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Bird cestodes from Huinay (Comau Fjord), Chilean Patagonia: several species of the family Dilepididae (Platyhelminthes, Cyclophyllidea), with the erection of two new genera

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Abstract

Birds in the Huinay area, Los Lagos region, Chile, were studied for parasites. Here we report 2 new genera and species of the family Dilepididae (Cyclophyllidea) found in common local passerines: *Janinellia peebeehi* **gen. n.**, **sp. n.** was found in *Elaenia albiceps* (Tyrannidae) and *Huinaylepis elegans* **gen. n.**, **sp. n.** was found in *Aphrastura spinicauda* (Furnariidae). Other dilepidid parasites are reported for the first time from *Xolmis pyrope* (Tyrannidae) and from 2 species of Rhinocryptidae. *Cotylorhipis sureshi* Jadhav & Shinde, 1981 is considered a species inquirenda. The very high diversity and endemism of the observed cestode fauna in the Valdivian temperate rain forests is noted.

Keywords

Biodiversity, Cestoda, Chile, COI, Dilepididae, Furnariidae, helminth parasites, Passeriformes, Rhinocryptidae, Tyrannidae

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Introduction

Chile is home to a very rich avifauna comprising more than 460 species (Jaramillo et al. 2003). However, apart from a few isolated reports limited to a small number of hosts (i.e. Babero et al. 1981; Torres et al. 1991; González-Acuña et al. 2017), very little is known of the cestode fauna of birds in this country. In the frame of a global and coordinated effort to improve our knowledge of the diversity of the Cestoda (Platyhelminthes) (Caira and Jensen 2017), the authors spent two weeks collecting bird tapeworms in coastal Valdivian temperate rain forests around the Huinay Scientific Field Station (HSFS) (Chile) in November and December 2008. A total of 87 birds belonging to 19 species were examined for parasites during this trip and 31 of them (36%) belonging to 12 species (63%) were found infected with one or more species of cestode. The diversity and novelty of this parasitic fauna is surprisingly high: all the parasite taxa recovered are new for Chile and several are new for science. Two earlier contributions based on this material described a new hymenolepidid genus from Trochilidae (Widmer et al. 2013) as well as a new species of the genus *Anonchotaenia* (Paruterinidae) from the tyrant flycatcher *Elaenia albiceps* (Tyrannidae) (Phillips et al. 2014).

This paper reports on a series of tapeworms of the family Dilepididae found in hosts belonging to the Furnariidae, Tyrannidae and Rhinocryptidae, including 2 new genera and species.

Methods

Hosts were caught with mist nets, kept in fabric bags for a short time, then killed with an overdose of diethyl-ether, and autopsied immediately after their death. The digestive system was entirely removed, cut in sections if necessary, and searched for parasites under a dissecting microscope. Cestodes were fixed in hot 4% formalin after a small fragment was preserved in ethanol for DNA studies. Fixed specimens were transferred to 70% ethanol for storage. Further treatment included staining with Mayer's hydrochloric carmine, dehydrating in an ethanol series, clearing in eugenol and mounting in Canada balsam. Some scoleces were prepared in Berlese's medium for examination of their rostellar armament.

Drawings and photographs were made respectively with a drawing tube and a digital camera on a Nikon 80i microscope. Unless otherwise stated all measurements are in micrometers. Minimum and maximum values are reported followed by the mean and number of observations in parentheses when applicable. Conventions for dilepidid descriptions follow Bona (1994). All material is deposited in the Invertebrates Department of the Museum of Natural History of Geneva (MHNG). The nomenclature of birds follows the latest available edition of Avibase (Lepage 2018). Partial COI (cox1) sequences were generated according to the methodology described in Scholz et al. (2013). These sequences are deposited in Genbank under accession numbers MH663460 to MH663465 (data by A. Waeschenbach, Natural History Museum London, UK).

Collections acronyms: MHNG-PLAT: Muséum d'Histoire Naturelle de Genève (Invertebrates Department, Platyhelminthes Collection), USNM: United States National Museum (Cestode Collection).

Results

Janinellia gen. n.

http://zoobank.org/0E3A0865-7B2B-4A17-AF2A-ADF1F9D880B8

Type species. *Janinellia peebeehi* sp. n. by original designation.

Diagnosis. Dilepididae, Dilepidinae. Body small to medium. Scolex without rostellum, apical structures consist of unarmed glandular pouch. Suckers weakly muscular. Genital pores irregularly alternating. Genital ducts passing between osmoregulatory canals. Cirrus sac weakly muscular, elongate. Cirrus unarmed. Vagina posterior to cirrus sac. Testes numerous, posterior, in one field. Uterus initially reticular. Parasite of South-American passerines (Tyrannidae).

Etymology. The genus name (feminine) is dedicated to Prof. Janine N. Caira (Storrs, Connecticut, USA) in recognition of her remarkable and tireless action in favour of tapeworm systematics.

Remarks. Dilepidids with distinct but unarmed apical structures are known from various avian hosts, and are presently classified within several genera as synthesized by Bona (1994). Their classification is difficult, as they are mostly known only from a few species (or even specimens) and show few distinctive characters. According to Bona (1994), they are presently attributed to genera according to their apical glandular or muscular structures. Most of them can easily be differentiated from the material described above: *Cotylorhipis* Blanchard, 1909 because of its armed suckers; *Unciunia* Skrjabin, 1914 because of its cirrus armament with a tuft of setae resembling those in the genus *Spiniglans* Yamaguti, 1959 (see Mariaux and Georgiev 2018 for a recent discussion); *Ptilotolepis* Spasskii, 1969 because its genital ducts pass the osmoregulatory canals dorsally and egg capsules; *Platyscolex* Spasskaya, 1962 because its genital ducts are dorsal to the osmoregulatory canals, scolex shape, genital atrium structure and testis distribution; *Eburneotaenia* Bona, 1994 (see Mariaux and Vaucher 1991 for description of its type and only species), and *Emberizotaenia* Spasskaya, 1970 because of the presence of an unarmed rudimentary rostellum in their apical apparatus (see Georgiev and Genov 1993; Bona 1994). Moreover all these groups are parasitic in very specific groups of birds and, with the exception of *Cotylorhipis* and *Unciunia*, have never been recorded in South America. Our material is most similar to *Pseudochoanotaenia* Burt, 1938. However, *Pseudochoanotaenia* spp. are very small (up to 10 mm long) and our material is at least 2–3 times larger; they have a clear apical cavity in the glandular pouch which is lacking in our material; they have a short pyriform vagina versus a longer straight one in our specimens. Furthermore, *Pseudochoanotaenia* is presently restricted to Apodiformes and has never been reported from South America. In consequence, we consider the present material as belonging to a new genus.

Janinellia peebeehi sp. n.

http://zoobank.org/3D7F502C-EA02-4F1D-A45E-EEED2758FF59
Figures 1–5

Host: *Elaenia chilensis* Hellmayr, 1927 (Passeriformes, Tyrannidae), Fio-fio, Chilean White-crested Elaenia.

Prevalence: 2/12 (16.7%).

Intensity: 1–2.

Site of infection: Small intestine.

Locality: HSFS, Comau Fjord, Los Lagos region, Chile, –42.39, –72.42. Altitude 10–30 m. (Type locality).

Date: 29.11.2008 and 2.12.2008.

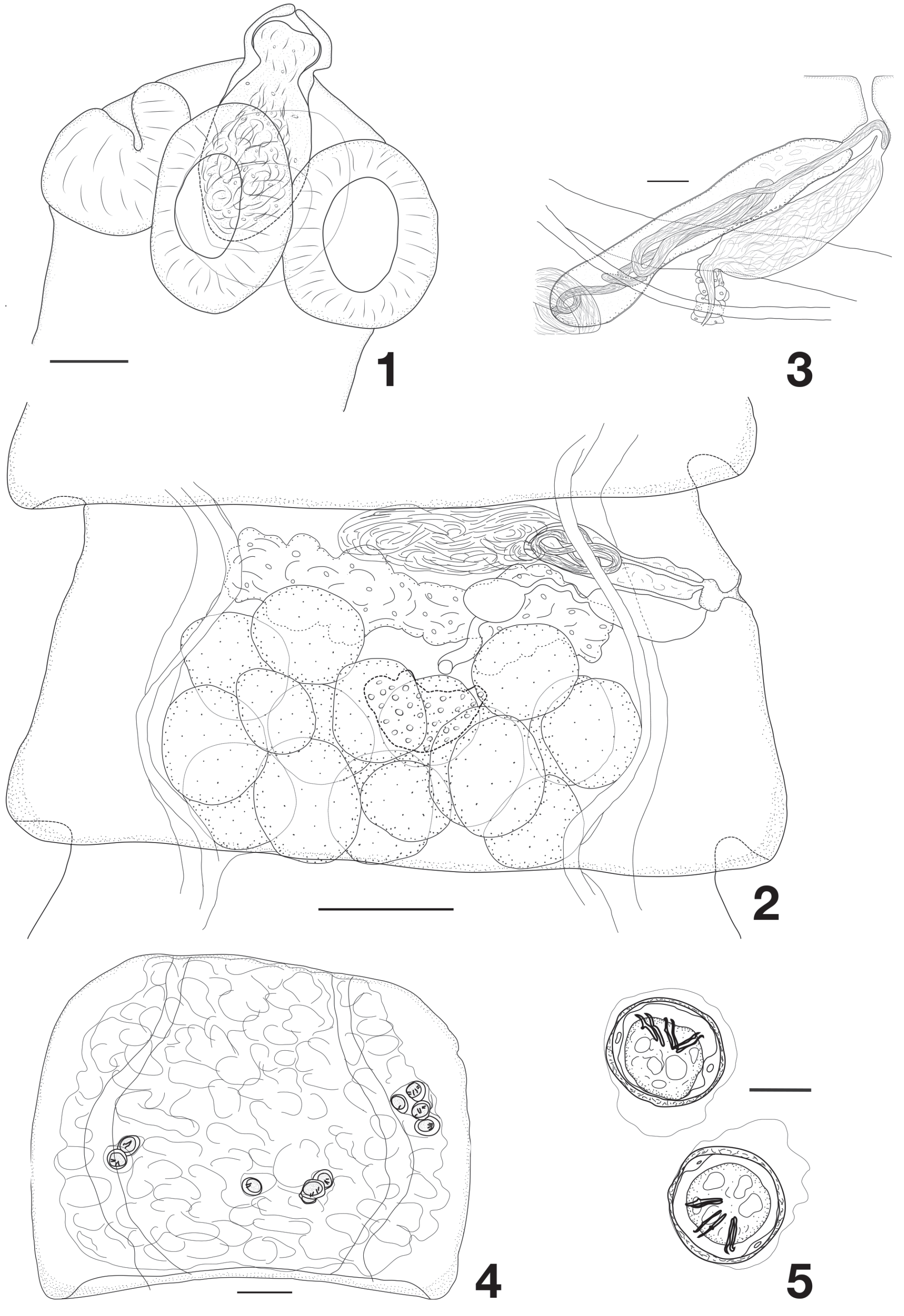
Specimens studied: 3 specimens. Holotype: MHNG-PLAT-82292 (on slide). Paratypes: MHNG-PLAT-120515; MHNG-PLAT-82293 (2 specimens, on slides).

Hologenophore (genseq-2 COI): MHNG-PLAT-82292 [CHIL-002/C2] and MHNG-PLAT-120515 [CHIL-038/C2]. Partial COI sequence, Genbank MH663460 and MH663461.

Etymology. The species name phonetically reminds one of the acronyms of the NSF program that was sponsoring the project (Planet Biodiversity Inventory, PBI).

Description. Body of small to medium size, up to 34 mm long (inferred from fragmented specimen). Strobila with almost parallel margins, gradually expanding in posterior direction: immature, mature, pregravid and gravid proglottides up to 250, 550, 700 and 1025 wide, respectively. Maximum width achieved at level of early gravid proglottides. Most complete specimens consisting of up to 157 proglottides. Proglottides weakly craspedote, wider than long except for very last gravid ones, which can be up to twice longer than wide. Two pairs of osmoregulatory canals. Ventral canals up to 50 in diameter, with posterior transverse anastomosis in each proglottis. Dorsal ones up to 11 in diameter.

Scolex (Fig. 1) not clearly separated from neck, 210–295 (258, n = 3) wide at middle of suckers; anterior part of scolex conically tapering; apex may form pipette-like protrusion. Suckers weakly muscular, oval 110–137 × 82–105 (120 × 96, n = 12). Apical apparatus consisting of oval rostellar pouch, 127–142 × 65–75, thin-walled, densely filled with glandular tissue, reaching to level of middle to posterior half of suckers. No rostellum. Neck straight, 225–325 wide. Genital ducts passing between osmoregulatory canals. Genital pores at border of first third of lateral proglottis margin, often forming genital papilla, irregularly alternating. Genital atrium simple, inconspicuous, thin-walled, tubular, with infundibular orifice.



Figures 1–5. *Janinellia peebeehi* gen. n., sp. n. **1** scolex **2** mature proglottis **3** cirrus sac **4** gravid proglottis **5** eggs. Scale bars: 50 µm (**1**), 100 µm (**2, 4**), 20 µm (**3, 5**).

Testes 13–17 (14.8, *n* = 25) in number, disposed in two dense layers, forming a continuous field filling most of posterior two thirds of median field of proglottides; posterior, lateral and dorsal to vitellarium, overlapping posterior parts of ovary; in younger proglottides, testes may occupy most of dorsal parenchyma (Fig. 2); testes 75–100 (89, *n* = 15) in diameter. External vas deferens very developed, forming multiple coils at extremity of cirrus-sac, filling the antero-poral and central part of median field. Cirrus-sac 130–182 × 25–38 (157 × 32, *n* = 30), oblique, straight, thin-walled, reaching or crossing poral osmoregulatory canals. Internal vas deferens coiled, making several loops in proximal half of cirrus-sac (Fig. 3). Evaginated cirrus short (up to 44 long), almost cylindrical, thin, 8–9 in diameter at its basal part, slightly tapering distally; unarmed.

Vitellarium large, up to 130 wide, central, lobate, oval or bean-shaped. Ovary transversely-elongate, massive and multilobulate, with two poorly marked and slightly asymmetrical wings, occupying entire width of median field and up to 30–40% of proglottis length. Mehlis' gland not distinct as glandular structure. Ootype central, just anterior to vitellarium. Seminal receptacle oval 45–58 × 35–45 when empty, up to 150 × 87 when full. Vagina posterior to cirrus-sac, straight, distally thin-walled, proximally bordered with a row of large, dense cells; distal part often dilated, sometimes filled with spermatozoa (Figs 2, 3).

Uterus initially as loose reticulated network, then becoming denser as eggs develop, overlapping osmoregulatory canals and filling most of proglottis, including part of lateral fields (Fig. 4). Embryophore thick, 37–42 × 30–38 (39.5 × 34.5, *n* = 25). Oncosphere 27–30 × 22–27 (28.5 × 24, *n* = 25). Embryonic hooks sub-equal: central pair 13–15 (14, *n* = 10) long, lateral pairs 13–15 (13.5, *n* = 12) long (Fig. 5).

Remarks. The new species is the type species of the newly erected monotypic genus *Janinellia* gen. n.

Huinaylepis gen. n.

http://zoobank.org/01B1BC94-EB49-4A9F-A145-A1A9B41F4D28

Type species. *Huinaylepis elegans* sp. n. by original designation.

Diagnosis. Dilepididae, Dilepidinae. Small strobila. Rostellum armed with two rows of hooks with peculiar and irregular 2-1 alternation. Rostellar pouch glandular. Suckers armed on anterior half, with largest antero-central hooks and progressively shorter ones laterally. Genital pores irregularly alternating. Genital ducts dorsal to osmoregulatory canals. Cirrus sac reaching osmoregulatory canals. Cirrus armed with strong spines. Testes in one field extending bilaterally and often also anteriorly to form circle reaching anterior proglottis margin. Ovary small. Uterus labyrinthic. Parasite of South American passerines (Furnariidae).

Etymology. The genus name (feminine) derives from the name of the locality and the Latin suffix –lepis (scales).

Remarks. Dilepidids with armed suckers, especially armed with true hooks and not merely spines, are very uncommon. The present material can only be compared with *Cotylorhipis* Blanchard, 1909, which is also found in South American furnariid birds. Although the general aspect of *C. furnarii* (Del Pont, 1906) and our specimens is similar because of the obvious sucker armament and despite an incomplete description of the former taxon [based on Del Pont (1906) as reported and completed in Blanchard (1909)], a number of characters easily separate them. *Cotylorhipis* specimens do not have any rostellum, their sucker armament is complete (all around the suckers circumference), and the testes never reach the anterior proglottis margin whereas our material shows an obvious armed rostellum in a large and distinctive rostellar pouch; sucker armament is restricted to the anterior half of suckers and testes are often far found anterior. Furthermore, the terminal gravid proglottides contain thousands of eggs and their length reaches up to 4–5 times their width in *Cotylorhipis*, while there are only a few hundreds of eggs and they are twice as long as wide in our specimens. These characters are sufficient to separate our material from *Cotylorhipis* and we propose to place it in the new genus *Huinaylepis*. It is, however, very likely that *Cotylorhipis* and *Huinaylepis* are closely related given the general appearance of their genital anatomy, presence of armed suckers, and shared host and geographical distribution.

Huinaylepis elegans **sp. n.**

http://zoobank.org/61C52012-B371-4B3A-B2D9-A2CD4E40678B
Figures 6–11

Host: *Aphrastura spinicauda* (Gmelin, 1789) (Passeriformes, Furnariidae), Rayadito, Thorn-tailed Rayadito.

Prevalence: 4/5 (80%).

Intensity: 4 to about 10 specimens.

Site of infection: Small intestine.

Locality: HSFS, Comau Fjord, Los Lagos region, Chile, –42.39, –72.42. Altitude 10–30 m. (Type locality).

Dates: 29.11–10.12.2008.

Specimens studied: Holotype: MHNG-PLAT-82294 (on slide). Paratypes: MHNG-PLAT-82295; MHNG-PLAT-120512 to MHNG-PLAT-120514 (about 30 specimens, on slides). Additional non-type material: Locality: “Valdivia Forest Reserve, First refuge” (according to Franco Bona’s field books, deposited in MHNG). MHNG-PLAT-87937 16 slides from *Pygarrhichas albogularis* (King, 1831) (Furnariidae), 19.01.1985, field number 657/5; MHNG-PLAT-87938, 5 slides from *Pygarrhichas albogularis*, 20.01.1985. Field number 667/10; MHNG-PLAT-87939 14 slides from *Aphrastura spinicauda*, 20.01.1985. Field number 672/12.

Hologenophore (genseq-2 COI): MHNG-PLAT-120512 [CHIL-013/C2] and MHNG-PLAT-82295 [CHIL-071/C2 and C/4]. Partial COI sequence, Genbank MH663462 to MH663464.

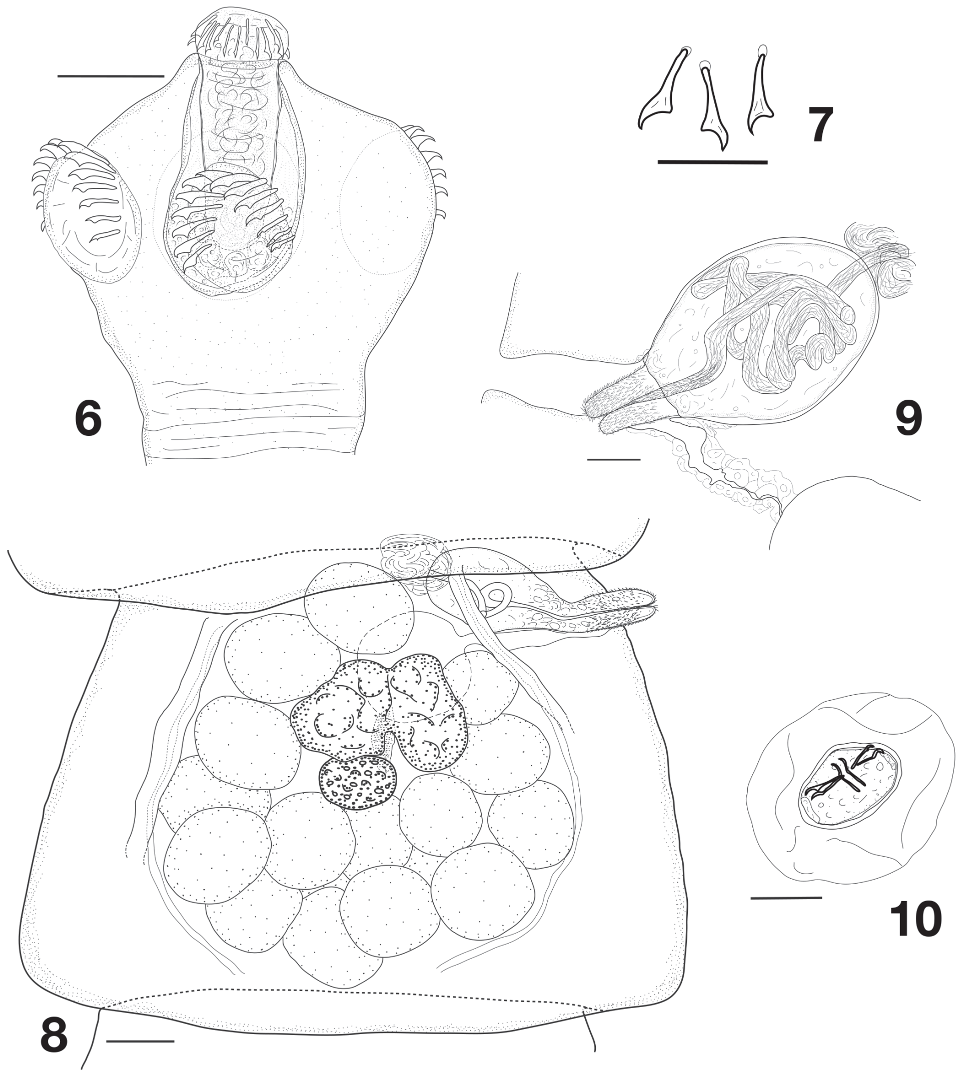
Etymology. The species name refers to the elegant (Latin: *elegans*) aspect of the worm's scolex.

Description. Body of small size, up to 18 mm long and with maximum width 600 at level of gravid or late mature proglottides. Up to 36 acraspedote proglottides (observed; maximum number of proglottides inferred from various fragments is about 44). Proglottides initially wider than long, progressively becoming as long as wide at level of male proglottides, then up to about twice as long as wide (terminal gravid proglottides). Development of strobila with marked steps instead of being progressive (similar to serial maturation sensu Spasskii 1951), i.e. with maturation of cirrus sac, testes or eggs sudden from one proglottis to next. Two pairs of osmoregulatory canals. Ventral canals with posterior transverse anastomoses in each proglottis.

Scolex (Fig. 6) rounded. Rostellum musculo-glandular, mushroom-shaped, elongate, 67–112 × 40–55 (96 × 48, *n* = 18), with maximum diameter at level of crown of hooks. Rostellar pouch oval, 105–142 × 65–92 (126 × 78, *n* = 17), densely filled with glandular masses, reaching but usually not exceeding posterior margin of suckers. Rostellar hooks 29–35 in number, 16–18 long, in two rows, with particular 1-2 arrangement (1 hook on anterior row alternates with two on posterior row) but with recurring irregularities (i.e. 1-1-1, 2-2-2, 1-3-1) or sometimes intermediate positions (Fig. 11C–E). Hooks with long handle with small epiphyses, short blade and massive guard (Figs 7, 11E, F). Suckers round to slightly oval, with maximum diameter 60–90 (76, *n* = 79), bearing highly visible and very typical anterior semicircle of 12–17 (14.3, *n* = 109) hooks of similar shape as those of rostellum but with proportionally longer handle (Fig. 11A, B); epiphyses of sucker-hooks not always well marked but maybe conspicuous on handle (Fig. 11F); hooks of suckers up to 40 long, larger centrally and becoming gradually shorter (20–25) laterally (Fig. 11A B). Neck very short, formation of proglottides appears immediately behind scolex. Genital ducts dorsal to osmoregulatory canals. Genital pores alternating irregularly in short series, at border of first fifth of lateral proglottis margin.

Testes 16–22, rarely only 14 or up to 24 (19, *n* = 84) in number, disposed in entire median field reaching anterior proglottis margin and forming U-shaped field, with converging branches, often forming circle with one or two anterior testes linking the two lateral fields (Fig. 8), essentially in one layer, although some posterior testes may be superimposed; testes reaching up to 85 in diameter in late mature proglottides. Vas deferens coiled just at antiporal end of cirrus sac, often poorly visible but occasionally well-developed (up to 12 in diameter) and filling antero-central space. Cirrus-sac (Fig. 9) 90–137 × 50–77 (119 × 62, *n* = 55), ovoid, thin walled, anterior, with proximal extremity often touching anterior limit of proglottis, usually crossing poral osmoregulatory canals. Cirrus massive, armed with clearly visible spines (about 2 long) except on apex, 22–25 in diameter and reaching up to 145 long when evaginated. Internal vas deferens forming several coils.

Ovary central, small, compact, bilobed, anterior and dorsal to vitellarium. Vitellarium massive, central, compact, oval. Vagina posterior or ventral to cirrus pouch, straight, often dilated. Conductive part surrounded by thick but not dense cellular layer. Seminal receptacle oval, very large, commonly over 170 × 120, up to 217 × 160.



Figures 6–10. *Huinaylepis elegans* gen. n., sp. n. **6** scolex **7** rostella hooks **8** mature proglottis **9** cirrus sac **10** eggs. Scale bars: 40 µm (**6**), 20 µm (**7, 9, 10**), 100 µm (**8**).

Young uterus saccular, becoming labyrinthic, filling space between osmoregulatory canals, containing a limited number (less than 200) of large eggs situated in 3 or 4 layers. Oncospheres ovoid, 29–37 × 19–25 (33 × 21.5, *n* = 21). Embryonic hooks 11–13 long (Fig. 10).

Remarks. The new species is the type species of the newly erected monotypic genus *Huinaylepis* gen. n.

In 2005, the late Prof. Franco V. Bona (Torino) left his tapeworm collection to the MHNG. Among this rich material we found 35 slides of worms collected in *Aphrastura spinicaudata* and *Pygarrhichas albogularis*. All material was collected in the Valdivia

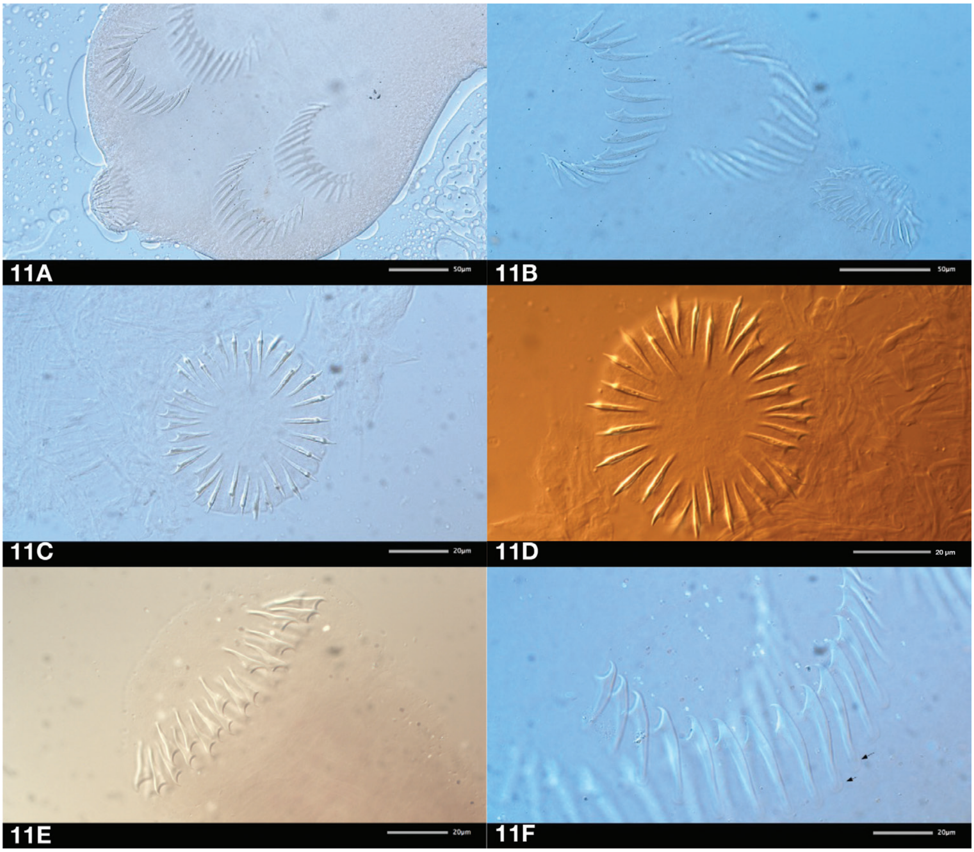


Figure 11. *Huinaylepis elegans* gen. n., sp. n. **A–B** rostellar armament **C–D** rostellar hooks, showing irregular alternations, apical views **E** lateral view of rostellar hooks **F** sucker hooks with epiphyses (arrows).

Forest (about 250 km N of our study area) on 19–20 January 1985. On his accompanying notes, Bona noticed the interest of this material and indicated that it belonged to a new genus on some slides. Most of Bona's specimens are juveniles, a few are mature and only a couple of proglottides are pregravid. We have examined all these slides and this materiel fully corresponds to *Huinaylepis elegans* sp. n. as described above. The only minor variations we noticed were two specimens with a slightly higher number of hooks than in the type series (36 and 38). These observations imply that *H. elegans* is probably more widespread in southern Chile than the few occurrences reported here may suggest. Over 30 species of Furnariidae are known in the country and, so far, have never been investigated for their parasites.

Cotylorhipis was a monotypic genus until Jadhav and Shinde (1981) described *C. sureshi* in domestic fowl from Aurangabad in India. Both the description and illustrations of this species are extremely succinct and of substandard quality. It is not even clear whether hooks reported by Jadhav and Shinde (1981) as "fanlike outgrowth", and illustrated by asterisks, are present on suckers or not! In addition, and according to B. Jadhav (personal communication to M. Oros), there is no type material for *C. sureshi*.

The disjoint geographic distribution, unrelated host, as well as the few morphological details given by Jadhav and Shinde (1981) make it highly dubious that their material belongs to *Cotylorhipis*. There is no possibility of checking the validity or taxonomic position of the material described as *Cotylorhipis sureshi*, which must consequently be considered a species inquirenda.

***Kintneria* (?) sp.**

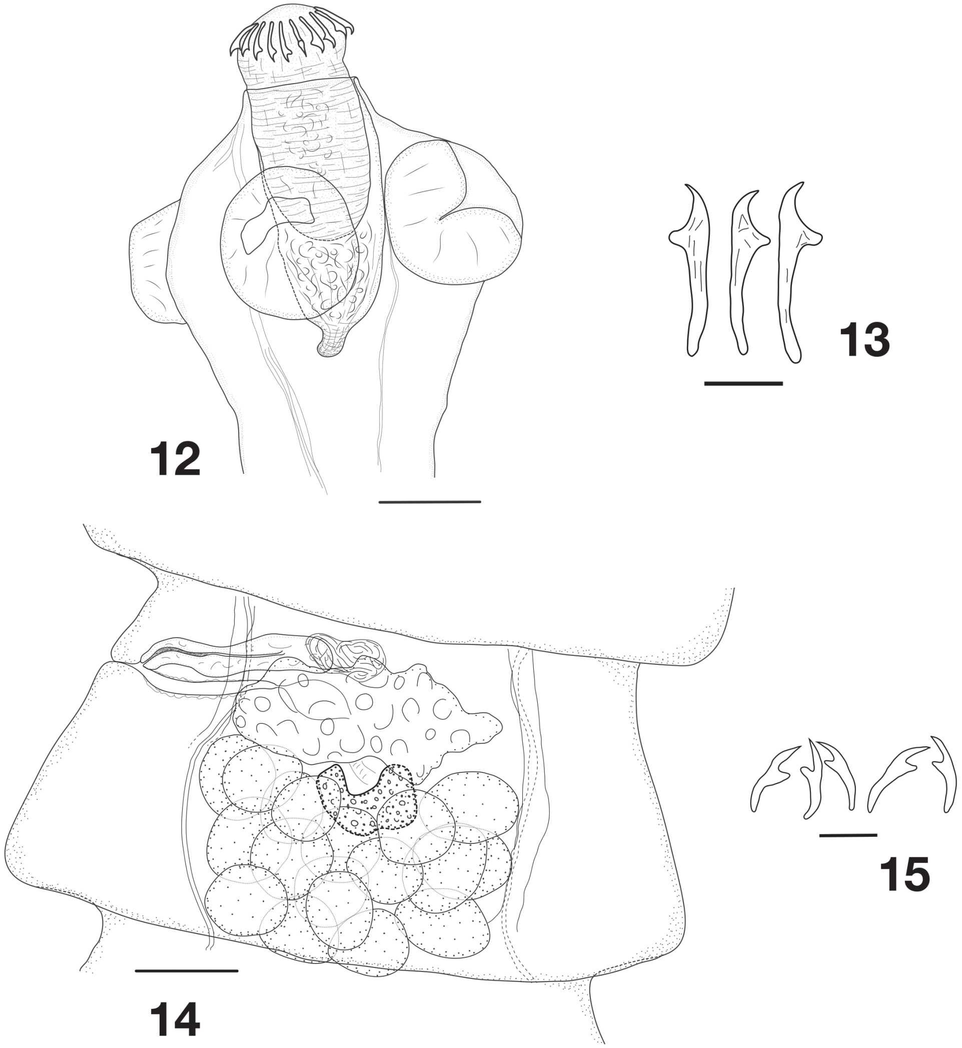
Figures 12–14

Host: *Xolmis pyrope* (Gmelin, 1789) (Passeriformes, Tyrannidae), Diucon, Fire-eyed Diucon.
Prevalence: 1/1.
Intensity: 3 specimens.
Site of infection: Small intestine.
Locality: HSFS, Comau Fjord, Los Lagos region, Chile, –42.39, –72.42. Altitude 10–30 m.
Date: 1.12.2008.
Specimens studied: MHNG-PLAT-87930.
Hologenophore (genseq-2 COI): MHNG-PLAT-87930 [CHIL-028/C2]. Partial COI sequence, Genbank MH663465.

