margin straight, dorsal lobe barely visible in ventral view (Fig. 4A–D); tip reaching beyond pleonal locking tubercle but not exceed sternites 4/5 in situ (Fig. 2F); clear boundary between terminal segment and subterminal segment, latter length about 0.7 × length of terminal segment (Fig. 4A, C). G2 basal segment ovate, about 1.5 × length of terminal segment, tip of terminal segment flat rather than sharp (Fig. 4E).

Etymology. The species is named after the type locality, Binchuan County, Dali Bai Autonomous Prefecture, Yunnan Province.

Distribution. The new species is presently known only from the type locality, Binchuan County, Dali Bai Autonomous Prefecture, Yunnan Province.

Remarks. *Aparapotamon binchuanense* sp. nov. closely resembles congeners in general carapace morphology. However, *A. binchuanense* sp. nov. can be distinguished from other species by the terminal segment of G1, which is claviform, with distal end tapering and distinctly bent (Fig. 9A) [vs. terminal segment of G1 disc-shaped, straight in *A. inflomanum* and *A. molarum* (Fig. 9C, D), terminal segment of G1 of *A. emineoforaminum* tapering distally but not bent (Fig. 9E), terminal segment of G1 arc-shaped in *A. arcuatum* and *A. muliense* (Fig. 9H, I), and terminal segment of G1 of *A. tholosum*, *A. protinum*, *A. grahami*, *A. huiliense*, *A. similium* and *A.gracilipedum* claviform, not bent (Fig. 9F, G, J-M)]. In addition, in *A. binchuanense* sp. nov., the pterygostomial region is densely covered with round granules, while in the sub-orbital region the granules are sparse.

(Fig. 1C). This character can also distinguish *A. binchuanense* sp. nov. from congeners. For detailed differences between this new species and congeners, see Table 2.

Aparapotamon huizeense sp. nov.

http://zoobank.org/9b44a1c4-162b-4db0-be6c-dce5124412b0
Figures 5–8

Material examined. *Holotype*: NCU MCP 179801, 1♂ (25.9 × 21.2 mm), China, Yunnan Province, Qujing City, Huize County, Nagu Town, Zebu Village, 26°30'41"N, 103°10'25"E, alt. 1954 m, 25 Aug 2011, Yue Huang leg. *Paratypes*: NCU MCP 179802, 1♂ (26.9 × 21.9 mm) and NCU MCP 179803–179808, 6♀♀ (31.0 × 24.8 mm, 30.7 × 23.6 mm, 27.3 × 21.5 mm, 23.5 × 18.4 mm, 25.5 × 20.5 mm, 29.8 × 22.6 mm), same data as holotype.

Diagnosis. Carapace trapezoidal, dorsal surface slightly convex, regions defined. External orbital angle round, separated from anterolateral margin, postorbital cristae convex, postfrontal lobe prominent. Cervical groove shallow, H-shaped groove distinct, especially in female specimen. Epibranchial tooth distinct, especially in female specimen. Third maxilliped exopod without flagellum. Ambulatory legs slender. Male pleon broad triangular, telson triangular, apex rounded. Vulva ovate, covering anterior half of sternite 6, with the posterior margin distinctly convex. G1 very slender,
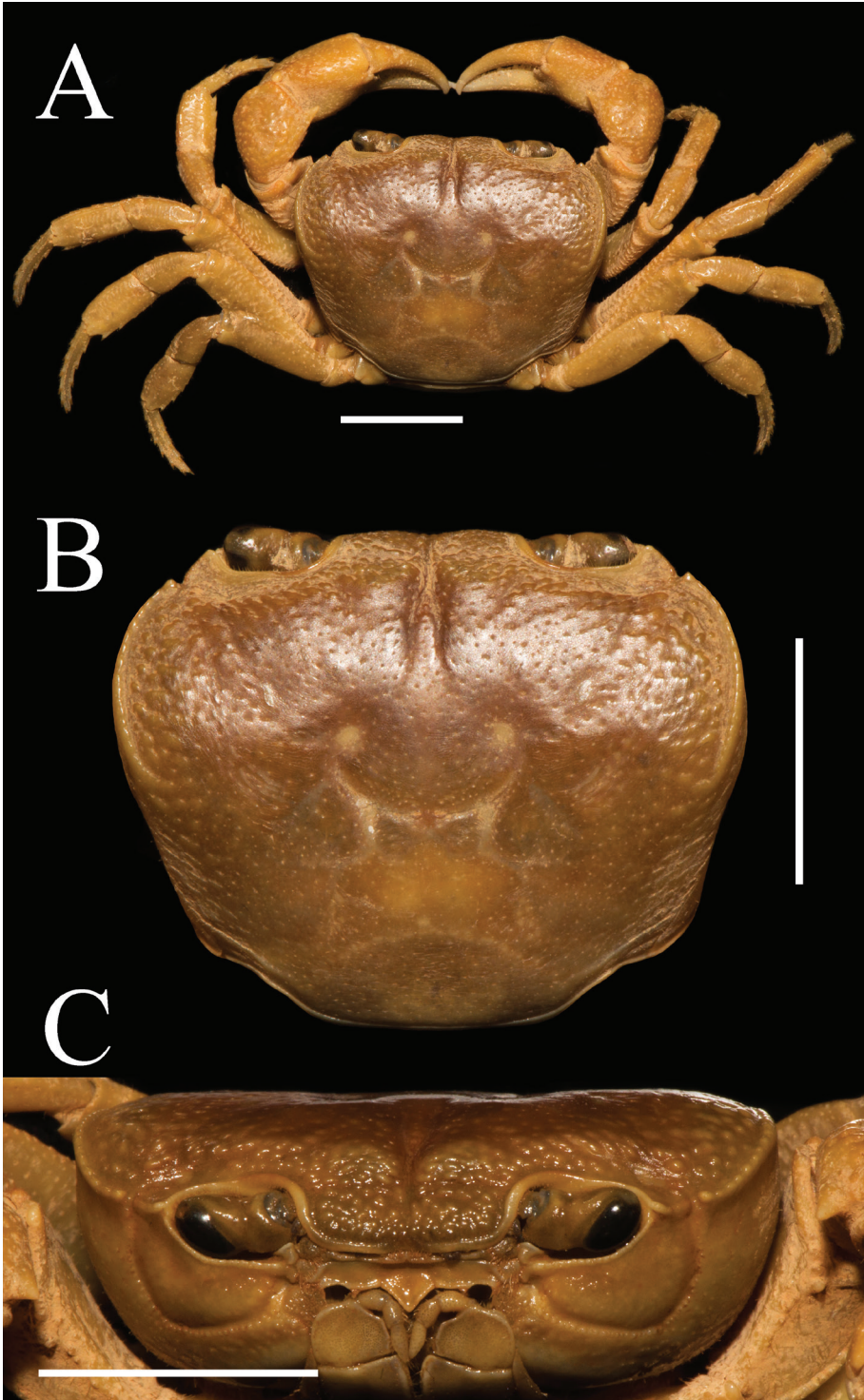
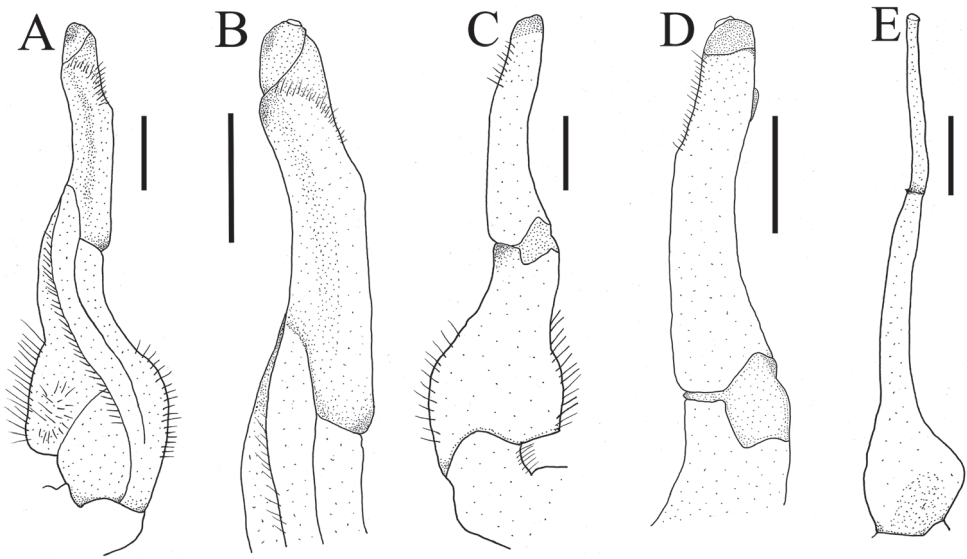**Figure 5.** *Aparapotamon huizeense* sp. nov. Holotype male (25.9 × 21.2 mm) (NCU MCP 179801) **A** overall habitus **B** dorsal view of carapace **C** frontal view of cephalothorax. Scale bars: 1 cm.
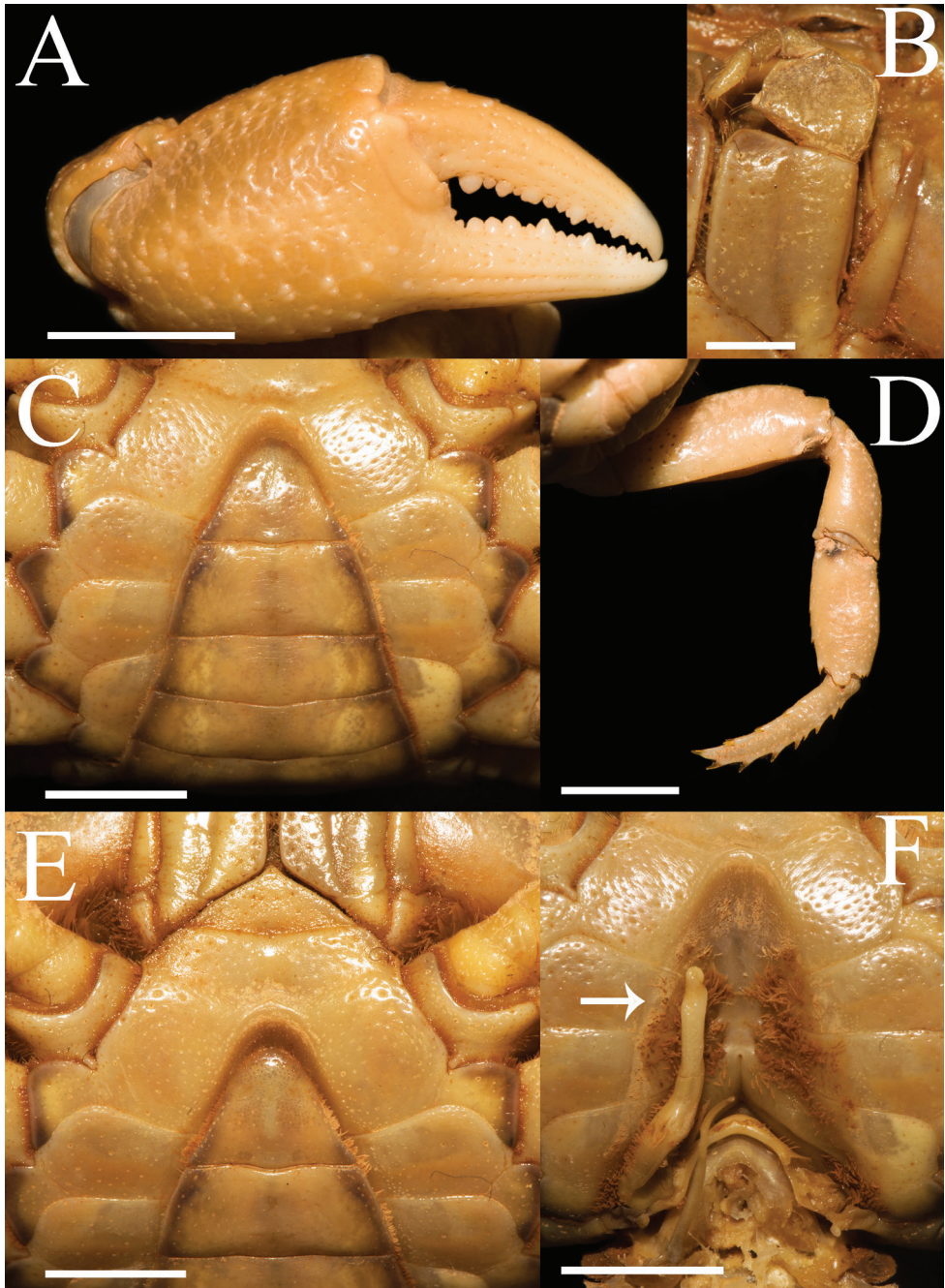
Figure 6. *Aparapotamon huizeense* sp. nov. Holotype male (25.9 × 21.2 mm) (NCU MCP 179801) **A** outer view of right cheliped **B** left third maxilliped **C** ventral view of pleon **D** right fourth ambulatory leg **E** ventral view of anterior thoracic sternum and telson **F** ventral view of sterno-pleonal cavity with right G1 in situ; arrow indicates pleonal locking tubercle. Scale bars: 2 mm (**B**); 5 mm (**A, C–F**).
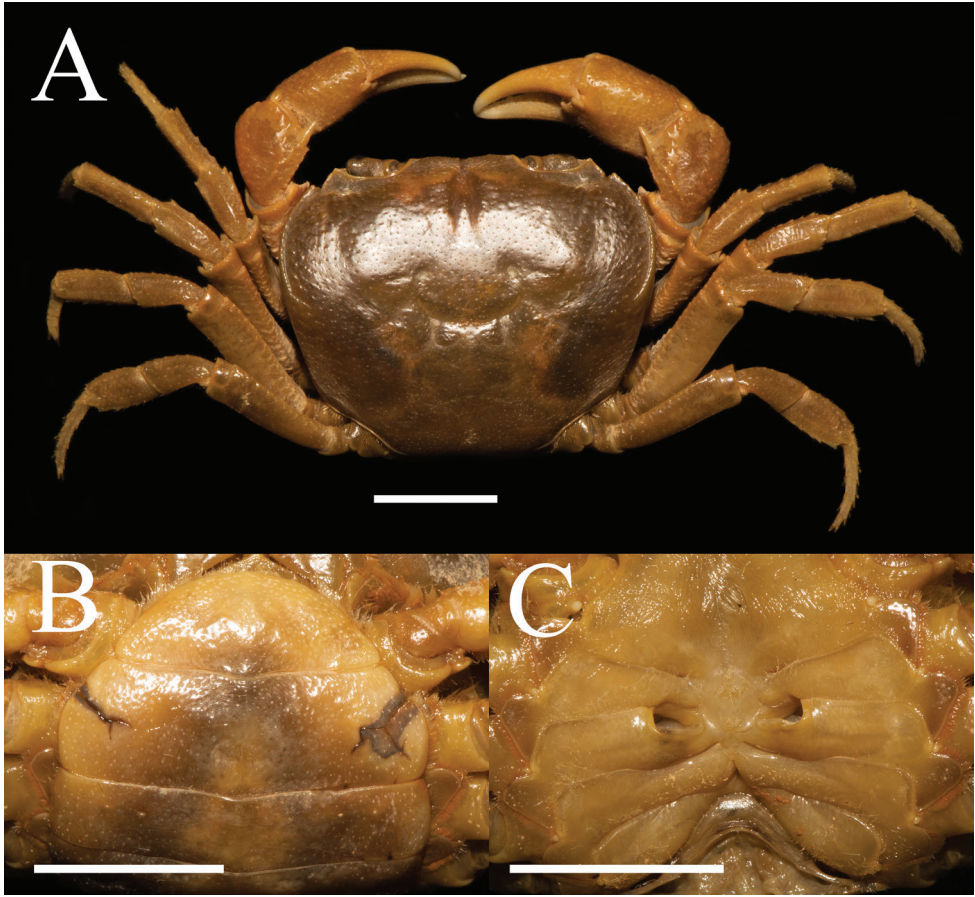
Figure 7. *Aparapotamon huizeense* sp. nov. Paratype female (31.0 × 24.8 mm) (NCU MCP 179803) **A** overall habitus **B** ventral view of pleon **C** vulvae. Scale bars: 10 mm.

dorsal lobe well developed, exceeding suture 4/5 in situ, G2 basal segment ovate, tip of terminal segment round.

Description. Carapace width 1.25 × length (n = 8), regions distinctly defined; dorsal surface slightly convex, anterolateral and frontal region covered with conspicuous round granules (Fig. 5A, B). External orbital angle triangular, round, separated from anterolateral margin by deep notch (Figs 5A–C, 7A). Postorbital cristae convex, not continuous to epibranchial tooth; postfrontal lobe prominent, separated medially by a Y-shaped groove extending to the frontal region (Figs 5A, B, 7A). Cervical groove shallow; H-shaped gastro-cardiac groove distinct, especially in female specimen (Figs 5A, B, 7A). Epibranchial tooth sharp, distinct, especially in female specimen; anterolateral margin cristae distinct, curved inwards posteriorly, lined with approximately 10–13 ambiguous granules; posterolateral surface smooth, with some inconspicuous oblique striae, converging towards posterior carapace margin (Figs 5A, B, 7A). Orbits

Figure 8. *Aparapotamon huizeense* sp. nov. Holotype male (25.9 × 21.2 mm) (NCU MCP 179801) **A** ventral view of left G1 **B** ventral view of terminal segment of left G1 **C** dorsal view of left G1 **D** dorsal view of terminal segment of left G1 **E** ventral view of left G2. Scale bars: 1 mm.

and eyes medium-size; supraorbital margin ridged, infraorbital margins cristate, minutely granulated (Fig. 5C). Sub-orbital smooth, pterygostomial and sub-hepatic regions covered with sparse round granules (Fig. 5C). Epistome posterior margin median lobe broad triangular, lateral margin with small projection (Fig. 5C).

Third maxilliped exopod without flagellum, claviform, reaching proximal 1/3 of merus lateral margin (Figs 5C, 6B). Ischium about 1.4 times as long as broad, rectangular, longitudinal median sulcus indistinct (Fig. 6B). Merus about 1.3 times as broad as long, subquadrate, median slightly depressed (Figs 5C, 6B). Chelipeds unequal in both adult male and female, palm of larger cheliped length 1.4 × height (n = 8); dactylus 0.6 × palm length (n = 8); slightly shorter than pollex (Figs 5A, 6A). Merus outer surface punctate; carpus surface covered with several prominent granules and sharp spine at inner-distal angle (Figs 5A, 7A). Occlusal margins of fingers of adult male with numerous round blunt teeth, with narrow gap when fingers closed (Fig. 6A). Ambulatory legs slender; second ambulatory legs longest; fourth ambulatory leg propodus 1.9 × as long as broad (n = 8), shorter than dactylus, which accompanied with several thorn-like setae (Figs 5A, 6D).