Partial description (based on only a few available mature proglottides): Body of small size, largest specimen 12.8 mm long and maximum width 675 mm wide. Up to 86 proglottides observed (up to mature stage, no complete specimens available), wider than long, craspedote. Scolex 275–330 (*n* = 2) in diameter, bearing four elongated and rather weak unarmed suckers155–175 (164, *n* = 7) in diameter. Rostellar pouch 280–285 × 123–148 (*n* = 2) with dense posterior glandular zone. Rostellum large, 243–265 × 95–118 (*n* = 2) present, strongly muscular but with distinct central glandular zone (Fig. 12). Rostellar hooks 17–18 (*n* = 2) in number, in one row, 41–47 long (44.5, *n* = 17), with long handle (Fig. 13). Neck well marked 162–250 (206, *n* = 3) wide. Formation of proglottides distinct at 242–312 (277, *n* = 3) from posterior margin of suckers. Genital pores situated in first third of length of lateral proglottis margin, alternating irregularly in small series (i.e. 3, 2, 1, 3), up to 6 consecutive pores on same side observed. Ventral osmoregulatory canals connected posteriorly in each proglottis by transverse anastomosis. Genital ducts passing between osmoregulatory canals.

Testes 16–21 (18, *n* = 10) in number, situated in single posterior field, in 2–3 layers, not extending beyond osmoregulatory canals. External vas deferens coiled, forming compact aggregation. Cirrus sac thin-walled 139–168 × 30–36 (149 × 33, *n* = 7) extending past the osmoregulatory canals. Cirrus armed with very fine spines.

Vitellarium immediately anterior to testes field, central, slightly V-shaped. Ovary lobulated and elongate transversely, anterior (poorly visible in our material). Vagina in same plane as, and posterior to, cirrus sac; wide, straight, opening in simple genital



Figures 12–15. *Kintneria* (?) sp. **12** scolex **13** rostellar hooks **14** mature proglottis. Dilepididae gen. sp. 2 **15** rostellar hooks. Scale bars: 100 µm (**12, 14**), 20 µm (**13, 15**).

atrium about 15 deep (Fig. 14). No gravid proglottides and no early uterine development visible.

Remarks. This material is likely to represent a new species. However a complete description is not possible without observations of the uterine development. Its generic position remains uncertain. According to Bona's (1994) keys, it could belong to one of two very similar genera: *Monosertum* Bona, 1994 or *Kintneria* Spaskii, 1968, both parasitic in passerine birds. These genera differ from one another essentially by the structure of their uterus, with or without capsules, a character, which we cannot determine in the present material due to the lack of gravid proglottides. A few other diagnostic characters are given by Bona (1994). Among them, the small size of the body of our specimens rather resembles *Monosertum*; however, this character can often vary among species in many dilepidid genera. On the other hand, it corresponds to the diagnosis of *Kintneria* because of its larger rostellar hooks, the ovary that doesn't reach the anterior proglottis margin and its cirrus armament consisting of short spines. For these reasons, we consider that it most likely belongs to the genus *Kintneria*. This genus was erected by Spasskii (1968) for a parasite of introduced European sparrows *Passer domesticus* (L.) in North America. The type species of this genus was identified as *Choanotaenia passerina* (Fuhrmann, 1908) by Kintner (1938). Spasskii (1968) considered it a distinct species, differing from the Palaearctic *Monopylidium passerinum* (Fuhrmann, 1908); he also placed it in the newly erected subgenus *Kintneria* Spasskii, 1968 within the genus *Monopylidium* as *M.* (*Kintneria*) *capsulata* Spasskii, 1968. Bona (1994) eventually elevated *Kintneria* to the generic rank and its validity was accepted by Mariaux et al. (2017). *Kintneria* is known from the Nearctic and members of *Xolmis* are restricted to the Neotropics; however, other tyrant-flycatchers are known to migrate between North and South America, suggesting that genera of avian cestodes may have rather Pan-American than restricted distributions. This is the first cestode ever reported from the genus *Xolmis*.

To our knowledge the genus is monotypic and *K. capsulata* can easily be separated from our material by its shorter rostellar hooks and longer cirrus sac. Thus, should the observation of gravid segments confirm the placement of the present material into *Kintneria*, it would belong to a new species.

The two species belonging to the other similar genus, *Monosertum parinum* (Dujardin, 1845) and *M. mariae* (Mettrick, 1958), are known from European passerine birds only; furthermore, they are characterized by an osmoregulatory system forming a complicated reticular formation in the scolex and the neck (Komisarovas and Georgiev 2007). Such complicated network of osmoregulatory canals has not been observed in the present material.

Dilepididae from Rhinocryptidae

A few specimens were retrieved from 2 species of terrestrial Rhinocryptidae with a limited distribution. Unfortunately, our material does not allow for complete descriptions of these worms. The limited available characters are briefly reported below.

Dilepididae. gen. sp. 1: Three fragments of 2 or 3 incomplete specimens, no gravid proglottides. Max length 2.6 mm for 20 proglottides weakly craspedote and wider than long, max width 560. A single scolex 312 wide. Powerful suckers 195–205 in diameter. Rostellar pouch indistinct, about 135 long. Rostellum muscular 107 × 40 with hooks mostly lost. Remaining hook fragments suggest 2 rows and a length of about 12. Neck short. Very rapid development of strobila with testes appearing in 7th proglottides and mature proglottides in 12th to 14th. Genital pores regularly alternating and genital ducts passing between osmoregulatory canals. 10–14 testes (12, $n = 10$) in one posterior field and 1 to 2 layers, not extending past osmoregulatory canals. Cirrus pouch 155–168 × 28–38, crossing excretory canals, slightly oblique. Cirrus armed with small spines. Ovary transverse anterior, bi-winged. Vitellarium posterior central and massive up to 58 × 96. Vagina posterior to cirrus pouch, finely armed.

MHNG-PLAT-120516. Host: *Scelorchilus rubecula* (Kitlitz, 1831) (Passeriformes, Rhinocryptidae), Chucao, Chucao Tapaculo. Small intestine. Prevalence: 1/6 (17%). Locality: HSFS, Comau Fjord, Los Lagos region, Chile, –42.39, –72.42, 50 m, 7.12.2008.

Dilepididae gen. sp. 2 (Fig. 15): A single immature specimen with scolex. Scolex 20 in diameter, suckers circular 100–115 in diameter. Rostellum pouch 230 × 80, tapered and elongated posteriorly, with glandular mass at suckers level. Rostellum 152 × 70 strongly muscular. 20 subequal hooks 27–30 in length on 2 rows. Blade long, strong guard and handle slightly curved (Fig. 15). Neck short. About 15 immature proglottides with no anatomy visible.

MHNG-PLAT-120517. Same host and collection data as previous material.

Dilepididae gen. sp. 3: A single specimen in 2 parts, no scolex. Length 1.55 mm and 675 maximum width at gravid proglottides level. 75 proglottides, craspedote, mostly wider than long, becoming slightly longer than wide when gravid. Genital pores irregularly alternating in short series. Genital ducts in between osmoregulatory canals. Cirrus pouch 155–205 × 23–31, oblique, crossing osmoregulatory canals opening at anterior third of proglottides margin. Cirrus armed with small spines. Testes 12–16, in 2 layers, in a compact posterior field, in between osmoregulatory canals. Ovary bi-winged, anterior, difficult so see. Vitelline gland central, massive, up to 130 in diameter. Vagina posterior to cirrus pouch, copulatory part lined with short hairs/spines. Seminal receptacle large, central, anterior to vitellarium. Uterus multilobate, progressively filling entire proglottides. Eggs with thick external envelope.

MHNG-PLAT-120518. Host: *Pteroptochos tarnii* (King, 1831) (Passeriformes, Rhinocryptidae), Black-throated Huet-huet, Hued-hued del sur. Small intestine. Prevalence: 1/5 (20%). Locality: HSFS, Comau Fjord, Los Lagos region, Chile, –42.39, –72.42, 10 m, 10.12.2008.

Remarks

It is the first record of tapeworms in this family of birds. Despite the limited material available, key characters confirm that at least 3 different species of cestodes are present. Thus an interesting diversification of dilepidids has occurred, at least locally, in these rather elusive hosts. It would obviously be very interesting to collect more of them in various areas of their range, which encompasses most of South America.

Discussion

It is widely accepted that biodiversity is particularly important in tropical rainforests (Mittermeier et al. 2003). However, our observations in Chile serve as a reminder that other biodiversity hotspots might be of great interest for parasitologists. This is particularly the case of Mediterranean-climate regions in general, and those with unique ecological conditions like the Chilean coastal forests (i.e. Ormazabal 1993; Smith-Ramirez 2004). In the humid temperate Chilean forests we have explored, the local diversity of birds is relatively poor, and we could only sample a small number of hosts. Nevertheless, not only the global prevalence (at 36% vs about 20% on average for similar studies according to our experience) and diversity of tapeworms in these hosts was high but their originality was also exceptional. *Elaenia chilensis* for example was previously found to harbour another new and, until now, endemic cestode species, *Anonchotaenia prolixa* Phillips, Georgiev, Waeschenbach & Mariaux, 2014 (Phillips et al. 2014). The presence of several new endemic lineages (that may even be more numerous once the study of the remaining material from this mission is achieved) is remarkable for the region, and should stimulate more research in similar non-tropical areas. Although more observations are desirable before generalizing these results, they already confirm the interest of the Chilean Valdivian Temperate Forest as a biodiversity hotspot as recognized by Myers et al. (2000). Although some of these forests are relatively well protected compared to those in other parts of the world, parts of them remain highly vulnerable to progressive fragmentation and other human driven influence (Wilson et al. 2005; Echeverria et al. 2008; Schmitt et al. 2009; Gillespie et al. 2012). This is also an opportunity to point out that active research programs on parasites should be part of all studies involving the collection of vertebrate specimens in such areas.

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RESEARCH ARTICLE

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A revision of dragon millipedes IV: the new genus *Spinaxytes*, with the description of nine new species (Diplopoda, Polydesmida, Paradoxosomatidae)

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Abstract

Nine new species constituting the '*spiny*' group of dragon millipedes are assigned to the new genus *Spinaxytes* Srisonchai, Enghoff & Panha, **gen. n.** Seven new species are described from Thailand: *S. biloba* Srisonchai, Enghoff & Panha, **sp. n.** and *S. palmata* Srisonchai, Enghoff & Panha, **sp. n.** from Surat Thani Province, *S. hasta* Srisonchai, Enghoff & Panha, **sp. n.** from Chumphon Province, *S. krabiensis* Srisonchai, Enghoff & Panha, **sp. n.** (type species) and *S. sutchariti* Srisonchai, Enghoff & Panha, **sp. n.** from Krabi Province, *S. uncus* Srisonchai, Enghoff & Panha, **sp. n.,** and *S. macaca* Srisonchai, Enghoff & Panha, **sp. n.** from Phang Nga Province; as well as one from Malaysia, *S. tortioverpa* Srisonchai, Enghoff & Panha, **sp. n.**, and one from Myanmar, *S. efefi* Srisonchai, Enghoff & Panha, **sp. n.** The new genus is endemic to South Myanmar, South Thailand, and Malaysia, and all new species are restricted to limestone habitats. All were exclusively found living on humid rock walls and/or inside small caves. Complete illustrations of external morphological characters, an identification key, and a distribution map are provided.

Keywords

dragon millipede, endemic, new species, taxonomy, Thailand

Introduction

This is the fourth paper in a series of articles about revision of the dragon millipedes. Srisonchai et al. (2018a) provided general information on dragon millipedes, split *Desmoxytes* Chamberlin, 1923, sensu Golovatch and Enghoff (1994) into five genera based on morphological and genetic data, and revised the genus *Desmoxytes* in its new, restricted sense. Subsequently, Srisonchai et al. (2018a, b) described two new genera of dragon millipedes containing several new species and several species transferred from *Desmoxytes*. In the present study, we describe nine new species constituting the group that we (Srisonchai et al. 2018a) provisionally named the '*spiny*' group, of which no species has hitherto been named, and assign them to *Spinaxytes* gen. n.

The new genus is narrowly distributed in the Malay Peninsula (Malaysia, Myanmar, and Thailand).

Materials and methods

Specimen collection and preservation

Specimens were hand-collected from many localities throughout South Thailand, in some parts of Malaysia and in southern Myanmar. We also observed the habitats of all specimens. Specimens were mostly stored in 70% ethanol for morphological study and partly in 95% ethanol for molecular analysis. Latitude, longitude, and elevation were recorded by using a Garmin GPSMAP 60 CSx, and all coordinates and elevations were checked with Google Earth.

The main collectors in this work were staff and students of the Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University which we here refer to as 'ASRU members'.

Illustrations

All living specimen photos were taken with a Nikon D700 equipped with a AF-S VR Micro-Nikkor 105 mm lens during fieldwork. Newly collected specimens preserved in ethanol were imaged with an Olympus DP72 camera on an Olympus SZX16 stereomicroscope, using image stacking Cell-D auto-montage software. Scanning electron micrographs were generated with a JEOL – JSM–5410 LV. All samples studied with SEM were carefully dissected under a microscope, mounted on aluminium stubs, and coated with gold. After imaging with SEM, all objects were removed and kept in dry condition. Drawings were outlined under a stereo microscope (Leica Wild M10) with a drawing tube and finished using dot-line technique (stipple). Plates were composed in Adobe Photoshop CS6.

Morphological descriptions

We use morphological terminology according to previous taxonomic publications (Chamberlin 1923; Jeekel 1964, 1980, 2003; Golovatch and Enghoff 1994; Enghoff et al. 2007; Golovatch et al. 2012; Srisonchai et al. 2016, 2018a, 2018b, 2018c. Details of gonopodal terms are shown in the gonopod terminology section below.

Gonopod terms for the genus *Spinaxytes* gen. n., and their abbreviations

acropodite	Apical part of the gonopod; including femur, postfemoral part, solenophore and solenomere
ca	Cannula: a tube, lever-like, curved and slender; originating from coxa, tip inserted into concavity in prefemoral part
cx	Coxa: basal part of the gonopod, rather long, connecting to seventh body ring, attached to apertural rim dorsally; with a distoanterior group of setae
fe	Femur: longest part of the gonopod, straight; with lateral and mesal sulci distally; accommodates seminal groove (terminology for femorite vs femur, see Jeekel (2003 p. 48)
ll	Lamina lateralis: a small lobe on distal part of gonopod; seen in lateral view
lm	Lamina medialis: the longest part distally on the gonopod, very long, curved
ls	Lateral sulcus: a distinct sulcus distally on femur, seen obviously in lateral view
ms	Mesal sulcus: a distinct sulcus distally on femur, seen obviously in mesal view
pfe	Prefemoral part (=prefemur): basal portion of the telopodite, densely setose
pof	Postfemoral part (=postfemur): short part of telopodite, supporting solenophore and solenomere, demarcated from femur by lateral and mesal sulci
sg	Seminal groove: a conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femur in mesal view
sl	Solenomere: a long and curved, flagellum-like appendage, originating from base of solenophore
sph	Solenophore (=tibiotarsus): apical part of telopodite, consisting of lamina lateralis and lamina medialis
telopodite	Main part of the gonopod, pivoting on coxa; including prefemoral part, femur, postfemoral part, solenophore and solenomere

Deposition of holotypes, paratypes, and other new specimens

All holotypes and most paratypes are kept at CUMZ. Some paratypes are deposited at NHMUK, NHMW, ZMUC, and ZMUM.

Abbreviations:

ASRU	Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
CUMZ	Chulalongkorn University Museum of Zoology, Bangkok, Thailand
FFI	Fauna and Flora International, Myanmar
NHMUK	Natural History Museum of London, England
NHMW	Natural History Museum, Vienna, Austria
ZMUC	Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
ZMUM	Zoological Museum, University of Moscow, Russia
a.s.l.	above sea level

Positional and directional terms in gonopod descriptions

Traditionally the gonopods are depicted as rotated 90° up from their in situ position. Following Srisonchai et al. (2018a), we use the following terms:

Dorsal	nearest to the body ring,	**Dorsad**	towards the body ring,
Ventral	farthest away from the body ring,	**Ventrad**	away from the body ring,
Mesal	nearest to the midline,	**Mesad**	towards the midline,
Lateral	furthest from the midline,	**Laterad**	away from the midline.

We use “sub-” as a prefix referring to positions and directions slightly different from the ones given above. For example, “subdorsal” means a position close to, but not quite on the dorsal side.

Taxonomy

Class Diplopoda Blainville in Gervais, 1844
Order Polydesmida Pocock, 1887
Family Paradoxosomatidae Daday, 1889
Subfamily Paradoxosomatinae Daday, 1889
Tribe Orthomorphini Brölemann, 1916

Spinaxytes Srisonchai, Enghoff & Panha, gen. n.
http://zoobank.org/EB550BAF-CFF4-4683-9E00-D00C17227870

Type species. *Spinaxytes krabiensis* Srisonchai, Enghoff & Panha, gen. et sp. n.

Diagnosis. The genus *Spinaxytes* gen. n. is characterized by:

1. Paraterga spiniform.
2. Metaterga with two rows of tubercles/cones/spines.
3. Postfemoral part of gonopod conspicuous, demarcated from femur by deep mesal and lateral sulci.
4. Lamina lateralis distinctly demarcated from lamina medialis.
5. Lamina medialis very long, curved, larger and longer than lamina lateralis.

Etymology. The name is a noun in apposition; from the Latin '*spina*', referring to the spine-like paraterga of all constituent species; '*–xytes*' ensures harmony with *Desmoxytes* (and its synonym '*Pteroxytes*').

Included species.

1. *Spinaxytes biloba* Srisonchai, Enghoff & Panha, sp. n.
2. *Spinaxytes efefi* Srisonchai, Enghoff & Panha, sp. n.
3. *Spinaxytes hasta* Srisonchai, Enghoff & Panha, sp. n.
4. *Spinaxytes krabiensis* Srisonchai, Enghoff & Panha, sp. n.
5. *Spinaxytes macaca* Srisonchai, Enghoff & Panha, sp. n.
6. *Spinaxytes palmata* Srisonchai, Enghoff & Panha, sp. n.
7. *Spinaxytes sutchariti* Srisonchai, Enghoff & Panha, sp. n.
8. *Spinaxytes tortioverpa* Srisonchai, Enghoff & Panha, sp. n.
9. *Spinaxytes uncus* Srisonchai, Enghoff & Panha, sp. n.

Remarks. The new genus is easily distinguished from other genera of dragon millipedes by having spiniform paraterga, lamina lateralis smaller and shorter than lamina medialis, lamina medialis long and curved. Some species of the genus *Hylomus* Cook & Loomis, 1924, share spine-like paraterga; however, the gonopod details are totally different.

General description of the genus *Spinaxytes*. The description applies to adult males and females, except for the gonopods and when "male" is specified (Figs 1, 2, 4). The general description of the gonopods is based mainly on *Spinaxytes krabiensis* gen. et sp. n. (Figs 3, 5).

Size. Body length ca. 18–33 mm (male) ca. 16–33 mm (female), width 1.0–2.2 mm (male) 1.3–2.9 mm (female), size varies between species, usually female a bit longer than male.

Colour. Most species in life with dark brown colour. Colour in alcohol: all specimens partly faded to pale brown after 5 years' preservation in alcohol; specimens kept in darkness faded more slowly.

Antennae (Figure 1A–C). Extremely long and slender, covered by delicate setation, usually reaching backwards to body rings 7–10 (male) and 6–8 (female) when stretched dorsally. Antennomere 3 = 4 > 5 ≥ 2 > 6 > 1 > 7 > 8.

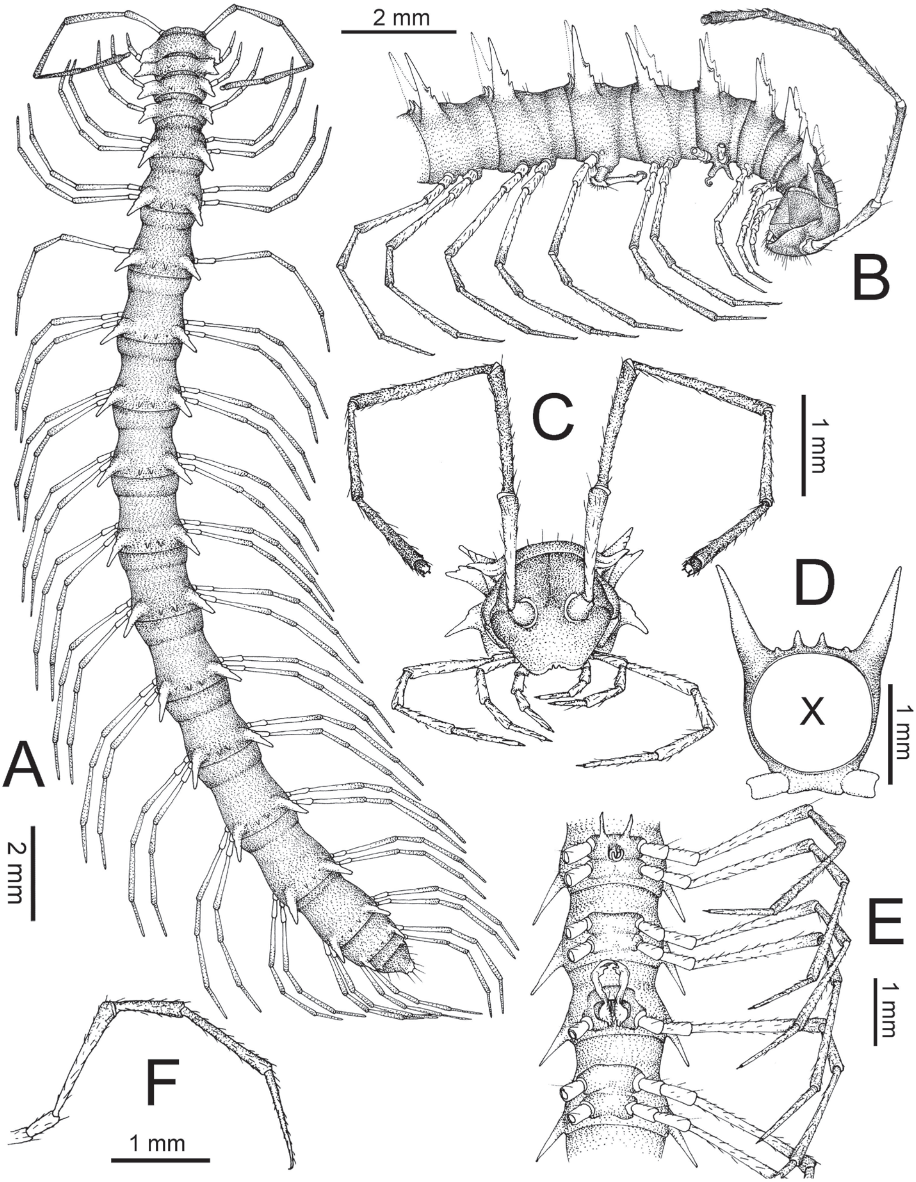

Figure 1. General body characters of *Spinaxytes* gen. n. (*S. tortioverpa* sp. n., ♂ paratype, CUMZ-pxDGT00220) **A** whole body **B** anterior body part **C** head and antennae **D** midbody ring **E** body rings 5–8, showing gonopods and sternal lobe between coxae 4 **F** leg 13.

Head. Delicately setose; vertex, labrum and genae sparsely setose; epicranial suture conspicuous as a deep, brown or black stripe.

Collum (Figure 2A, C). With three regular transverse rows of setiferous tubercles/cones; number of tubercles/cones in each row varies between species. Paraterga wing-like/spiniform, usually elevated at ca. 10°–30°, directed laterad/caudolaterad/caudad, with one or two conspicuous/inconspicuous notches at lateral margin.

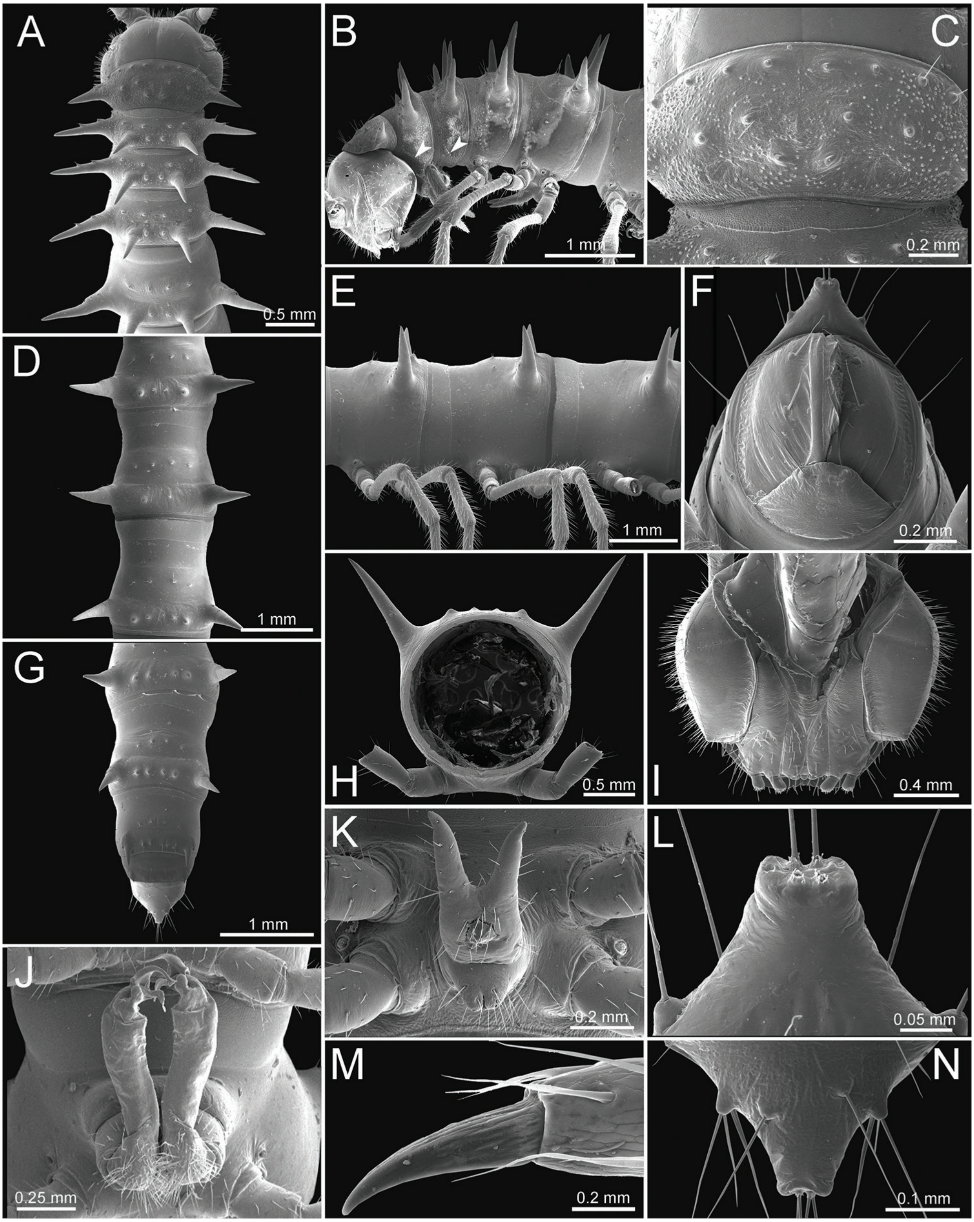

Figure 2. General body characters of *Spinaxytes* gen. n. (*S. palmata* sp. n., ♂ paratype, CUMZ-pxDGT00216) – SEM images **A, B** anterior body part (arrowheads point to pleurosternal carinae) **C** collum **D, E** body rings 9–11 **F** telson **G** posteriormost rings and telson **H** body ring 10 **I** mouth parts, ventral view **J** gonopods **K** sternal lobe between coxae 4 **L, N** tip of epiproct **M** tip of tarsus and claw of leg 13.

Tegument. Quite dull, sometimes shining; collum, metaterga and surface below paraterga smooth/microgranulate; prozona finely shagreened; paraterga, epiproct and sterna smooth. Stricture between prozona and metazona shallow, wide.

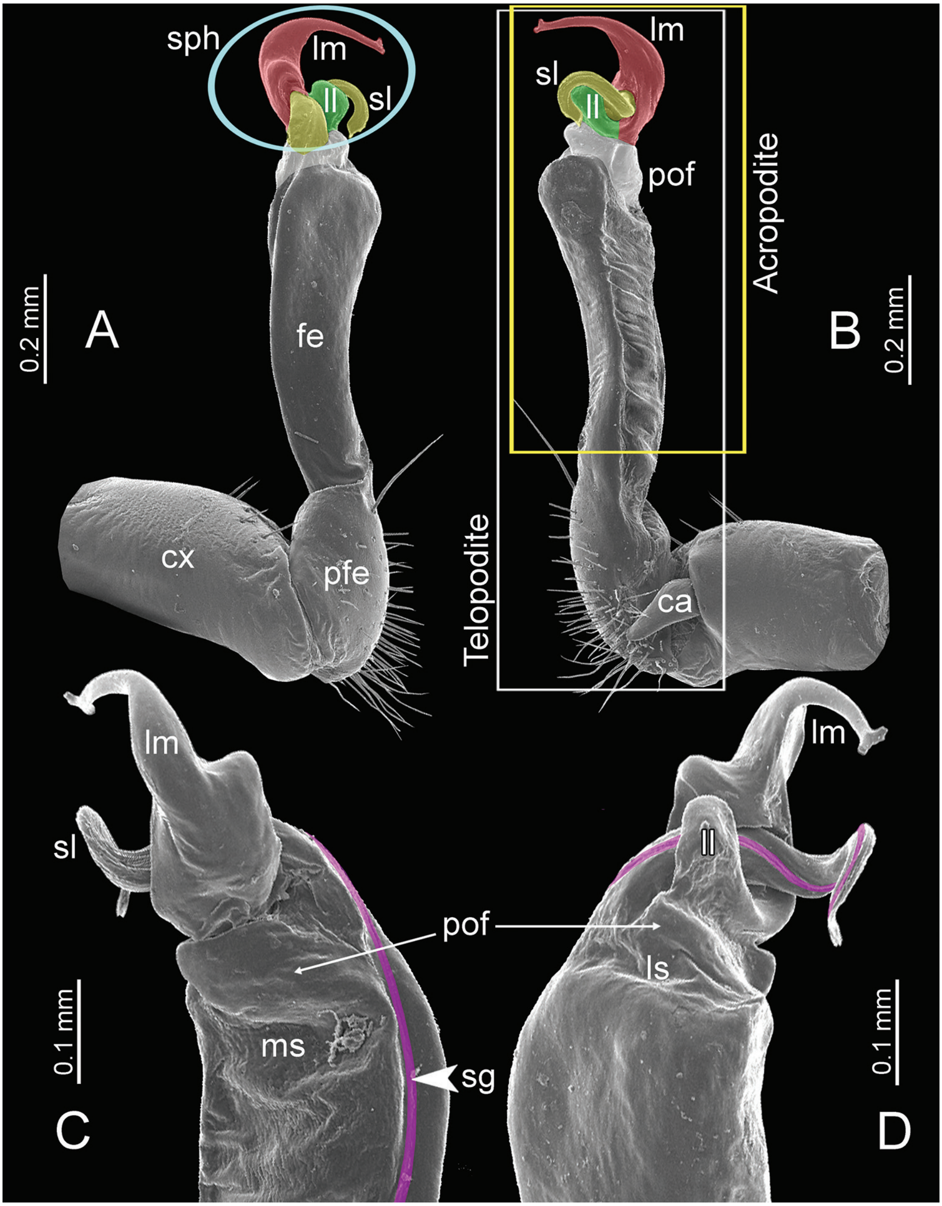

Figure 3. SEM images of right gonopod of *Spinaxytes* gen. n. (*Spinaxytes krabiensis* sp. n., ♂ paratype, CUMZ-pxDGT00212) **A** lateral view **B** mesal view **C** dorsal view **D** ventral view. Key: red = lamina medialis (lm), yellow = solenomere (sl), green = lamina lateralis (ll), purple = seminal groove (sg).

Metaterga (Figure 2A, D, G). With two regular transverse rows of setiferous cones/tubercles (in anterior row) and cones/spines (in posterior row); number of tubercles/cones/spines in each row varies between species. Transverse sulcus on metaterga shallow and wide in body rings 5–18. Mid-dorsal (axial) line missing.

Pleurosternal carinae (Figure 2B). Forming a complete, tooth-like crest on ring 2, a short ridge on ring 3, missing on remaining body rings.

Paraterga (Figs 1A, B, D; 2A, B, D, E, G, H). Spiniform, long (except *S. biloba* sp. n.: quite short), extremely elevated at ca. 45°–80° (male) 40°–70° (female). Callus and shoulder poorly developed, inconspicuous. Anterior margin with two distinct denticles; on body rings 9, 10, 12, 13, 15–19 without a third denticle at lateral margin near tip. Degree of elevation of paraterga in male usually higher than in female. Posterior angle straight. Tip pointed and sharp. Ozopore visible from dorsal/dorsolateral/lateral view, round, small.

Telson (Figure 2F, G, L, N). Epiproct usually long, apically with two pairs of conspicuous setae (spinnerets) arranged at the corners of a square, not in a depression, anterior pair close to apical tubercles. Paraprocts convex. Hypoproct usually subtrapeziform, sometimes subsemicircular/subtriangular; caudal margin often round, sometimes subtruncate/angular, with two conspicuous/ inconspicuous setiferous tubercles.

Sterna (Figs 1E, 2K). Sparsely setose, cross-impressions shallow in all species. Sternal lobe between male coxae 4 varies in shape; subtrapeziform/long subrectangular/bifurcate/spear-like; one or two pores seen in posterior view.

Legs (Figs 1F, 2M). Extremely long and slender. Relative length of podomeres: femur ≥ tibia > tarsus ≥ postfemur > prefemur > coxa > claw. Male femora mostly without modification, sometimes male femora 6, 7 or 7 or 8, 9 with hump/apophysis ventrally in distal part.

Gonopods (Figure 3). Coxa shorter than femur, sometimes subequal in length to femur. Cannula long and slender. Telopodite erect. Prefemoral part usually almost half as long, sometimes ca. 2/3 as long as femur. Acropodite erect. Femur long and straight. Seminal groove running entirely on mesal surface of femur. Mesal sulcus and lateral sulcus conspicuous, deep. Postfemoral part conspicuous, usually small and narrow, sometimes broad and wide, rarely very large. Solenophore variously modified in shape between species: lamina lateralis obviously demarcated from lamina medialis, smaller and shorter than lamina medialis; lamina medialis long, base stout, slightly attenuated near the curved tip. Solenomere long, slender, curved, supported by solenophore.

Distribution and habitat. All species of the new genus are allopatric. However, some of the new species can be found in syntopy with some species of *Desmoxytes*. The nine species described here are confined to limestone habitats and have narrow distributions; we therefore regard them as endemic. All species blend perfectly with habitat environment, mostly living on humid rock walls and/or inside small caves.

According to the current knowledge, *Spinaxytes* gen. n. is distributed only in the Malay Peninsula (south Myanmar, south Thailand, and north Malaysia): Myanmar: Thanintharyi Region; Thailand: Chumphon Province (Thung Tako, Mueng Chumphon, Lang Suan and Sawi Districts), Surat Thani Province (Phanom District), Phang Nga Province (Mueng Phang Nga and Takua Thung Districts), Krabi Province (Ao Luek and Muaeng Krabi Districts); Malaysia: Perak State (Figure 30).

Key to species of *Spinaxytes* gen. n. (based mainly on males)

1 Male femora 6–9 without modification (e.g., Figs. 4E, G; 10J; 13J) **2**

– Male femora 6 and 7, or 7, or 8 and 9 humped/with apophyses (e.g., Figs. 4B, C, L, M; 7J; 15J) **6**

2 Collum with 5+5 tubercles in anterior row, 2+2 tubercles in intermediate row, 3+3 tubercles in posterior row (Figure 10A). Metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–19 with 3+3 cones in anterior row and 4+4 cones in posterior row (Fig. 2A, C, E) .... ***S. efefi* sp. n.**

– Collum with 4+4 tubercles/cones in anterior row, 1+1 in intermediate row, 2+2 in posterior row (e.g., Figs 16A, 28A). Metaterga 2–19 with 2+2 tubercles/cones in anterior row and 2+2/3+3 tubercles/cones/spines in posterior row (e.g., Figs 16A, C, E; 28A, C, E) **3**

3 Sternal lobe between male coxae 4 bilobed/bifurcate/subtrapeziform (e.g., Figs 4A, K, P, R; 7F, G; 19F, G) **4**

– Sternal lobe between male coxae 4 spear-like (not bilobed, not bifurcate, not subtrapeziform) (Figs 4F; 13F, G) .... ***S. hasta* sp. n.**

4 Postfemoral part very large, angled 90 degrees with femoral part (Figs 5H, 26C–F). Lamina lateralis divided into two lobes; first lobe spine-like, long; second lobe smaller, ridge-like (Figs 5H; 26A, C, D). Lamina medialis curving up (Figs 5H; 26C, E). Solenomere longer than lamina medialis (Figs 5H; 26A–D) ..... ***S. tortioverpa* sp. n.**

– Postfemoral part small, not angled 90 degrees with femoral part (e.g., Figs 5F, G; 23C; 25C). Lamina lateralis not divided into two lobes (e.g., Figs 5F, G; 23C; 25C, F). Lamina medialis curving down (e.g., Figs 5F, G; 23C; 25C, D). Solenomere approximately equal in length to lamina medialis (e.g., Figs 5F, G; 23C; 25C).......... **5**

5 Lamina lateralis small (Figs 5F, 23C). Solenomere circular in transverse section, curving down (Fig. 23C, E) .... ***S. palmata* sp. n.**

– Lamina lateralis large (Figs 5G; 25C, F). Solenomere flat in transverse section, curving up (Fig. 25C–E) .... ***S. sutchariti* sp. n.**

6 Only male femora 7 modified (Figs 4V, 28J) .... ***S. uncus* sp. n.**

– Male femora 6 and 7, or 8 and 9 modified (e.g. Figs 4B, C, L, M; 7J; 19J) **7**

7 Lamina medialis with process-like lobe at base (Fig. 8D). Sternal lobe between male coxae 4 subtrapeziform (Figs 4A; 7F, G). Male femora 8 and 9 with apophyses .... ***S. biloba* sp. n.**

– Lamina medialis without process-like lobe at base (Figs 17D, E; 20D, E). Sternal lobe between male coxae 4 incompletely bilobed, fork-like (Figs 4H, K; 16F, G; 19F, G). Male femora 6 and 7 modified as humped ventrally in distal portion . **8**

8 Paraterga extremely long (Fig. 16D). Lamina lateralis distally round (Fig. 17C). Tip of lamina lateralis terminating in two lobes (Figs 3C, D; 17C, D, E) .... ***S. krabiensis* sp. n.**

– Paraterga moderately long (Fig. 19D). Lamina lateralis distally protruding, lobe-like (Fig. 20C). Tip of lamina lateralis bent, terminating in one lobe (Fig. 20C, D, E) .... ***S. macaca* sp. n.**

Species descriptions

Spinaxytes biloba Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/DAC03327-012B-4096-846C-468C40558DDE
Figs 4A–C, 5A, 6–8

Material examined. Holotype. ♂, THAILAND, Surat Thani Province, Phanom District, near Khlong Phanom National Park, Pha Daeng, 8°53'41"N, 98°33'12"E, ca. 67 m a.s.l., 7 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00205). **Paratypes.** 17 ♂♂, 24 ♀♀, same data as for holotype (CUMZ- pxDGT00206); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040249); 1 ♂, 1 ♀, same data as for holotype (NHMW9423). **Further specimens, not paratypes.** 5 ♂♂, 3 ♀♀, THAILAND, Surat Thani Province, Phanom District, near Khlong Phanom National Park, Pha Daeng, 8°53'41"N, 98°33'12"E, ca. 67 m a.s.l., 6 Aug. 2015, ASRU members leg. (CUMZ).

Etymology. The species name is an adjective, refers to the two additional process-like lobes on the solenophore (one on lamina lateralis and one on lamina medialis).

Diagnosis. Differs from other species by having: metaterga 5–19 with 2+2 cones in anterior row and 3+3 cones in posterior row; sternal lobe between male coxae 4 subtrapeziform; male femora 8 and 9 with apophyses distally; lamina lateralis with an additional process-like protruding lobe; lamina medialis basally with an additional protruding process-like lobe.

Description. SIZE. Length 15–17 mm (male), 16–18 mm (female); width of midbody metazona 1.0–1.2 mm (male), 1.3–1.5 mm (female). Width of rings 2 = 3 < 4 < collum < 5 < head = 6–17, thereafter body gradually tapering towards telson.

Colour (Figure 6A, B). Specimens in life brown/pale brown; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8) and collum brown; prozona, metaterga (except white spines in posterior row) and surface below paraterga brown/pale brown; sterna pale brown/whitish brown; epiproct and legs whitish brown; a few basal podomeres whitish brown/white.

Antennae. Reaching to body ring 7 or 8 (male) and 6 (female) when stretched dorsally.

Collum (Figure 7A). With three transverse rows of setiferous cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with one inconspicuous setiferous notch at lateral margin; paraterga wing-like, quite short, tip blunt, elevated at ca. 15°–20° (male) 10°–20° (female), directed almost caudad.

Tegument. Quite shining; collum coarsely microgranulate; metaterga and surface below paraterga finely microgranulate.

Metaterga (Figure 7A, C, E). With two transverse rows of setiferous cones; metaterga 2–4 with 2+2 cones in anterior row and 2(3)+2(3) cones in posterior row; metaterga 5–19 with 2+2 cones in anterior row and 3+3 cones in posterior row; all cones subequal in length and size. An additional cone-like denticle at base of paraterga near anterior row of cones.

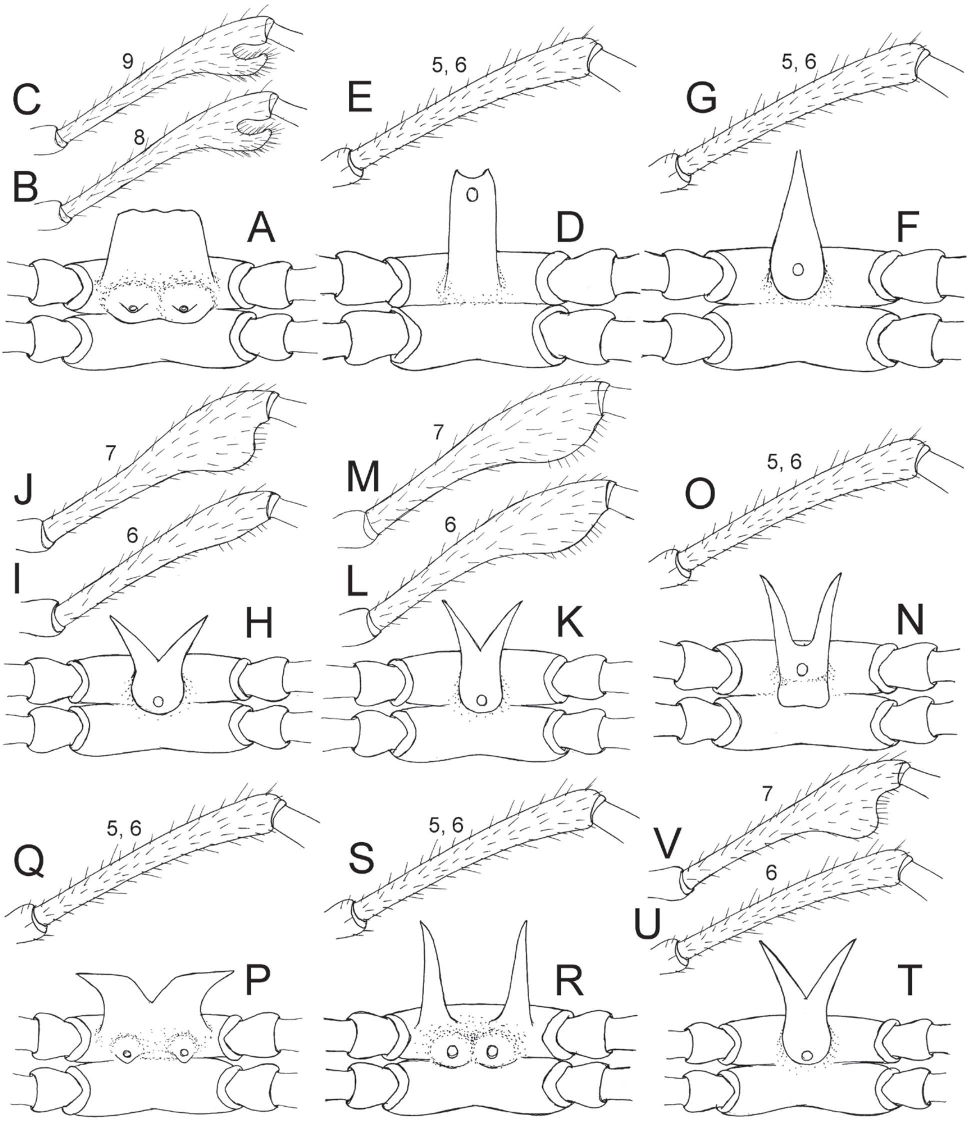

Figure 4. Male femora and sternal lobe between male coxae 4 of *Spinaxytes* gen. n. **A–C** *S. biloba* sp. n. (**A** Sternal lobe **B** Femur 8 **C** Femur 9) **D, E** *S. efefi* sp. n. (**D** Sternal lobe **E** Femur 5 or 6) **F, G** *S. hasta* sp. n. (**F** Sternal lobe **G** Femur 5 or 6) **H–J** *S. krabiensis* sp. n. (**H** Sternal lobe **I** Femur 6 **J** Femur 7) **K–M** *S. macaca* sp. n. (**K** Sternal lobe **L** Femur 6 **M** Femur 7) **N, O** *S. palmata* sp. n. (**N** Sternal lobe **O** Femur 5 or 6) **P, Q** *S. sutchariti* sp. n. (**P** Sternal lobe **Q** Femur 5 or 6) **R, S** *S. tortioverpa* sp. n. (**R** Sternal lobe **S** Femur 5 or 6) **T–V** *S. uncus* sp. n. (**T** Sternal lobe **U** Femur 6 **V** Femur 7).

Paraterga (Figure 7A–D, H). Quite short; directed dorsocaudad on body rings 3–17, elevated at ca. 60°–70° (male) 55°–70° (female), directed more caudad on body ring II and increasingly so on rings 18 and 19. Denticle of paraterga located at base of paraterga and very close to anterior row of cones on metaterga. Ozopore visible in lateral view.

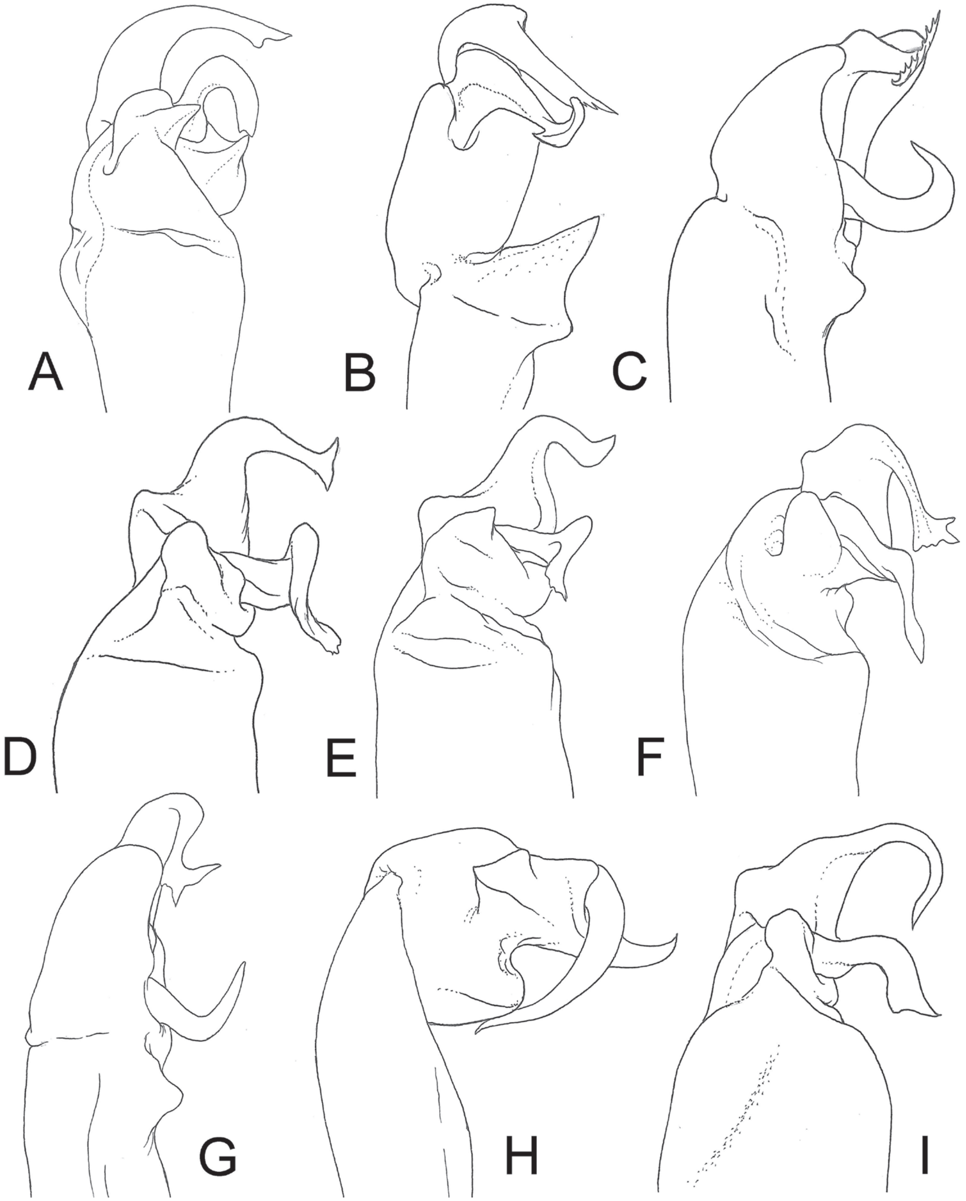

Figure 5. Right gonopods of *Spinaxytes* gen. n. (ventral view) **A** *S. biloba* sp. n. **B** *S. efefi* sp. n. **C** *S. hasta* sp. n. **D** *S. krabiensis* p. n. **E** *S. macaca* sp. n. **F** *S. palmata* sp. n. **G** *S. sutchariti* sp. n. **H** *S. tortioverpa* sp. n. **I** *S. uncus* sp. n.

Telson (Figure 7E, I, H). Epiproct quite long; tip subemarginate; lateral setiferous tubercles conspicuous; apical tubercles conspicuous. Hypoproct subtrapeziform, wide; caudal margin round (in some specimens subtruncate), with inconspicuous setiferous tubercles.

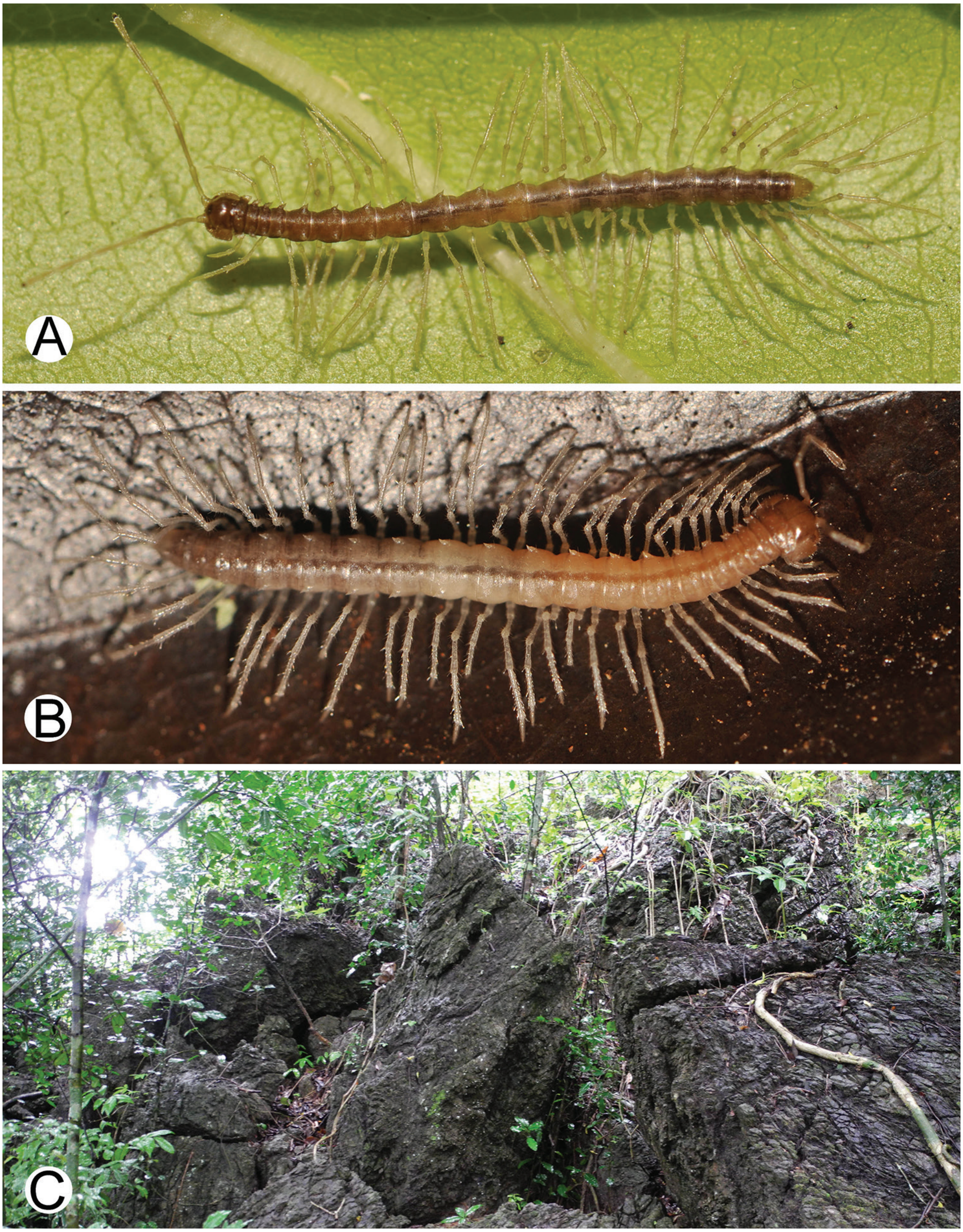

Figure 6. Photographs of live *Spinaxytes biloba* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00206 **B** ♀ paratype, CUMZ-pxDGT00206 **C** Habitat.

Sterna (Figs 4A; 7F, G). Sternal lobe between male coxae 4 subtrapeziform, broad, and thin, tips subtruncate, in situ directed ventroanteriad; posterior surface of sternal lobe with two pores borne on swollen and short lobe.

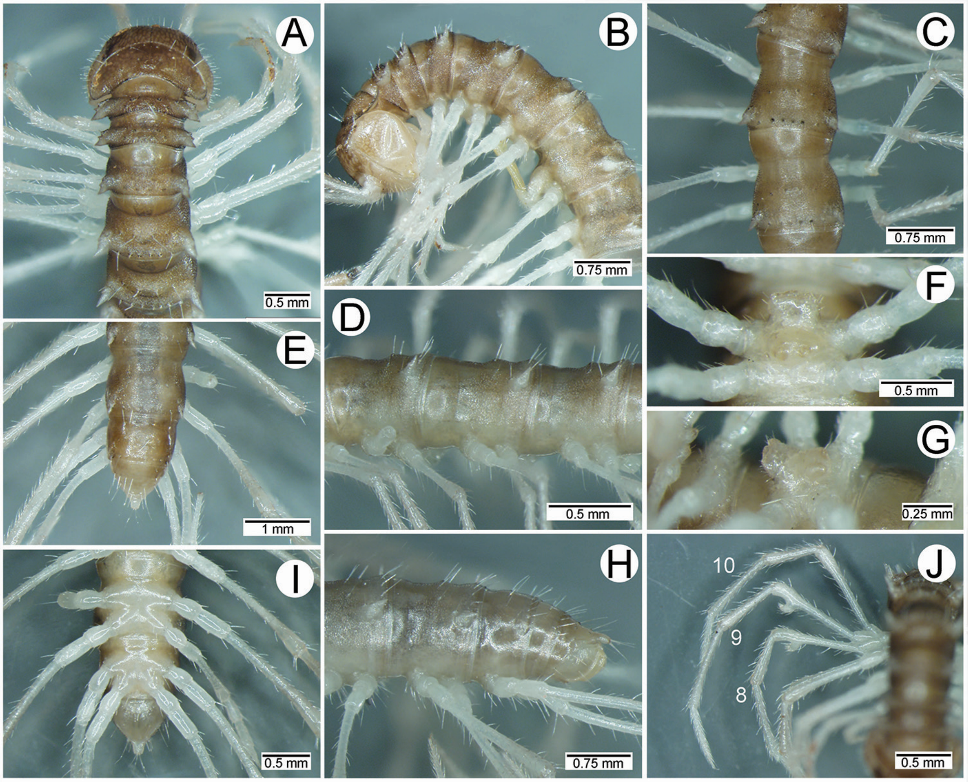

Figure 7. *Spinaxytes biloba* sp. n., ♂ paratype, CUMZ-pxDGT00206 **A, B** anterior body part **C, D** body rings 8–10 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 6–10.

Legs (Figs 4B, C; 7J). Male femora 8 and 9 with apophyses distally.

Gonopods (Figs 5A, 8). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur not enlarged distally. Postfemoral part broad. Mesal sulcus wide; lateral sulcus narrow. Solenophore subequal in size to postfemoral part: lamina lateralis small and short; with a protruding lobe, process-like, directed mesad; apically round: lamina medialis long; base enlarged and stout, slightly attenuated near the tip, basally with a protruding lobe, process-like, directed mesad; tip curving down, bifurcating into two small spines. Solenomere curving down, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 6C). Known only from the type locality which is a small isolated limestone mountain between Khao Sok and Khlong Phanom National Parks. The new species blended perfectly with the humid rock walls, and most specimens were found inside rock holes/crevices. *S. biloba* sp. n. co-occurs with *Desmoxytes cervina* (Pocock, 1895) (Srisonchai et al. 2018a) in the same habitat. Several attempts (2017–2018) have been made to find further specimens near the type locality, but none were found. As the new species has only been found at the type locality only, we regard *S. biloba* sp. n. as endemic to Thailand.

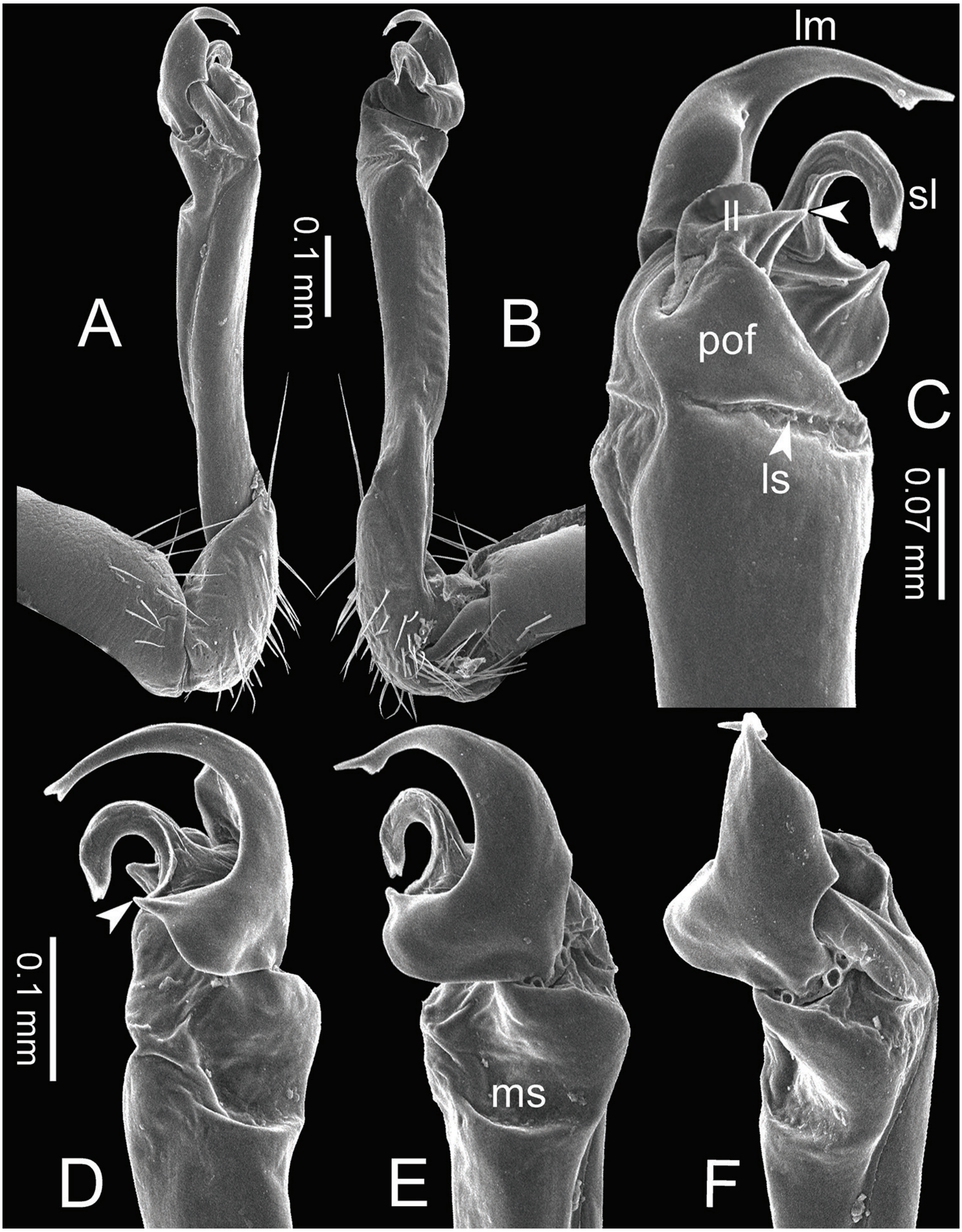

Figure 8. *Spinaxytes biloba* sp. n., paratype, CUMZ-pxDGT00206 – right gonopod **A** lateral view **B** mesal view **C** ventral view (unlabelled arrowhead points to lobe on lamina lateralis) **D** mesodorsal view (arrowhead points to lobe at base of lamina medialis) **E** dorsal view **F** laterodorsal view.

Remarks. Among all *Spinaxytes* species, *S. biloba* sp. n. is obviously the smallest (length 15–18 mm, width of midbody metazona 1.0–1.5 mm), and the live pale brown colouration is lighter than that of other species.

Spinaxytes efefi **Srisonchai, Enghoff & Panha, sp. n.**

http://zoobank.org/935306A6-160D-4903-B3B4-BE046F963661
Figs 4D, E; 5B; 9–11

Material examined. Holotype. ♂, MYANMAR, Tanintharyi Region, Myeik, 20 km northeast of Monoron, Lenya National Park, limestone mountain near Ngawun Chaung River, 11°40'20"N, 99°13'30"E, ca. 64 m a.s.l., 9 Jun. 2015, FFI staff and ASRU members leg. (CUMZ-pxDGT00207). **Paratypes.** 20 ♂♂, 25 ♀♀, same data as for holotype (CUMZ-pxDGT00208); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040250); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9422); 1 ♂, 1 ♀, same data as for holotype (NHMUK).

Etymology. The name is an artificially constructed homophone (*efefi* = FFI) honouring FFI (Fauna and Flora International, Myanmar), an organization for biodiversity conservation; in recognition of their hard work to protect wildlife including invertebrates.

Diagnosis. Sternal lobe between male coxae 4 not bilobed and male femora without modification. Similar in this respect to *S. hasta* sp. n., but differs by having: collum with 5(4)+5(4) tubercles in anterior row, 2+2 tubercles in intermediate row and 3+3 tubercles in posterior row; metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–18 with 3+3 cones in anterior row and 4+4 cones in posterior row; metatergum 19 with 3+3 tubercles/cones in anterior row and 4+4 tubercles/cones in posterior row; postfemoral part of gonopod with a triangular process and a triangular ridge.