Male thoracic sternum punctate, formed by tidy depression; sternites 1–4 broad, sternites 1/2 completely continuous; suture 2/3 complete, transverse; suture 3/4 visible, mesially reaching distolateral part of sterno-pleonal cavity (Fig. 6C, E). Male sterno-pleonal cavity deep; median longitudinal groove between sternites 7, 8 long; male pleonal locking tubercle barely visible, almost middle of sternite 5 (Fig. 6F, arrow). Male pleon broad triangular (Fig. 6C); telson triangular, apex rounded, width 1.4 × length in males (n = 2), 2.5 × in females (n = 6); somite 6 trapezoidal, width 2.3 × length in males (n = 2), 3.0 × in females (n = 6) (Figs 6C, 7B). Vulva medium-size, ovate, superior mar-
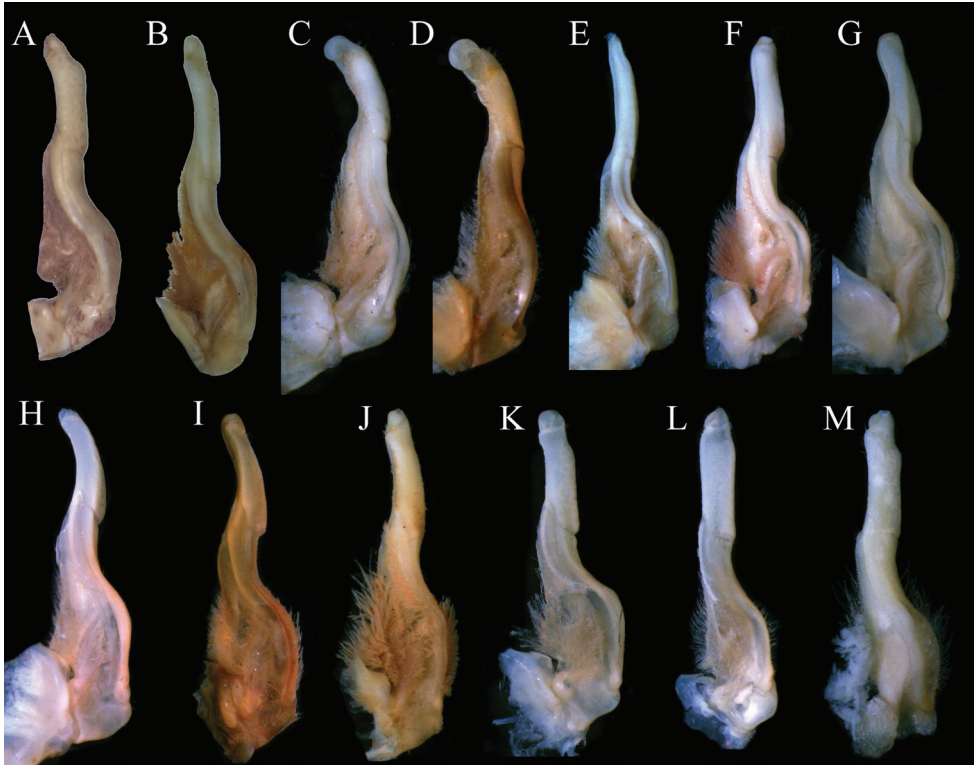
Figure 9. Left G1s. **A** *Aparapotamon binchuanense* sp. nov. NCU MCP 170701 **B** *Aparapotamon huizeense* sp. nov. NCU MCP 179801 **C** *Aparapotamon inflomanum* (Dai & Chen, 1985), IZCAS CB 05096 **D** *Aparapotamon molarum* (Dai & Chen, 1985), CAS CB 05094 **E** *Aparapotamon emineoforaminum* (Dai & Chen, 1985), CAS CB 05090 **F** *Aparapotamon tholosum* (Dai & Chen, 1985), CAS CB 05092 **G** *Aparapotamon protinum* (Dai & Chen, 1985), CAS CB 05093 **H** *Aparapotamon arcuatum* (Dai & Chen, 1985), CAS CB 05091 **I** *Aparapotamon muliense* (Dai & Chen, 1990), CAS CB 05088 **J** *Aparapotamon grahami* (Rathbun, 1929), CAS CB 00142 **K** *Aparapotamon huiliense* (Dai & Chen, 1985), CAS CB 05089 **L** *Aparapotamon similium* (Dai & Chen, 1985), CAS CB 05095 **M** *Aparapotamon gracilipedum* (Chen & Chang, 1982), CAS CB 05148.

gin reaching suture 5/6 in situ, opening inward, posterior margin distinctly convex, the sternal vulvar cover broadly triangular and relatively low (Fig. 7C).

G1 very slender; terminal segment claviform, slightly bent distally, inner margin arc-shaped, outer margin straightly, dorsal lobe well developed and gonopod pore located in it (Fig. 8A–D); exceeding suture4/5 in situ (Fig. 6F); clear boundary between terminal segment and subterminal segment, the latter length about 0.9 × length of terminal segment (Fig. 8A, C). G2 basal segment ovate, about 1.9 × length of terminal segment, tip of terminal segment round (Fig. 8E).

Etymology. The species is named after the type locality, Huize County, Qujing City, Yunnan Province.

Distribution. The new species is presently known only from the type locality presently, Huize County, Qujing City, Yunnan Province.

Remarks. *Aparapotamon huizeense* sp. nov. closely resembles *A. grahami* in the general carapace morphology and G1 structure. However, *A. huizeense* sp. nov. can be distinguished from *A. grahami* by the following characters: G1 exceeding suture 4/5 in situ (Fig. 6F) [vs. reaching pleonal locking tubercle but not reaching suture 4/5 in situ (Dai 1999: fig. 187)]; and the G1 is very slender, terminal segment slightly bent distally, dorsal lobe well developed (Fig. 9B) [vs. slender, terminal segment without bending (Fig. 9J), dorsal lobe variably developed]. *A. huizeense* sp. nov. is also similar to *A. huiliense*. But, in *A. huiliense*, G1 extends to pleonal locking tubercle but not exceeding suture 4/5 in situ (Dai 1999: fig. 189) and its dorsal lobe roundly developed (Fig. 9K). For detailed differences between this new species and congeners, see Table 2.

Phylogenetic analyses

Thirty 529 bp 16S rRNA gene sequences were used to construct BI and ML trees. The phylogenetic tree in this study included five species of *Aparapotamon*, and the results showed that they were clustered into one clade (Fig. 10). Eight sequences of
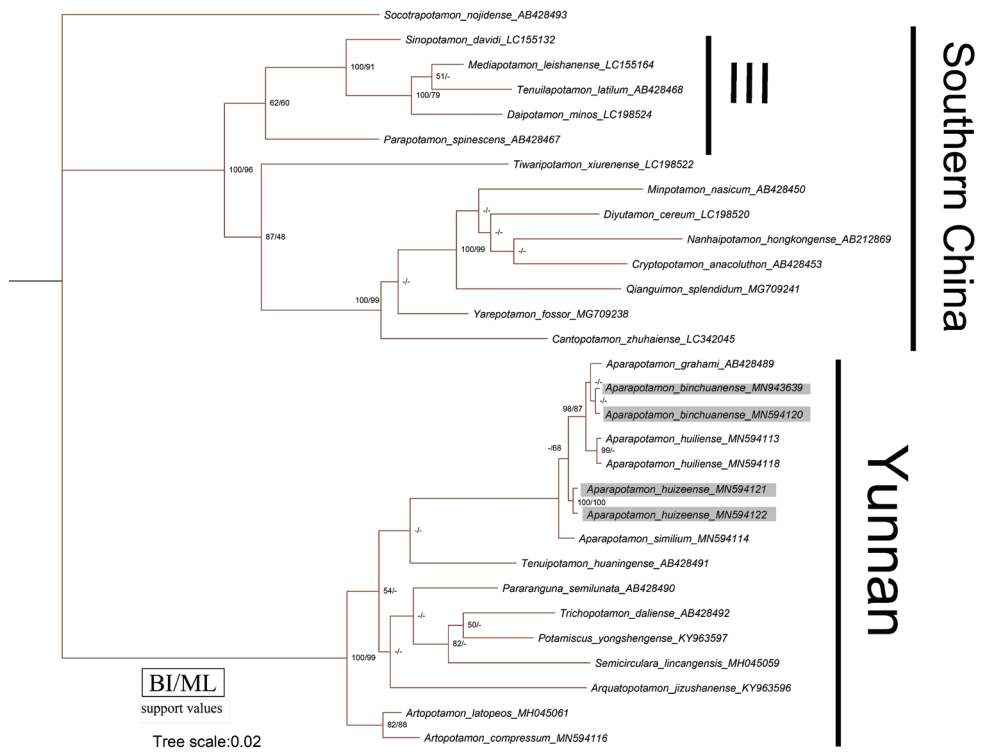
Figure 10. Bayesian inference (BI) phylogenetic tree based on 16S rRNA gene for two new species with their sequence accession numbers see Table 1. Probability values at nodes represent support values for BI and ML. Only values > 50% are shown.

Table 2. Morphological differences among species of *Aparapotamon*.

Species/characters	Epibranchial tooth	Pterygostomial and sub-hepatic regions	Sub-orbital region	G1 in situ	Terminal segment of G1	Vulva
A. binchuanense sp. nov.	Blunt (Fig. 1A)	Densely covered with round granules (Fig. 1C)	Sparely covered with round granules (Fig. 1C)	Exceeding pleonal locking tubercle but not suture 4/5 (Fig. 2F)	Slender, distal end tapering, distinctly bent (Fig. 9A)	Ovate, posterior margin not convex (Fig. 3C)
A. huizeense sp. nov.	Sharp (Fig. 5A)	Sparely covered with round granules (Fig. 5C)	Smooth (Fig. 5C)	Exceeding suture 4/5 (Fig. 6F)	Very slender, distal end slightly bent, dorsal lobe well developed inward (Fig. 9B)	Ovate, posterior margin distinctly convex (Fig. 7C)
A. inflomanum (cf. Dai 1999: fig. 196)	Blunt	Smooth	Smooth	Reaching suture 4/5	Slender, distal end disc-shaped (Fig. 9C)	Ovate, posterior margin not convex
A. molarum (cf. Dai 1999: fig. 195)	Blunt	Smooth	Smooth	Exceeding suture 4/5	Slender, distal end disc-shaped (Fig. 9D)	Transversely ovate, posterior margin not convex
A. emineoforaminum (cf. Dai 1999: fig. 197)	Blunt	Densely covered with round granules	Smooth	Exceeding suture 4/5	Very slender, tapering distally (Fig. 9E)	Ovate, posterior margin distinctly convex
A. tholosum (cf. Dai 1999: fig. 194)	Sharp	Densely covered with round granules	Smooth	Exceeding pleonal locking tubercle but not suture 4/5	Slender, dorsal lobe well developed upwards (Fig. 9F)	Transversely ovate, posterior margin distinctly convex
A. protinum (cf. Dai 1999: fig. 193)	Sharp	Densely covered with round granules	Smooth	Exceeding pleonal locking tubercle but not suture 4/5	Slender, dorsal lobe slightly developed upwards (Fig. 9G)	Transversely ovate, posterior margin arching to form semicircular structure
A. arcuatum (cf. Dai 1999: fig. 191)	Blunt	Sparely covered with round granules	Smooth	Exceeding pleonal locking tubercle but not suture 4/5	Slender, arc-shaped, dorsal lobe slightly developed upwards (Fig. 9H)	Transversely ovate, posterior margin not convex
A. muliense (cf. Dai 1999: fig. 192)	Blunt	Sparely covered with round granules	Smooth	Exceeding pleonal locking tubercle but not suture 4/5	Slender, arc-shaped, dorsal lobe well developed upwards (Fig. 9I)	Transversely ovate, posterior margin distinctly convex
A. grahami (cf. Dai 1999: fig. 187)	Sharp	Sparely covered with round granules	Smooth	Reaching pleonal locking tubercle	Slender, dorsal lobe variably developed inwards (Fig. 9J)	Ovate, posterior margin slightly convex
A. huiliense (cf. Dai 1999: fig. 189)	Sharp	Sparely covered with round granules	Smooth	Exceeding pleonal locking tubercle but not suture 4/5	Slender, dorsal lobe roundly developed (Fig. 9K)	Transversely ovate, posterior margin slightly convex
A. similium (cf. Dai 1999: fig. 188)	Blunt	Densely covered with round granules	Sparely covered with round granules	Exceeding pleonal locking tubercle but not suture 4/5	Slender, dorsal lobe slightly developed inwards, tapering distally (Fig. 9L)	Transversely ovate, posterior margin distinctly convex
A. gracilipedum (cf. Dai 1999: fig. 190)	Sharp	Densely covered with round granules	Sparely covered with round granules	Exceeding pleonal locking tubercle but not suture 4/5	Slender, dorsal lobe slightly developed inwards, distal end blunt (Fig. 9M)	Ovate, posterior margin slightly convex

five species were clustered into one branch, including the two new species reported in this paper, along with *A. huiliense*, *A. similium*, and *A. grahami*. The pairwise distance based on the K2P model showed that the pairwise genetic distances among five species of *Aparapotamon* range from 0.0019 to 0.0095 (Table 3). The minimum genetic distance is between *A. grahami* and *A. binchuanense* sp. nov., indicating that they have a close relationship. The minimum genetic distances between *A. huizeense* sp. nov. and other four species is 0.0038, which is same as the genetic distance between *A. grahami* and *A. huiliense*.

Table 3. The pairwise genetic distances among five species from *Aparapotamon*.

species	1	2	3	4	5	6	7	8
A. grahami AB428489								
A. similium MN594114	0.0095							
A. huiliense MN594113	0.0038	0.0095						
A. huiliense MN594118	0.0038	0.0095	0.0000					
A. binchuanense sp. nov. MN943639	0.0019	0.0076	0.0019	0.0019				
A. binchuanense sp. nov. MN594120	0.0019	0.0076	0.0019	0.0019	0.0000			
A. huizeense sp. nov. MN594121	0.0057	0.0038	0.0057	0.0057	0.0038	0.0038		
A. huizeense sp. nov. MN594122	0.0057	0.0038	0.0057	0.0057	0.0038	0.0038	0.0000	

Discussion

There are currently 13 species in this genus including those described in this study. The original eleven species of *Aparapotamon* are morphologically diverse, with the distal end of G1s of *A. inflomanum* and *A. molarum* being disc-shaped but that of *A. emineoforaminum* tapering distally, and the three G1s extend to suture 4/5, while the other eight species have G1s that are claviform in terminal segment and distal ends do not extend to suture 4/5 (Dai 1999). *A. binchuanense* sp. nov. and *A. huizeense* sp. nov. can be distinguished from above eleven species by their G1s, which distinctly bent in distal end and very slender, dorsal lobe distinctly developed, distal end exceeds suture 4/5 respectively.

In this study, 30 sequences of 16S rRNA gene from 27 species of 22 genera were used to performed phylogenetic analyses. Since the two new species cluster with other *Aparapotamon* species form a separate branch in clade (Fig. 10), the phylogenetic tree supports the assignment of these two new species to *Aparapotamon*. However, the genetic distances between species of *Aparapotamon* are small, ranging from 0.0019 to 0.0095 (Table 3). *A. grahami* and *A. binchuanense* sp. nov. are close at molecular level, with the genetic distance 0.0019, but they are significantly different in morphology (Table 2). Most importantly, *A. binchuanense* sp. nov. can be distinguished from *A. grahami* by the terminal segment of G1, which is claviform, with distal end tapering and distinctly bent (Fig. 9A) [vs. terminal segment of G1 *A. grahami* claviform, not bent (Fig. 9J)]. In this study, the molecular results of 16S rRNA gene were not sufficient for species identification in *Aparapotamon*. Therefore, it is recommended to use other markers (e.g. COI and nuclear genes) for further phylogenetic studies of this genus. If the results of other makers indicate that the genetic distance between *Aparapotamon* is also too small compared to other freshwater crab genera, revision of *Aparapotamon* is necessary.

The present molecular results show five species of *Aparapotamon* were clustered into one clade. And *Aparapotamon* cluster with other genera from Yunnan form 'Yunnan' clade. The genera in the branch of 'Yunnan' have many similarities in terms of morphological structure, such as the G1 slender, the terminal segment is longer than the half of subterminal segment, third maxilliped exopod without flagellum, and the ability to live at an altitude of 1500–2900 meters (Dai and Chen 1985; Dai 1999; Chu et al. 2017). Specimens of *A. molarum* were collected at Baishui River, Yulong Naxi Autonomous County, Lijiang City, Yunnan Province at an altitude of 2910 meters, which is the highest altitude at which freshwater crab specimens have been discovered in China so far (Dai 1999).

Acknowledgements

References

Bai J, Xu SX, Nie ZH, Wang YF, Zhu CC, Wang Y, Min WP, Cai YX, Zou JX, Zhou XM (2018) The complete mitochondrial genome of *Huananpotamon lichuanense* (Decapoda: Brachyura) with phylogenetic implications for freshwater crabs. Gene 646: 217–226. https://doi.org/10.1016/j.gene.2018.01.015

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chu KL, Zhou LJ, Sun HY (2017) A new genus and new species of freshwater crab (Decapoda: Brachyura: Potamidae Ortmann, 1896) from Yunnan Province, China. Zootaxa 4286: 241–253. https://doi.org/10.11646/zootaxa.4286.2.7

Chu KL, Wang PF, Sun HY (2018b) A new genus and species of primary freshwater crab and a new species of *Artopotamon* Dai & Chen, 1985 (Crustacea, Brachyura, Potamidae) from western Yunnan, China. Zootaxa 4422: 115–131. https://doi.org/10.11646/zootaxa.4422.1.7

Chu KL, Ma XP, Zhang ZW, Wang PF, Lü LN, Zhao Q, Sun HY (2018a) A checklist for the classification and distribution of China's freshwater crabs. Biodiversity Science 26: 274–282. https://doi.org/10.17520/biods.2018062

Cumberlidge N, Ng PKL, Yeo DCJ, Naruse T, Meyer KS, Esser LJ (2011) Diversity, endemism and conservation of the freshwater crabs of China (Brachyura: Potamidae and Gecarcinucidae). Integrative Zoology 6: 45–55. https://doi.org/10.1111/j.1749-4877.2010.00228.x

Dai AY (1999) Fauna Sinica (Arthropoda. Crustacea. Malacostraca. Decapoda. Parathelphusicae. Potamidae). Science Press, Beijing, 501 pp. [In Chinese with English summary]

Dai AY, Chen GX (1985) A preliminary report on the freshwater crabs of Hengduan Mountains Area. Sinozoologia 3: 39–72.