Description. SIZE. Length 26–30 mm (male), 30–32 mm (female); width of midbody metazona 2.1–2.2 mm (male), 2.7–2.9 mm (female). Width of collum = ring 2 = 3 = 4 < head = 5–17, thereafter body gradually tapering towards telson.

Colour (Figure 9A, B). Specimens in life with body brown/yellowish brown; paraterga yellow; antennae (except whitish distal part of antennomeres 7 and 8), head and prozona brown/blackish brown; collum, metaterga and surface below paraterga brown/yellowish brown; sterna, epiproct and legs brown; a few basal podomeres pale brown/whitish brown.

Antennae. Reaching to body ring 9 or 10 (male) and 7 or 8 (female) when stretched dorsally.

Collum (Figure 10A). With three transverse rows of setiferous tubercles, 5(4)+5(4) tubercles in anterior row, 2+2(1) tubercles in intermediate row and 3+3 tubercles in posterior row; with two inconspicuous setiferous notches at lateral margin; paraterga wing-like, quite short and small, tip obtuse, elevated at ca. 15°–25° (male) 10°–15° (female), directed caudolaterad.

Tegument. Quite dull; collum, metaterga (posterior part) and surface below paraterga coarsely microgranulate; metaterga (anterior part) smooth.

Metaterga (Figure 10A, C, E). With two transverse rows of setiferous cones; metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–19 with 3(4)+3(4) cones in anterior row and 4(5)+4(5) cones in posterior row; all cones subequal in length and size.

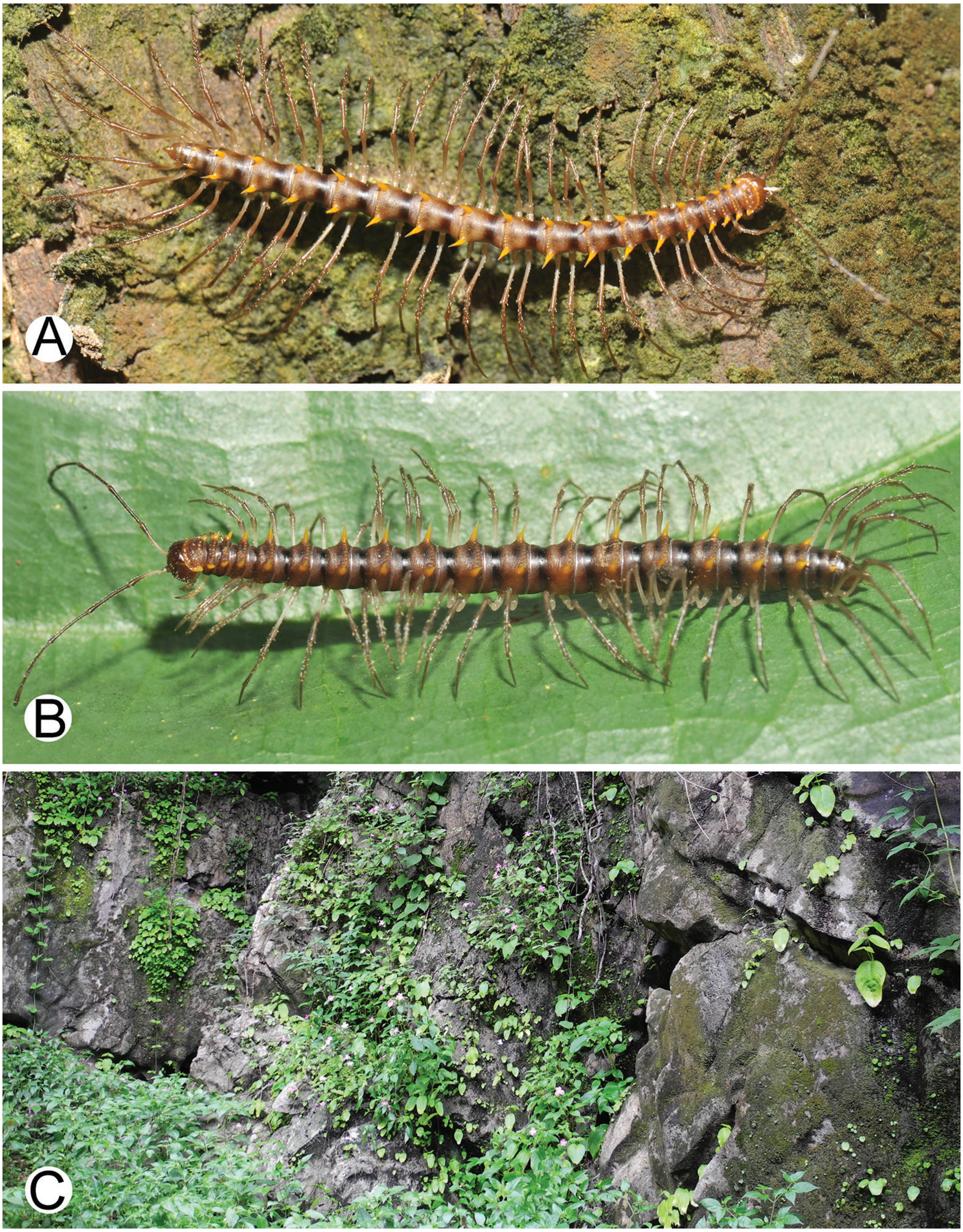

Figure 9. Photographs of live *Spinaxytes efefi* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00208 **B** ♀ paratype, CUMZ-pxDGT00208 **C** habitat.

Paraterga (Figure 10A–E, H). Very long; directed almost dorsad on body rings 2–16, elevated at ca. 65°–80° (male) 60°–70° (female); directed dorsocaudad on ring 17; directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

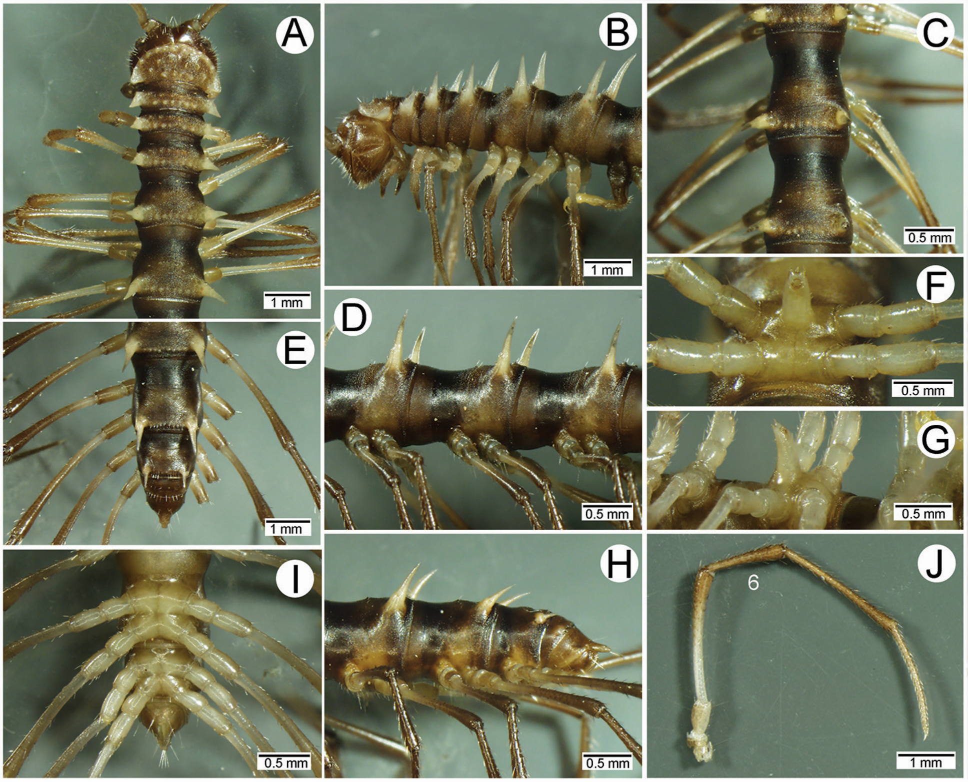

Figure 10. *Spinaxytes efefi* sp. n., ♂ paratype, CUMZ-pxDGT00208 **A, B** anterior body part **C, D** body rings 9–11 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** leg 6.

Telson (Figure 10E, H, I). Epiproct quite long; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular; caudal margin round (in some specimens angular), with conspicuous setiferous tubercles.

Sterna (Figs 4D; 10F, G). Sternal lobe between male coxae 4 erect, subrectangular, very long; tips emarginate, in situ directed ventrad; posterior surface bearing one pore near tip.

Legs (Figs 4E, 10J). Male femora without modification.

Gonopods (Figs 5B, 11). Coxa subequal in length to femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally, ventrally swollen in middle part. Postfemoral part broad; mesally with a long triangular process (directed mesoanteriad) and a long triangular ridge, between process and ridge with a wide furrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part; basally very broad: lamina lateralis long and slender, curved, tip round: lamina medialis long and slender; with two ridges in middle portion; slightly attenuated near tip; tip in situ resting very close to solenomere, terminating in small spines. Solenomere flat, curving down; tip terminating in three sharp spines, directed mesoventrad.

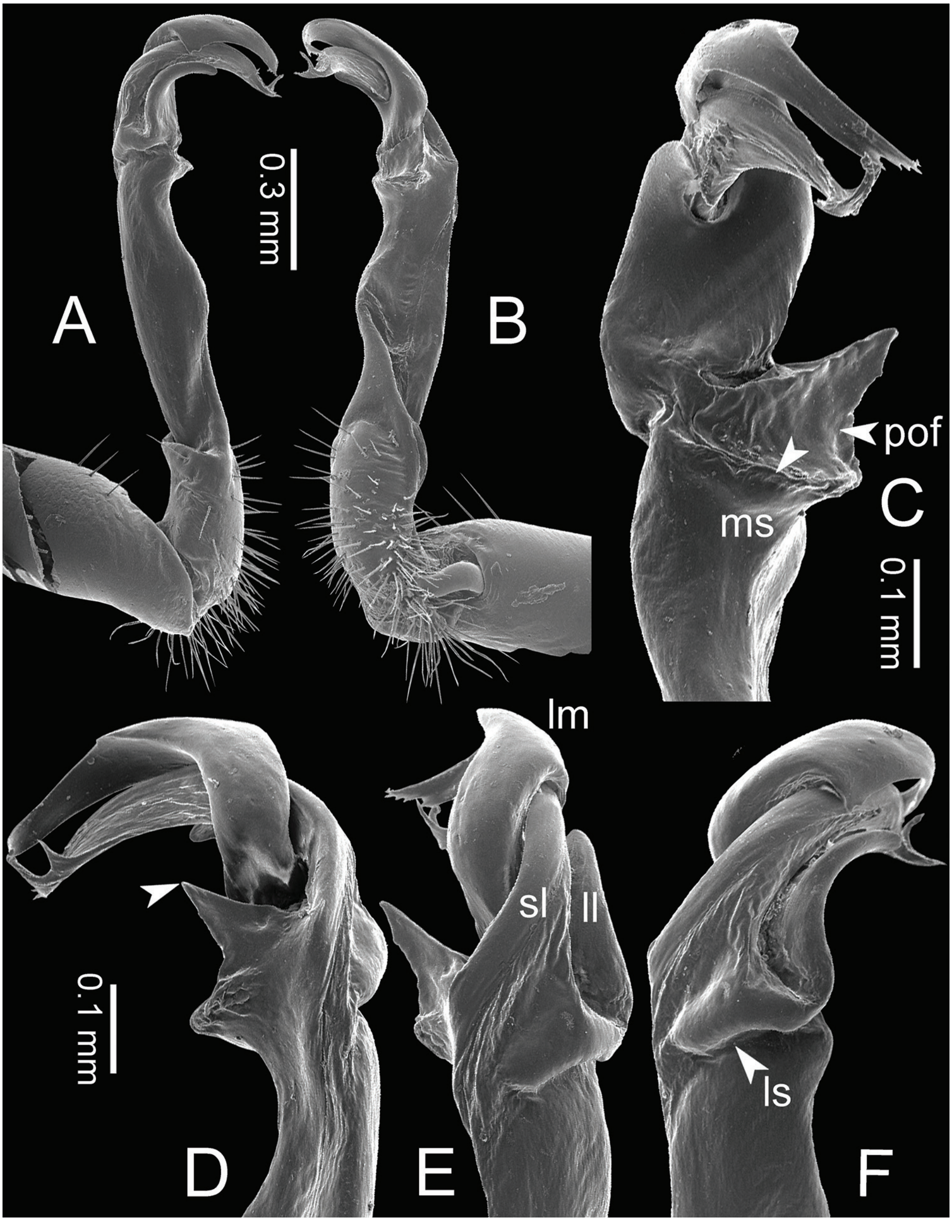

Figure 11. *Spinaxytes efefi* sp. n., paratype, CUMZ-pxDGT00208 – right gonopod **A** lateral view **B** mesal view **C** ventral view (unlabelled arrowhead points to a ridge on postfemoral part) **D** mesodorsal view (arrowhead points to a triangular process on postfemoral part) **E** dorsal view **F** laterodorsal view.

Distribution and habitat (Figure 9C). Known only from the type locality. The specimens were found exclusively on rock walls or in caves. We have tried to find this species in other places near the type locality, but no further specimens have been collected. Given the finding only at the type locality, the new species is considered to be endemic to southern Myanmar.

Remarks. No variation was found. Body ring 19 of *S. efefi* sp. n. seems to be shorter than in other species, and the tip of paraterga on collum is obtuse whereas in other species (except *S. biloba* sp. n.) it is sharp.

Spinaxytes hasta Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/C9605402-C710-4E70-8A7B-9F41F4249C0E

Figs 4F, G; 5C; 12–14

Material examined. Holotype. ♂, THAILAND, Chumphon Province, Thung Tako District, Khao Ma Ngaen, 10°05'27"N, 99°04'25"E, ca. 28 m a.s.l., 23 Oct. 2016, ASRU members leg. (CUMZ-pxDGT00209). **Paratypes.** 5 ♂♂, 6 ♀♀, same data as for holotype (CUMZ-pxDGT00210); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040251). **Further specimens, not paratypes, all from THAILAND, Chumphon Province. Mueang Chumphon District:** 8♂♂, 1 ♀, Wat Tham Sanook, 10°28'52"N, 99°04'29"E, ca. 54 m a.s.l., 3 Jul. 2017, ASRU members leg. (CUMZ). **Lang Suan District:** 2 ♀♀, Wat Ratcha Burana School, 9°56'21"N, 99°02'26"E, ca. 34 m a.s.l., 10 Sep. 2016, ASRU members leg. (CUMZ); 1 ♂, 5 ♀♀, Wat Tham Khao Kriap (Khao Kriap Cave), 9°49'08"N, 99°02'22"E, ca. 102 m a.s.l., 5 Jun. 2009, ASRU members leg. (CUMZ). **Sawi District:** 8 ♂♂, 3 ♀♀, Wat Nam Cha, 10°17'54"N, 99°01'57"E, ca. 95 m a.s.l., 5 Jun. 2009, ASRU members leg. (CUMZ).

Etymology. The name is a Latin noun in apposition meaning spear, referring to the shape of the sternal lobe between male coxae 4 which is somewhat similar to a spear.

Diagnosis. Sternal lobe between male coxae 4 not bilobed, not bifurcate; male femora without modification. Similar in this respect to *S. efefi* sp. n., but differs by having: collum with 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row; metaterga 2–8 with 2+2 cones in anterior row and 2+2 cones in posterior row; metaterga 9–18 with 2+2 cones in anterior row and 2+2 cones in posterior row; metatergum 19 with 2+2 tubercles/cones in anterior row and 2+2 tubercles/cones in posterior row; lamina medialis (lm) with a large lobe in middle part.

Description. SIZE. Length 23–33 mm (male), 26–33 mm (female); width of midbody metazona 1.7–2.2 mm (male), 2.1–2.8 mm (female). Width of collum = ring 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 12A–C). Specimens in life with body black/brownish black; paraterga white/yellowish white/whitish yellow; antennae (except whitish distal part of antennomeres 7 and 8) and metaterga (posterior part) brown/brownish black; head and collum brown/blackish brown; prozona and metaterga (anterior part) black; surface below paraterga black/brownish black; sterna and epiproct brown; legs brown/pale brown; a few basal podomeres pale whitish brown.

Antennae (Figure 13M). Reaching to body ring 9 or 10 (male) and 7 (female) when stretched dorsally.

Collum (Figure 13A). With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1(0)+1 tubercles in intermediate row and 2+2 tubercles in posterior row; with two inconspicuous setiferous notches at lateral margin; paraterga

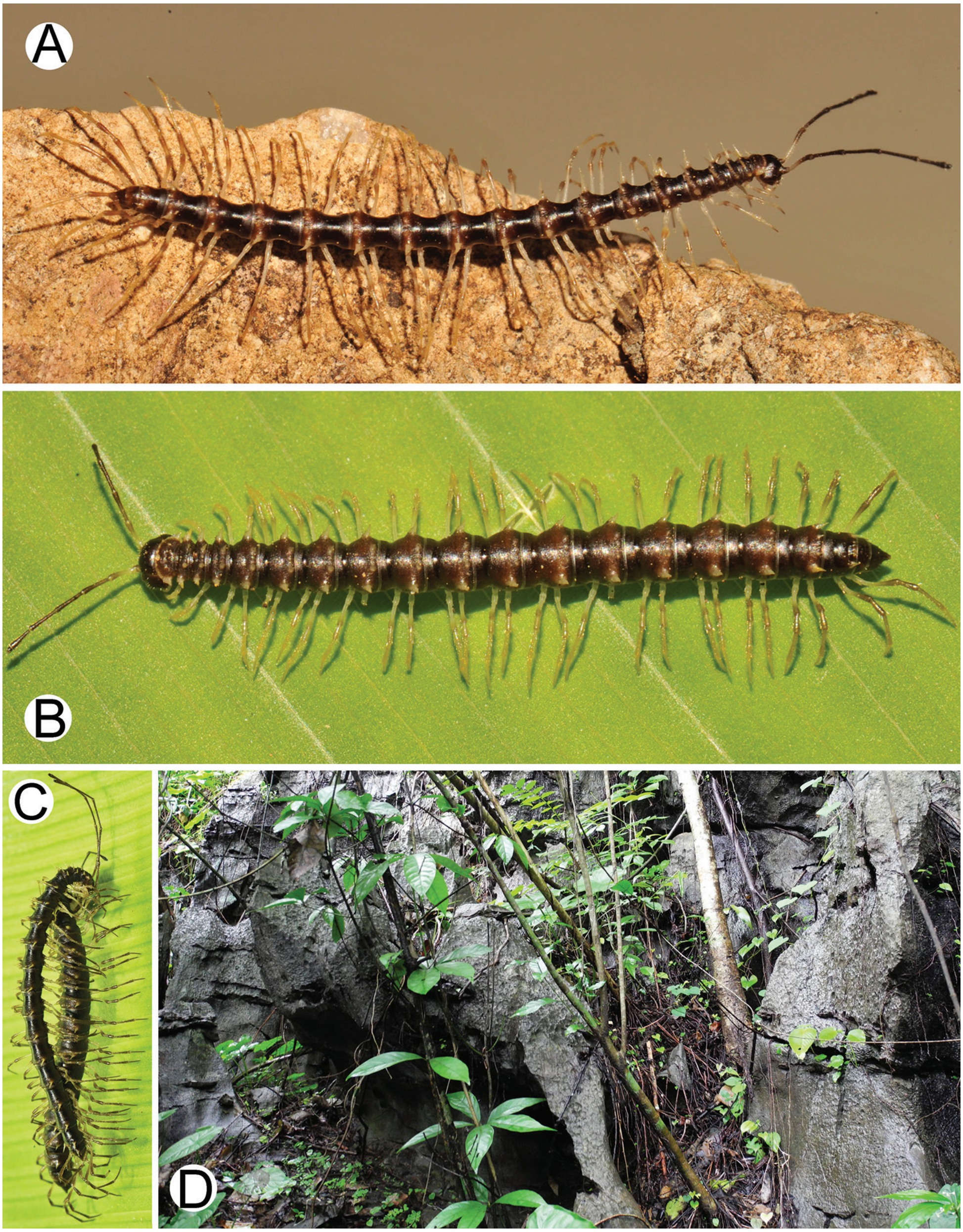

Figure 12. Photographs of live *Spinaxytes hasta* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00210 **B** ♀ paratype, CUMZ-pxDGT00210 **C** mating couple **D** habitat.

wing-like, quite short and broad, tip sharp, elevated at ca. 10°–15° (male) 10°–15° (female), directed caudolaterad.

Tegument. Quite dull; collum, metaterga and surface below paraterga finely microgranulate.

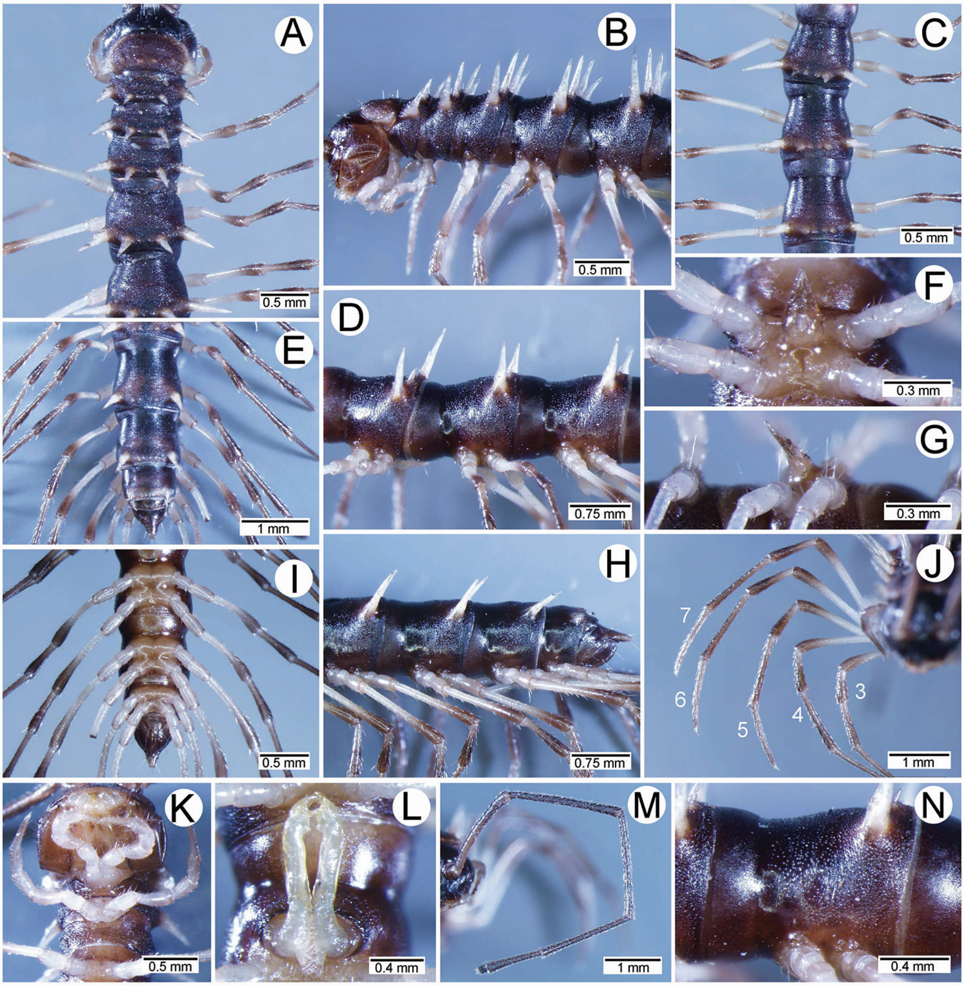

Figure 13. *Spinaxytes hasta* sp. n., ♂ paratype, CUMZ-pxDGT00210 **A, B** anterior body part **C, D** body rings 8–10 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 3–7 **K** legs 1–3 **L** gonopods **M** left antenna **N** sculpture of body ring 10.

Metaterga (Figure 13A, C, E). With two transverse rows of setiferous tubercles/cones and spines; metaterga 2–8 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; metaterga 2–18 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; metatergum 19 with 2+2 tubercles in anterior row and 2+2 tubercles in posterior row; lateral spines of posterior row bigger and longer than mesal ones, gradually reduced in length and size on the following rings.

Paraterga (Figure 13A–E, H). Very long; directed dorsolaterad on body rings 4–16, elevated at ca. 60°–70° (male) 50°–60° (female); directed caudolaterad on rings 2, 3 and 17; directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

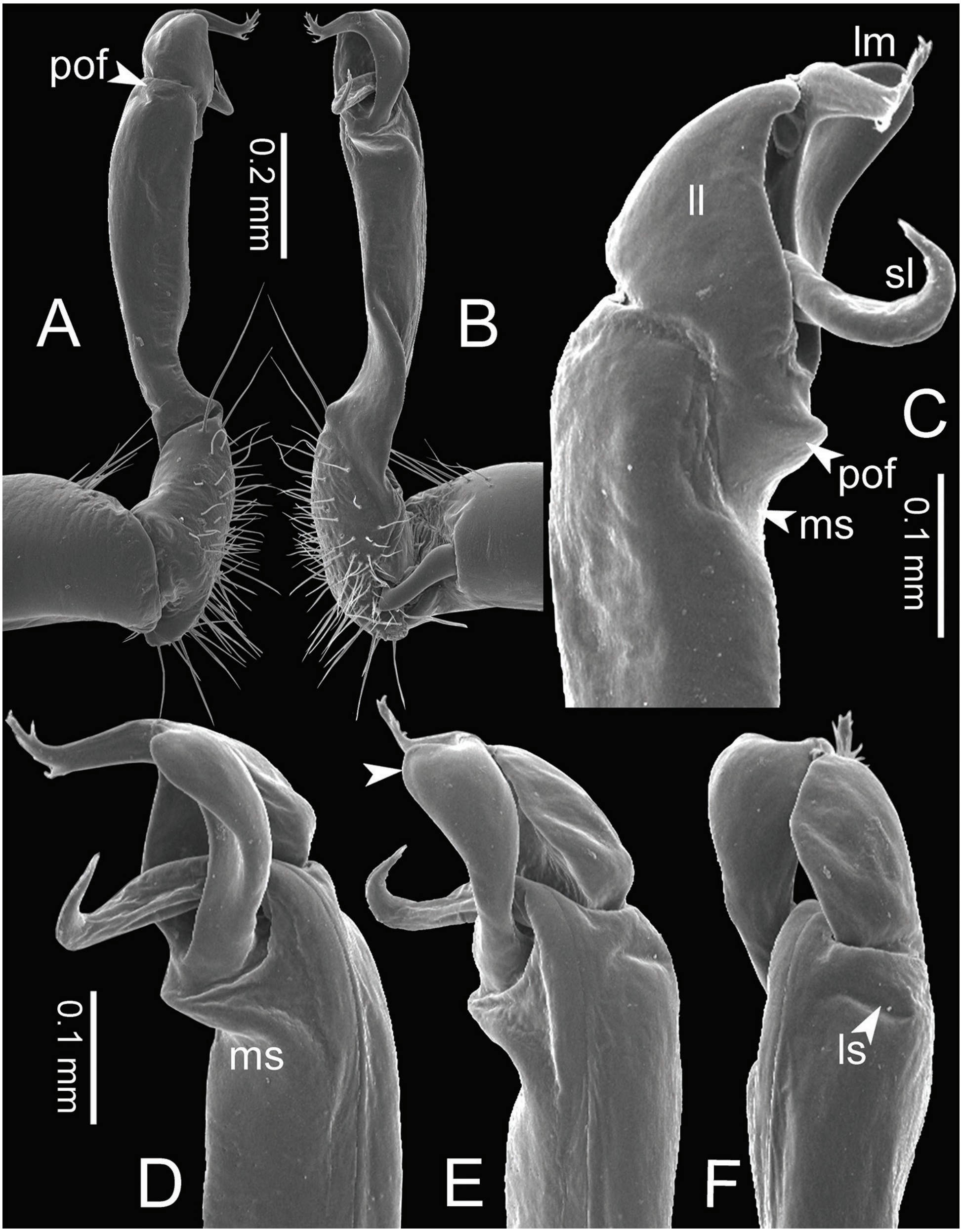

Figure 14. *Spinaxytes hasta* sp. n., paratype, CUMZ-pxDGT00210 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view (arrowhead points to lobe on lamina medialis) **F** laterodorsal view.

Telson (Figure 13E, H, I). Epiproct long; tip subtruncate; lateral setiferous tubercles conspicuous (in some specimens inconspicuous); apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subsemicircular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

Sterna (Figs 4F; 13F, G). Sternal lobe between male coxae 4 coniform, long, spear-like; base stout; tips sharp, in situ directed almost ventrad; posterior surface bearing one pore.

Legs (Figs 4G, 13J). Male femora without modification.

Gonopods (Figs 5C, 14). Coxa shorter than femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally, basally indented. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part: lamina lateralis broad and long, flattened laterally: lamina medialis long; base enlarged, slightly attenuated near the tip; middle part with a large lobe; tip a bit curving up, terminating in several small spines. Solenomere circular in transverse section, curving up, tip directed anteriad.

Distribution and habitat (Figure 12D). The specimens were found on rocks or walls with plants, and some were found in a small cave. *S. hasta* sp. n. is distributed only in Chumphon Province, and we regard the new species as endemic for the Thai fauna. At Wat Nam Cha the new species coexists with *Desmoxytes cervina*.

Remarks. There are some variations: the lateral setiferous tubercles of the epiproct are conspicuous in some specimens, inconspicuous in others; the hypoproct is subtrapeziform in some individuals, subsemicircular in others; the caudal margin of the hypoproct is rounded in some specimens, angular in others.

Spinaxytes krabiensis Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/DCB1E283-74DC-48F6-9876-FE1E70F8AB8A
Figs 3; 4H–J; 5D; 15–17

Material examined. Holotype. ♂, THAILAND, Krabi Province, Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ-pxDGT00211). **Paratypes.** 5 ♂♂, 9 ♀♀, 1 juvenile, same data as for holotype (CUMZ-pxDGT00212); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040252). **Further specimens, not paratypes, all from THAILAND, Krabi Province. Ao Luek District:** 2 ♂♂, 1 ♀, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 14 Jan. 2013, ASRU members leg. (CUMZ); 5 ♂♂, 1 ♀, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 23 Aug. 2014, ASRU members leg. (CUMZ); 12 ♂♂, 7 ♀♀, 1 juvenile, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 3 ♂♂, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., Jan. 2016, ASRU members leg. (CUMZ); 1 ♂, 5 ♀♀, P.N. Mountain Resort, 8°24'09"N, 98°44'18"E, ca. 46 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 1 ♂, 1 broken ♂, Tham Sa Yuan Thong (Sa Yuan Thong Cave), 8°23'29"N, 98°46'17"E, ca. 7 m a.s.l., 9 Oct. 2006, ASRU members leg. (CUMZ). **Muaeng Krabi District:** 1 broken ♂, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 25 Oct. 2007, ASRU members leg. (CUMZ); 1 broken ♂, 1 ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 7 Oct. 2009, ASRU members leg. (CUMZ); 1 ♂, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N,

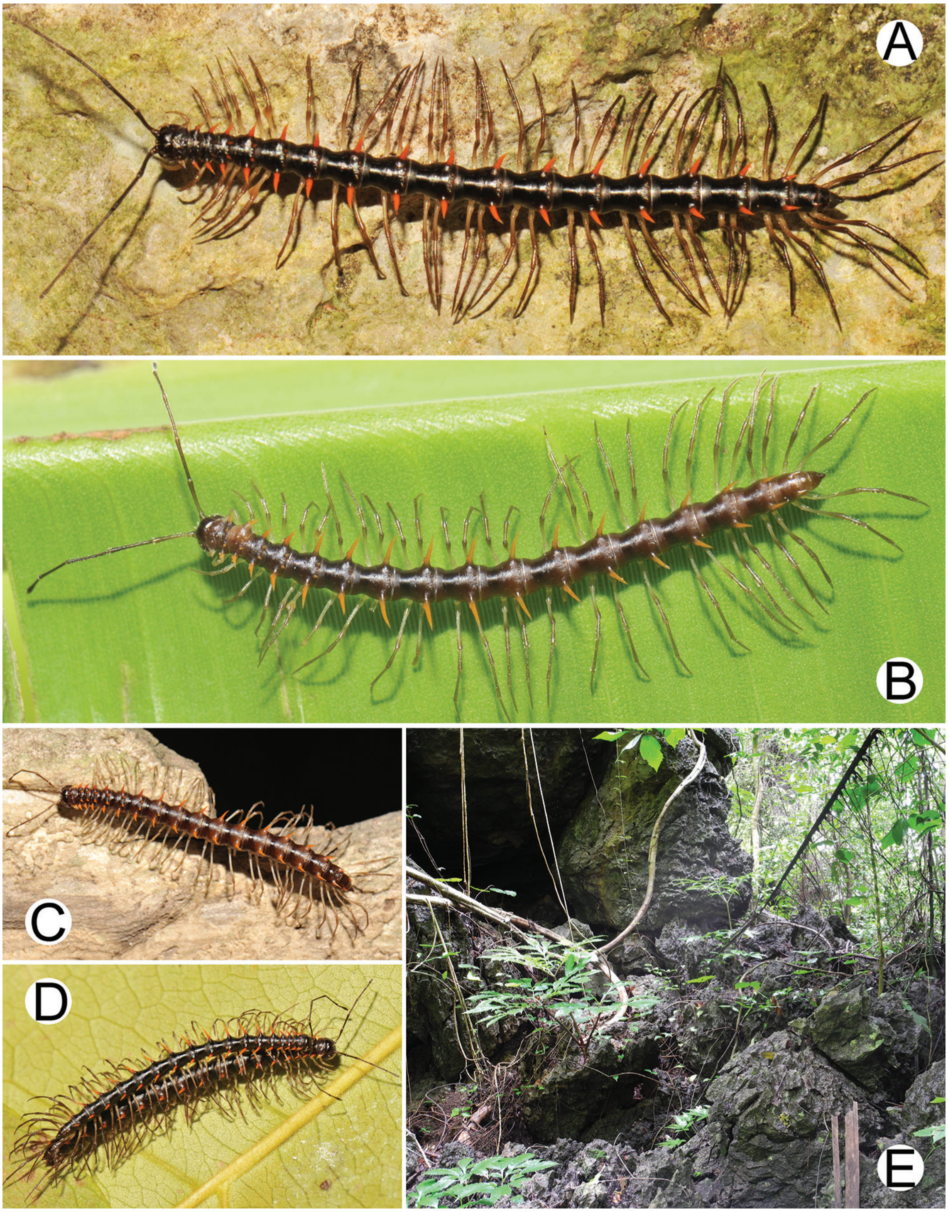

Figure 15. Photographs of live *Spinaxytes krabiensis* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00212 **B** ♂, specimen from Tham Sa Yuan Thong (Sa Yuan Thong Cave) **C** ♀ paratype **D** mating couple **E** habitat.