Davie PJF, Guinot D, Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram F, Von Vaupel Klein C (Eds) Treatise on Zoology – Anatomy, Taxonomy, Biology – The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie, 9(C)(I), Decapoda: Brachyura (Part 1), 11–163. https://doi.org/10.1163/9789004190832_004

Fang F, Ji YK, Zhao Q, Wang YJ, Gao W, Chu KL, Sun HY (2015) Phylogeography of the Chinese endemic freshwater crab *Sinopotamon acutum* (Brachyura, Potamidae). Zoologica Scripta 44: 653–666. https://doi.org/10.1111/zsc.12131

Gao N, CuiYY, Wang SB, Zou JX (2019) Two new species and the molecular phylogeography of the freshwater crab genus *Bottapotamon* (Crustacea: Decapoda: Brachyura: Potamidae). PeerJ 7: e7980. https://doi.org/10.7717/peerj.7980

Harrison TM, Copeland P, Kidd WSF, Yin A (1992) Raising tibet. Science 255: 1663–1670. https://doi.org/10.1126/science.255.5052.1663

Huang C (2018) Revision of *Yarepotamon* Dai & Türkay, 1997 (Brachyura: Potamidae), freshwater crabs endemic to southern China, with descriptions of two new genera and four new species. Journal of Crustacean Biology 2018: 1–17. https://doi.org/10.1093/jcbiol/rux120

Huang C, Ahyong ST, Shih HT (2017a) *Cantopotamon*, a new genus of freshwater crabs from Guangdong, China, with descriptions of four new species (Crustacea: Decapoda: Brachyura: Potamidae). Zoological Studies 56: e41. https://doi.org/10.6620/ZS.2017.56-41

Huang C, Shih HT, Ng PKL (2017b) A new genus and new species of Potamidea (Crustacea: Decapoda: Brachyura: Potamoidae), the first stygomorphic cave crab known from China and East Asia. Zootaxa 4232(1): 071–084. https://doi.org/10.11646/zootaxa.4232.1.5

Huang C, Shih HT, Ahyong ST (2018a) Two new genera and two new species of narrow-range freshwater crabs from Guangdong, China (Decapoda: Brachyura: Potamidae). Journal of Crustacean Biology 38: 614–624. https://doi.org/10.1093/jcbiol/ruy050

Huang C, Wong KC, Ahyong ST (2018b) The freshwater crabs of Macau, with the description of a new species of *Nanhaipotamon* Bott, 1968 and the redescription of *Nanhaipotamon wupingense* Cheng, Yang, Zhong & Li, 2003 (Crustacea, Decapoda, Potamidae). Zookeys 810: 91–111. https://doi.org/10.3897/zookeys.810.30726

Huang C, Huang SZ, Shen ZX (2020a) A new long-legged terrestrial freshwater crab, *Calcipotamon puglabrum* gen. nov. et sp. nov. (Crustacea: Decapoda: Potamidae), from Hainan Island, China. Zootaxa 4766: 447–456. https://doi.org/10.11646/zootaxa.4766.3.4

Huang C, Ahyong ST, Shih HT (2020b) The second known stygomorphic freshwater crab from China, *Phasmon typhlops* gen. nov. et sp. nov. (Crustacea, Decapoda, Potamidae), diverged at the beginning of the Late Miocene. ZooKeys 1008: 1–15. https://doi.org/10.3897/zookeys.1008.58854

Ji YK, Sun YF, Gao W, Chu KL, Wang RC, Zhao Q, Sun HY (2016) Out of the Sichuan Basin: Rapid species diversification of the freshwater crabs in *Sinopotamon* (Decapoda: Brachyura: Potamidae) endemic to China. Molecular Phylogenetics and Evolution 100: 80–94. https://doi.org/10.1016/j.ympev.2016.04.003

Jia XN, Xu SX, Bai J, Wang YF, Nie ZH, Zhu CC, Wang Y, Cai YX, Zou JX, Zhou XM (2018) The complete mitochondrial genome of *Somanniathelphusa boyangensis* and phylogenetic analysis of Genus *Somanniathelphusa* (Crustacea: Decapoda: Parathelphusidae). PLoS ONE 13: e0192601. https://doi.org/10.1371/journal.pone.0192601

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Mao SY, Huang C (2020) Descriptions of a new species of *Minpotamon* Dai & Türkay, 1997, and a monotypic new genus of aquatic freshwater crab (Brachyura, Potamidae) from east-

ern Guangdong, China. Crustaceana 93: 1295–1313. https://doi.org/10.1163/15685403-bja10060

Nakamura T, Yamada KD, Tomii K, Katoh K (2018) Parallelization of MAFFT for large-scale multiple sequence alignments. Bioinformatics 34: 2490–2492. https://doi.org/10.1093/bioinformatics/bty121

Naruse T, Chia JE, Zhou XM (2018) Biodiversity surveys reveal eight new species of freshwater crabs (Decapoda: Brachyura: Potamidae) from Yunnan Province, China. PeerJ 6: e5497. https://doi.org/10.7717/peerj.5497

Nylander JAA (2004) MrModeltest, version 2.3. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Schubart CD (2000) Use of mitochondrial 16S rRNA gene for phylogenetic and population studies in Crustacea. The biodiversity crisis and Crustacea 12: 817–830.

Shih HT, Ng PKL (2011) Diversity and biogeography of freshwater crabs (Crustacea: Brachyura: Potamidae, Gecarcinucidae) from East Asia. Systematics and Biodiversity 9: 1–16. https://doi.org/10.1080/14772000.2011.554457

Shih HT, Ng PKL, Chang HW (2004) Systematics of the genus *Geothelphusa* (Crustacea, Decapoda, Brachyura, Potamidae) from southern Taiwan: A molecular appraisal. Zoological Studies 43: 561–570.

Shih HT, Chen GX, Wang LM (2005) A new species of freshwater crab (Decapoda: Brachyura: Potamidae) from Dongyin Island, Matsu, Taiwan, defined by morphological and molecular characters, with notes on its biogeography. Journal of Natural History 39: 2901–2911. https://doi.org/10.1080/00222930500214010

Shih HT, Yeo DCJ, Ng PKL (2009) The collision of the Indian Plate with Asia: molecular evidence for its impact on the phylogeny of freshwater crabs (Brachyura: Potamidae). Journal of Biogeography 36: 703–719. https://doi.org/10.1111/j.1365-2699.2008.02024.x

Shih HT, Huang C, Ng PKL (2016) A re-appraisal of the widely-distributed freshwater crab genus *Sinopotamon* Bott, 1967, from China, with establishment of a new genus (Crustacea: Decapoda: Potamidae). Zootaxa 4138: 309–331. https://doi.org/10.11646/zootaxa.4138.2.5

Shih HT, Zhou XM, Chen GX, Chien IC, Ng PKL (2011) Recent vicariant and dispersal events affecting the phylogeny and biogeography of East Asian freshwater crab genus *Nanhaipotamon* (Decapoda: Potamidae). Molecular Phylogenetics and Evolution 58: 427–438. https://doi.org/10.1016/j.ympev.2010.11.013

Wang SB, Huang C, Zou JX (2019a) Description of a new species of freshwater crab of the genus *Qianguimon* Huang, 2018 (Crustacea: Decapoda: Brachyura: Potamidae) from Yulin, Guangxi, Southern China. Zoological Studies 58: e31. https://doi.org/10.6620/ZS.2019.58-31

Wang SB, Zhou XM, Zou JX (2019b) A new species of freshwater crab of the genus *Mediapotamon* Turkay & Dai, 1997 (Crustacea, Decapoda, Brachyura, Potamidae) from Guizhou, China. Zookeys 873: 9–23. https://doi.org/10.3897/zookeys.873.36702

Wang SB, Zhang YN, Zou JX (2020a) A new species of freshwater crab of the genus *Qianguimon* Huang, 2018 (Decapoda: Brachyura: Potamidae) from Guangxi, Southern China. PeerJ 8: e9194. https://doi.org/10.7717/peerj.9194

Wang SB, Xu YY, Zou JX (2020b) Description of two new species of the genus *Heterochelamon* Türkay & Dai, 1997 (Crustacea: Decapoda: Brachyura: Potamidae), from southern China. PeerJ 8: e9565. https://doi.org/10.7717/peerj.9565

Wang PF, Zhang ZW, Sun HY (2020) *Ruiyupotamon*, a new genus and four new species of freshwater crabs from northwestern Yunnan, China (Decapoda, Brachyura, Potamidae). Crustaceana 93: 1315–1341. https://doi.org/10.1163/15685403-bja10059

Yeo DCJ, Ng PKL, Cumberlidge N, Magalhaes Cl, Daniels SR, Campos MR (2008) Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. Hydrobiologia 595: 275–286. https://doi.org/10.1007/978-1-4020-8259-7_30

Zou JX, Bai J, Zhou XM (2018) A new species of karst-dwelling freshwater crab of the genus *Chinapotamon* Dai & Naiyanetr, 1994 (Crustacea: Decapoda: Brachyura: Potamidae), from Guizhou, southwest China. PeerJ 6: e5947. https://doi.org/10.7717/peerj.5947

Supplementary material 1

BI tree
Authors: Qi-Hong Tan, Xiao-Juan Zhou, Jie-Xin Zou
Data type: Tre. file
Explanation note: Phylogenetic.
Link: https://doi.org/10.3897/zookeys.1056.63755.suppl1

Supplementary material 2

ML tree
Authors: Qi-Hong Tan, Xiao-Juan Zhou, Jie-Xin Zou
Data type: MTSX file
Explanation note: Phylogenetic.
Link: https://doi.org/10.3897/zookeys.1056.63755.suppl2

Supplementary material 3

Sequences

Authors: Qi-Hong Tan, Xiao-Juan Zhou, Jie-Xin Zou

Data type: FASTA. file

Explanation note: Genomic.

Link: https://doi.org/10.3897/zookeys.1056.63755.suppl3

RESEARCH ARTICLE

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Two new species of the millipede genus *Glyphiulus* Gervais, 1847 (Diplopoda, Spirostreptida, Cambalopsidae) from caves in northern Thailand

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Abstract

Two new species of the genus *Glyphiulus* Gervais, 1847 are described and illustrated. The first species, *G. longus* **sp. nov.**, is the second species of the *javanicus*-group to be found in Thailand. It resembles *G. guangnanensis* Jiang, Guo, Chen & Xie, 2018, from southern China, but is distinguished by a smaller size and the carinotaxic formula of the collum, combined with ♂ legs 1 bearing very strongly reduced telopodites, the anterior gonopods showing a pair of very long and slender apicomesal processes, and the denser plumose and stout flagella of the posterior gonopods. The second species, *G. promdami* **sp. nov.**, the fifth member of the *granulatus*-group in Thailand, seems to be particularly similar to *G. subbedosae* Likhitrakarn, Golovatch & Panha, 2017, from Laos. However, it can be distinguished from the latter species mainly by showing a uniformly yellow collum and the posterior gonopod coxite bearing several strong setae in median and lateral views, coupled with the anterior gonopod coxosternum being microsetose in the anterior and medial parts in caudal view. An identification key to, and a distribution map of, all seven *Glyphiulus* species currently known to occur in Thailand are also provided.

Introduction

The millipede family Cambalopsidae Cook, 1895 is very common, abundant and widespread in subterranean habitats of Thailand. Within this family, three genera are well-represented in Thai caves: *Glyphiulus* Gervais, 1847 (4 species), *Plusioglyphiulus* Silvestri, 1923 (14 species) and *Trachyjulus* Peters, 1864 (5 species) (Golovatch et al. 2009, 2011a, b, 2012b; Likhitrakarn et al. 2020). *Glyphiulus* is the most speciose and characteristic genus of the family Cambalopsidae (Golovatch et al. 2007a). Most *Glyphiulus* species are considered endemic to Southeast Asia and southern China, narrow endemism prevailing because, like most Diplopoda, their dispersal capacities are very limited (Golovatch et al. 2007b; Jiang et al. 2017, 2018; Likhitrakarn et al. 2017). Only two species, *G. granulatus* (Gervais, 1847), pantropical through numerous anthropochoric introductions (Golovatch et al. 2007a), and *G. javanicus* Carl, 1911, described from a sugar cane plantation in Java, Indonesia (Carl 1911), but from a still unclear area of origin lying somewhere in Indochina or China, are assumed to be truly widespread (Golovatch et al. 2007b, 2012a).

Two distinct species groups are currently recognized in *Glyphiulus*, based on the conformation of ♂ legs 1 (Golovatch et al. 2007a, b). The *granulatus*-group is distinguished by these legs usually being very strongly reduced to 1- or 2-segmented telopodite rudiments, coupled with two widely separated and curved prongs on the sternum. In the *javanicus*-group, ♂ legs 1 are usually with nearly normal 4- or 5-segmented telopodites, coupled with medially contiguous, but not entirely fused central coxal processes, and special carinotaxy patterns on the collum and following metaterga.

Five *Glyphiulus* species have hitherto been described from Thailand. The first species recorded was *G. siamensis* Mauriès, 1983, an epigean millipede from Doi Suthep, Chiang Mai (Mauriès 1983), which represents the *javanicus*-group (Golovatch et al., 2007a). All four following congeners have been reported from cave environments (Golovatch et al. 2011b) and they belong to the *granulatus*-group: *G. sattaa* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b from three caves (Tham Ku Kan (Ban Tham), Tham Nam Cham, and Tham Prah) in Mae Sai District, Chiang Rai Province; *G. duangdee* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b from Tham Chan, Khlong Trong National Park, Tong Saen Khan District, Uttaradit Province, *G. mongkon* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b from Tham Maho Lan, Ban Non Hin District, Loei Province, and *G. maidtreejit* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b from Tham Pha Hong, Lom Sak District, Phetchabun Province. All five species have narrow distributions and seem to be endemic to Thailand (Fig. 5 and Table 1).

In the present study, we describe two additional new species of *Glyphiulus* from northern Thailand. Furthermore, we provide a distributional map of, and a key to, all seven species of the genus currently known to occur in Thailand.

Materials and methods

New material was collected in northern Thailand, in particular in limestone mountain and cave habitats. They were searched for and hand-collected using forceps. All

populations were found to be sufficiently large and associated with bat guano in the twilight to deep and dark zones of the caves. The specimens taken were euthanized using a two-step method following AVMA Guidelines for the Euthanasia of Animals (AVMA 2013).

Specimens were then preserved in 95% ethanol for morphological and future molecular studies. All specimens were examined, measured, and photographed under a Nikon SMZ 745T trinocular stereo microscope, equipped with a Canon EOS 5DS R digital SLR camera. Digital images obtained were processed and edited with Adobe Photoshop CS6. Line drawings were based on photographs and examined under the stereo microscope equipped with a digital SLR camera.

Collecting sites were located by GPS using the WGS84 datum using a Garmin GPSMAP 60 CSx, and all coordinates and elevations were checked with Google Earth. The distribution maps of all *Glyphiulus* species recorded from Thailand were prepared using QGIS 3.18.0 (QGIS Development Team 2021). Google satellite maps were downloaded via the QuickMapServices plugin. The images were enhanced and arranged in plates with Adobe Photoshop CS6 software.

The terminology used and the carinotaxic formulae in the descriptions follow those in Golovatch et al. (2007a, b, 2009, 2011a, 2011b), while body segment counts are after Enghoff et al. (1993) and Golovatch et al. (2007a).

The holotypes, as well as most of the paratypes are housed in the Museum of Zoology, Chulalongkorn University (**CUMZ**), Bangkok, Thailand; some paratypes have been shared with the collections of the Zoological Museum, State University of Moscow, Russia (**ZMUM**) and the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University (**NHM-PSU**), Songkhla, Thailand, as indicated in the text.

Taxonomy

Family Cambalopsidae Cook, 1895
Genus *Glyphiulus* Gervais, 1847

Glyphiulus longus **sp. nov.**
http://zoobank.org/B99F5675-C67F-4AA8-A777-6D987C2A975C
Figs 1, 2

Type material. *Holotype* ♂: Thailand, Nan Province, Pon, Thung Chang District, Tham Nam Lod, 19°25'13"N, 101°04'15"E, ca 1420 m a.s.l., 30.05.2018, S. Jantarit leg.; CUMZ-CAM171. *Paratypes***:** 3 ♀: same locality as holotype; CUMZ-CAM171; 1 ♀: same locality as holotype; ZMUM; 1 ♀: same locality as holotype; NHM-PSU.

Name. The species is so named to emphasize the long medial processes of the anterior and posterior gonopods; adjective.

Diagnosis. This new species seems to be particularly similar to *G. guangnanensis* Jiang, Guo, Chen & Xie, 2018, from Yunnan Province, China (Jiang et al. 2018), with which it shares the following diagnostic characters: very strong metatergal crests
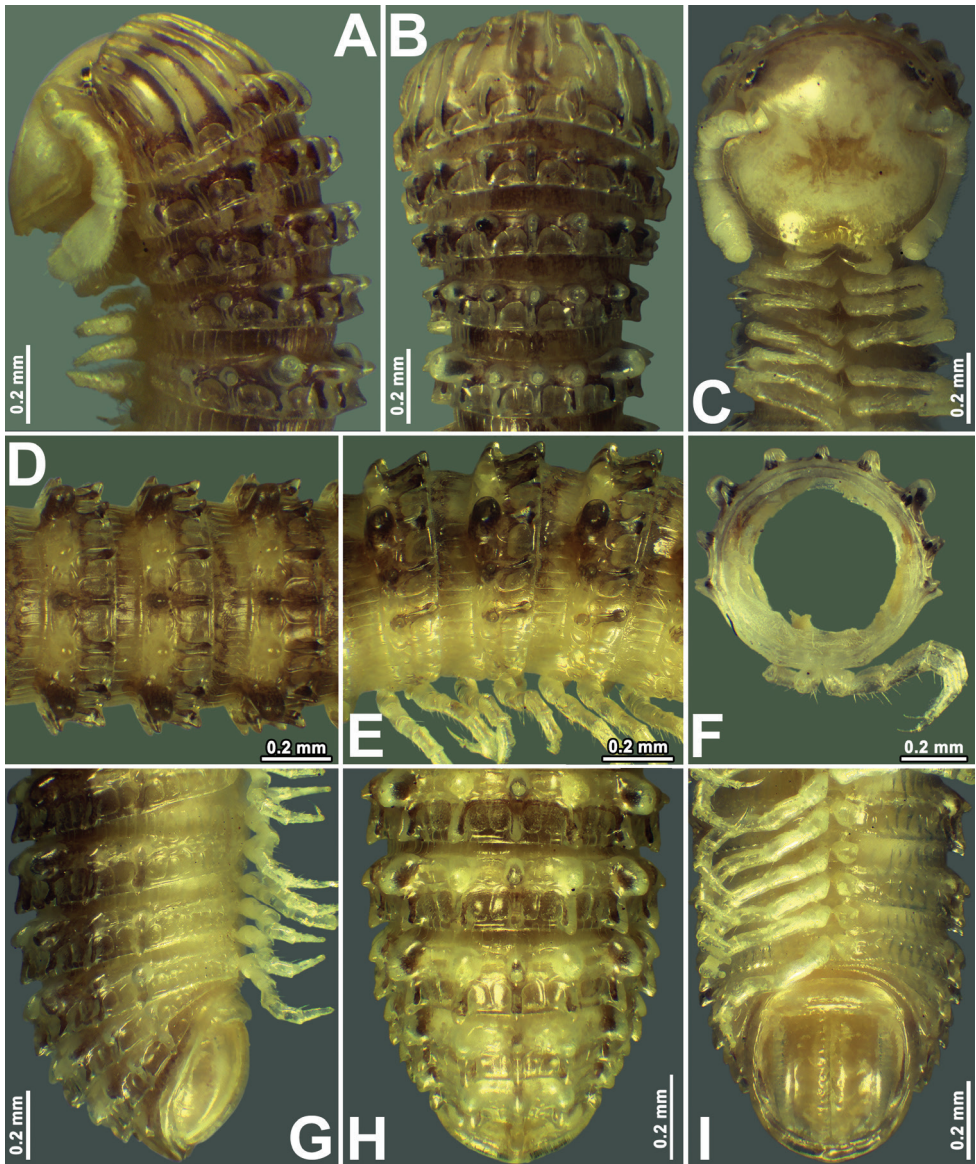
Figure 1. *Glyphiulus longus* sp. nov., ♂ holotype **A–C** anterior part of body, lateral, dorsal, and ventral views, respectively **D, E** midbody rings, dorsal and lateral views, respectively **F** cross-section of a midbody ring **G–I** posterior part of body, lateral, dorsal, and ventral views, respectively.

and unique carinotaxic formulae, coupled with certain anterior and posterior gonopod structural details. *Glyphiulus longus* sp. nov. differs from *G. guangnanensis* by the smaller body size, 22–26 mm long (vs. larger, 38–54 mm long) and the carinotaxic formula of the collum: 1+2a+3c+4–5+6c+7a+pc+ma (vs. 1a+2c+3–4+5c+6a+pc+ma) (Fig. 1A, B), coupled with ♂ legs 1 showing very strongly reduced telopodites (Fig. 2C, D) (vs.
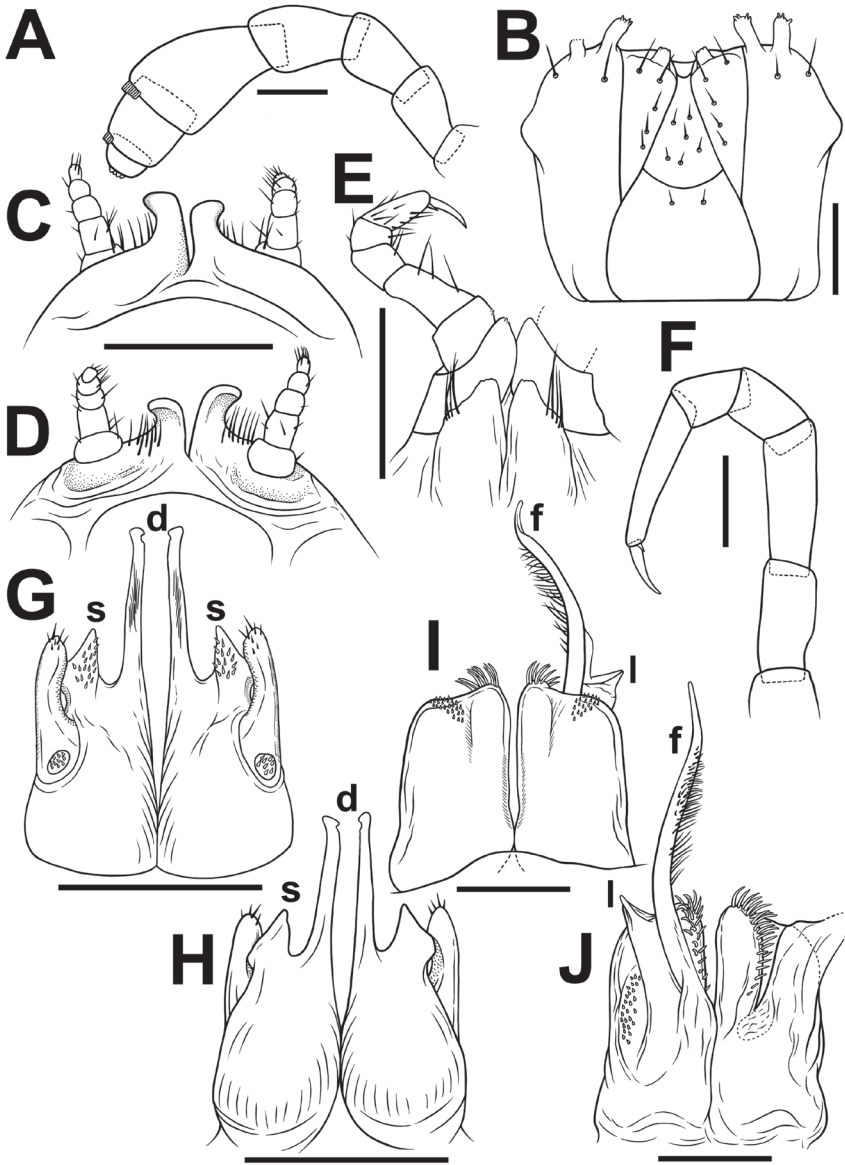
Figure 2. *Glyphiulus longus* sp. nov., ♂ holotype **A** antenna, lateral view **B** gnathochilarium, ventral view **C, D** legs 1, oral and caudal views, respectively **E** legs 2, caudal view **F** midbody leg **G, H** anterior gonopods, caudal and oral views, respectively **I, J** posterior gonopods, oral and caudal views, respectively. Abbreviations: **d** apicomesal processes, **s** subsecuriform process, **f** flagellum process, **l** lamelliform lobe. Scale bar: 0.1 mm.

nearly normal telopodites), the apicomesal processes (d) on the anterior gonopods being very long and slender (Fig. 2G, H) (vs. shorter and digitiform), and the presence of a very long, medially densely plumose and stout flagellum process (f) on the posterior gonopods (Fig. 2I, J) (vs. slim and smooth flagellum process).

Table 1. Comparison of all seven *Glyphiulus* species known to occur in Thailand; n/a = no information.

Characters/ Species	G. duangdee	G. longus sp. nov.	G. maidtreejit	G. mongkon	G. promdami sp. nov.	G. sattaa	G. siamensis
Group	*granulatus*	*javanicus*	*granulatus*	*granulatus*	*granulatus*	*granulatus*	*javanicus*
Length (mm)							
♂	14–22	23.5	22–24	12–20	14.5–18.4	23–40	23
♀	14–22	22.8–26.5	n/a	n/a	14.2–24.3	23–40	n/a
colour	uniformly brown to dark brown	uniformly red-brownish or dark castaneous brown to grey-brown, dorsal crests and porosteles usually dark brownish	dark grey-brown to dark brown, most of tergal crests/tubercles and ozopoiferous cones very dark brown	uniformly light yellow-brown	uniformly red-yellownish to grey-brown, dorsal crests and porosteles usually dark brownish	uniform light brown or brown, with tergal crests/ tubercles and ozoporiferous cones dark brown	reddish brown
Eyes	8–13, blackish	2–5, blackish to brownish	14–16, blackish	6–8, light greyish	8–13, blackish to brownish	9–13, brown	n/a
Antennae	Long and moderately clavate; extending beyond segment 4 laterally	short and clavate, extending past ring 3 laterally	short and moderately clavate; extending beyond segment 3 laterally	short and moderately clavate; extending beyond segment 3 laterally	short and clavate, extending past ring 3 laterally	Long and moderately clavate; extending beyond segment 4 laterally	n/a
Body							
Holotype	52p+2a+T	56p+2a+T	52p+2a+T	31p+2a+T	58p+1a+T	58p+1a+T	53+2a+T
♂	40-56p+4-2a+T	n/a	46p+2a+T	31–43p+2a+T	35-58p+1–2a+T	44–72p+5-1a+T	n/a
♀	40-56p+4-2a+T	50–57p+2(1)a+T	n/a	31–43p+2a+T	39–51p+1-3a+T	44-72p+5-1a+T	n/a
Carinotaxy formula of collum	1a+2-5+pc+ma	1+2a+3c+4-5+6c+7a+pc+ma	1-6+7a+pc+ma	1-4+5a+pc+ma	1–6+7a+pc+ma	1-4+5a+6a+pc+ma	6/6+ma
Carinotaxy formula of midbody rings	3/3+I/ i+4//3+I/i+3/3	2/2+I/i+3/3+I/ i+2/2	(2)3/(2)3+I/ i+4//3+I/i+3/3	3/3+I/ i+4//3+I/i+3/	3/3+I/i+4/3+I/ i+3/3	2/2+I/ i+4/3(2)/3+I/ i+2/2	3/3+I/i+3/3I/ i+3/3
Ratio of leg length comparing to their ring height	0.7–0.8	0.67	0.9–1.0	1.1–1.2	0.5	1.0–1.1	n/a
Habitat	caves	caves	caves	caves	caves	caves	epigean
Locality	Tong Saen Khan District, Uttaradit	Thung Chang District, Nan	Lom Sak District, Phetchabun	Ban Non Hin District, Loei	Na Noi District and Na Muen District, Nan; Rong Kwang District, Phrae	Mae Sai District, Chiang Rai	Doi Suthep, Chiang Mai

Description. Length of holotype ♂, 23.5 mm; that of paratypes, 22.8–26.5 mm (♀); midbody segments round in cross-section (Fig. 1F), their width (horizontal diameter) and height (vertical diameter) being similar; width of holotype ♂, 1.0 mm, of ♀ paratypes, 0.9–1.2 mm.

Coloration in alcohol (Fig. 1), after three years of preservation, uniformly red-brownish or dark castaneous brown to grey-brown, dorsal crests and porosteles usually dark brownish (Fig. 1A, B, D, E, H). Antennae and venter yellowish to pallid (Fig. 1A, C, E–G, I). Eyes blackish to brownish (Fig. 1A, C).

Body with 56p+2a+T rings/segments (♂ holotype); ♀ paratypes with 50–57p+2(1) a+T rings. Eye patches transversely ovoid, each composed of 2–5 rather flat ocelli in a single longitudinal row (Fig. 1A, C). Antennae short and clavate (Figs 1A, C, 2A), extending past ring 3 laterally, antennomeres 5 and 6 each with a small distoventral

group or corolla of bacilliform sensilla (Fig. 2A). Gnathochilarium with a clearly separated promentum (Fig. 2B).

In width, head = ring 2 < collum = midbody rings (close to 13th to 15th) < ring 4 = 5 = 7 = 3 < 8 = 10; body abruptly tapering towards telson on a few posteriormost rings (Fig. 1B). Postcollar constriction very evident (Fig. 1B).

Collum nearly smooth, carinotaxic formula 1+2a+3c+4–5+6c+7a+pc+ma (Fig. 1A–C), with 6+6 longitudinal crests starting from anterior edge, but both median crests interrupted in about caudal 2/3–3/4, being replaced there by similar 1+1+1 crests.

Following metaterga very strongly crested (Fig. 1A, B, D–H), especially from ring 5 on, whence porosteles commence (Fig. 1A, B), smaller tubercles in their stead on legless rings in front of telson due to loss of ozopores (Fig. 1G, H). Porosteles large, conical, round, directed caudolaterad, rather higher than wide (Fig. 1A, B, D–H). Midway metatergal crests on ring 5 distinctly divided into two at about 1/3 metatergal height, each half evident and well rounded, nearly undivided small tubercles in their stead in legless rings in front of telson (Fig. 1G, H). Carinotaxic formulae 2/2+I/i+3/3+I/i+2/2, all dorsal crests subdivided transversely and sharper, especially so lateral crests (Fig. 1B, D–H).

Tegument rather smooth, shining throughout (Fig. 1A, B, D–H). Fine longitudinal striations in front of stricture between pro- and metazonae, remaining surface of prozonae very delicately shagreened (Fig. 1D, E). Metatergal setae absent. Rings 2 and 3 each with long pleural flaps. Epiproct (Fig. 1G–I) simple, with a long dorsal crest in middle and small paramedian tubercles, regularly rounded caudally, faintly convex medially. Paraprocts regularly convex, each with premarginal sulci medially and a row of sparse setae at medial margin (Fig. 1I). Hypoproct transversely bean-shaped, slightly concave caudally, with 1+1 strongly separated setae near caudal margin (Fig. 1I).

Ventral flaps behind gonopod aperture on ♂ ring 7 barely distinguishable as low swellings forming no marked transverse ridge.

Legs short, on midbody rings about 2/3 length of body height (Figs 1A, C, E–G, 2F). Claw at base with a very small accessory spine about 1/6 the length of main claw (Fig. 2F).

♂ legs 1 highly characteristic (Fig. 2C, D) in being very strongly reduced, 5-segmented telopodites and a pair of large, subdigitiform, medially contiguous, but apically diverging coxal processes with groups of long and strong setae at base.

♂ legs 2 nearly normal (Fig. 2E), claw long and slender; only anteriorly, prefemur somewhat reduced, and femur abbreviated on oral face; penes broad, rounded, each with four or five strong setae distolaterally (Fig. 2E).

♂ legs 3 missing, lost.

Anterior gonopods (Fig. 2G, H) with a typical shield-like coxosternum, the latter modestly microsetose on caudal face (Fig. 2G), on each side with a very long, slender, chopstick-shaped, apicomesal process (d) and an evident subsecuriform process (s), tip narrowly rounded. Telopodite rather small, stout, movable, 1-segmented, lateral in position, with three or four strong apical setae and a field of microsetae at base (Fig. 2G, H), about as long as adjacent lateral corner of coxosternum, but lower than paramedian processes (d) of coxosternum.

Posterior gonopods (Fig. 2I, J) compact, broadly subquadrate, micropapillate medially on oral face; with a very long, medially densely plumose and stout flagellum

process (f) (Fig. 2I, J); lamelliform lobe (l) higher than caudal piece of coxite, membranous, smooth, with an apical field of coniform microsetae laterally (Fig. 2J); each median and lateral part of coxite with dense, strong and curved setae (Fig. 2J).

Remarks. This new species belongs to the *javanicus*-group which currently encompasses 32 described species (Golovatch et al. 2007b, 2011b, 2012a; Likhitrakarn et al. 2017; Jiang et al. 2017, 2018, 2020). The above new congener is the second one in this group to be reported from Thailand. Due to the absence of any potential morphological cave adaptations, i.e., of a longer body, of a lighter coloration, and of elongated femora and tarsi of walking legs (Liu et al. 2017), *G. longus* sp. nov. is only to be considered as troglophilic at most. The cave where the species was discovered is located at an elevation of ca 1420 m a.s.l. in Nan Province. The cave is rather narrow, hidden in a steep-sided doline in a riparian area. It consists of a streamway and a series of oxbow passages, with many links between these two parts to the cave. The areas where the cave was developed are surrounded by agricultural landscapes, i.e., cabbage and corn fields. The specimens were found on the cave floor with scattered bat guano and some debris brought in by the stream, ca 50 meters from the entrance. The temperature of the cave was 20.8–22.4 °C (mid-May), and the relative humidity was 85–90%. In the same cave and habitat, we also found Collembola (*Coecobrya* sp. and *Lepidocyrtus* sp.), Formicidae (*Ponera* sp.), Thelyphonida, mites and pseudoscorpions.

Glyphiulus promdami sp. nov.
http://zoobank.org/31975FDC-B9BF-4130-9BE3-B06B9C0921EE
Figs 3, 4

Type material. *Holotype* ♂: Thailand, Nan Province, Na Noi District, Tham Chetawan, 18°16'26"N, 100°34'43"E; 520 m a.s.l., 18.05.2018, S. Jantarit leg.; CUMZ-CAM169. *Paratypes:* 5 ♂, 5 ♀: same locality as holotype; CUMZ-CAM169; 1 ♂, 1 ♀: same locality as holotype; ZMUM; 1 ♂, 1 ♀: same locality as holotype; NHM-PSU; 1 ♂, 3 juv.: same Province, Na Muen District, Tham La-ong, 18°14'18"N, 100°34'55"E, 648 m a.s.l., 18.05.2018, S. Jantarit leg.; CUMZ-CAM170; 3 ♂, 2 ♀: Phrae Province, Rong Kwang District, Tham Pha Phrai Wan, 18°25'18"N, 100°28'10"E, 419 m a.s.l., 17.05.2019, S. Jantarit leg.; CUMZ-CAM166.

Name. The species is so named to honour Mr. Rueangrit Promdam, a carcinologist and researcher at the Princess Maha Chakri Sirindhorn Natural History Museum of Prince of Songkla University (NHM-PSU), who is interested in cave fauna in the country and who has collected many millipedes, including this new species, from various Thai caves.

Diagnosis. This new species seems to be particularly similar to *G. subbedosae* Likhitrakarn, Golovatch & Panha, 2017, from Laos (Likhitrakarn et al. 2017), with which it shares the following diagnostic characters: body size, colour pattern and unique carinotaxic formulae, coupled with certain anterior and posterior gonopod structural details. It differs from *G. subbedosae* primarily by a uniformly yellow collum (Fig. 3A–C) (vs. its anterior half darker) and the median and lateral parts of the posterior gonopod
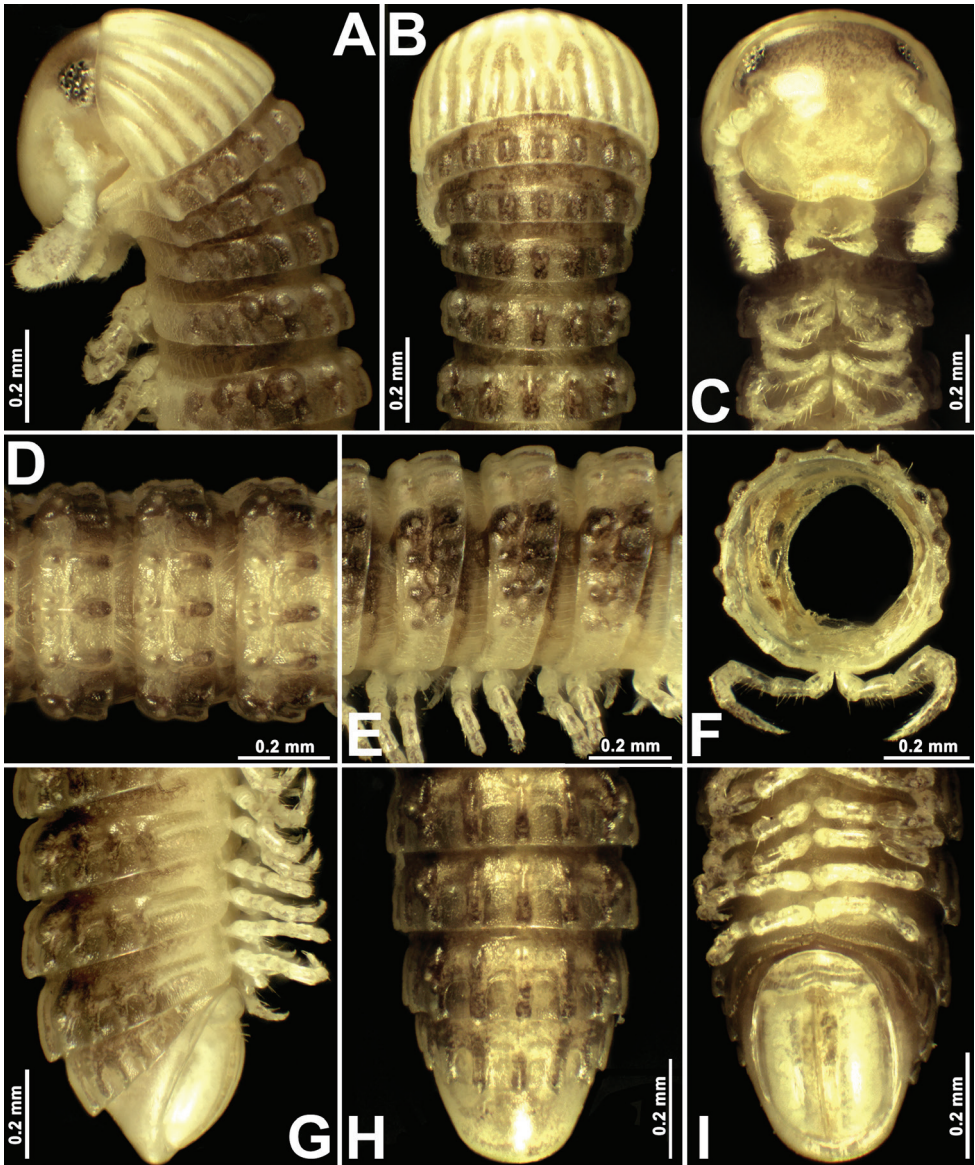
Figure 3. *Glyphiulus promdami* sp. nov., ♂ paratype **A–C** anterior part of body, lateral, dorsal and ventral views, respectively **D, E** midbody rings, dorsal and lateral views, respectively **F** cross-section of a midbody ring **G–I** posterior part of body, lateral, dorsal and ventral views, respectively.

coxite with 10–12 strong setae (Fig. 4K) (vs. six strong setae), coupled with the anterior gonopod coxosternum being moderately microsetose in the anterior and medial parts on the caudal face (Fig. 4H) (vs. only in medial part).