98°55'26"E, ca. 87 m a.s.l., 24 Aug. 2014, ASRU members leg. (CUMZ); 1 ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 30 Aug. 2015, P. Pimvichai, P. Prasankok and N. Natarat leg. (CUMZ); 2 ♂♂, 1 ♀, 1 broken ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 25 Jul. 2017, ASRU members leg. (CUMZ).

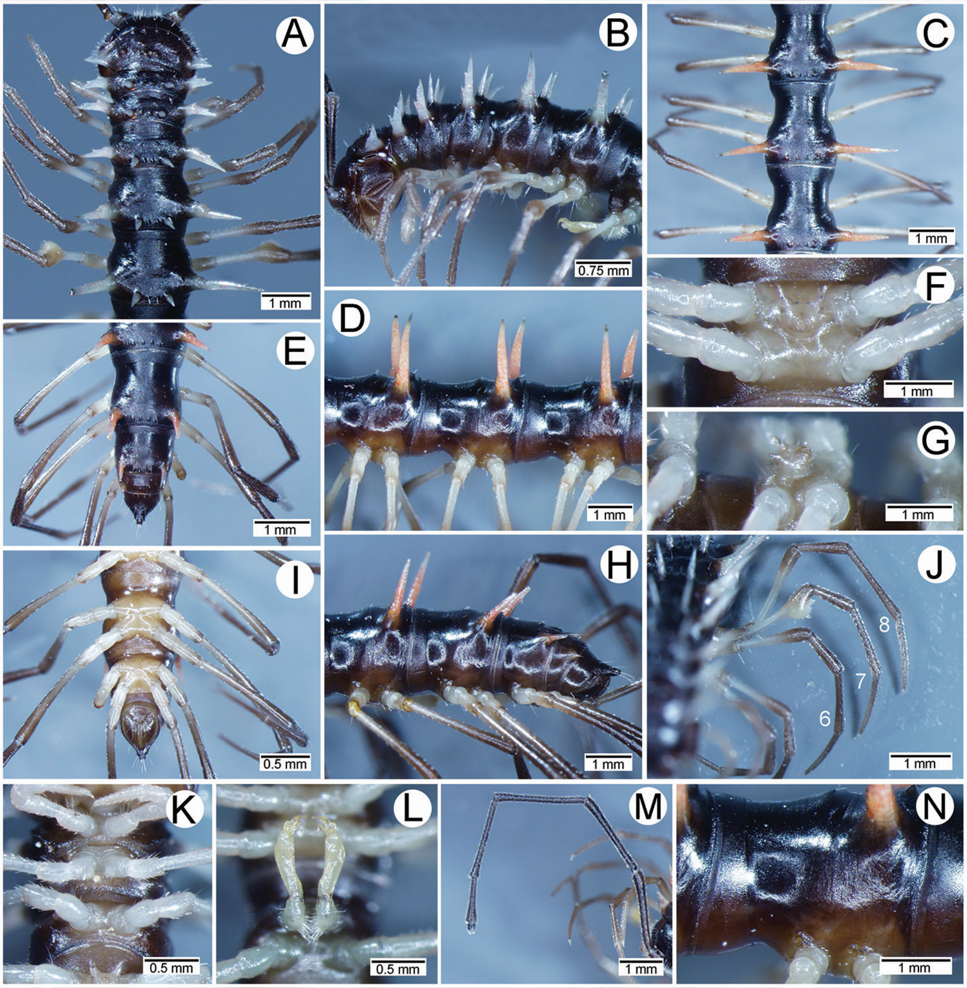

Figure 16. *Spinaxytes krabiensis* sp. n., ♂ paratype, CUMZ-pxDGT00212 **A, B** anterior body part **C, D** body rings 9–11 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 4–8 **K** legs 1–3 **L** gonopods **M** right antenna **N** sculpture of body ring 10.

Etymology. The new species is named after the province where the type locality lies.

Diagnosis. Male femora 6 and 7 humped distally. Similar in this respect to *S. macaca* sp. n., but differs by having: paraterga orange, longer; male femora 6 smaller; tip of lamina lateralis round, not protuding as digitiform; tip of lamina medialis terminating in two lobes.

Description. SIZE. Length 28–31 mm (male), 30–33 mm (female); width of midbody metazona 1.8–2.0 mm (male), 2.2–2.5 mm (female). Width of rings 2 = 3 = 4 < collum < head = 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 15A–D). Specimens in life with body black/brownish black; paraterga orange; head, antennae (except whitish distal part of antennomeres 7 and 8),

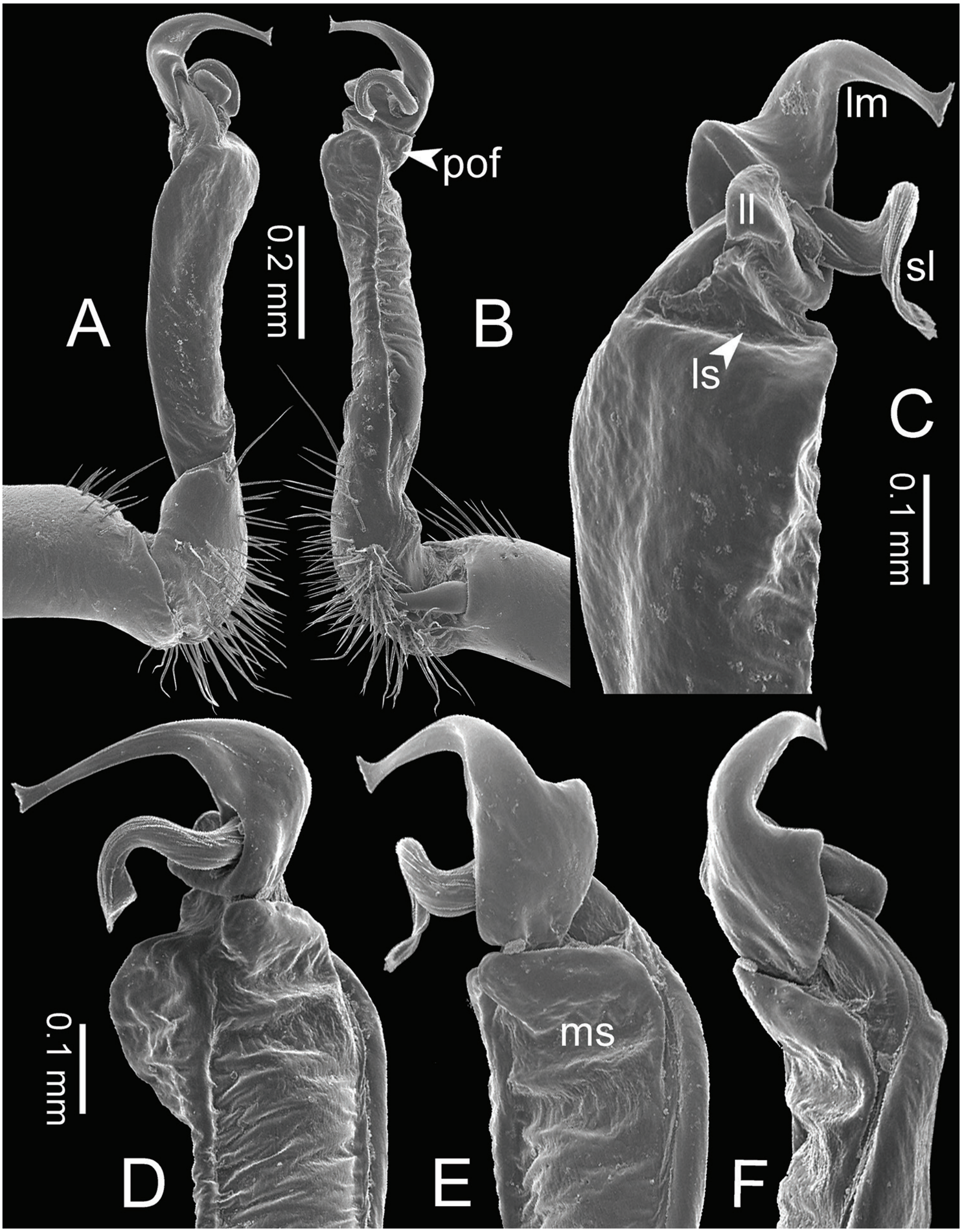

Figure 17. *Spinaxytes krabiensis* sp. n., paratype, CUMZ-pxDGT00212 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

collum, prozona and epiproct black; metaterga and surface below paraterga black/brownish black; sterna brown; legs brown/blackish brown; a few basal podomeres whitish brown.

Antennae (Figure 16M). Reaching to body ring 8 (male) and 6 (female) when stretched dorsally.

Collum (Figure 16A). With three transverse rows of setiferous tubercles/cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 20°–30° in both male and female, directed caudolaterad.

Tegument. Quite shining; collum coarsely microgranulate; metaterga and surface below paraterga smooth.

Metaterga (Figure 16A, C, E). With two transverse rows of setiferous tubercles and setiferous cones/spines; metaterga 2–7 with 2+2 tubercles in anterior row and 2+2 spines in posterior row; 8–19 with 2+2 tubercles in anterior row and 2+2 cones in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in size and length on the following rings.

Paraterga (Figure 16A–E, H). Extremely long; directed dorsolaterad on body rings 2–16, elevated at ca. 45°–60° (male) 40°–50° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in subdorsal view.

Telson (Figure 16E, H, I). Epiproct long; tip subtruncate; lateral setiferous tubercles mostly inconspicuous (in some specimens conspicuous); apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with inconspicuous setiferous tubercles.

Sterna (Figs 4H; 16F, G). Sternal lobe between male coxae 4 bifurcate, long; tips sharp, in situ directed ventroanteriad; posterior surface bearing one pore.

Legs (Figs 4I, J; 16J). Male femora 6 a bit humped; male femora 7 strongly humped.

Gonopods (Figs 3, 5D, 17). Coxa subequal in length to femur. Prefemoral part ca. half as long as femur. Femur obviously enlarged distally. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger than postfemoral part: lamina lateralis small, compact, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip a bit curved, terminating in two lobes. Solenomere curved and twisted, compressed in transverse section, tip directed lateroposteriad.

Distribution and habitat (Figure 15E). *S. krabiensis* sp. n. inhabits Krabi Province. Considering its narrow distribution, we regard this species as endemic for the Thai fauna. It is syntopic with *Desmoxytes delfae* (Jeekel, 1964), *Desmoxytes cervina* and *Gigaxytes gigas* (Golovatch & Enghoff, 1994), which were collected from the same location (Than Bok Khorani and Wat Tham Sue (Tiger Cave)), but the new species was encountered living on rock walls or in small caves while the others were usually found on leaf litter or on tree branches.

Remarks. We found variations in the lateral setiferous tubercles of the epiproct: conspicuous in some specimens, inconspicuous in others.

Spinaxytes macaca Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/21BACA0B-8E80-43D5-8E1F-2BB1902962C2
Figs 4K–M; 5E; 18–20

Material examined. Holotype. ♂, THAILAND, Phang Nga Province, Takua Thung District, Wat Suwan Khuha (Monkey Cave), 8°25'42"N, 98°28'22"E, ca. 27 m a.s.l.,

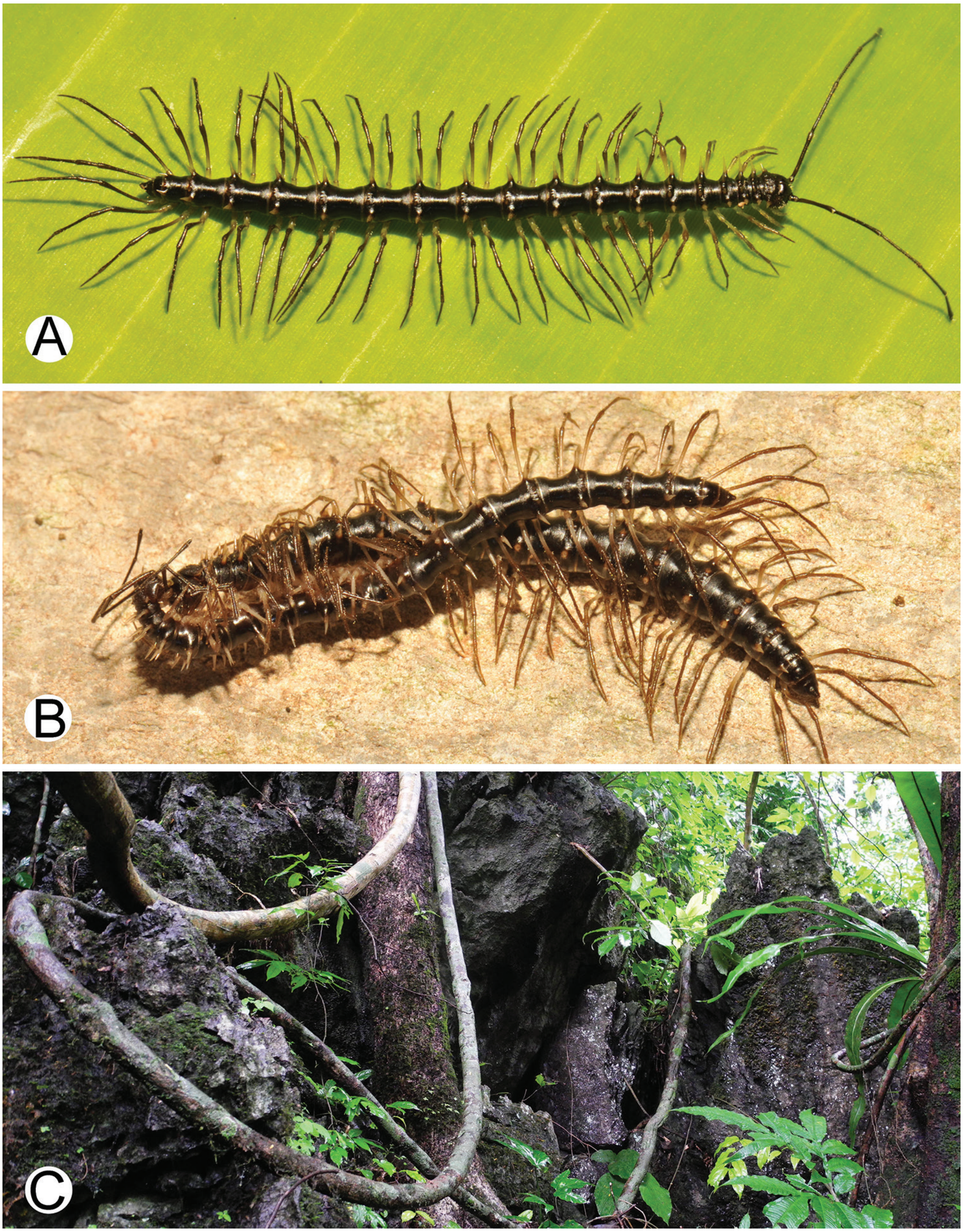

Figure 18. Photographs of live *Spinaxytes macaca* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00214 **B** mating couple **C** habitat.

8 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00213). **Paratypes.** 7 ♂♂, 2 ♀♀, same data as for holotype (CUMZ-pxDGT00214); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040253); 1 ♂ same data as for holotype (ZMUM).

Etymology. The species is named after the monkey, long-tailed macaque (*Macaca fascicularis*) living at the type locality (Monkey Cave).

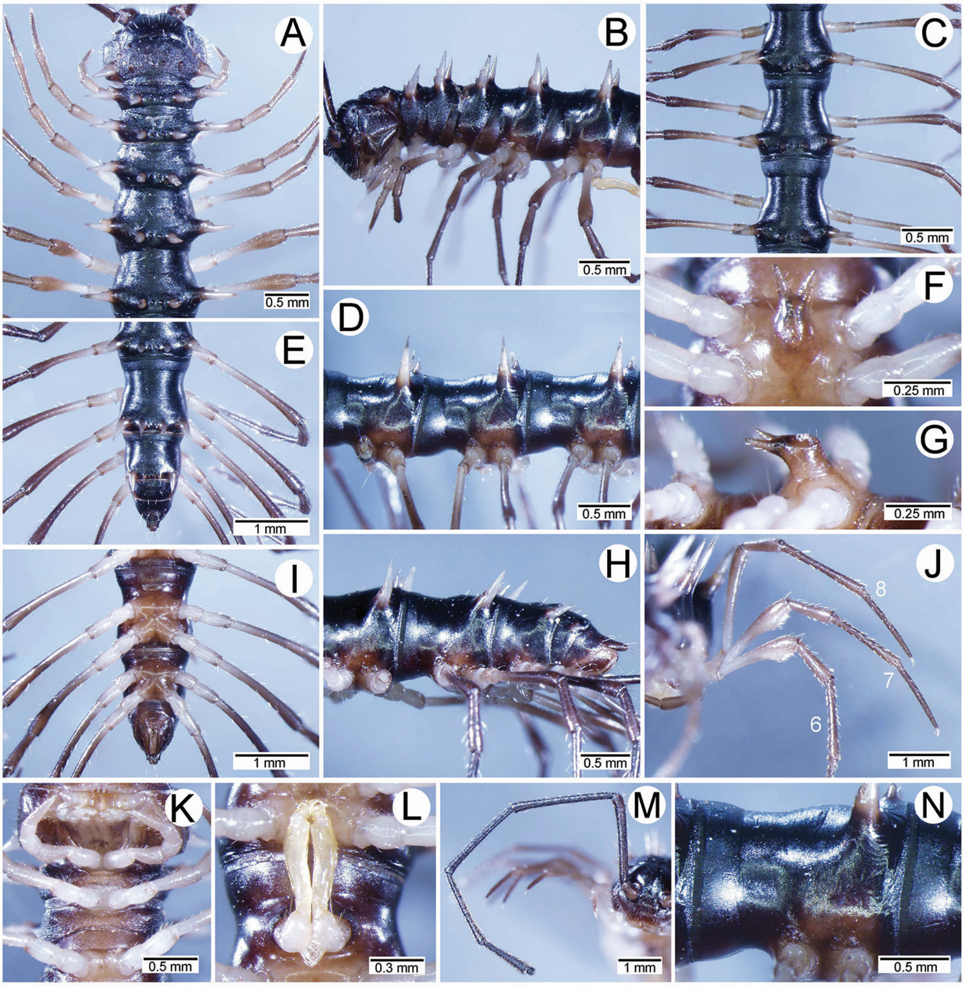

Figure 19. *Spinaxytes macaca* sp. n., ♂ paratype, CUMZ-pxDGT00214 **A, B** anterior body part **C, D** body rings 8–10 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 6–8 **K** legs 1–3 **L** gonopods **M** right antenna **N** sculpture of body ring 10.

Diagnosis. Male femora 6 and 7 humped distally. Similar in this respect to *S. krabiensis* sp. n., but differs from it by having: paraterga brownish white, shorter; male femora 6 larger; tip of lamina lateralis (ll) protruding as a small lobe, digitiform; tip of lamina medialis (lm) bent, terminating in one lobe.

Description. SIZE. Length 27–29 mm (male), 29–32 mm (female); width of midbody metazona 1.8–1.9 mm (male), 2.0–2.3 mm (female). Width of collum = 2 = 3 < 4 < head = 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 18A, B). Specimens in life with body black; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, metaterga, prozona and surface below paraterga black; sterna brown; epiproct black/brownish black; legs blackish brown; a few basal podomeres pale brown/whitish brown.

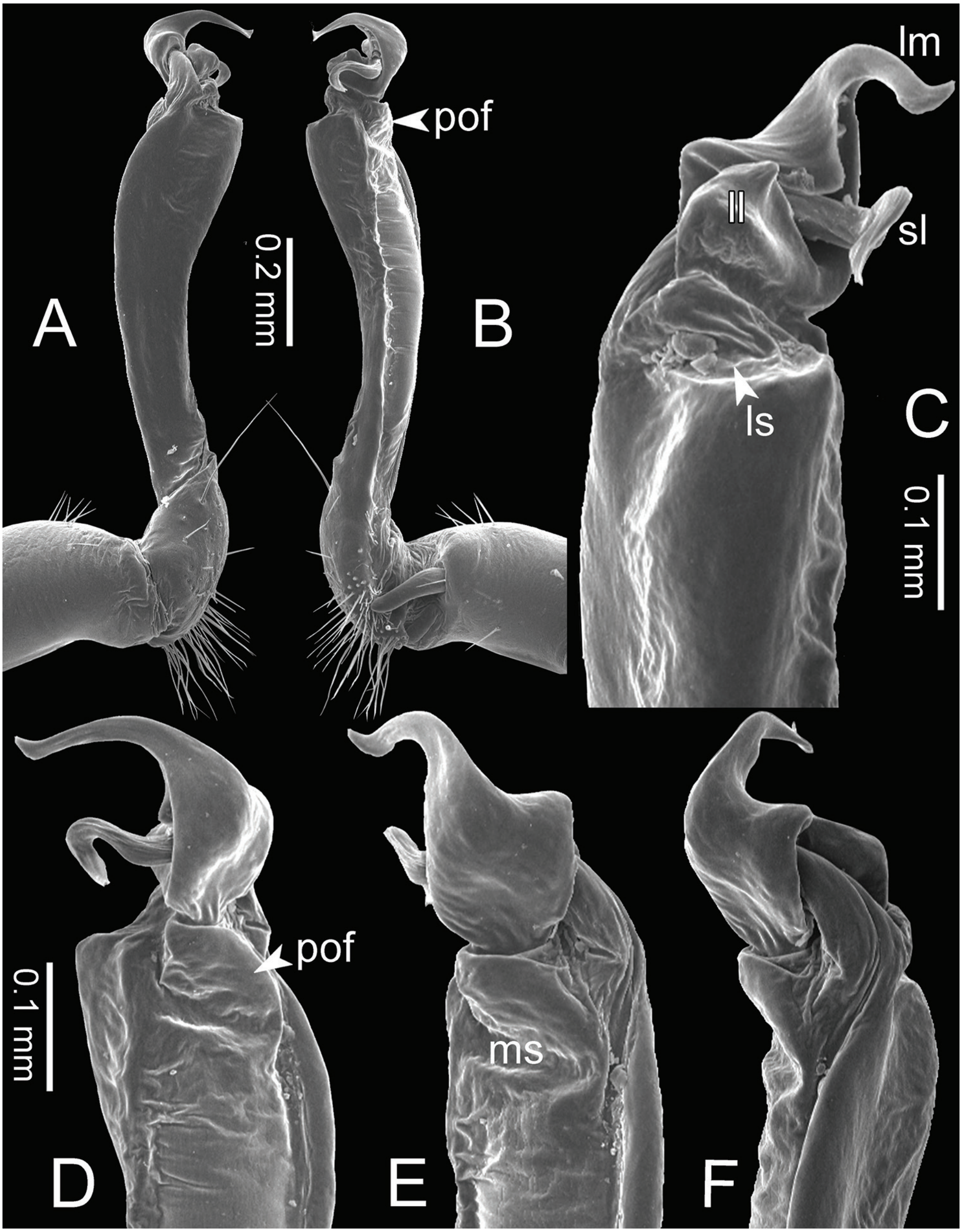

Figure 20. *Spinaxytes macaca* sp. n., paratype, CUMZ-pxDGT00214 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

Antennae (Figure 19M). Reaching to body ring 8 or 9 (male) and 7 (female) when stretched dorsally.

Collum (Figure 19A). With three transverse rows of setiferous tubercles/cones, 4+4 tubercles/cones in anterior row, 1+1 tubercles/cones in intermediate row and 2+2 tubercles/cones in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

Tegument. Quite shining; collum, metaterga and surface below paraterga smooth.

Metaterga (Figure 19A, C, E). With two transverse rows of setiferous tubercles and cones/spines; metaterga 2–19 with 2+2 tubercles in anterior row and 2+2 cones/spines in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in length and size on the following rings.

Paraterga (Figure 19A–E, H). Long; directed dorsolaterad on body rings 2–16, elevated at ca. 60°–70° (male) 50°–60° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

Telson (Figure 19E, H, I). Epiproct quite short; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with conspicuous setiferous tubercles.

Sterna (Figs 4K; 19F, G). Sternal lobe between male coxae 4 bifurcate, long; base stout; tips very sharp, in situ directed ventroanteriad; posterior surface bearing 1 pore.

Legs (Figs 4L, M; 19J). Male femora 6 and 7 humped ventrally in distal part.

Gonopods (Figs 5E, 20). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur quite enlarged distally. Postfemoral part short and narrow. Mesal sulcus and lateral sulcus wide. Solenophore longer than postfemoral part: lamina lateralis small, compact; apically protruding as a small lobe, directed mesoventrad: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip bent, sharp and curving up. Solenomere curved and twisted, metazona in transverse section, tip directed posteriad.

Distribution and habitat (Figure 18C). All specimens were collected in small caves near the big Monkey Cave, crawling on rock walls. It is difficult to see the new species without using a flashlight/torch as the black body colour blends in with dark rocks. This species can be found in syntopy with *Desmoxytes cervina*. For the time being, *S. macaca* sp. n. is known only from the type locality and we regard it as endemic to Thailand.

Remarks. *S. macaca* sp. n. is morphologically similar to *S. krabiensis* sp. n. and *S. uncus* sp. n. with which it shares a fork-like sternal lobe between male coxae 4 and a small lamina lateralis.

Spinaxytes palmata Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/2A4B8447-3443-44D7-B463-0A6A2AB840C9

Figs 2; 4N, O; 5F; 21–23

Material examined. Holotype. ♂, THAILAND, Surat Thani Province, Phanom District, Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 6 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00215). **Paratypes.** 23 ♂♂, 22 ♀♀, same data as for holotype (CUMZ-pxDGT00216); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040254); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9425); 1 ♂, 1 ♀, same data as for holotype (NHMUK).

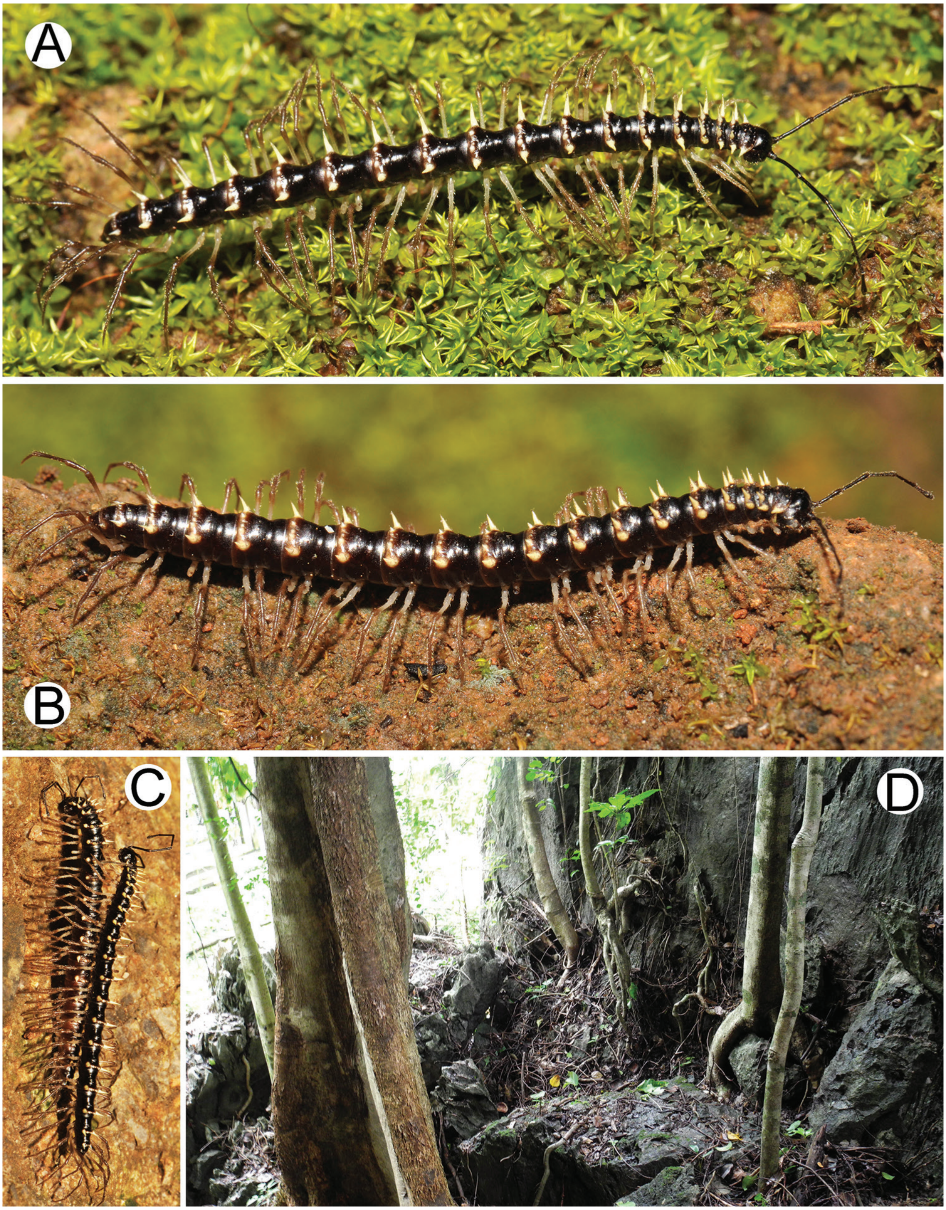

Figure 21. Photographs of live *Spinaxytes palmata* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00216 **B** ♀ paratype, CUMZ-pxDGT00216 **C** mating couple **D** habitat.

Further specimens, not paratypes. THAILAND: 1 ♂, 2 ♀♀, Surat Thani Province, Phanom District, Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 5 Aug. 2014, ASRU members leg. (CUMZ).

Etymology. The species name is a Latin adjective, referring to the tip of lamina medialis which is somewhat hand-shaped.