Description. Length of holotype, 21.8 mm; adult paratypes 14.5–18.4 (♂) or 14.2–24.3 mm long (♀), juveniles 6.5–12.3 mm long; midbody rings round in cross-
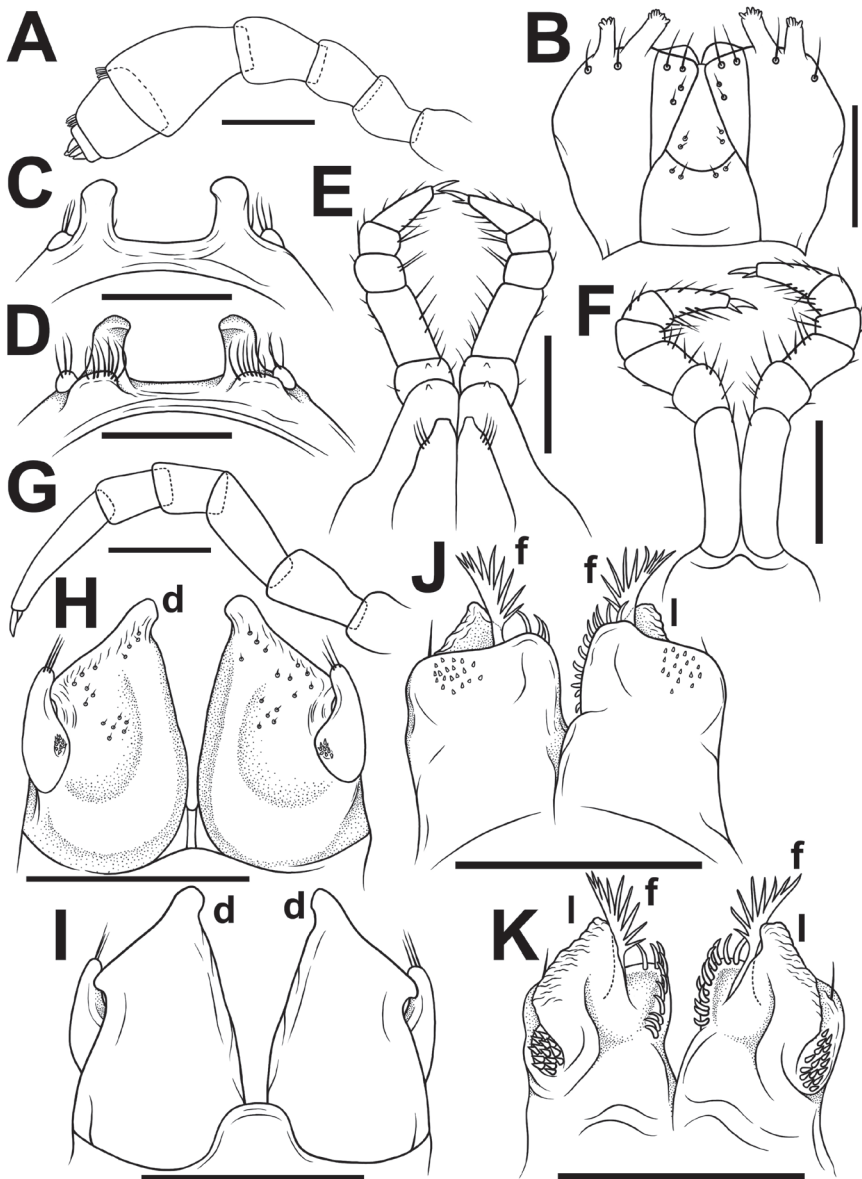
Figure 4. *Glyphiulus promdami* sp. nov., ♂ holotype **A** antenna, lateral view **B** gnathochilarium, ventral view **C, D** legs 1, oral and caudal views, respectively **E** legs 2, caudal view **F** leg 3, caudal view **G** midbody leg **H, I** anterior gonopods, caudal and oral views, respectively **J, K** posterior gonopods, oral and caudal views, respectively. Abbreviations: **d** apicomesal processes, **f** flagellum process, **l** lamelliform lobe. Scale bar: 0.1 mm.

section (Fig. 5L), their width (horizontal diameter) and height (vertical diameter) being similar; width in holotype, 0.9 mm; in paratypes, 0.7–1.0 (♂), 0.8–1.1 (♀) or 0.5–0.7 mm (juveniles).

Coloration in alcohol (Fig. 3), after three years of preservation, uniformly red-yellownish to grey-brown, dorsal crests and porosteles usually dark brownish (Fig. 3A, B, D, E, H). Head, collum, antennae and venter yellowish to pallid (Fig. 3A, C, E–G, I). Eyes blackish to brownish (Fig. 3A, C).

Body with 58p+1a+T rings (♂ holotype); paratypes with 35–58p+1–2a+T (♂), 39–51p+1–3a+T (♀) or 25–35+2–5a+T (juveniles). Eye patches transversely ovoid, each composed of 8–13 blackish, rather flat ocelli in three or four irregular longitudinal rows (Fig. 3A). Antennae short and clavate (Figs 3A, C, 4A), extending past ring 3 laterally, antennomeres 5 and 6 each with a small distoventral group or corolla of bacilliform sensilla (Fig. 4A). Gnathochilarium with a clearly separated promentum (Fig. 4B).

In width, head = ring 4 = 5 < 6 < 7 < 3 < midbody rings (close to 8th to 10th) < 2 < collum; body abruptly tapering towards telson on a few posteriormost rings (Fig. 3B). Postcollar constriction very evident (Fig. 3B).

Collum nearly smooth, carinotaxic formula 1–6+7a+pc+ma (Fig. 3A–C), with 7+7 longitudinal crests starting from anterior edge, but both median crests interrupted in about caudal 2/3–3/4, being replaced there by similar 1+1+1 crests.

Following metaterga similarly strongly crested (Fig. 3A, B, D–H), especially from ring 5 on, whence porosteles commence (Fig. 3A, B), smaller tubercles in their stead on legless rings in front of telson due to loss of ozopores (Fig. 3G, H). Porosteles large, conical, round, directed caudolaterad, wider than high. Midway metatergal crests on ring 5 distinctly divided into two at about 1/3 metatergal height, each half evident and well rounded, nearly undivided small tubercles in their stead in legless rings in front of telson (Fig. 3G, H). Carinotaxic formulae 3+I/i+3/3+I/i+3 on rings 2–4, as well as on the last one or two leg-bearing, and on legless rings (Fig. 3A, B, G, H); midbody rings showing mostly dorsal crests distinctly divided into two at about 1/3 metatergal height, each half rather evident and well rounded (carinotaxic formulae 3/3+I/i+4/3+I/i+3/3) and sharper, especially so lateral crests (Fig. 3D, E).

Tegument rather smooth, dull throughout (Fig. 3A, B, D, E, G, H). Fine longitudinal striations in front of stricture between pro- and metazonae, remaining surface of prozonae very delicately shagreened (Fig. 3D, E). Metatergal setae absent. Rings 2 and 3 each with long pleural flaps (Fig. 3A). Epiproct (Fig. 3G, I) simple, regularly rounded caudally, faintly convex medially. Paraprocts regularly convex, each with premarginal sulci medially and a row of sparse setae at medial margin (Fig. 3I). Hypoproct transversely bean-shaped, slightly concave caudally, with 1+1 strongly separated setae near caudal margin (Fig. 3I).

Ventral flaps behind gonopod aperture on ♂ ring 7 distinguishable as low swellings forming a bare transverse ridge.

Legs rather short, on midbody rings about half the length of ring height (Figs 3A, C, E–G, 4G). Claw at base with an evident accessory spine about 1/3–1/4 the length of main claw (Fig. 4G).

♂ legs 1 highly characteristic (Fig. 4C, D) in being very strongly reduced, represented only by a sternum devoid of any median or paramedian structures,

but carrying 1+1 strongly separated prongs, both evidently curved posteriad and bearing several strong setae, and rudimentary, 1-segmented leg vestiges at base on caudal face (Fig. 4C, D).

♂ legs 2 nearly normal (Figs 4E), prefemur somewhat reduced only anteriorly; penes broad, oblong-subtrapeziform, each with 3–5 strong setae distolaterally (Fig. 4E).

♂ legs 3 modified in having coxa especially slender and elongate (Fig. 4F).

Anterior gonopods (Fig. 4H, J) with a typical shield-like coxosternum, the latter moderately microsetose in anterior and medial parts on caudal face (Fig. 4H), with a high, digitiform, apicomesal process (d). Telopodite rather small, movable, 1-segmented, lateral in position, with two or three strong apical setae and a field of microsetae at base (Fig. 4H), moderately higher than adjacent lateral corner of coxosternum.

Posterior gonopods (Fig. 4J, K) compact, broadly subquadrate, micropapillate medially on oral face; coxite medio-apically with a long, plumose, apical flagellum (f) with evident spikes paramedially (Fig. 4J, K); lamelliform lobe (l) high, subquadrate, membranous, wrinkled frontolaterally, with an apical field of coniform microsetae laterally (Fig. 4K); each mediolateral part of coxite with 10–12 strong and curved setae (Fig. 4K).

Remarks. The *granulatus*-group currently encompasses 36 described species, including our new species (Golovatch et al. 2007a, 2011a; Likhitrakarn et al. 2017; Liu and Wynne 2019). The new species is the fifth in this group to be reported from Thailand.

Three populations have been collected inside caves, with the longest distance of about 25 air-km between the collecting localities, and all show similar morphological characters as described above. *Glyphiulus promdami* sp. nov. fails to show any morphological adaptations to cave life and is considered here as a troglophilic species. It appears to have a rather narrow distribution, but has been found in a wide range of cave environments from the twilight (Tham Chetawan) to the dark and deep zones of the caves (all three caves). The temperature in the caves where the species was collected ranged between 24.2 and 29.8 °C, while the relative humidity was 70–94%. All populations were found to be quite large and associated with bat guano.

Key to *Glyphiulus* species presently known to occur in Thailand, based mainly on male characters

1   First male legs either normal or reduced in size, but with a pair of paramedian coxal processes (Fig. 2C, D) .... **2 (the *javanicus*-group)**
–   First male legs very strongly reduced, completely lacking any median structures (Fig. 4C, E) .... **3 (the *granulatus*-group)**
2   Carinotaxic formula of collum, 6+6, all complete crests. Each anterior gonopod with a typical, digitiform, apicomesal process (d) (Fig. 4H, I). Each posterior gonopod with a short and bare flagellum....................***G. siamensis***
–   Carinotaxic formula of collum, 1+2a+3c+4–5+6c+7a+pc+ma (Fig. 1A, B). Each anterior gonopod with a very long, slender, apicomesal process (d)

(Fig. 2G, H). Each posterior gonopod with a very long, medial, densely plumose flagellum (Fig. 2I, J).. *G. longus* **sp. nov.**

3   Body usually larger: length 23–40 mm. Carinotaxic formula of midbody rings, 2/2+I/i+4/3+I/i+2/2 .... ***G. sattaa***

–   Body usually smaller: length 14–24 mm. Carinotaxic formula of midbody rings, 3/3+I/i+4/3+I/i+3/3 ....**4**

4   Carinotaxic formula of collum, 1–4+5+6c+7a+pc+ma. Ocelli unpigmented, mostly invisible, only sometimes traceable as light greyish, with 6–8 translucid ocelli. Legs long, about 1.1–1.2 the length of ring height.... ***G. mongkon***

–   Carinotaxic formula of collum different. Ocelli pigmented, with 8–16 blackish ocelli either side of head. Legs short, about 0.5–1.0 the length of ring height **5**

5   Carinotaxic formula of collum, 1a+2–5+pc+ma. Telopodites of first male leg-pair two-segmented... ***G. duangdee***

–   Carinotaxic formula of collum, 1–6+7a+pc+ma (Fig. 3A, B). Telopodites of first male leg-pair one-segmented (Fig. 4C, D) **6**

6   14–16 ocelli in three or four irregular transverse rows. Each anterior gonopod with a very short apicomesal process (d), the latter as high as telopodites ....***G. maidtreejit***

–   8–13 ocelli in three or four irregular transverse rows, always black. Each anterior gonopod with an elongated apicomesal process (d), the latter obviously higher than telopodites (Fig. 4H, I) ....***G. promdami* sp. nov.**

Discussion

The millipede family Cambalopsidae is known to be the most common, highly abundant and species-rich group dominating the cave diplopod faunas of Southeast Asia and China (Golovatch 2015). *Glyphiulus* is the largest genus and it presently comprises 68 described species. Most of the species (43, or > 63%) have been recorded from southern China, followed by Vietnam (nine species), northern Thailand (seven species), Laos (six species), Japan (the Ryukyu Islands) and Indonesia (north-central Java) (one species each) (Golovatch et al. 2007a, b; 2011a, b, 2012a; Likhitrakarn et al. 2017; Jiang et al. 2017, 2018, 2020; Liu and Wynne 2019). However, the diversity of this genus in Thailand is incompletely assessed, with only a small area having yet to be revealed as being confined to the northern, mountainous parts of the country (Fig. 5).

Only five *Glyphiulus* species have been found, and four described from caves, in Thailand: *G. duangdee* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b, *G. maidtreejit* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b, *G. mongkon* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b, and *G. sattaa* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011b (Table 1). Now the diversity has been increased to seven, considering both new species documented in this study. On the other hand, since Thailand and the neighboring countries are known to be extremely
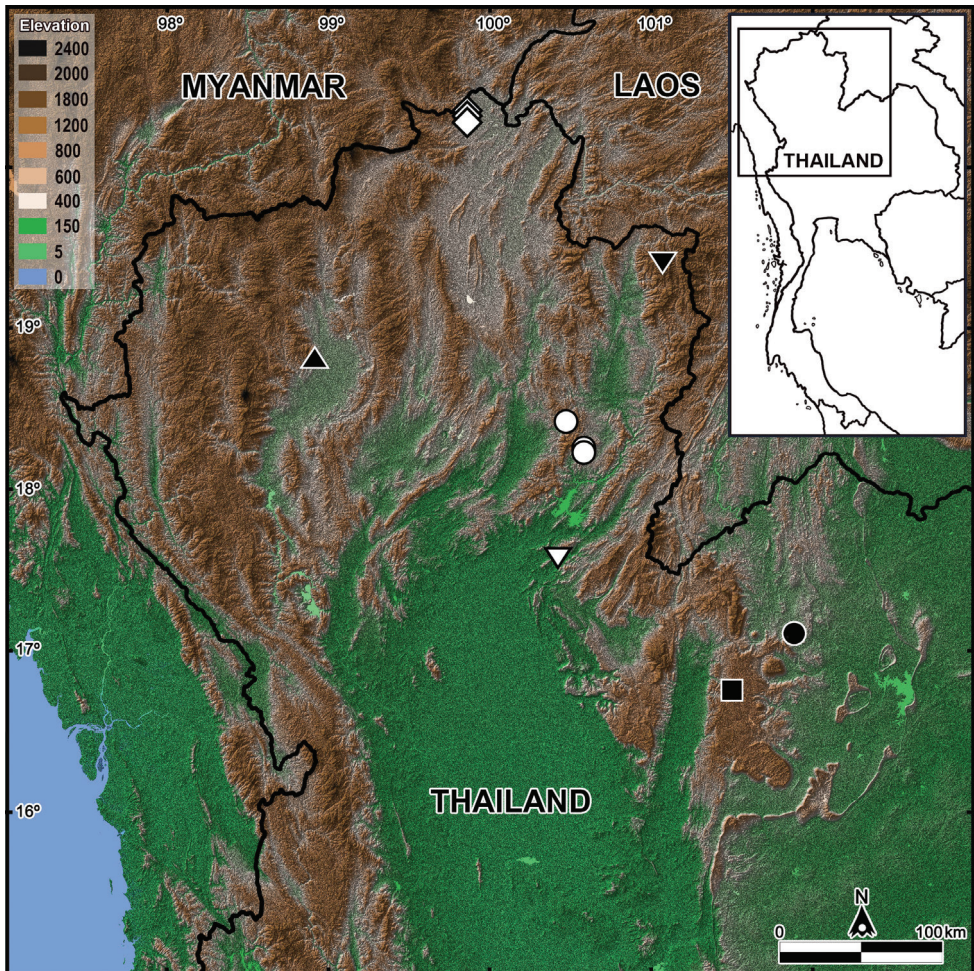
Figure 5. Distribution of *Glyphiulus* species in Thailand (seven species): Open diamond: *Glyphiulus sattaa* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011; Inverted filled triangle: *Glyphiulus longus* sp. nov.; Filled triangle: *Glyphiulus siamensis* Mauriès, 1983; Open circle: *Glyphiulus promdami* sp. nov.; Inverted open triangle: *Glyphiulus duangdee* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011; Filled circle: *Glyphiulus mongkon* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011; Filled square: *Glyphiulus maidtreejit* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2011.

rich in karst and caves, there can hardly be any doubt that additional species of *Glyphiulus* still await discovery. In contrast to the distribution of cave *Glyphiulus*, which is restricted to northern Thailand with all species being narrowly endemic, the similarly mostly cavernicolous genera *Plusioglyphiulus* and *Trachyjulus* are widespread throughout Thailand, while their species are likewise mostly narrowly endemic.

Most species of *Glyphiulus* in Thailand are known from caves or surrounding karst areas, except for *G. siamensis* Mauriès, 1983 which has been recorded from Kontathan (= Montha Than) waterfall area, Doi Suthep National Park, Chiang Mai Province

(Mauriès 1983; Enghoff 2005). Similarly, *G. formosus* (Pocock, 1895) has been found and redescribed from under stones in a typical deciduous forest habitat in Guangdong Province, China (Jiang et al. 2020). This is evidence that many more cambalopsids can also be expected to be revealed outside caves, as they also live epigeically on the forest floor. Still, because locating millipedes inside caves or grottos on guano seems to be easier than searching for them in forest litter or tree stumps, the obvious bias to spotting "cavernicolous" Cambalopsidae is easy to comprehend. There is little doubt that, with further study of the millipede fauna of Thailand, both epigean and cavernicolous, many more novelties are to be expected.

Acknowledgements

References

AVMA (2013) AVMA guidelines for the euthanasia of animals. https://www.avma.org/KB/Policies/Documents/euthanasia.pdf [Accessed on: 2019-2-2]

Carl J (1911) Drei neue Diplopoden des Genfer Museums. Revue suisse de Zoologie 19: 397–407.

Enghoff H (2005) The millipedes of Thailand (Diplopoda). Steenstrupia 29(1): 87–103.

Enghoff H, Dohle W, Blower JG (1993) Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. Zoological Journal of the Linnean Society 109: 103–234. https://doi.org/10.1111/j.1096-3642.1993.tb00305.x

Gervais P (1847) Myriapodes. In: Walckenaer CA, Gervais P (Eds) Histoire naturelle des Insectes Aptères Vol. 4. Librairie encyclopédique de Roret, Paris, 1–133.

Golovatch SI (2015) Cave Diplopoda of southern China with reference to millipede diversity in Southeast Asia. ZooKeys 510: 79–94. https://doi.org/10.3897/zookeys.510.8640

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2007a) Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 1: the *granulatus*-group. Zoosystema 29(1): 7–49.

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2007b) Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia

(Diplopoda, Spirostreptida, Cambalopsidae). Part 2: the *javanicus*-group. Zoosystema 29(3): 417–456.

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2009) Review of the millipede genus *Plusioglyphiulus* Silvestri, 1923, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Zoosystema 31(1): 71–116. https://doi.org/10.5252/z2009n1a5

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2011a) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *granulatus*-group (Diplopoda: Spirostreptida: Cambalopsidae). Arthropoda Selecta 20(2): 65–114. http://kmkjournals.com/journals/AS/AS_Index_Volumes/AS_20/AS_20_2_065_114_Golovatch_et_al

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2011b) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *javanicus*-group (Diplopoda: Spirostreptida: Cambalopsidae). Arthropoda Selecta 20(3): 149–165. http://kmkjournals.com/journals/AS/AS_Index_Volumes/AS_20/AS_20_3_149_165_Golovatch_et_al

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2012a) An unusual new species of the millipede genus *Glyphiulus* Gervais, 1847 from Borneo (Diplopoda: Spirostreptida: Cambalopsidae). Russian Entomological Journal 21(2): 133−137. https://doi.org/10.15298/rusentj.21.2.04

Golovatch SI, Geoffroy JJ, Mauriès JP, VandenSpiegel D (2012b) New or poorly-known species of the millipede genus *Trachyjulus* Peters, 1864 (Diplopoda: Spirostreptida: Cambalopsidae). Arthropoda Selecta 21(2): 103–129. https://doi.org/10.15298/arthsel.21.2.01

Jiang X, Guo X, Chen H, Xie Z (2018) Four new species of the *Glyphiulus javanicus* group from southern China (Diplopoda, Spirostreptida, Cambalopsidae). In: Stoev P, Edgecombe GD (Eds) Proceedings of the 17th International Congress of Myriapodology, Krabi, Thailand. ZooKeys 741: 155–179. https://doi.org/10.3897/zookeys.741.23223

Jiang XK, Hennen DA, Chen HM, Xie ZC (2020) First description of the male of *Glyphiulus formosus* (Pocock, 1895) (Diplopoda: Spirostreptida: Cambalopsidae) from China. Zootaxa 4861(2): 281–289. https://doi.org/10.11646/zootaxa.4861.2.8

Jiang XK, Lv JC, Guo X, Yu ZG, Chen, HM (2017) Two new species of the millipede genus *Glyphiulus* Gervais, 1847 from Southwest China (Diplopoda: Spirostreptida: Cambalopsidae). Zootaxa 4323(2): 197–208. http://dx.doi.org10.11646/zootaxa.4323.2.3

Likhitrakarn N, Golovatch SI, Inkhavilay K, Sutcharit C, Srisonchai R, Panha S (2017) Two new species of the millipede genus *Glyphiulus* Gervais, 1847 from Laos (Diplopoda, Spirostreptida, Cambalopsidae). ZooKeys 722: 1–18. https://doi.org/10.3897/zookeys.722.21192

Likhitrakarn N, Golovatch SI, Jeratthitikul E, Srisonchai R, Sutcharit C, Panha S (2020) A remarkable new species of the millipede genus *Trachyjulus* Peters, 1864 (Diplopoda, Spirostreptida, Cambalopsidae) from Thailand, based both on morphological and molecular evidence. ZooKeys 925: 55–72. https://doi.org/10.3897/zookeys.925.49953

Liu W, Golovatch S, Wesener T, Tian M (2017) Convergent evolution of unique morphological adaptations to a subterranean environment in cave millipedes (Diplopoda). PLoS ONE 12(2): e0170717. https://doi.org/10.1371/journal.pone.0170717

Liu W, Wynne JJ (2019) Cave millipede diversity with the description of six new species from Guangxi, China. Subterranean Biology 30: 57–94. https://doi.org/10.3897/subt-biol.30.35559

Mauriès JP (1983) Cambalides nouveaux et peu connus d'Asie, d'Amérique et d'Océanie. I, Cambalidae et Cambalopsidae (Myriapoda, Diplopoda). Bulletin du Muséum national d'Histoire naturelle, Série 2, 42(3): 509–519.

Pocock RI (1895) Report upon the Chilopoda and Diplopoda obtained by Bassett-Smith PW, Esq., Surgeon RN, Walker JJ, Esq RN, during the cruise in the Chinese Seas of HMS 'Penguin', Commander W. U. Moore commanding. Annals and Magazine of Natural History, ser. 6, 15: 346–368. https://doi.org/10.1080/00222939508677895

QGIS Development Team (2021) QGIS Geographic Information System. Open source geo-spatial foundation project. http://qgis.osgeo.org

RESEARCH ARTICLE

Two new species and one new record of *Neoperla* (Plecoptera, Perlidae) from Guangxi Zhuang Autonomous Region, China

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Abstract

Three species of the *Neoperla montivaga* group are described from Guangxi Zhuang Autonomous Region of southern China, including two new species, *N. falcatata* **sp. nov.** and *N. shangsiensis* **sp. nov.**, and a new record for Guangxi: *N. bilineata* Wu & Claassen, 1934. Illustrations and color images are provided for the three species mentioned above, and the new species is compared with related congeners in the group. Notes on the distribution of the *Neoperla* species known from Guangxi are also given.

Keywords

Neoperla montivaga group, Perlinae, southern China, Stoneflies, taxonomy

Introduction

Neoperla Needham, 1905, of the subfamily Perlinae (Plecoptera, Perlidae), is one of the most species-rich and widely distributed stonefly genera, with at least 271 species worldwide (DeWalt et al. 2020). To date, 104 *Neoperla* species have been reported in China, comprising about 38% of species in the genus (Yang and Li 2018; DeWalt et

al. 2020). The *N. montivaga* species group was first proposed by Zwick (1983) and currently includes 119 species worldwide (Yang and Li 2018; DeWalt et al. 2020; Mo et al. 2020a). In the present paper, we describe two new species and provide one new record of *Neoperla* from Guangxi, southern China. The three species are members of the *Neoperla montivaga* species group as defined by Zwick (1983), because of the incomplete sclerotization on the ventral surface of the aedeagal tube. The distribution and number of *Neoperla* species in cities of Guangxi are also presented.

Materials and methods

Specimens were collected using an aerial net or by light traps with white lamps and stored in 75% ethanol. The holotype of the new species and other studied specimens are deposited in the Insect Collection of the Henan Institute of Science and Technology (**HIST**), Xinxiang, China and in the National Museum Prague (**NMP**), Czech Republic, as indicated in the text. Specimens were examined with the aid of a Leica M420 dissecting microscope and the color illustrations were made with a Leica S8APO. Aedeagi were everted using the cold maceration technique of Zwick (1983), and terminology follows Sivec et al. (1988). The map (Fig. 10) was prepared using a base map of the Guangxi Zhuang Autonomous Region downloaded from the standard map service of the online government service platform of the Ministry of Natural Resources, People's Republic of China (http://bzdt.ch.mnr.gov.cn/; map number GuiS(2017)47).

Results and discussion

Neoperla bilineata Wu & Claassen, 1934
Figs 1, 2

Neoperla bilineata: Wu and Claassen 1934: 120; Wu 1938: 107; Claassen 1940: 158; Wu 1948: 75; Illies 1966: 268; Zwick 1973: 258; Du et al. 1999: 62; Li et al. 2017: 199; Yang and Li 2018: 39; Mo et al. 2020b: 375.

Material examined. 1 male (HIST), 1 male (NMP), Guangxi Zhuang Autonomous Region, Guilin City, Multinational Autonomous County of Longsheng, Jiangdi Village, terraced fields surrounded with shrubs and bamboo forest, 365m, 25°55.6'N, 110°14.8'E, 12.IV.2013, leg. M. Fikáček, J. Hájek and J. Růžička.

Diagnosis. Males of this species are characterized by tergum 7 with an anteromedian pair of nipple-shaped processes, the straight aedeagal tube and the spinulose aedeagal sac with a small dorsoapical butterfly-shaped sclerite.

Distribution. China (Guangxi, Sichuan).

Ecology. The Jiangdi Village is located in the northeast of the Multinational Autonomous County of Longsheng, Guangxi, and is bordered by the Xing'an, Lingchuan and Ziyuan counties of Guangxi and by Chengbu County of Hunan Province. The
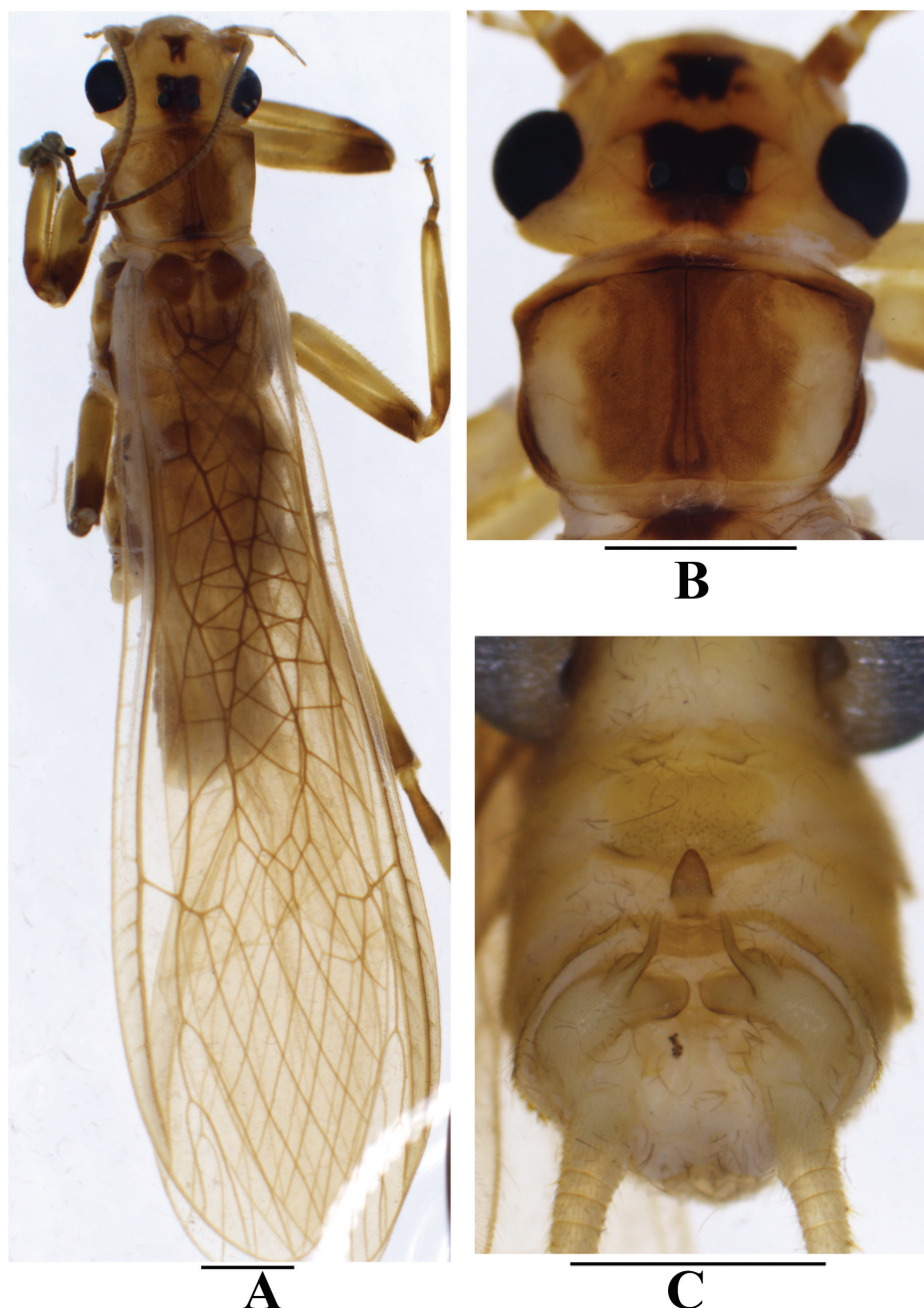
Figure 1. *Neoperla bilineata* Wu & Claassen, 1934 (male) **A** adult habitus, dorsal view **B** head and pronotum, dorsal view **C** terminalia, dorsal view. Scale bars: 1.0 mm.

Sangjiang River system flows through the village. In addition, both Jiangdi Village and Huaping National Nature Reserve of the same county belong to the Nanling area. The village is more than 600 km from Yibin City of Sichuan Province, where the type
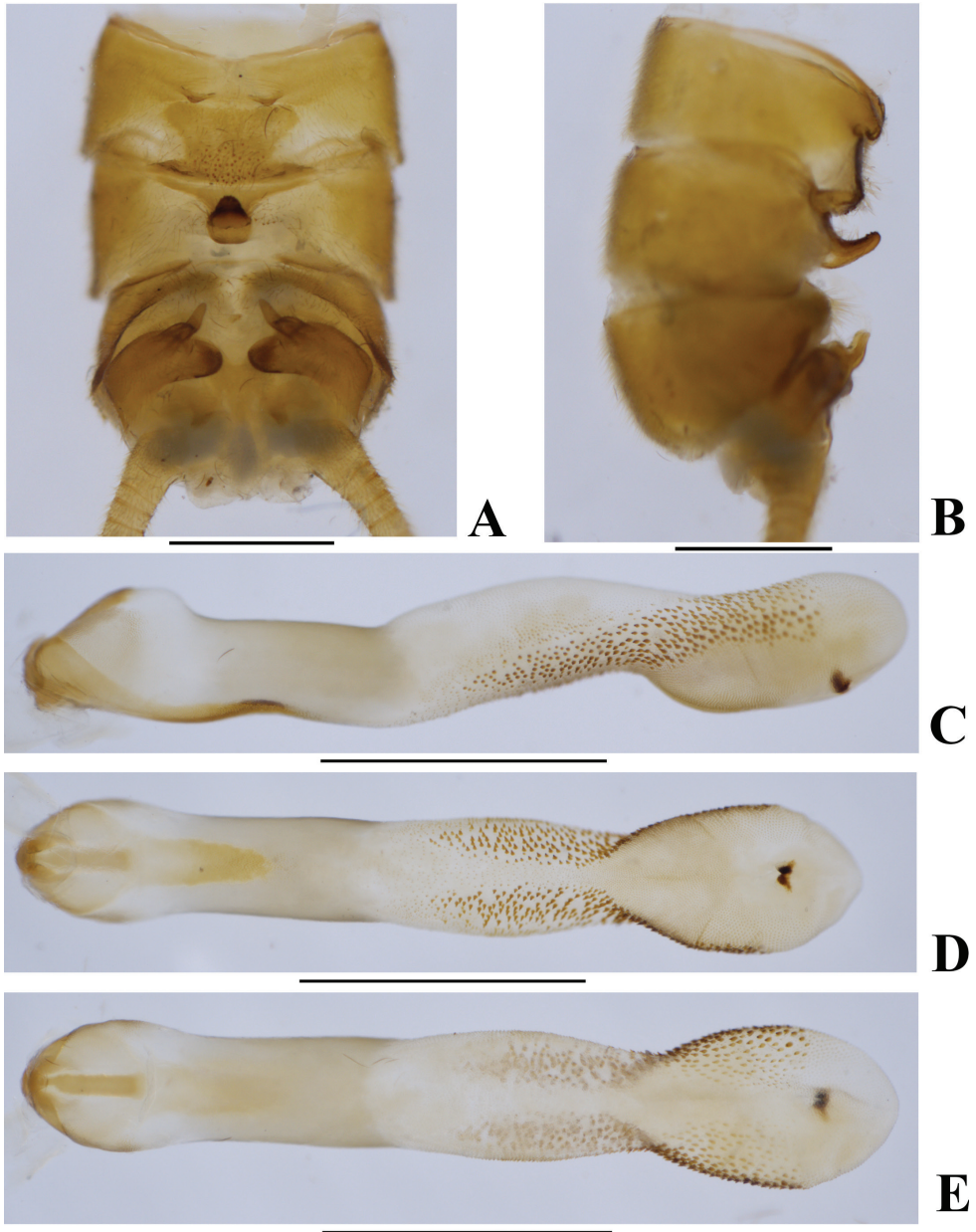
Figure 2. *Neoperla bilineata* Wu & Claassen, 1934 (male) **A** terminalia after being cleared, dorsal view **B** terminalia after being cleared, lateral view **C** aedeagus, lateral view **D** aedeagus, dorsal view **E** aedeagus, ventral view. Scale bars: 1.0 mm.

material of this species were collected. The adults of the species fly in spring and occur at low altitude. At the same locality, accompanying stoneflies were *Neoperla delphina* Li, Mo & Wang, 2020 and one unidentified female *Togoperla* sp.