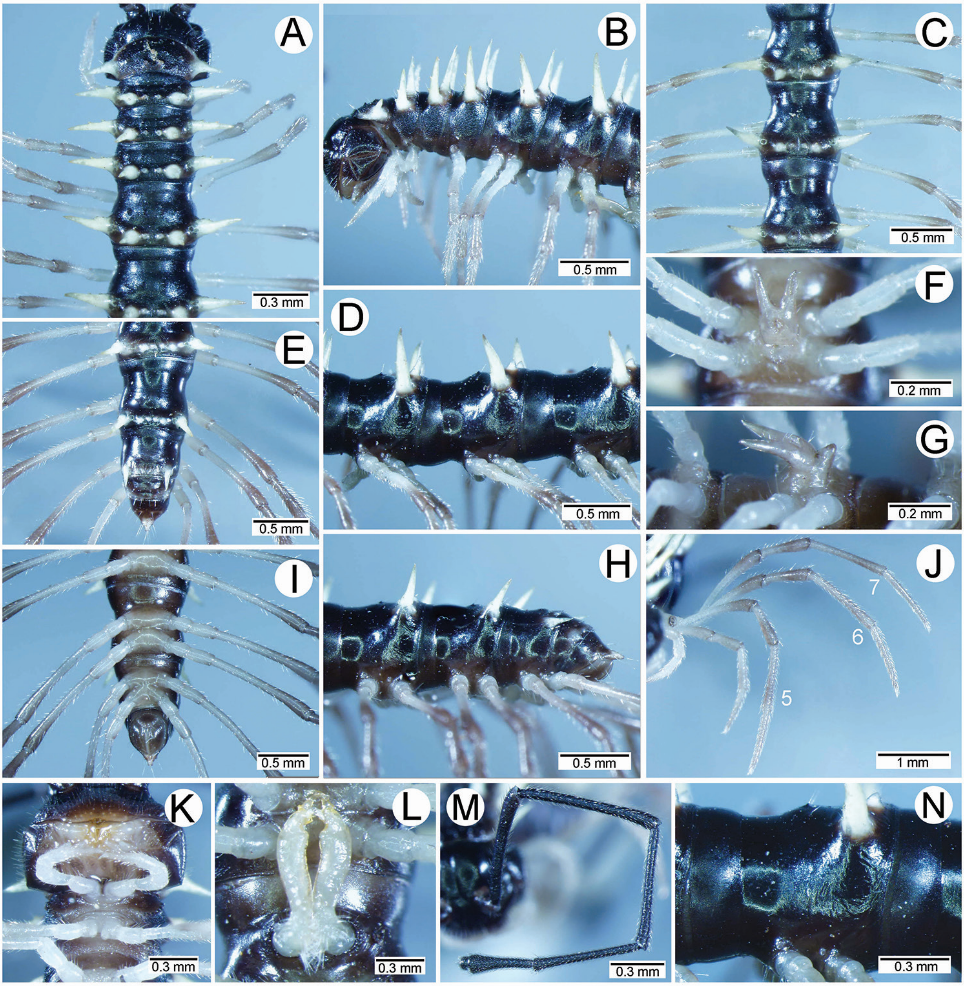

Figure 22. *Spinaxytes palmata* sp. n., ♂ paratype, CUMZ-pxDGT00216 **A, B** anterior body part **C, D** body rings 8–10 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 5–7 **K** legs 1–3 **L** gonopods **M** left antenna **N** sculpture of body ring 10.

Diagnosis. Male femora without modification. Similar in this respect to *S. efefi* sp. n., *S. hasta* sp. n., *S. sutchariti* sp. n. and *S. tortioverpa* sp. n., but differs from them by having: anterior part of sternal lobe between male coxae 4 bifurcate, fork-like; tip of lamina medialis expanded, hand-shaped.

Description. SIZE. Length 26–30 mm (male), 27–32 mm (female); width of midbody metazona 1.9–2.2 mm (male), 2.0–2.4 mm (female). Width of collum = 2 = 3 = 4 < head < 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 21A–C). Specimens in life with body black; paraterga orange; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, prozona,

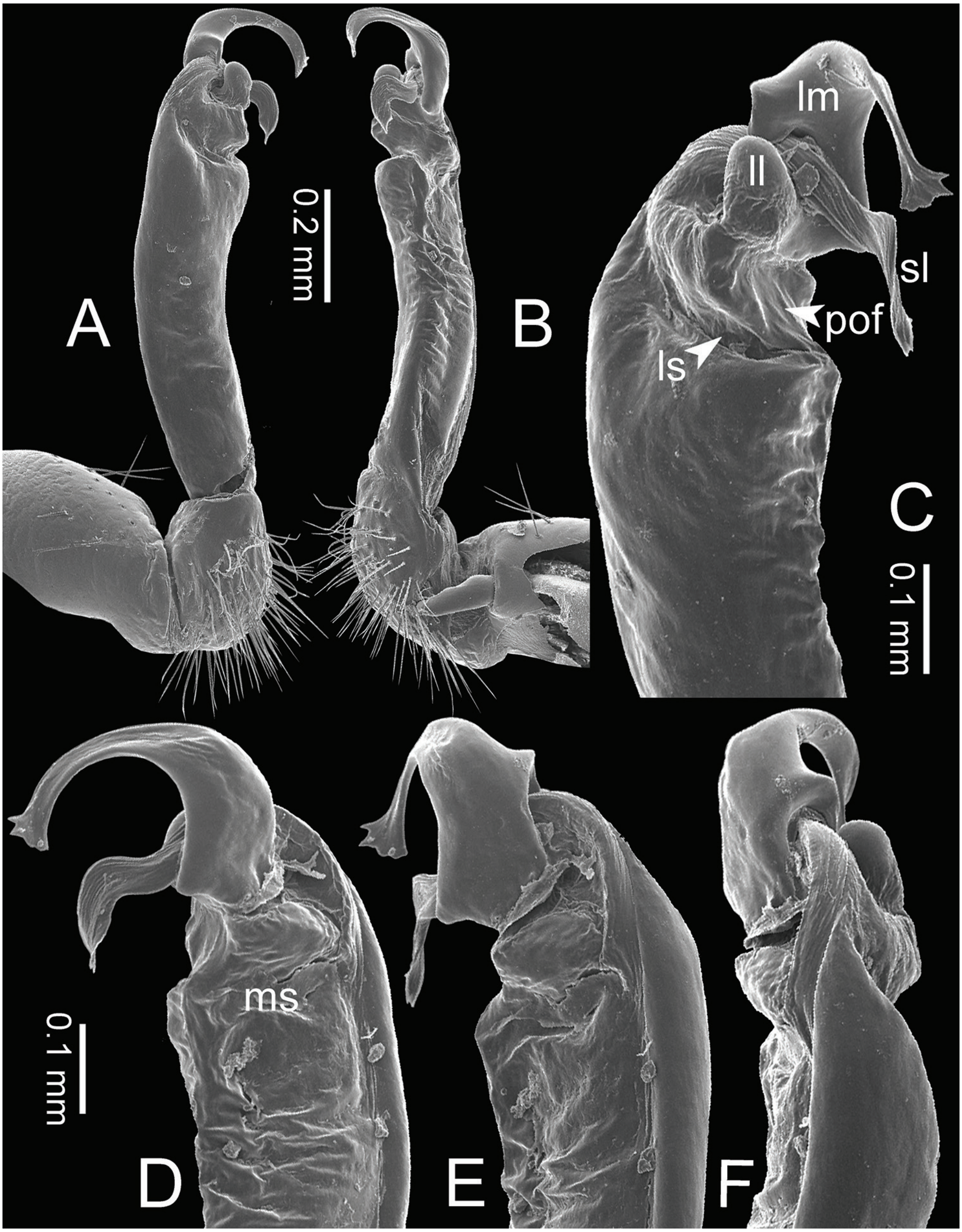

Figure 23. *Spinaxytes palmata* sp. n., paratype, CUMZ-pxDGT00216 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

metaterga (except white spines in posterior row) and surface below paraterga black; sterna and legs brown; epiproct pale brown; a few basal podomeres whitish brown.

Antennae (Figure 22M). Reaching to body ring 8 (male) and 6 or 7 (female) when stretched dorsally.

Collum (Figure 22A). With three transverse rows of setiferous tubercles/cones, 4+4 in anterior row, 1(0)+1(0) in intermediate row and 2(1)+2(1) in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 15°–20° (male) 10°–15° (female), directed almost laterad.

Tegument. Very shining; collum coarsely microgranulate; metaterga and surface below paraterga smooth.

Metaterga (Figure 22A, C, E). With two transverse rows of setiferous cones and setiferous spines; metaterga 2–19 with 2+2 cones in anterior row and 2+2 spines in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in size and length on the following rings.

Paraterga (Figure 22A–E, H). Very long; directed dorsolaterad on body rings 2–17, elevated at ca. 50°–60° (male) 45°–60° (female), directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

Telson (Figure 22E, H, I). Epiproct quite short; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subtriangular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

Sterna (Figs 4N; 22F, G). Sternal lobe between male coxae 4 with two parts; anterior part bifurcate, tuning-fork-like, long, tips sharp, in situ directed ventroanteriad; posterior margin of anterior part bearing 1 pore; posterior part swollen, short.

Legs (Figs 4O, 22J). Male femora without modification.

Gonopods (Figs 5F, 23). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur not enlarged distally. Postfemoral part broad. Mesal sulcus and lateral sulcus wide. Solenophore a bit bigger than postfemoral part: lamina lateralis small, oval, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip fringed, hand-shaped; tip curving down, in situ resting close to solenomere. Solenomere curved and twisted, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 21D). *S. palmata* sp. n. is known only from the type locality. We regard this species as endemic for the Thai fauna. The new species can be found in syntopy with *Desmoxytes corythosaurus* Srisonchai, Enghoff & Panha, 2018, crawling on humid rock walls.

Remarks. There are variations in the hypoproct: subtrapeziform in some specimens, subtriangular in the others; caudal margin in some individuals round, angular in the others.

Spinaxytes sutchariti Srisonchai, Enghoff & Panha, sp. n.

http://zoobank.org/4E54ED20-66AB-4BF7-B40D-D6F6699CF282
Figs 4P, Q; 5G; 24; 25

Material examined. Holotype. ♂, THAILAND, Krabi Province, Muang Krabi District, Tham Na Mee (Na Mee Cave), 8°08'12"N, 98°48'23"E, ca. 70 m a.s.l., 31 Aug.

2015, C. Sutcharit leg. (CUMZ-pxDGT00217). **Paratypes.** 7 ♂♂, 4 ♀♀, same data as for holotype (CUMZ-pxDGT00218).

Etymology. The name honours associate professor Dr. Chirasak Sutcharit, malacologist of ASRU (CUMZ), collector of this new species and numerous other dragon millipedes.

Diagnosis. Male femora without modification, sternal lobe between male coxae 4 incompletely bilobed. Similar in these respects to *S. palmata* sp. n., but differs by having: a large and round lamina lateralis; tip of lamina medialis terminating in two spines; distal part of solenomere circular in tranverse section.

Description. SIZE. Length 20–25 mm (male), 23–27 mm (female); width of midbody metazona 1.5–1.8 mm (male), 1.9–2.2 mm (female). Width of collum = 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 24A–C). Specimens in life with body black; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, prozona, metaterga and epiproct black; surface below paraterga black/brownish black; sterna brown; legs brown/blackish brown; a few basal podomeres whitish brown.

Antennae. Reaching to body ring 8 or 9 (male) and 6 (female) when stretched dorsally.

Collum. With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row; with one inconspicuous setiferous notch at lateral margin; paraterga spiniform, quite short, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

Tegument. Quite dull; collum and metaterga (posterior part) coarsely microgranulate; metaterga (anterior part) and surface below paraterga smooth.

Metaterga. With two transverse rows of setiferous tubercles and setiferous spines; metaterga 2–19 with 2+2 tubercles in anterior row and 2+2 spines in posterior row; lateral spines of posterior row bigger and longer than mesal ones, subequal in size and length on all body rings.

Paraterga. Long; directed dorsolaterad on body rings 2–16, elevated at ca. 45°–50° (male) 40°–50° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

Telson. Epiproct quite long; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subtriangular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

Sterna (Figure 4P). Sternal lobe between male coxae 4 incompletely bilobed; tips sharp, in situ directed laterad; posterior surface bearing 2 pores.

Legs (Figure 4Q). Male femora without modification.

Gonopods (Figs 5G, 25). Coxa subequal in length to femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part: lamina lateralis oval, large, long, tip round: lamina medialis long and slender; base enlarged, slightly attenuated near the tip; tip curving down, with two sharp spines (one smaller, one bigger). Solenomere curving up, circular in transverse section, tip directed anteriad.

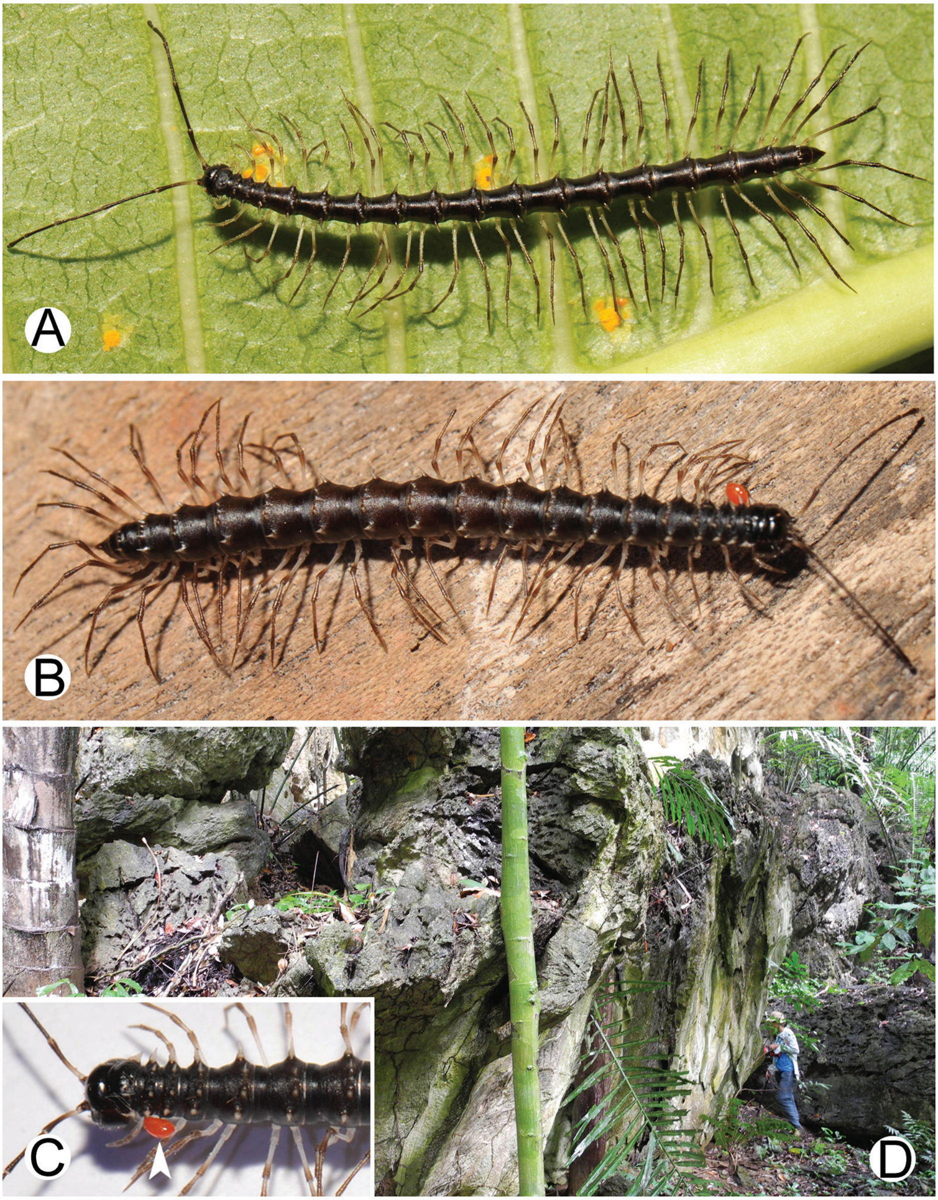

Figure 24. Photographs of live *Spinaxytes sutchariti* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00218 **B** ♀ paratype, CUMZ-pxDGT00218 **C** parasitic mite (arrowhead) **D** habitat.

Distribution and habitat (Figure 24D). *S. sutchariti* sp. n. is known only from the type locality, and we regard it as endemic to Thailand. The new species can be found in the same area as *Gigaxytes gigas*, but we assume that they live in different microhabitats: *G. gigas* was collected from the ground in leaf litter, whereas the new species was found on humid rock walls.

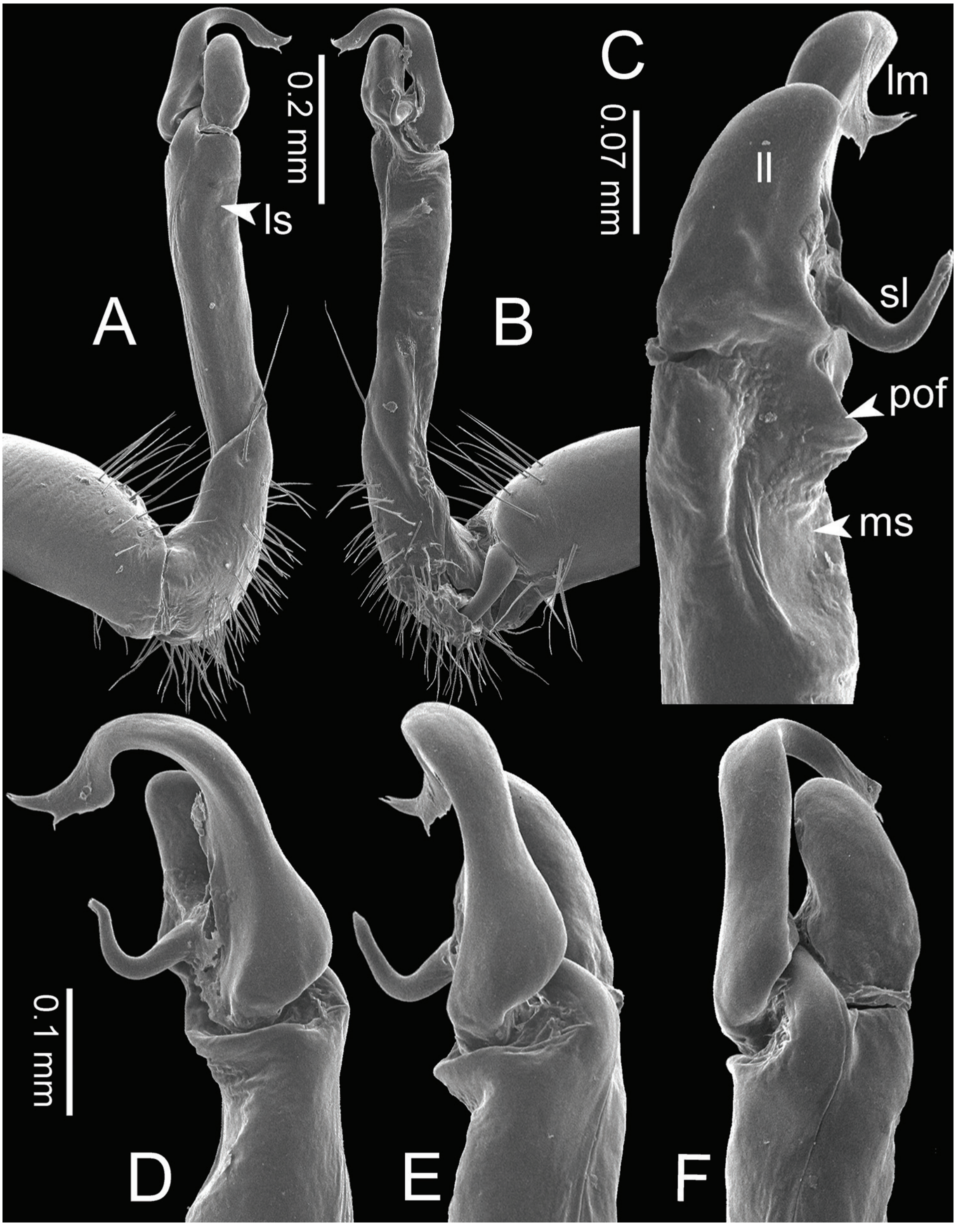

Figure 25. *Spinaxytes sutchariti* sp. n., paratype, CUMZ-pxDGT00218 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

Remarks. We found variation in the hypoproct: in some specimens subtrapeziform, in others subtriangular; caudal margin in some individuals round, in others angular. Parasitic mite larvae, probably of the genus *Leptus* Latreille, 1796, were found attached to the anterior body part of some female specimens. Larvae of ?*Leptus* have previously been found on species of *Desmoxytes* (*D. cervina*) and *Nagaxytes* (*N. acantherpestes* (Golovatch & Enghoff, 1994)) (Srisonchai et al. 2018a, 2018b, see also Southcott 1992).

Spinaxytes tortioverpa **Srisonchai, Enghoff & Panha, sp. n.**

http://zoobank.org/97E5F638-2A4D-4834-B93C-838548BAD087

Figs 1; 4R, S; 5H; 26

Material examined. Holotype. ♂, MALAYSIA, Perak State, Ipoh City, Gua Tempurung, limestone mountain, 4°24'58"N, 101°11'16"E, ca. 92 m a.s.l., 27 Sep. 2007, B. W. Ng and ASRU members leg. (CUMZ-pxDGT00219). **Paratypes.** 1 ♂, 1 ♂ gonopods missing, 1 ♀, same data as for holotype (CUMZ-pxDGT00220).

Etymology. The name is a noun in apposition, from the Latin *tortio* meaning torsion and *verpa* for penis, refers to the distal part of gonopod (postfemoral part, solenophore and solenomere) which makes a 90 degrees torsion relative to the femoral part.

Diagnosis. Male femora without modification; collum with 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row. Similar in these respects to *S. hasta* sp. n. and *S. palmata* sp. n., but differs from them by having: a completely bilobed sternal lobe between male coxae 4; postfemoral part, solenophore and solenomere angled 90 degrees with femoral part; lamina lateralis with two lobes – the lateral one spine-like, the mesal one shorter and ridge-like; solenomere very long, longer than lamina medialis.

Description. SIZE. Length 28–30 mm (male), 30–33 mm (female); width of midbody metazona 2.0 mm (male), 2.8 mm (female). Width of rings 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

Colour. Specimens in life with body black/brownish black. Colour in alcohol: after 10 years changed to brown; paraterga brownish white; antennae brown (except whitish distal part of antennomeres 7 and 8); head, collum, metaterga and prozona blackish brown; surface below paraterga brown/blackish brown; sterna, epiproct and legs pale brown; a few basal podomeres whitish brown.

Antennae. Reaching to body ring 8 or 9 (male) and 6 or 7 (female) when stretched dorsally.

Collum. With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row; anterior margin truncate; with one inconspicuous setiferous notch at lateral margin; paraterga wing-like, long and broad, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

Tegument. Quite dull; collum, metaterga and surface below paraterga finely microgranulate.

Metaterga. With two transverse rows of setiferous tubercles/cones and spines; metaterga 2–8 with 2+2 cones in anterior row and 2+2 spines in posterior row; metaterga 9–19 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; mesal spines of posterior row bigger and longer than lateral ones, gradually reduced in length and size on posterior rings.

Paraterga. Very long; directed dorsolaterad on body rings 2–17, elevated at ca. 65°–70° (male) 60°–70° (female), directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

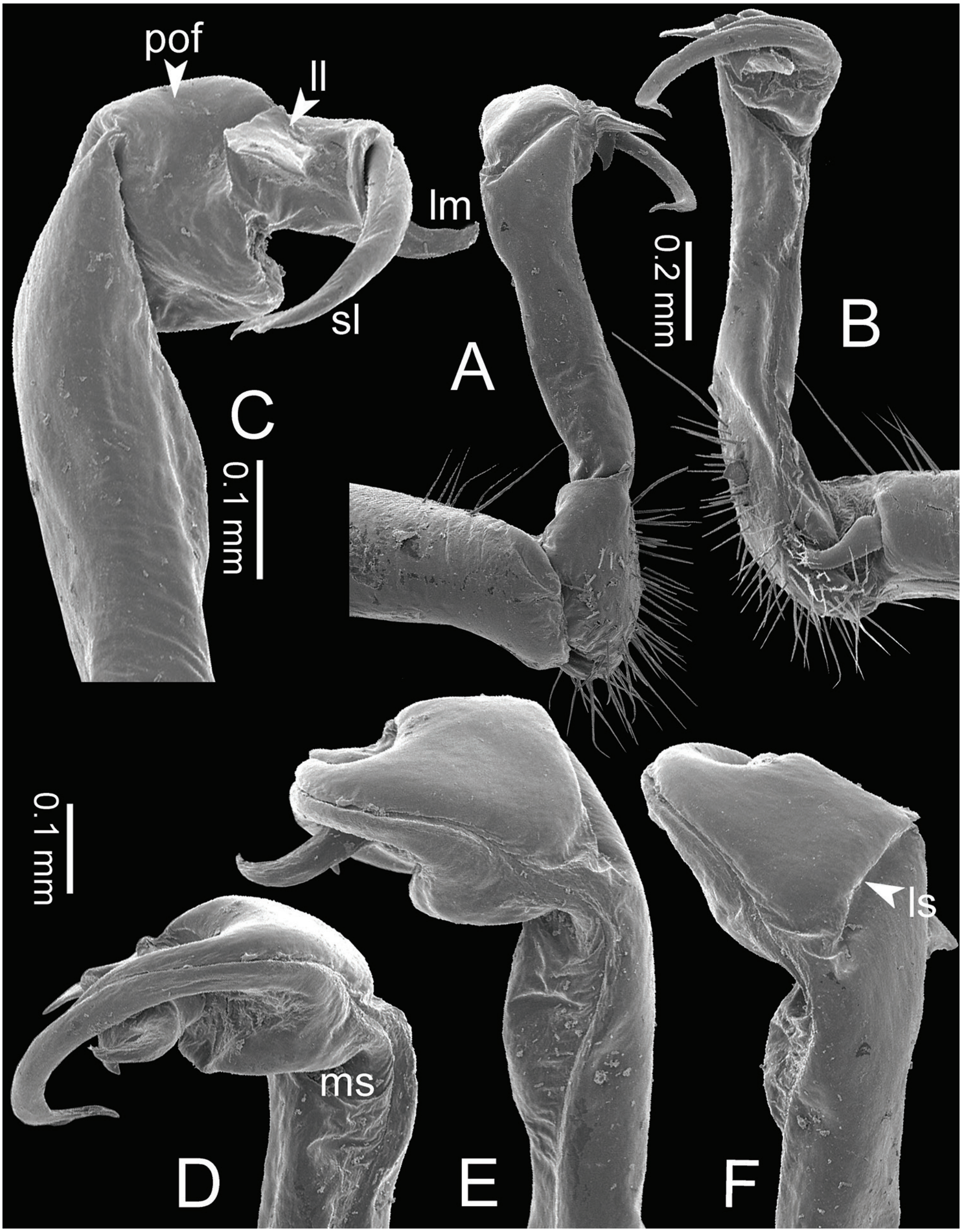

Figure 26. *Spinaxytes tortioverpa* sp. n., paratype, CUMZ-pxDGT00220 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

Telson. Epiproct quite short; tip subtruncate; lateral setiferous tubercles inconspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular; caudal margin round, with inconspicuous setiferous tubercles.

Sterna (Figure 4R). Sternal lobe between male coxae 4 completely divided into two lobes, long, spine-like; tips in situ directed ventrad; posterior surface a bit swollen, bearing 2 pores.

Legs (Figure 4S). Male femora without modification.

Gonopods (Figs 5H, 26). Coxa subequal in length to femur. Prefemoral part about 2/3 as long as femur. Femur quite enlarged distally. Postfemoral part large, broad and wide; angled 90 degrees with femur. Mesal sulcus and lateral sulcus wide. Solenophore smaller than postfemoral part: lamina lateralis apparently with two lobes demarcated from each other; lateral lobe very long, process-like, its tip in situ directed ventrad; mesal lobe short and wide, supporting solenomere: lamina medialis long, base not enlarged, tip directed mesad. Solenomere obviously longer than lamina medialis, circular in transverse section, curving down, tip directed laterad.

Distribution and habitat. Known only from the type locality which is currently a tourist attraction (cave). We regard this species as endemic to Malaysia.

Remarks. A photograph of a live specimen was not taken during the field survey, but our collector noticed its black or brownish black colour. All specimens were seen crawling on rock walls where they seem to blend perfectly with the substrate. No variation in morphological characters was found.

Spinaxytes uncus **Srisonchai, Enghoff & Panha, sp. n.**

http://zoobank.org/1C0878B4-7450-472D-A495-4C75B44CA4E0
Figs 4T–V; 5I; 27–29

Material examined. Holotype. ♂, THAILAND, Phang Nga Province, Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 8 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00221). **Paratypes.** 15 ♂♂, 16 ♀♀, same data as for holotype (CUMZ-pxDGT00222); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040255); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9424). **Further specimens, not paratypes, all from THAILAND, Phang Nga Province. Muaeng Phang Nga District:** 4 ♂♂, 2 ♀♀, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 6 Aug. 2014, ASRU members leg. (CUMZ); 4 ♂♂, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 5 Aug. 2015, ASRU members leg. (CUMZ); 2 ♂♂, 4 broken ♀♀, Tham Nam Pud, 8°27'50"N, 98°32'36"E, ca. 58 m a.s.l., 8 Oct. 2006, ASRU members leg. (CUMZ); 3 ♂♂, 2 ♀♀, Tham Nam Pud, 8°27'50"N, 98°32'36"E, ca. 58 m a.s.l., 5 Aug. 2015, ASRU members leg. (CUMZ); 2 ♂♂, 1 ♀, Wat Tham Bang Toei, 8°27'52"N, 98°34'10"E, ca. 24 m a.s.l., 10 Jul. 2017, ASRU members leg. (CUMZ); 8 ♂♂, 2 ♀♀, Tham Pha Phueng Bureau of Monks, 8°28'24"N, 98°32'15"E, ca. 78 m a.s.l., 10 Jul. 2017, ASRU members leg. (CUMZ). **Thap Put District:** 11 ♂♂, 3 ♀♀, Wat Kerewong (Tham Koab), 8°31'52"N, 98°34'39"E, ca. 76 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ).

Etymology. The name is a Latin noun in apposition (*uncus*), meaning hook, and refers to the hook-like lamina medialis of gonopod.

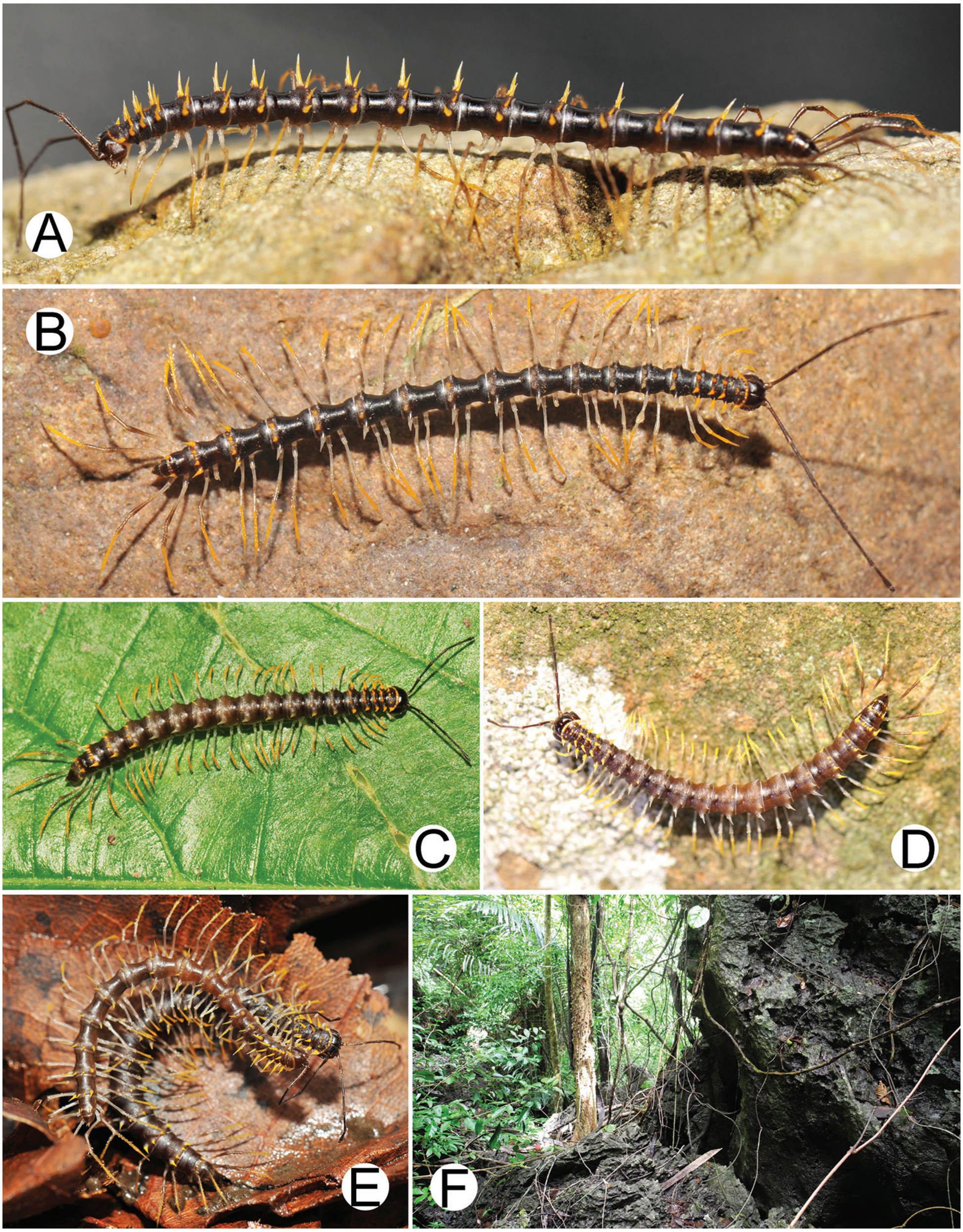

Figure 27. Photographs of live *Spinaxytes uncus* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00222 **B** ♂, specimen from Wat Kerewong (Tham Koab) **C** ♀ paratype, CUMZ-pxDGT00222 **D** ♀, specimen from Wat Kerewong (Tham Koab) **E** mating couple **F** habitat.