Remarks. *Neoperla bilineata* Wu & Claassen, 1934 was originally described from the Sichuan Province of southwest China, without full eversion of the aedeagus. Li et al. (2017) made a complementary description, including that of the completely everted aedeagus. In the present study, two males of this species from Guangxi agree well with original and complementary illustrations and descriptions of the head pattern, the dorsal aspects of the terminalia and the aedeagus (Wu and Claassen 1934; Wu 1938; Li et al. 2017). We provide additional illustrations (Figs 1, 2) for aiding the recognition of this species from the Guangxi Zhuang Autonomous Region of southern China.

Neoperla falcatata sp. nov.
http://zoobank.org/1FD1B32C-B857-46DF-837D-0F5CF8F29A70
Figs 3–6

Type Material. *Holotype*: male (NMP), China: Guangxi Zhuang Autonomous Region, Shangsi County, Shiwandashan National Forest Park, forested river valley, 290–360m, 21°54.4'N, 107°54.2'E, 5–9.IV.2013, light trap, leg. M. Fikáček, J. Hájek and J. Růžička. *Paratypes*: 2 males (NMP), 1 female and 1 male (mating pair, HIST), same data as for holotype.

Diagnosis. This species is characterized by a median dark brown oval area on the head. The aedeagus is sickle-shaped, mostly covered with mixed armatures of spines and spinules. Females of this species have a small truncate tab-like subgenital plate of sternum 8.

Description. Adult habitus (Figs 3, 4, 5A, 6C). Body color brown. Head brown, with a dark brown subtrapezoidal stigma on anterior part of frons and a distinct median dark brown oval area covering the posterior ocelli; mouthparts brown, palpi paler, antennae dark brown; biocellate, the distance between ocelli ca. 1.5× the diameter of each ocellus; head slightly wider than pronotum. Pronotum rectangular, brown, with scattered darker rugosities; anterior corners sharp, posterior corners rounded. Wings brownish and transparent, veins dark brown; legs brown except femora yellow-brown at base; cerci dark brown.

Male (Figs 3, 4A, 5, 6A). Forewing length 10.0–10.5 mm. Hindwing length 8.3–8.8 mm. Posterior process of tergum 7 trapezoidal, covered with many basiconic sensilla. Tergum 8 with a tongue-shaped upcurved process, with many basiconic sensilla at apex. Tergum 9 with two paramedial patches of long hairs, without sensilla patches. Hemitergal processes of tergum 10 sclerotized, slender, finger-like, S-shaped: basally incurved, curved outward medially but incurved again apically, nearly extending to tongue-shaped process of tergum 8 (Fig. 5B, D, E). Aedeagus mostly membranous, sickle-shaped (Figs 5C, F, 6A). Aedeagal tube plump, straight, distinctly sclerotized basally and dorsally, with many spinules on dorsal surface (Fig. 5F). Aedeagal sac ca. 2.0× as long as tube, membranous, strongly curved ventrad, forming an open loop with a blunt tip; ventral surface fully armed with spinules; dorsal surface of basal half covered with brownish spines; distal half mostly covered with larger brown dorsal spines before spinous apex (Figs 5C, F, 6A).

Figure 3. *Neoperla falcatata* sp. nov. (mating pair). Scale bar: 2.0 mm.

Figure 4. *Neoperla falcatata* sp. nov. **A** male adult habitus, dorsal view **B** female adult habitus, dorsal view. Scale bars: 2.0 mm.

Female (Figs 3, 4B, 6B–D). Forewing length 13.8–14.5 mm. Hindwing length 12.2–12.8 mm. Generally similar to male. Posteromedial portion of sternum 8 slightly produced, forming a small, rectangular subgenital plate with a truncate tip.

Etymology. The name refers to the sickle-shaped aedeagus. The Latin "falcatus" means sickle-shaped.
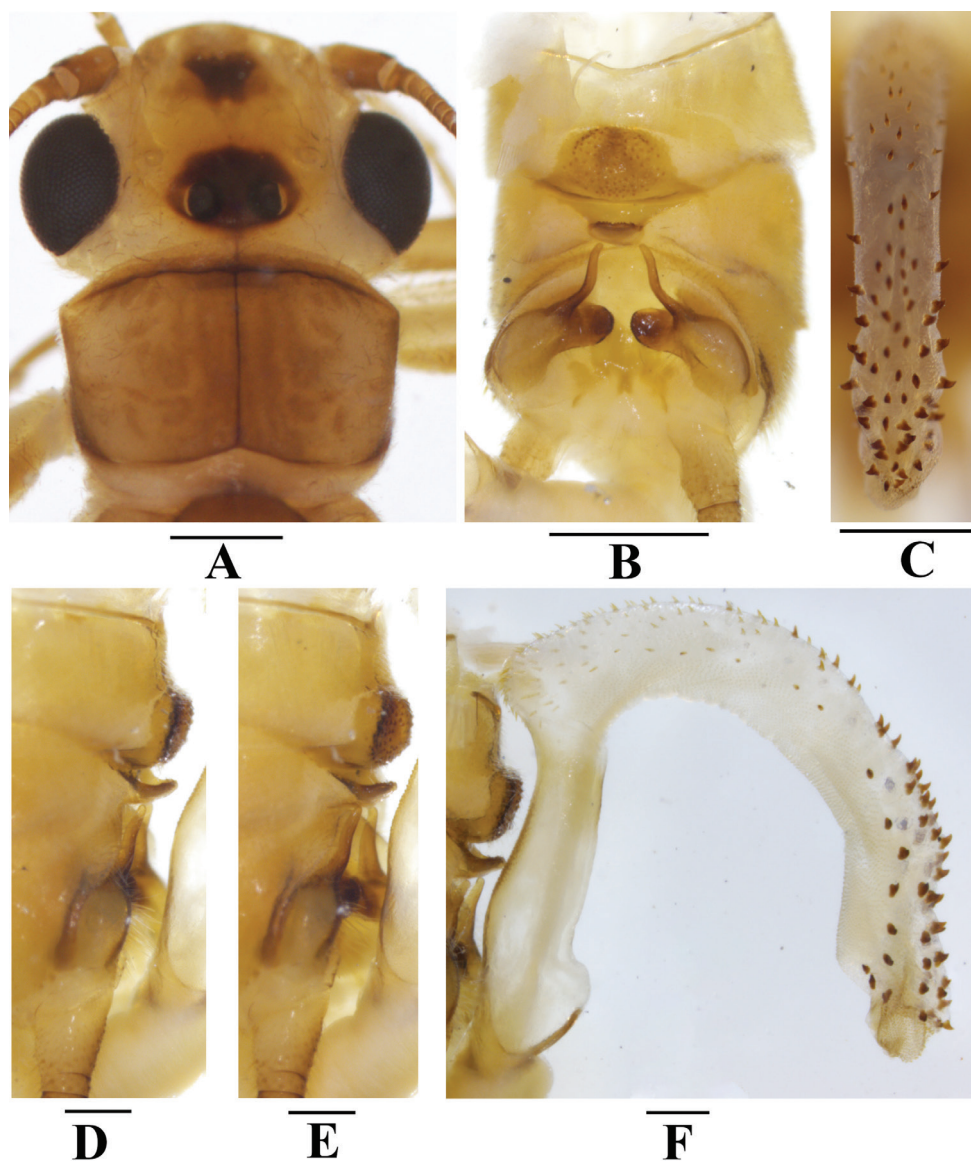
Figure 5. *Neoperla falcatata* sp. nov. (male) **A** head and pronotum, dorsal view **B** terminalia after being cleared, dorsal view **C** apical half of aedeagal sac, dorsal view **D** terminalia after being cleared, lateral view **E** terminalia after being cleared, oblique lateral view **F** aedeagus, lateral view. Scale bars: 0.5 mm (**A–C**); 0.2 mm (**D–F**).

Distribution. China (Guangxi).

Ecology. Shiwandashan National Forest Park is located in the southwest of Shangsi County of Fangchenggang City, Guangxi, and it belongs to the Shiwanda Mountains. The adults of the new species fly in spring and occur at low altitude. Other accompany-
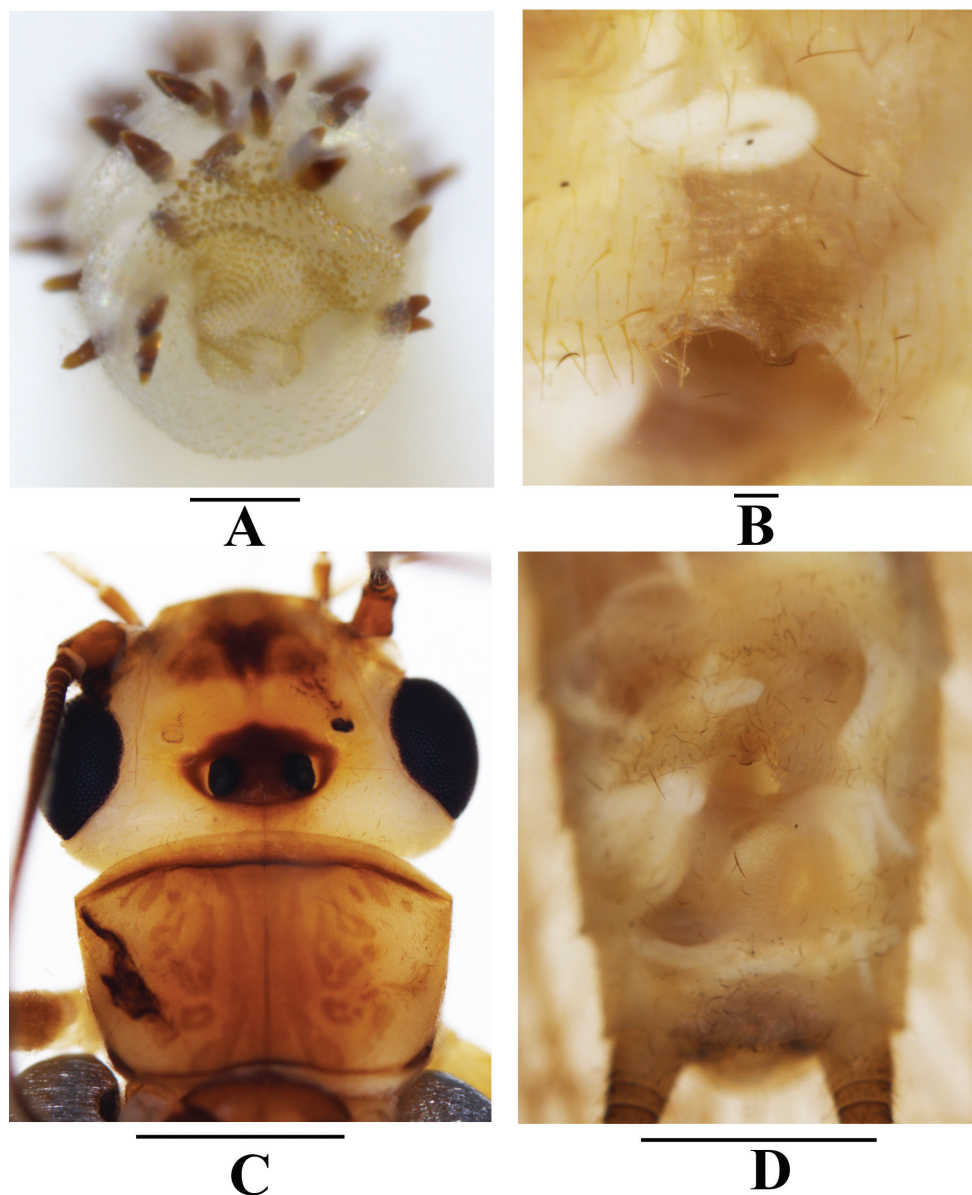
Figure 6. *Neoperla falcatata* sp. nov. **A** tip of aedeagal sac, dorsal view **B** female subgenital plate, ventral view **C** female head and pronotum, dorsal view **D** female terminalia, ventral view. Scale bars: 0.1 mm (**A, B**); 1.0 mm (**C, D**).

ing stoneflies were: *Amphinemura hamiornata* Li & Yang, 2008, *Neoperla shangsiensis* sp. nov., *N. yentu* Cao & Bae, 2007, *N. yao* Stark, 1987, an unidentified *Neoperla* sp. found only as a female, *Rhopalopsole cestroidea* Li, Murányi & Gamboa, 2017, and *Togoperla perpicta* Klapálek, 1921.

Remarks. The new species shares a similar shape of the aedeagus with *Neoperla nigromarginata* Li & Zhang, 2014 from Henan Province, central China. However, the new species can be easily separated from the latter by the markings on the head and pronotum (see Li and Zhang 2014: fig. 1a). The new species can also be distinguished from *N. nigromarginata* by the hemitergal processes of tergum 10 and details of tergum 7. In *N. falcatata*, the hemitergal processes of tergum 10 are longer and nearly extend to the process of tergum 8, and tergum 7 only bears a trapezoidal posterior process, whereas in *N. nigromarginata* the hemitergal processes of tergum 10 are short and only extend to the posterior margin of tergum 9, and tergum 7 has a pair of upraised, nipple-shaped processes in addition to the distal subquadrate process. Additionally, both species can be distinguished by details of the aedeagal armature (see Li and Zhang 2014: figs 1d, 2). Additionally, the aedeagal sac of *N. nigromarginata* bears paired apical flagella, whereas in the new species the aedeagal sac lacks the apical flagella.

Finally, the female subgenital plates of the two species have different details. In *N. falcatata*, the posterior margin of the subgenital plate is truncate, while in *N. nigromarginata* the posterior margin of the subgenital plate has a slightly emarginate tip.

Neoperla shangsiensis sp. nov.

http://zoobank.org/89F9F7F0-D72F-49E2-A9FC-AD9C72F31DC9
Figs 7–9

Type Material. *Holotype***:** male (NMP), China: Guangxi Zhuang Autonomous Region, Shangsi County, Shiwandashan National Forest Park, forested river valley, 290–360m, 21°54.4'N, 107°54.2'E, 5–9.IV.2013, light trap, leg. M. Fikáček, J. Hájek and J. Růžička.

Diagnosis. This species is characterized by head with a median dark-brown rectangular marking covering the posterior ocelli, with a pair of posterior wing-like extensions. In the male, the aedeagus is characterized by a short ventral spinulose lobe, a pair of small dorsal spinulose lobes, and a low ventroapical lobe fully armed with spines.

Description. Adult habitus (Fig. 7A, B). Body color brown. Head brown, with a dark brown fishtail stigma on anterior part of frons and a distinct median dark-brown rectangular marking covering posterior ocelli, with a pair of posterior wing-like extensions; mouthparts brown, palpi paler, antennae dark brown; biocellate, the distance between ocelli slightly wider than the diameter of one ocellus; head slightly wider than pronotum. Pronotum trapezoidal, brown, with scattered darker rugosities; anterior corners sharp, posterior corners rounded. Wings brownish and transparent, veins dark brown; legs brown except femora yellow-brown at base; cerci brown.

Male (Figs 7–9). Forewing length ca. 12.0 mm. Hindwing length ca. 10.4 mm. Posterior process of tergum 7 small, triangular, covered with many marginal basiconic sensilla. Tergum 8 without a process but covered by a small median spine patch. Tergum 9 with a pair of patches of basiconic sensilla and long hairs. Hemitergal processes of tergum 10 sclerotized, finger-like, bent ventrally in basal half, apical half slightly
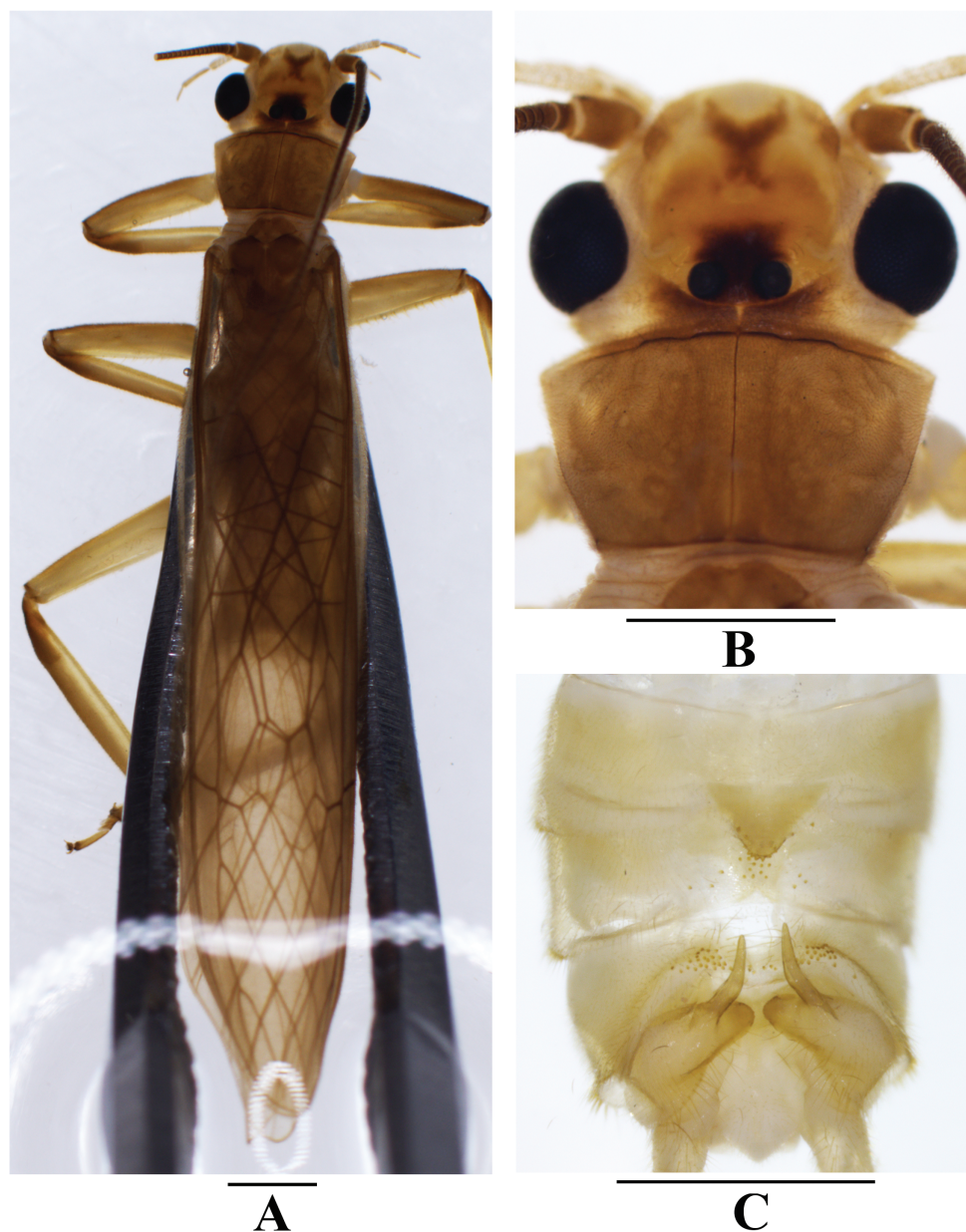
Figure 7. *Neoperla shangsiensis* sp. nov. (male) **A** adult habitus, dorsal view **B** head and pronotum, dorsal view **C** terminalia, dorsal view. Scale bars: 1.0 mm.

outcurved, tapering to an acute tip and nearly extending over tergum 9 (Figs 7C, 8A, B). Aedeagus mostly membranous, nearly straight (Figs 8C–F, 9). Aedeagal tube plump, straight, sclerotized basally and dorsally, with a pair of dorsoapical spinose lobes (Figs 8E, F, 9). Aedeagal sac about as long as tube, membranous, with a blunt
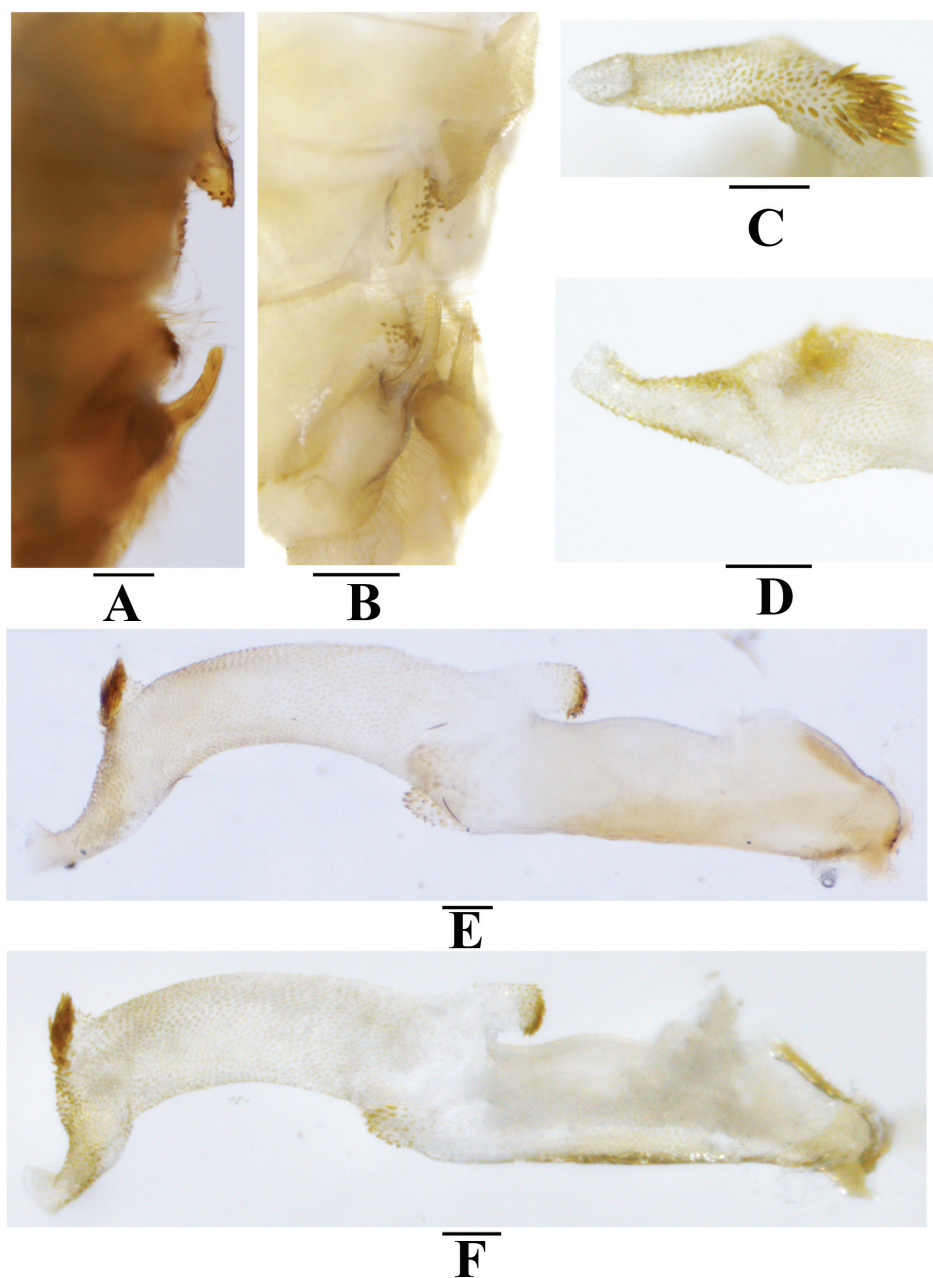
Figure 8. *Neoperla shangsiensis* sp. nov. (male) **A** terminalia after being cleared, lateral view **B** terminalia after being cleared, oblique lateral view **C** tip of aedeagal sac, dorsal view **D** tip of aedeagal sac, ventral view **E** aedeagus, oblique lateral view **F** aedeagus, lateral view. Scale bars: 0.2 mm (**A, B**); 0.1 mm (**C–F**).

trumpet-shaped tip; basoventral lobe distinctly shorter than corresponding width of sac, cylindrical, nearly parallel with aedeagus, with spinose apex; apical dorsal lobe small, triangular in lateral view, covered with a group of long spines; most of surface
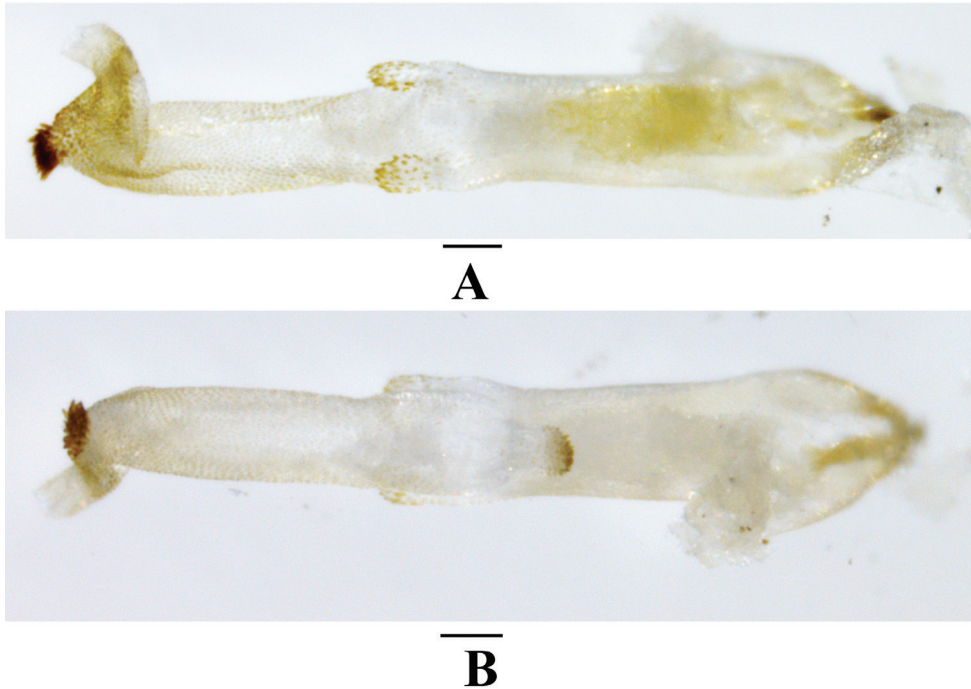
Figure 9. *Neoperla shangsiensis* sp. nov. (male) **A** aedeagus, dorsal view **B** aedeagus, ventral view. Scale bars: 0.1 mm.

armed with dense spinules; apical portion covered with large spines, ventral spines smaller (Figs 8C–F, 9).

Female. Unknown.

Etymology. The species name refers to the Shangsi County, where the type locality is located.

Distribution. China (Guangxi).

Ecology. See ecology of *Neoperla falcatata* sp. nov.

Remarks. The new species belongs to the *Neoperla oculata* species complex of the *montivaga* species group as defined by Zwick (1983, 1986), because of the wide lobe of tergum 7 and the four lobes of the aedeagus. The new species seems closely related to *N. furcomaculata* Kong & Li, 2016 from Hainan Province in having similar terminalia and aedeagal structures. However, the new species is easily distinguishable from the latter by the distinctively pigmented head pattern. Additionally, both species can be distinguished by the details of the aedeagal structure (see Kong et al. 2014: figs. 5d, 6). In *N. shangsiensis*, the paired dorsoapical spinose lobes of the aedeagal tube are higher and larger, and the ventroapical lobe of the aedeagal sac is distinctly enlarged. In *N. furcomaculata*, the paired dorsoapical spinose lobes of the aedeagal tube are obviously lower and smaller, and the ventroapical part of the aedeagal sac is not enlarged and is without a lobe. In addition, the basoventral lobe of aedeagal sac of the new species is nearly parallel with the aedeagal tube and distinctly shorter than the corresponding
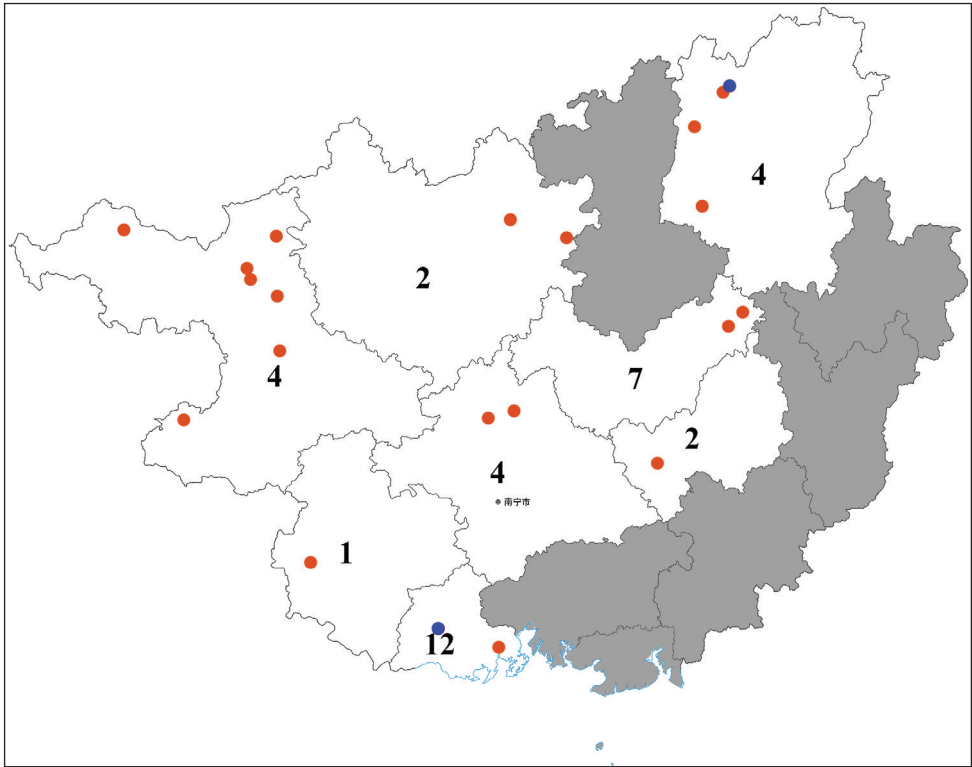
Figure 10. Distribution and species numbers of *Neoperla* Needham, 1905 in cities of Guangxi. Cities without records shaded in grey; blue dots indicate location of the two new species and new record.

width of the sac, whereas in *N. furcomaculata* the basoventral lobe of the aedeagal sac is perpendicular to the aedeagal tube and subequal in length to the width of the corresponding portion of the sac.

Concluding remarks

Guangxi Zhuang Autonomous Region is located in southern China. The Region borders Guangdong Province to the east, Beibu Gulf to the south and Hainan across the sea, Yunnan Province to the west, Hunan Province to the northeast, and Guizhou Province to the northwest. The Region also borders Vietnam to the southwest. To date, 24 species of *Neoperla* known from Guangxi had been studied, mainly by Wu (1948), Yang and Yang (1990), Du (1998), Du and Sivec (2004), Li et al. (2013, 2020), Wang et al. (2013a, 2013b), Yang et al. (2017), and Mo et al. (2019, 2020a). The type locality of one of these species, *Neoperla quadrispina* Li, Mo & Wang, 2020, was misspelled in the original description and it should be revised to Pingtianshan National Forest Park. In the checklist of Yang and Li (2018), *N. han* Stark, 1987 was recorded from

Guangxi by mistake, but this species do not occur in Guangxi (Stark 1987; Du et al. 1999; Wang et al. 2013; Mo et al. 2020b). The stonefly genus *Neoperla* primarily occurs in the Baise, Fangchenggang, Guilin, Laibin and Nanning cities of Guangxi (Fig. 10). There are famous reserves or parks in these five cities, including Cenwanglaoshan National Natural Reserve, Damingshan National Natural Reserve, Dayaoshan National Nature Reserve, Huaping National Nature Reserve, Jinhuacha Nature Reserve, and Shiwandashan National Forest Park. The genus *Neoperla* is widely distributed in Guangxi, which nearly covers two-thirds of the region. It has been poorly collected in southeast Guangxi. In the present study, two additional new species of *Neoperla* are described and one new species record of the genus for Guangxi is provided.

Acknowledgments

References

Claassen PW (1940) A Catalogue of the Plecoptera of the world. Memoirs of the Cornell University Agricultural Experiment Station 232: 1–235.

DeWalt RE, Maehr MD, Hopkins H, Neu-Becker U, Stueber G (2020) Plecoptera Species File Online. Version 5.0/5.0. http://Plecoptera.SpeciesFile.org [accessed 23 November 2020]

Du YZ (1998) Two new record species of genus *Neoperla* Needham (Plecoptera: Perlidae) from China. Journal of Zhejiang Agricultural University 24: 392–394.

Du YZ, Sivec I (2004) Plecoptera: Perlidae, Nemouridae, Leuctridae. In: Yang XK (Ed.) Insects from Mt. Shiwandashan area of Guangxi. China forestry Publishing House, Beijing, 39–45.

Du YZ, Sivec I, He JH (1999) A checklist of the Chinese species of the family Perlidae (Plecoptera: Perloidea). Acta Entomologica Slovenica 7: 59–67.

Illies J (1966) Katalog der rezenten Plecoptera. Das Tierreich, Berlin, 632 pp.

Kong, FB, Li WH (2016) Type designation for *Neoperla furcomaculata* Kong, Li, 2014 (Plecoptera: Perlidae). Illiesia 12(10): e59.

Kong FB, Lv JF, Li WH (2014) Three new species of *Neoperla* in the montivaga group (Plecoptera: Perlidae) from China. Zootaxa 3841(3): 429–438. https://doi.org/10.11646/zootaxa.3841.3.7

Li WH, Mo RR, Wang GQ (2020) Two new species of *Neoperla montivaga* group (Plecoptera: Perlidae) from Guangxi Zhuang Autonomous Region of southern China. Zootaxa 4718(4): 573–583. https://doi.org/10.11646/zootaxa.4718.4.10

Li WH, Wang GQ, Qin XF (2013) Two new species of *Neoperla* (Plecoptera: Perlidae) from China. ZooKeys 290: 21–30. https://doi.org/10.3897/zookeys.290.4568

Li WH, Wang Y, Wang RF (2017) Taxonomic notes on *Neoperla* (Plecoptera: Perlidae) from Sichuan Province of China with the description of two new species. Zootaxa 4221(2): 191–204. https://doi.org/10.11646/zootaxa.4221.2.3

Li WH, Zhang SQ (2014) Two new species of *Neoperla* (Plecoptera, Perlidae) from Dabie Mountains of China. ZooKeys 438: 45–55. https://doi.org/10.3897/zookeys.438.8230

Mo RR, Liu RJ, Li WH, Shi MW (2020b) Rediscovery of two species of *Neoperla* (Plecoptera: Perlidae) from China. Zootaxa 4758(2): 369–377. https://doi.org/10.11646/zootaxa.4758.2.10

Mo RR, Wang GQ, Li WH (2020a) A new species and two new records of the *Neoperla diehli* subgroup of the *N. montivaga* group (Plecoptera: Perlidae) from China. Zootaxa 4790(3): 515–524. https://doi.org/10.11646/zootaxa.4790.3.6

Mo RR, Yao G, Wang GQ, Li WH (2019) One new species and one new Chinese record of *Neoperla* (Plecoptera: Perlidae) from Mount Shiwandashan of the Guangxi Zhuang Autonomous Region of southern China. Zootaxa 4652(3): 497–506. https://doi.org/10.11646/zootaxa.4652.3.6

Needham JG (1905) New genera and species of Perlidae. Proceedings of the Biological Society of Washington 17: 107–110.

Sivec I, Stark BP, Uchida S (1988) Synopsis of the world genera of Perlinae (Plecoptera: Perlidae). Scopolia 16: 1–66.

Stark BP (1987) Records and descriptions of Oriental Neoperlini (Plecoptera: Perlidae). Aquatic Insects 9(1): 45–50. https://doi.org/10.1080/01650428709361270

Wang GQ, Li WH, Yang J (2013a) New species and records of the stonefly genus *Neoperla* (Plecoptera, Perlidae) from Jinhuacha Nature Reserve, Guangxi of China. ZooKeys 351: 37–48. https://doi.org/10.3897/zookeys.351.6259

Wang HL, Wang GQ, Li WH (2013b) Two new species in the subfamily Perlinae (Plecoptera, Perlidae) from China. ZooKeys 313: 81–90. https://doi.org/10.3897/zookeys.313.5460

Wu CF (1938) Plecopterorum Sinensium: A Monograph of Stoneflies of China (Order Plecoptera). Yenching University, 225 pp.

Wu CF (1948) Fourth supplement to the stoneflies of China (Order Plecoptera). Peking Natural History Bulletin 17: 75–82.

Wu CF, Claassen PW (1934) Aquatic insects of China. Article XVIII. New species of Chinese stoneflies. (Order Plecoptera). Peking Natural History Bulletin 9: 111–129.

Yang CK, Yang D (1990) New and little-known species of Plecoptera from Guizhou Province (I). Guizhou Science 8(4): 1–4.

Yang D, Li WH (2018) Species Catalogue of China (Vol. 2). Animals, Insecta (III), Plecoptera. Science Press, Beijing, 71 pp.

Yang J, Zhang SJ, Li WH (2017) Description of two new species of the *Neoperla montivaga* group (Plecoptera: Perlidae) from Guangxi Zhuang Autonomous Region, China. Zootaxa 4238(3): 385–394. https://doi.org/10.11646/zootaxa.4238.3.5

Zwick P (1973) Insecta: Plecoptera Phylogenetisches System und Katalog. Das Tierreich 94: 1–465.

Zwick P (1983) The *Neoperla* of Sumatra and Java (Indonesia) (Plecoptera: Perlidae). Spixiana 6: 167–204.

Zwick P (1986) The Bornean species of the stonefly genus *Neoperla* (Plecoptera: Perlidae). Aquatic Insects 8: 1–53. https://doi.org/10.1080/01650428609361227