Diagnosis. Differs from other species by having only male femora 7 strongly humped distally, in combination with the distal part of lamina medialis hook-like, tip long and sharp.

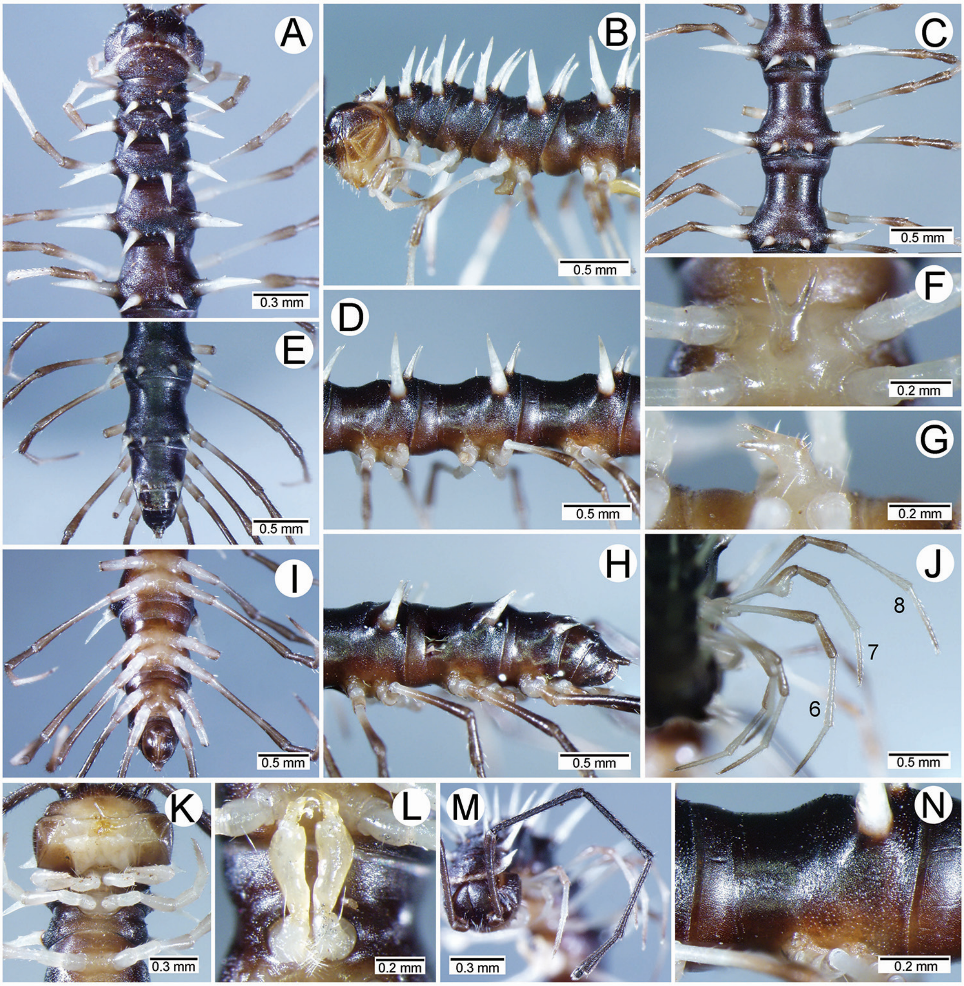

Figure 28. *Spinaxytes uncus* sp. n., ♂ paratype, CUMZ-pxDGT00222 **A, B** anterior body part **C, D** body rings 8–10 **E, H, I** posteriormost body rings and telson **F, G** sternal lobe between coxae 4 **J** legs 6–8 **K** legs 1–3 **L** gonopods **M** left antenna **N** sculpture of body ring 10.

Description. SIZE. Length 20–27 mm (male), 25–29 mm (female); width of midbody metazona 1.4–1.6 mm (male), 2.1–2.3 mm (female). Width of collum < 2 = 3 < 4 < head = 5–16, thereafter body gradually tapering towards telson.

Colour (Figure 27A–E). Specimens in life with body black; paraterga yellow/whitish yellow; head, antennae (except whitish distal part of antennomeres 7 and 8) and prozona black; collum, metaterga and surface below paraterga black/brownish black; sterna and epiproct brown; legs yellow; a few basal podomeres white.

Antennae (Figure 28M). Reaching to body ring 8 or 9 (male) and 6 or 7 (female) when stretched dorsally.

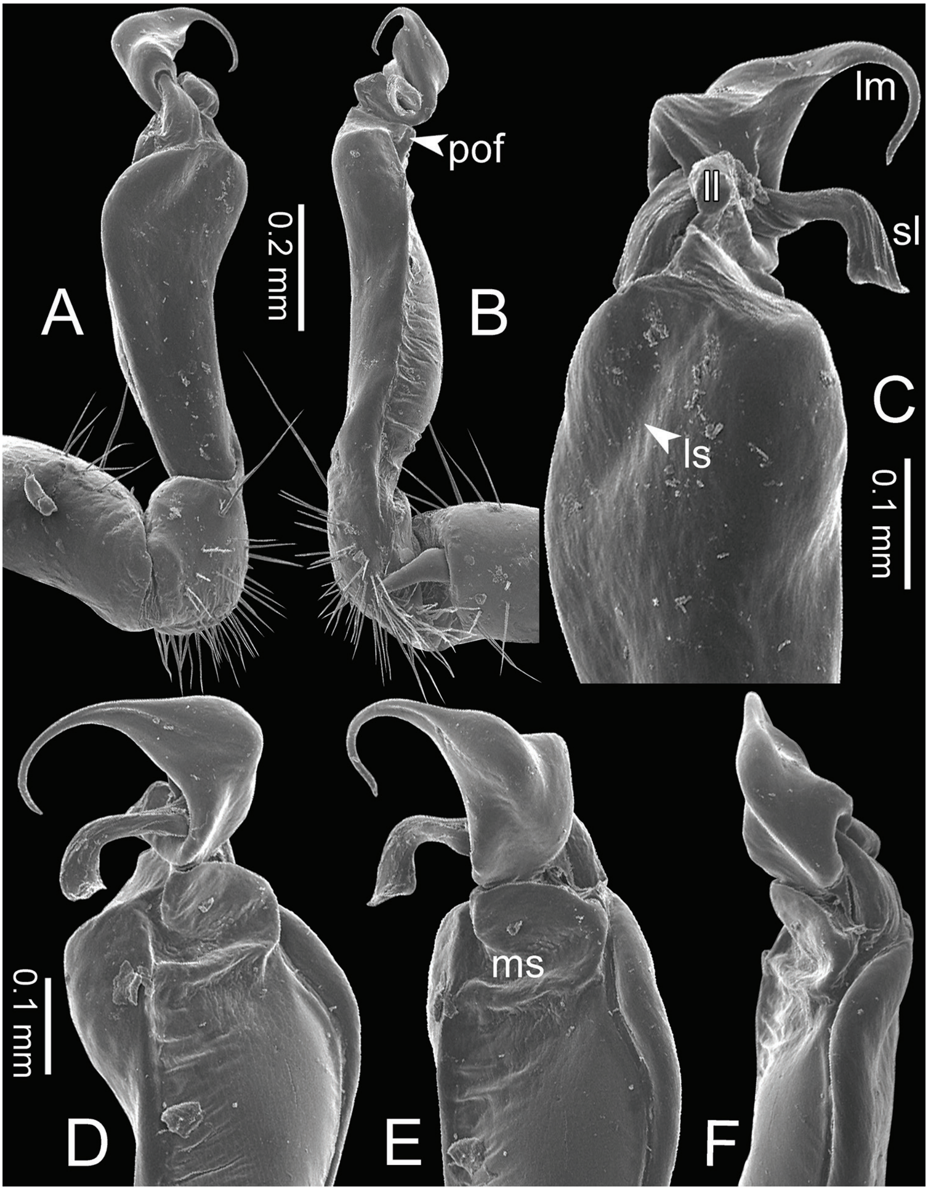

Figure 29. *Spinaxytes uncus* sp. n., paratype, CUMZ-pxDGT00222 – right gonopod **A** lateral view **B** mesal view **C** ventral view **D** mesodorsal view **E** dorsal view **F** laterodorsal view.

Collum (Figure 28A). With three transverse rows of setiferous cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with two conspicuous setiferous notches at lateral margin (first notch located at base of paraterga very close to cones of anterior row; paraterga spiniform, long, tip sharp, elevated at ca. 20°–30° in both male and female, directed almost laterad.

Tegument. Quite shining; collum, metaterga (posterior part) and surface below paraterga finely microgranulate; metaterga (anterior part) coarsely microgranulate.

Metaterga (Figure 28A, C, E). With two transverse rows of setiferous cones and setiferous spines; metaterga 2–19 with 2+2 cones in anterior row and 2+2 spines in posterior row; lateral spines of posterior row very long, bigger and longer than mesal ones.

Paraterga (Figure 28A–E, H). Very long; directed dorsolaterad on body rings 2–16, elevated at ca. 40°–50° (male) 40°–45° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

Telson (Figure 28E, I, H). Epiproct short; tip subtruncate; lateral setiferous tubercles inconspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subsemicircular); caudal margin round, with conspicuous setiferous tubercles (in some specimens inconspicuous).

Sterna (Figs 4T; 28F, G). Sternal lobe between male coxae 4 bifurcate, long; tips sharp, in situ directed ventroanteriad; posterior surface bearing one pore.

Legs (Figs 5U, V; 28J). Male femora 7 strongly humped ventrally in distal part.

Gonopods (Figs 5I, 29). Coxa subequal in length to femur. Prefemoral part almost half as long as femur. Femur obviously enlarged distally. Postfemoral part small, narrow. Mesal sulcus wide; lateral sulcus narrow. Solenophore bigger and longer than postfemoral part: lamina lateralis very small, compact, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; apically sharp, long, hook-like; tip curving down, in situ resting close to solenomere. Solenomere curved and twisted, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 27F). Known only from Phang Nga Province; we regard *S. uncus* sp. n. as endemic for the Thai fauna. Most specimens were found on rock walls near the cave, some were seen crawling on leaf litter on the rock. The new species has been encountered in syntopy with *Desmoxytes cervina* at Phung Chang Cave, Tham Nam Pud and Wat Kerewong (Tham Koab).

Remarks. Some variation in the hypoproct was observed in this species: in some specimens subtrapeziform, in others subsemicircular; caudal margin in some individuals conspicuous, in others inconspicuous. In addition, specimens from Wat Kerewong (Tham Koab) have smaller and shorter paraterga than other specimens.

Discussion

The new genus *Spinaxytes,* defined by Srisonchai et al. (2018a) as the "spiny" group of dragon millipedes, at that time without described members, adds to the challenge of understanding the patterns of paratergal and gonopod evolution in the dragon millipedes. The nine species, all new, described here are recorded from Malaysia, Myanmar, and Thailand. They are united in the new genus by sharing the diagnostic characters of subspiniform paraterga; lamina lateralis distinctly demar-

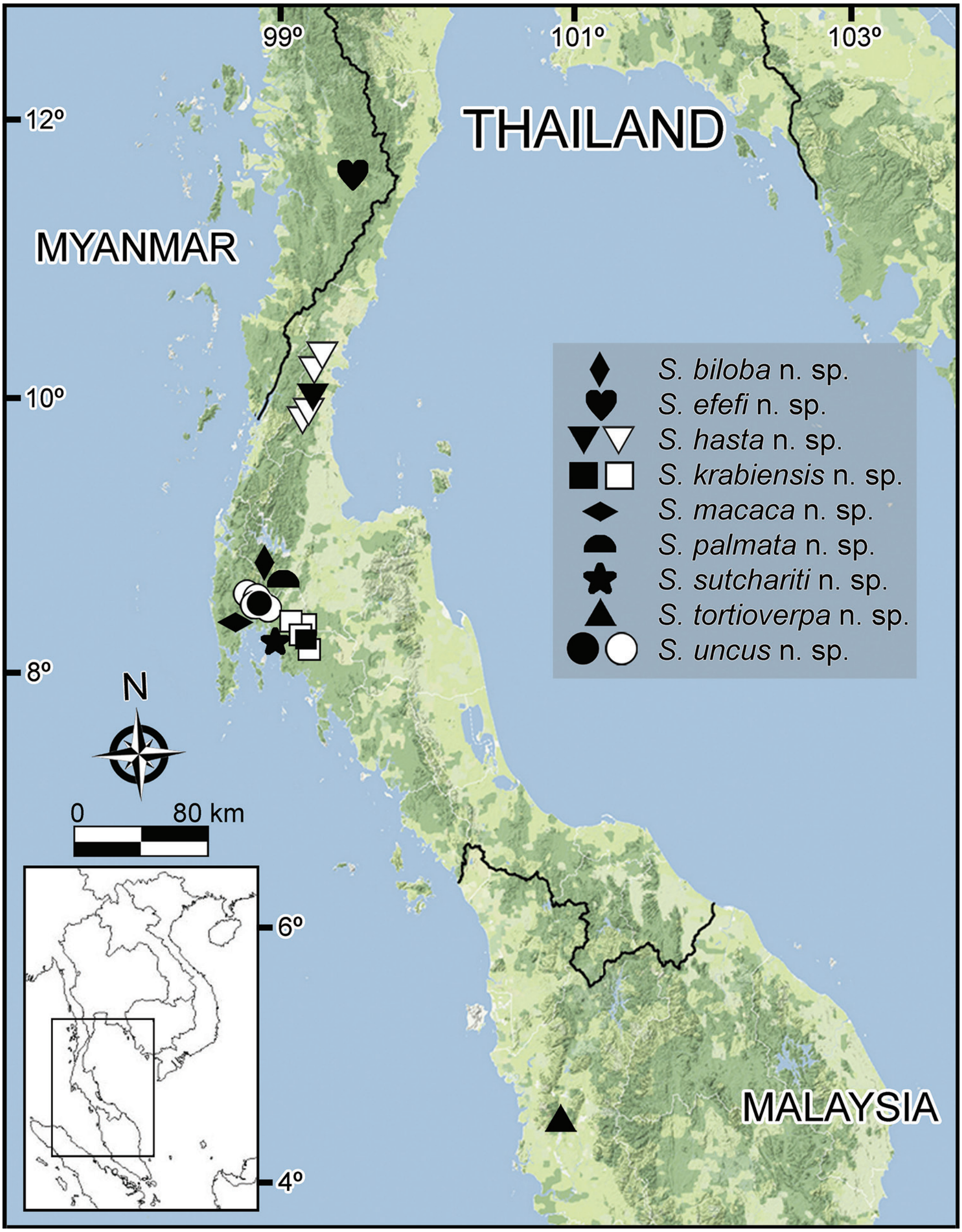

Figure 30. Known distribution of all *Spinaxytes* gen. n. species. Key: black symbols = type locality, white symbols = other localities.

cated from lamina medialis; and lamina medialis long and curved, larger and longer than lamina lateralis.

Based on a comparatively large number of specimens and species of the new genus, our study confirmed that gonopod characters can be used confidently to discriminate the species, just as we found in *Desmoxytes* and *Nagaxytes* (Srisonchai et al. 2018a, 2018b). Using the gonopods in combination with other morphological characters, such as modification of male femora, sternal lobe between male coxae 4, and number of tubercles/cones/spines on collum and on metaterga, further facilitates reliable taxonomic identification. It is particularly interesting that a process on the postfemoral part of the gonopod is found in *S. efefi* sp. n. Only two species of dragon millipede, *Hylomus specialis* (Nguyen et al. 2005) and *H. spectabilis* (Attems, 1937), have hitherto been known to have this process (z-spine) at the base of the solenophore. However, the overall gonopod characters of *S. efefi* sp. n. are markedly different from the gonopod of the two mentioned *Hylomus* species, warranting its inclusion in the new genus. *Spinaxytes* gen. n., is quite possibly a monophyletic group, considering both gonopodal and non-gonopodal characters. A phylogenetic study using molecular as well as morphological characters seems warranted in order to better understand the taxonomic position and the true relationship of the genus with other dragon millipede genera.

Almost all specimens collected by us were found on humid rock walls in small caves. Therefore, we strongly suspect that all species in this genus prefer to live on rock walls. The black or dark brown body colour makes them difficult to see against dark-coloured rocks. Quite often some specimens of *Desmoxytes* and *Gigaxytes* species are encountered in the same habitat as species of the new genus, but it seems likely that those species live on leaf litter, on the ground or on tree branches instead of rock walls. Considering currently known distributions of species of *Spinaxytes* gen. n., and their restriction to small limestone areas (Figure 30), we regard all described species here as locally endemic. Of the nine species of *Spinaxytes* gen. n., only one (*S. hasta* sp. n.) has been shown to have a somewhat wider range, but it still inhabits less than approximately 50 km^2 along the coast of Thailand.

The discovery rate of new dragon millipede species has been increasing in recent years (Liu et al. 2014, 2016; Likhitrakarn et al. 2015; Golovatch et al. 2016; Srisonchai et al. 2016, 2018a, 2018b, 2018c). Including the nine new species described here, the diversity of dragon millipedes (*Desmoxytes* + *Hylomus* + *Nagaxytes* + *Gigaxytes* + *Spinaxytes* gen. n.) has now reached 59 species. Dragon millipedes are thus a significant element in the biodiversity of Southeast Asia, especially Thailand and the Malay Peninsula. We believe that the number of endemic dragon millipede species will certainly increase further when collecting efforts in very remote or otherwise difficult-to-access places are made.

Acknowledgements

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History Museum of Denmark. We gratefully acknowledge the Plant Genetic Conservation Project under the Initiative of Her Royal Highness Maha Chakri Sirindhorn and Center of Excellence on Biodiversity for permission to field work in several restricted/remote areas. This work would not have been possible at all without the impressive collections made by ASRU members, especially Dr. Chirasak Sutcharit for his kind help in collecting numerous specimens. Thanks are due to B. W. Ng. (Malaysia) and Fauna & Flora International (Myanmar) for helping us to collect specimens in Malaysia and Myanmar. We are the most grateful to the subject editor R Mesibov, and journal referees, SI Golovatch and N Akkari, for all valuable comments and advices that greatly improved the manuscript. The first author also thanks to Ms Thita Krutchen for her kind teaching the drawing skills.

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RESEARCH ARTICLE

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Description of three new species of *Aposphragisma* Thoma, 2014 (Araneae: Oonopidae) from Sumatra, Indonesia

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Abstract

Three species from the family Oonopidae are newly described from leaf litter habitats in Sumatra, Indonesia based on male and female morphology. All three species belong to the genus *Aposphragisma* Thoma, 2014: *Aposphragisma globosum* **sp. n.,** *Aposphragisma jambi* **sp. n.**, and *Aposphragisma sumatra* **sp. n.**

Keywords

Arachnida, biodiversity, goblin spiders, systematics, taxonomy

Introduction

The family Oonopidae Simon, 1890 is a diverse group of spiders with over 1801 described species in 114 genera from all over the world (World Spider Catalog 2018). Oonopids are small (1–4 mm), two-clawed, ecribellate spiders (Saaristo 2001, Jocqué and Dippenaar-Schoeman 2007) that can be abundant in leaf litter, under bark of trees, in forest canopies and in subterranean habitats (Burger et al. 2002; Harvey and Edward 2007; Fannes and Jocqué 2008; Baehr et al. 2010). Currently 42 species of Oonopidae belonging to eight genera are known to occur in Indonesia, excluding Borneo (World Spider Catalog 2018). More than half of the species can be found on Sumatra (23 species), as well as most of the genera (six genera). The most species-rich genus, *Ischnothyreus* Simon, 1893 was recently revised by Richard et al. (2016) with eight species occurring on the island. It is followed by the genera *Gamasomorpha* Karsch, 1881 and *Prethopalpus* Baehr et al. 2012 (with six species each) revised by Eichenberger et al. (2011) and Baehr et al. (2012), respectively.

In 2014, Thoma described the new South East Asian genus *Aposphragisma* Thoma, 2014 including 19 new species, from which only one species was described from Sumatra, *A. borgulai* Thoma, 2014 (Thoma et al. 2014). Here we present the description of three new species of *Aposphragisma* from Sumatra.

Material and methods

All specimens were collected in the framework of the EFForTS (Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems) project that investigates the effects of transformation of lowland rainforests into agricultural systems (Drescher et al. 2016). Samples were taken from four forest types (primary degraded lowland rainforest, agroforest with a mixture of native vegetation and planted rubber trees (secondary degraded lowland rainforest), rubber monoculture, and oil palm monoculture). Material was collected during three sampling campaigns. The first was conducted in October–November 2012 (Barnes et al. 2014). From each of 32 sampling sites, three samples of 1×1 m were taken by sieving the leaf litter through a sieve of 2-cm mesh. Spiders visible by eye were hand-collected and stored in 65% ethanol. The second campaign was conducted in October–November 2013 (Klarner et al. 2017). From the same sampling sites three soil samples of 16×16 cm were taken with a spade, comprising the litter layer and the underlying mineral soil to a depth of 5 cm. Finally, the third collecting round was conducted in March, June, September and December 2017; specimens were collected by sieving 16×16cm of litter. All spiders from soil and litter were extracted by heat (Kempson et al. 1963) and collected in a dimethyleneglycol-water solution (1 : 1) and thereafter transferred into 70% ethanol. The material examined is deposited in the following institutions: Indonesian Institute of Sciences Cibinong, Indonesia (**LIPI**); Zoological Museum Hamburg, Germany (**ZMH**).

Specimens were examined in 65–75% ethanol under a Leica M125 dissection microscope and photographed with a custom-made BK Plus Lab System by company Dun, Inc. with integrated Canon camera, macro lenses (65 mm and 100 mm) and the Zerene stacking software (Zerene Systems LLC 2018). Female genitalia were excised using a sharp entomological needle, treated with Pancreatin (Álvarez-Padilla and Hormiga 2008), then placed in lactic acid and observed under a Leica DM2500 LED compound microscope. A Leica DMC 4500 digital camera attached to the microscope was used to photograph all the structures illustrated. All measurements are given in millimetres (mm). Males and females were matched based on the following criteria: (1) collected in the same sample, (2) body size, and (3) punctuation pattern and colouration. Morphological nomenclature follows Thoma et al. (2014).

Abbreviations

Somatic morphology:

ALE	anterior lateral eyes;	sli	slit;
bc	book lung cover;	s	spikes;
d	denticles;	sr	subterminal scutal ridges;
lap	lateral apodemes;	st	sternum tubercle;
PME	posterior median eyes;	tlp	tooth-like projection;
PLE	posterior lateral eyes;		

Male genitalia:

cb	conical bulge;	e	embolus;
c	conductor;	sp	sperm pore;

Female genitalia:

gap	globular appendix;	sa	sac-like structure;
na	nail-like structure;	tsc	transverse sclerites;
pa	papillae;	wl	wrinkle-lines;
re	receptaculum;		

Taxonomy

Family Oonopidae Simon, 1890

Genus *Aposphragisma* Thoma, 2014

Type species. *Aposphragisma helvetiorum* Thoma, 2014: 36–44

Diagnosis. The genus *Aposphragisma* most resembles the genera *Gamasomorpha* Karsch, 1881 and *Xestaspis* Simon, 1884 (Thoma et al. 2014) but they can be differentiated based on the combination of the following characters: hard-bodied spiders; sternum with microsculpture; dorsal and ventral abdominal scuta not fused; labium strongly incised; legs without spines. Furthermore, males are distinguished by their palpal bulb bearing an apical embolus closely associated with a laminar conductor (Thoma et al. 2014).

Distribution. Borneo, Indonesia (Sumatra), Malaysia, Singapore and Vietnam.

Aposphragisma globosum Fardiansah & Dupérré, sp. n.

http://zoobank.org/30F29C2E-E74A-4847-BAE1-1D83A77C2AAD
Figs 1–3

Type material. Holotype. ♂: Indonesia, Sumatra, Harapan, 02°09'09.9"S 103°21'43.2"E, secondary lowland rainforest, 26 November 2017, B. Klarner (LIPI). **Paratypes.** 1♀, Indonesia, Sumatra, Harapan, 01°54'35.6"S 103°15'58.3"E,

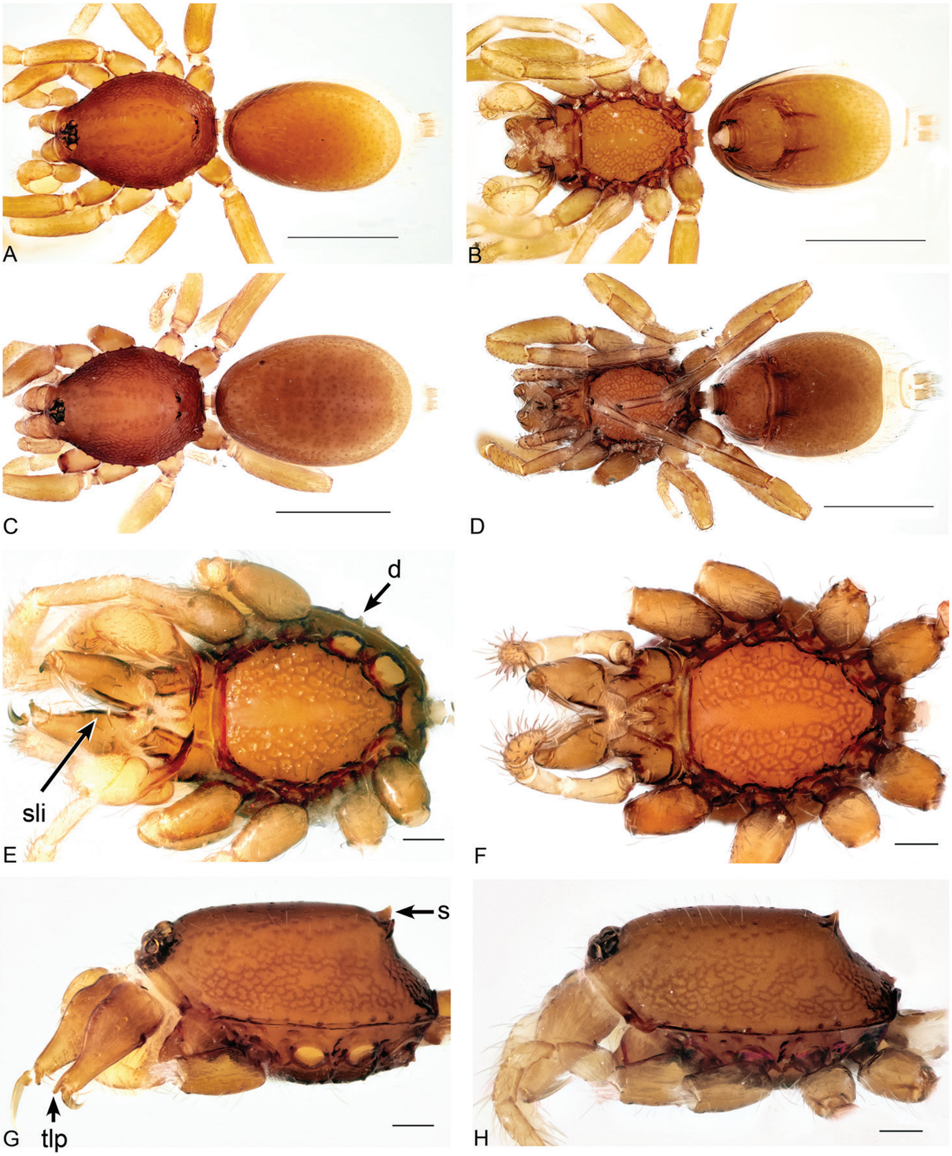

Figure 1. *Aposphragisma globosum* sp. n., Male (**A, B, E, G**); Female (**C, D, F, H**). **A, C** habitus dorsal view **B, D** habitus ventral view **E, F** prosoma ventral view **G, H** carapace lateral view. Scale bars: 0.5mm (**A–D**); 0.1mm (**E–H**).

oil palm plantation, October 2012, M. Jochum, A. Barnes (LIPI); 01°54'39.5"S 103°16'00.1"E, 2♂, rubber plantation, October 2013, B. Klarner (ZMH–A0000984, ZMH–A0000986); 02°09'09.9"S 103°21'43.2"E, 1♂2♀, secondary lowland rainforest litter, October 2013, B. Klarner (ZMH–A00001002, ZMH–A0001022, ZMH–A0001505); 01°55'44.0"S 103°15'33.8"E, 2♀, agroforest with a mixture of native vegetation and planted rubber trees, October 2012, M. Jochum, A. Barnes (ZMH–A0001304, ZMH–A0001305).

Etymology. The specific name is an adjective in apposition taken from Latin, meaning *globular* in reference to the shape of female genitalia.

Diagnosis. *Aposphragisma globosum* sp. n. males and females can be distinguished from most *Aposphragisma* species by the presence of prosomal spikes (Fig. 1G) and a coarsely reticulated sternum (Fig. 1F). From *A. brunomanseri* Thoma, 2014 it can be separated by the presence of only one pair of prosomal spikes (Fig. 1G), the latter species having two pairs of spikes (Thoma et al. 2014; fig. 2E, F); males are differentiated from *A. kolleri* Thoma, 2014 by their strongly twisted tip of the embolus (Fig. 3B), which is spatulate in the latter species (Thoma et al. 2014; fig. 27C).

Description. ***Male (holotype).*** Total length: 1.54; carapace length: 0.69; carapace width: 0.53; abdomen length: 0.85; abdomen width: 0.51. CEPHALOTHORAX. *Carapace*: Brownish orange, broadly oval in dorsal view, slightly elevated in lateral view, surface of elevated portion of pars cephalica smooth and with 1 pair of spikes at the apical end; sides and pars thoracica finely reticulated, partly interrupted by small smooth areas, lateral margin with blunt denticles (Fig. 1A, G). *Sternum:* Brownish orange; longer than wide, coarsely reticulated except of median stripe and smooth edges, covered by sparse setae; posterior margin extending posteriorly (Fig. 1E). *Eyes:*

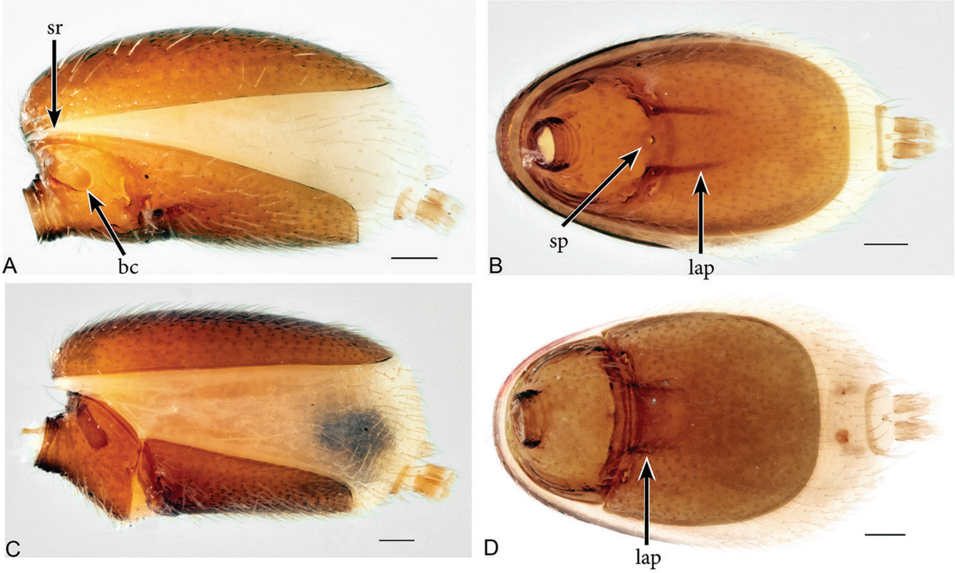

Figure 2. *Aposphragisma globosum* sp. n., Male (**A, B**); Female (**C, D**). **A, C** abdomen lateral view **B, D** abdomen ventral view. Scale bar: 0.1mm (**A–D**).

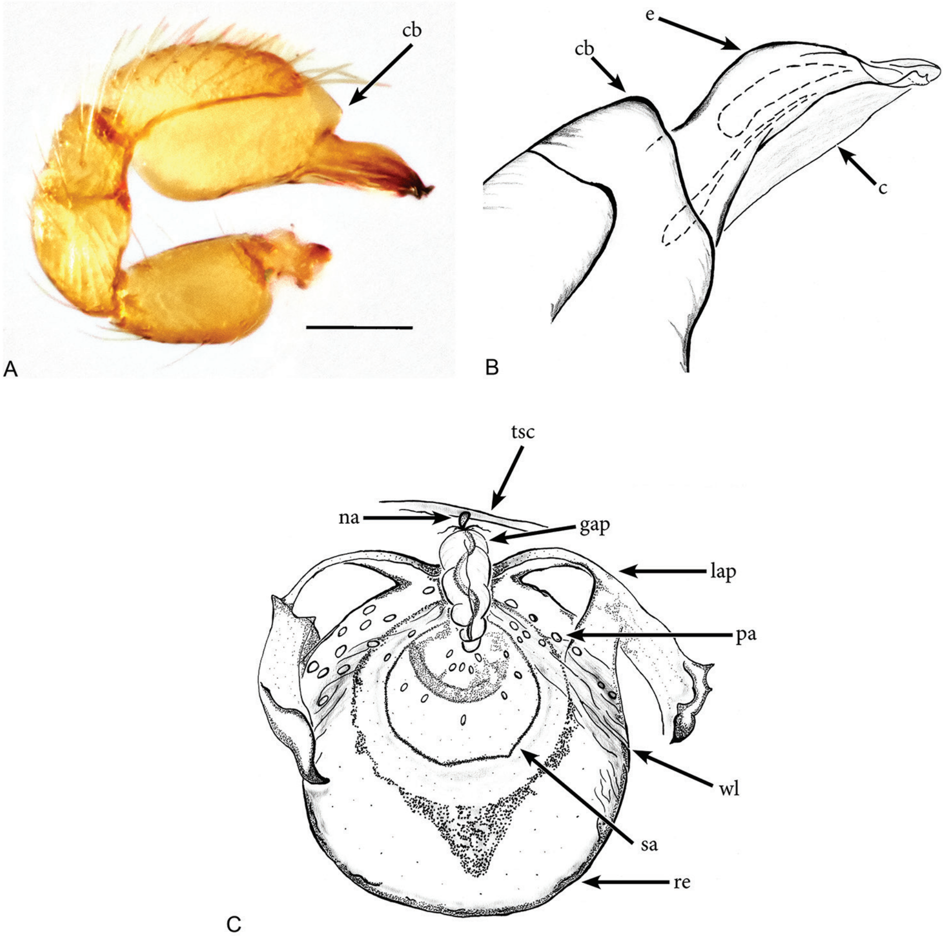

Figure 3. *Aposphragisma globosum* sp. n., Male (**A, B**); Female (**C**). **A, B** palp prolateral view **C** female genitalia dorsal view Scale bar: 0.1mm (**A**).

Six; ALE largest, ALE oval, PME circular, PLE oval; posterior eye row straight from above, procurved from front; ALE separated by their diameter, ALE-PLE separated by less than ALE radius, PMEs joint together, PLE-PME separated by less than PME radius (Fig. 1A). *Mouthparts*: chelicerae yellowish brown; straight in frontal view, convex in lateral view; anterior face strongly indented; posterior margin of inner surface proximally modified to a ridge with median slit (sli); promargin with row of flattened setae that extend distally into a short inward-pointing tooth-like projection (tlp) (Fig. 1G). Labium triangular, deeply incised, fused to sternum (Fig. 1E). Endites elongated; outer margin subdistally with a pair of long inward-bent setae. Abdomen. Dorsal scutum brownish yellow, ovoid; strongly sclerotized, covering most of dorsum (Fig. 1A); epigastric scutum strongly sclerotized, anteriorly with subterminal scutal ridge (sr) which is widely oval (Fig. 2A); book lung covers large (bc), oval (Fig. 2A). Postepigastric scutum long, strongly sclerotized, occupying most of the venter, with posteriorly directed lateral apodemes (lap) (Fig. 2B). *Legs:* yellowish orange. GENITALIA. *Epigastric region*: sperm pore (sp) situated at level of posterior spiracles (Fig. 2B). *Palp*: Yellowish bright, not strongly sclerotized (Fig. 3A); cymbium slightly ovoid in dorsal view; bulb stout; conical bulge (cb) strongly pronounced (Fig. 3A, B); embolus (e) tip twisted; conductor (c) with blunt tip (Fig. 3B).

Female (paratype). Total length: 1.75; carapace length: 0.77; carapace width: 0.55; abdomen length: 0.98; abdomen width: 0.65. Colouration: same as in male. CEPHALOTHORAX. *Carapace*: Same as in male. *Mouthparts*: chelicerae distally without pointing tooth-like projection. ABDOMEN. Epigastric scutum not fused to postepigastric scutum (Fig. 2D); postepigastric scutum with posteriorly directed lateral apodemes (lap) (Fig. 2D). *Legs:* yellowish white. GENITALIA. Dorsal view (Fig. 3C): receptaculum (re) large, globular, convex and sloping upward containing a globular sac-like structure (sa); anterior part covered with papillae (pa), mediolateral with wrinkle-like lines (wl); laterally framed by rectangular sclerites (apodemes, lap) that have wide and slightly folded tips, apodemes sloping upward; globular appendix (gap) lying dorsally of receptaculum and about 1/3 as long as receptaculum; a transverse sclerite (tsc) lies anteriorly to the receptaculum and bears a nail-like structure (na) more medially.

Natural History. Specimens were collected in four types of habitats: secondary lowland rainforest, oil palm plantation, and rubber plantation.

Distribution. Known only from the type locality: Harapan on Sumatra.

Aposphragisma jambi Fardiansah & Dupérré, sp. n.

http://zoobank.org/C8D21542-5234-48E1-BCC0-9AA0314AB504

Figs 4–6

Type material. Holotype ♂: Indonesia, Sumatra, Bukit Duabelas, 01°59'42.5"S 102°45'08.1"E, secondary lowland rainforest, October 2012, M. Jochum, A. Barnes (LIPI). **Paratypes:** 1♀, Indonesia, Sumatra, Bukit Duabelas, 02°08'26.6"S 102°51'04.3"E, agroforest with a mixture of native vegetation and planted rubber trees, October 2012, M. Jochum. A. Barnes (LIPI); 01°59'42.5"S 102°45'08.1"E, 2♀, secondary lowland rainforest litter, October 2013, B. Klarner (ZMH–A0000994, ZMH–A0000998), 01°59'42.5"S 102°45'08.1"E, 2♀, October 2012, M. Jochum, A. Barnes (ZMH–A0001273, ZMH–A0001282).

Etymology. The specific name is a noun in apposition and refers to the name of Jambi Province where Bukit Duabelas National Park is located.

Diagnosis. *Aposphragisma jambi* sp. n. males and females can be distinguished from most of the other *Aposphragisma* species by their finely reticulate carapace lacking spikes (Fig. 4A, C, G, H) and by their finely reticulated sternum with smooth median stripe (Fig. 4E, F); from *A. baltenspergerae* Thoma, 2014 and *A. retifer* Thoma, 2014 males are differentiated by their wider and strongly twisted embolus tip (Fig. 6B), not twisted in *A. baltenspergerae* and *A. retifer* (Thoma et al. 2014; figs. 4C and 37E respectively) and females by their elongated oval receptaculum (Fig. 6C), globose in *A. baltenspergerae* (Thoma et al. 2014; fig. 4G).

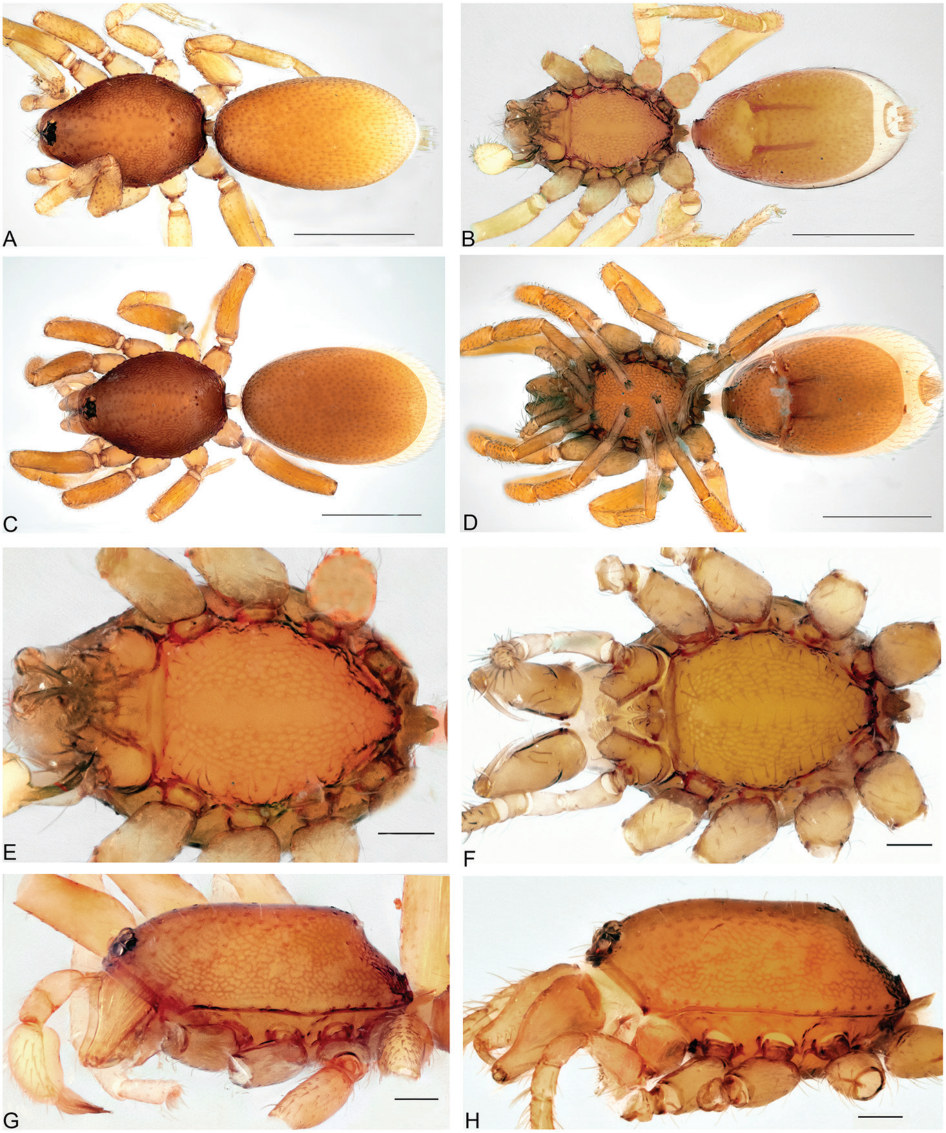

Figure 4. *Aposphragisma jambi* sp. n., Male (**A, B, E, G**); Female (**C, D, F, H**). **A, C** habitus dorsal view **B, D** habitus ventral view **E, F** prosoma ventral view **G, H** carapace lateral view. Scale bars: 0.5mm (**A–D**); 0.1mm (**E–H**).

Description. ***Male (holotype).*** Total length: 1.54; carapace length: 0.68; carapace width: 0.47; abdomen length: 0.86; abdomen width: 0.48. Cephalothorax. *Carapace*: Brownish orange, broadly oval in dorsal view, slightly elevated in lateral view, surface of elevated portion of pars cephalica smooth and without spikes, with 2 small tubercles at apical end that each bears a seta (Fig. 4A, G); sides of carapace finely reticulated; pars thoracica finely reticulated, sloping gradually; lateral margin with blunt

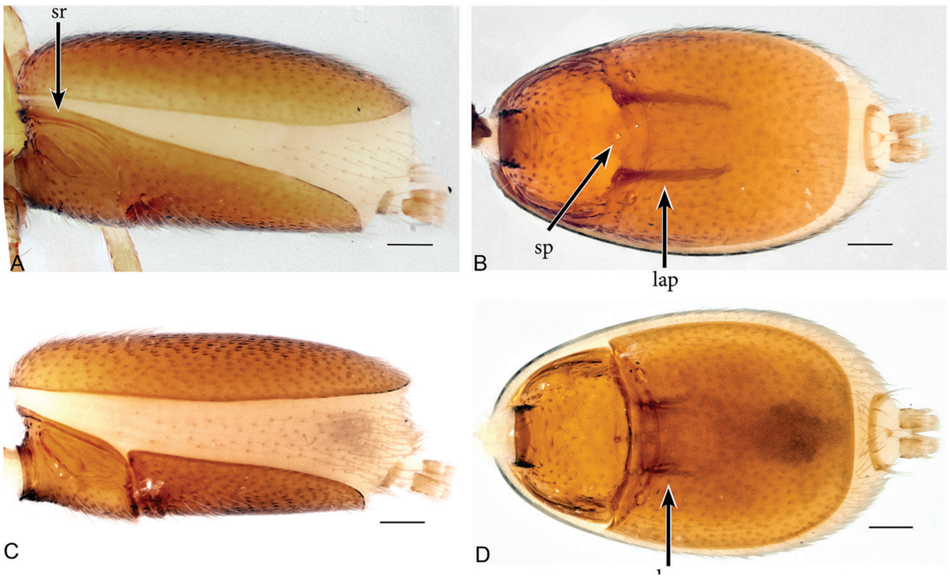

Figure 5. *Aposphragisma jambi* sp. n., Male (**A, B**); Female (**C, D**). **A, C** abdomen lateral view **B, D** abdomen ventral view. Scale bar: 0.1mm (**A–D**).

denticles (Fig. 4G). *Sternum:* Brownish orange; longer than wide, finely reticulated except median stripe and broadly smooth edges, surface covered by setae (Fig. 4E). *Eyes:* Six, all oval; ALE largest, posterior eye row straight from above; ALE separated by less than its radius, ALE-PLE touching, PME touching, PLE-PME touching (Fig. 4A). *Mouthparts*: chelicerae yellowish white, slightly divergent, anterior face convex in lateral view (Fig. 4G), inner surface covered by thick setae; posterior margin of inner surface proximally modified into a ridge with median slit; promargin with a row of flattened setae, distally extending into a short inwards-pointing tooth-like projection. Labium triangular, deeply incised, fused to sternum (Fig. 4E). Endites elongated, outer margin subdistally with a pair of long inward-bent setae. Abdomen. Dorsal scutum brownish yellow, ovoid; strongly sclerotized and covering full length of abdomen (Fig. 4A); book lung covers large, ovoid, surface smooth (Fig. 5A); epigastric scutum strongly sclerotized, anteriorly with widely oval subterminal, scutal ridge (sr) (Fig. 5A). Postepigastric scutum long, strongly sclerotized and occupying most of the venter, posteriorly-directed long lateral apodemes (lap) (Figs 4B, 5B). *Legs:* yellowish white. Genitalia. *Epigastric region*: sperm pore (sp) situated at level of posterior spiracles (Fig. 5B). *Palp:* Light yellow, not strongly sclerotized (Fig. 6A); cymbium slightly ovoid or rectangular in dorsal view; bulb stout; conical bulge (cb) only slightly pronounced (Fig. 6A, B); embolus (e) tip folded, conductor (c) with pointed tip (Fig. 6B).

Female (paratype). Total length: 1.54; carapace length: 0.70; carapace width: 0.49; abdomen length: 0.84; abdomen width: 0.53. Colouration: Same as in male. Cephalothorax. *Carapace*: Same as in male. *Mouthparts*: Chelicerae: distally without pointing tooth-like projection. Abdomen. Dorsal scutum not covering full length of the abdo-

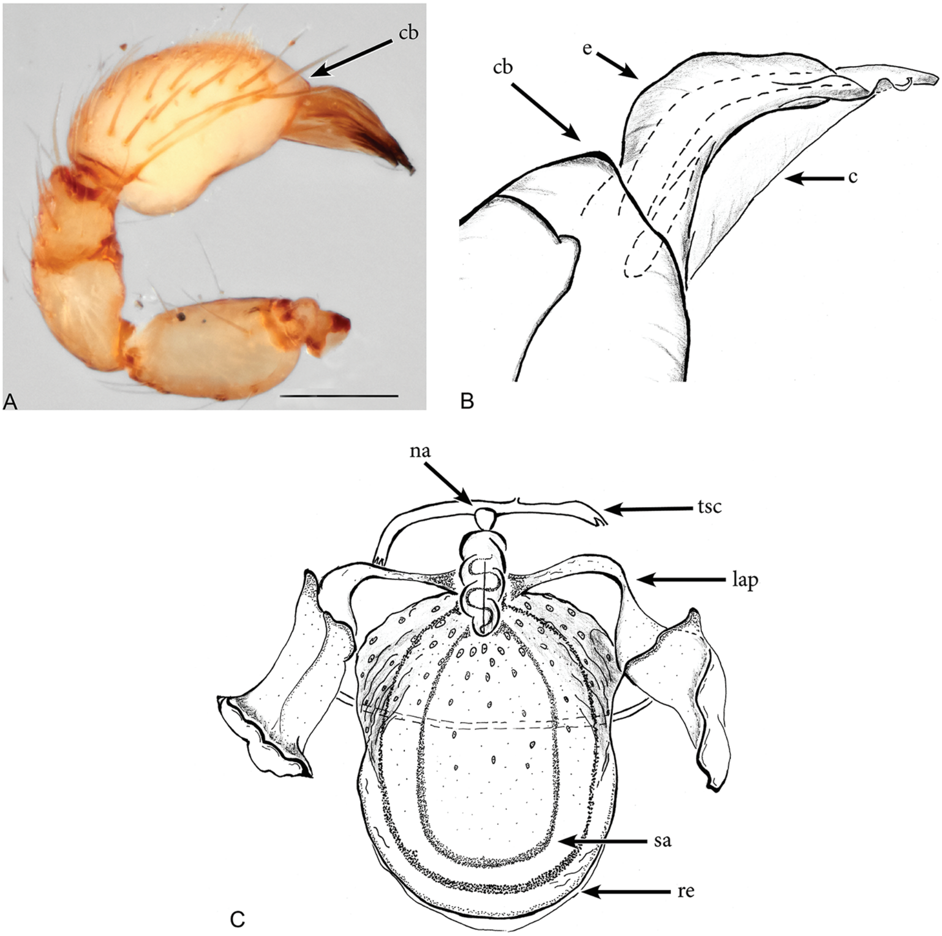

Figure 6. *Aposphragisma jambi* sp. n., Male (**A, B**); Female (**C**). **A, B** palp prolateral view **C** female genitalia dorsal view. Scale bar: 0.1mm (**A**).

men, soft tissue visible in dorsal view (Fig. 4C); epigastric scutum not fused to postepigastric scutum (Fig. 5C, D); postepigastric scutum with short posteriorly directed lateral apodemes (lap) (Fig. 5D). *Legs:* yellowish white. Genitalia. Dorsal view (Fig. 6C): Receptaculum (re) large, elongated oval, convex and sloping upward, containing an oval sac-like structure (sa), anterior and median part covered with papillae, anterolateral with wrinkle-like lines; laterally framed by rectangular sclerites (apodemes, lap) and with a wide and slightly folded tip; apodemes sloping upward; globular appendix lying dorsally of receptaculum and about 1/4 as long as receptaculum; a transverse sclerite (tsc) lies anteriorly to the receptaculum and has a nail-like structure (na) in medial position.

Natural History. Specimens were collected in a secondary degraded lowland rainforest only.

Distribution. Known only from the type locality, Bukit Duabelas National Park, Sumatra.

Aposphragisma sumatra Fardiansah & Dupérré, sp.n.

http://zoobank.org/97D45CA3-46CD-47A7-ADAA-9887F86711DC
Figs 7–9

Type material. Holotype ♂: Indonesia, Sumatra, Harapan, 02°09'09.9"S 103°21'43.2"E, secondary lowland rainforest, 10 June 2017, B. Klarner (LIPI). **Paratypes:** 2♀, Indonesia, Sumatra, Harapan, 02°09'09.9"S 103°21'43.2"E, secondary lowland rainforest, 4 September 2017 (LIPI) (ZMH–A0001198, ZMH–A0001203); 02°09'09.9"S 103°21'43.2"E, 1♂3♀, 8 March 2017, B. Klarner (ZMH–A0001196,

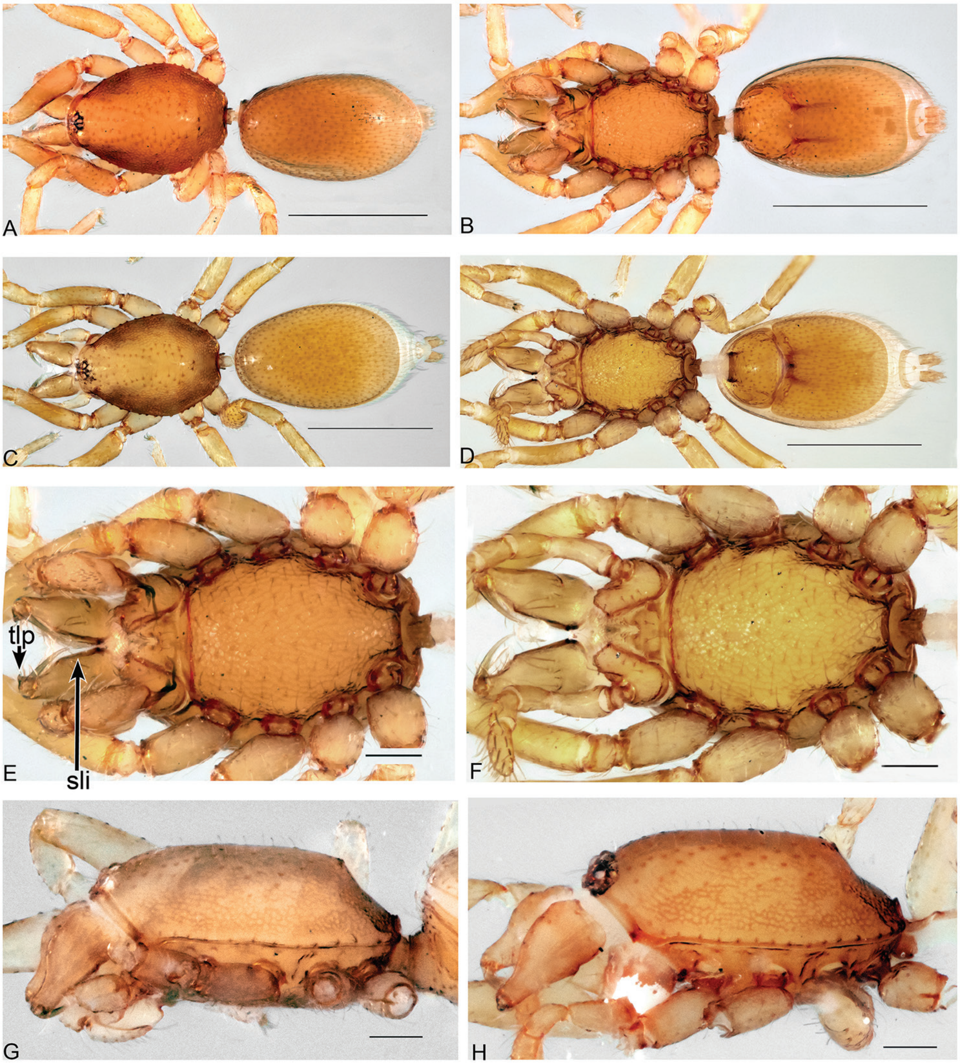

Figure 7. *Aposphragisma sumatra* sp. n., Male (**A, B, E, G**); Female (**C, D, F, H**). **A, C** habitus dorsal view **B, D** habitus ventral view **E, F** prosoma ventral view **G, H** carapace lateral view. Scale bars: 0.5mm (**A–D**); 0.1mm (**E–H**).

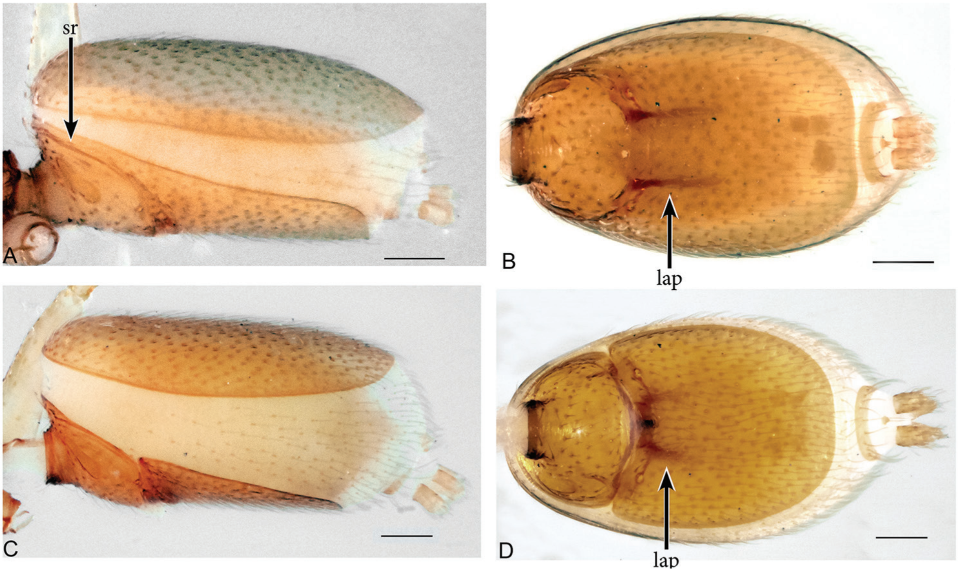

Figure 8. *Aposphragisma sumatra* sp. n., Male (**A, B**); Female (**C, D**). **A, C** abdomen lateral view **B, D** abdomen ventral view. Scale bar: 0.1mm (**A–D**).

ZMH–A0001197, ZMH–A0001199, ZMH–A0001202), 3♂4♀, 10 June 2017, B. Klarner (ZMH–A0001195, ZMH–A0001200, ZMH–A0001204), 1♂, 26 November 2017, B. Klarner (ZMH–A0001194).

Etymology. The specific name is a noun in apposition, the name of the island on which the types were collected.

Diagnosis. *Aposphragisma sumatra* sp. n. males and females can be distinguished from most of the other *Aposphragisma* species by their completely reticulate sternum (Fig. 7E, F); from *A. confluens* Thoma, 2014, *A. draconigenum* Thoma, 2014, *A. nocturnum* Thoma, 2014 and *A. scimitar* Thoma, 2014 by their blunt tubercles on the carapace margin (Fig. 7G, H); absent or reduced in the other species; from *A. stannum* Thoma, 2014 by their longer embolus (Fig. 9B), shorter in the latter species (Thoma et al. 2014; fig. 48D). From *A. rimba* Thoma, 2014, both males and females are differentiated by their reticulated carapace (Fig. 7G, H) and reduced eyes; in *A. rimba* the carapace and the eyes are of normal size (Thoma et al. 2014; fig. 38A).

Description. ***Male (holotype).*** Total length: 1.28; carapace length: 0.58; carapace width: 0.41; abdomen length: 0.70; abdomen width: 0.42. Cephalothorax. *Carapace*: Brownish orange, broadly oval in dorsal view, slightly elevated in lateral view, surface of elevated portion of pars cephalica smooth and without spikes, with 2 small tubercles at apical end that bear a terminal seta (Fig. 7A, G); sides finely reticulated; pars thoracica finely reticulated, sloping gradually, lateral margin with blunt denticles (Fig. 7G). *Sternum*: Brownish orange; longer than wide, finely reticulated, surface covered with setae (Fig. 7E). *Eyes*: Six, reduced, all oval; ALE largest; posterior eye row straight from above; ALE separated by their diameter, ALE-PLE separated by less ALE radius, PME separated by less than its radius, PLE-PME separated by less than its radius (Fig. 7A). *Mouthparts*:

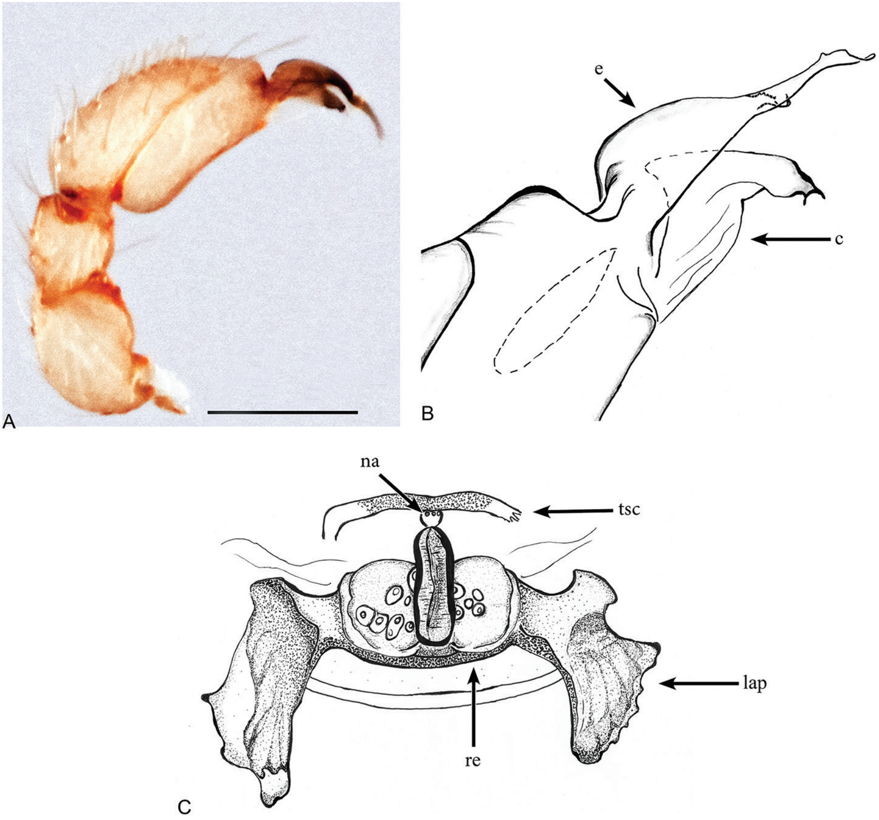

Figure 9. *Aposphragisma sumatra* sp. n., Male (**A, B**); Female (**C**). **A, B** palp prolateral view **C** female genitalia dorsal view. Scale bar: 0.1mm (**A**).

chelicerae yellowish white, straight in frontal view, convex in lateral view (Fig. 7G); posterior margin of inner surface proximally modified to a ridge with a median slit (sli); promargin with a row of flattened setae, distally extending into a short inward-pointing tooth-like projection (tlp) (Fig. 7E). Labium triangular, deeply incised, fused to sternum (Fig. 7E). Endites elongated, outer margin subdistally with a pair of long inward bent setae. ABDOMEN. Dorsal scutum yellowish white, ovoid; strongly sclerotized and covering full length abdomen (Fig. 7A); epigastric scutum strongly sclerotized, anteriorly with widely oval subterminal scutal ridge (sr) (Fig. 8A), book lung covers large, ovoid, surface smooth (Fig. 8A). Postepigastric scutum long, strongly sclerotized, venter fully occupied, posteriorly directed lateral apodemes (lap) long (Figs 7B, 8B). *Legs*: yellowish white. GENITALIA. *Epigastric region*: sperm pore situated at level of posterior spiracles (Fig. 8B). *Palp*: White, not strongly sclerotized (Fig. 9A); cymbium slightly rectangular in dorsal view; bulb stout; conical bulge slightly flat (Fig. 9A, B); embolus (e) basally narrowed, very long, twisted and with wavy tip; conductor (c) medially triangular and with wide tip (Fig. 9B).

Female (paratype). Total length: 1.46; carapace length: 0.61; carapace width: 0.43; abdomen length: 0.85; abdomen width: 0.48. Colouration: same as in male. CEPHALOTHORAX. *Carapace*: Same as in male. *Mouthparts*: chelicerae distally without pointed tooth-like projection (tlp). ABDOMEN: Dorsal scutum not covering full length of the abdomen, soft tissue visible in dorsal view (Fig. 7C); epigastric scutum not fused to postepigastric scutum; postepigastric scutum not fully covering the venter, and with short posteriorly directed lateral apodemes (lap) (Fig. 8D). *Legs:* yellowish white. GENITALIA. Dorsal view (Fig. 9C): Receptaculum (re) small, slightly rectangular; median part with papillae; laterally framed by rectangular sclerites (apodemes, lap) with wide and slightly bumpy tip, apodemes sloping upward; rectangular appendix lying dorsally of receptaculum about as long as receptaculum; a transverse sclerite (tsc) lies anteriorly to the receptaculum and bears medially a nail-like structure (na).

Natural History. Specimens were collected in a secondary degraded lowland rainforest only.

Distribution. Known only from the type locality, Bukit Duabelas National Park, Sumatra.

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RESEARCH ARTICLE

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Descriptions of four new species of *Bactrocera* and new country records highlight the high biodiversity of fruit flies in Vietnam (Diptera, Tephritidae, Dacinae)

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Abstract

Recent snap-shot surveys for fruit flies in Vietnam in 2015 and 2017 using traps baited with the male Dacinae fruit fly lures methyl eugenol, cue-lure and zingerone, collected 56 species, including 11 new country records and another 11 undescribed species, four of which are described in this paper. This increases the number of described species known to occur in Vietnam from 78 to 93. Species accumulation curves, based on the Chao 2 mean estimate, suggest that we collected 60–85 % of the local fauna at the sites sampled, and that species diversity decreases with increasing latitude. The four new species are named: *Bactrocera* (*Tetradacus*) *ernesti* Leblanc & Doorenweerd **sp. n.**, *B.* (*Asiadacus*) *connecta* Leblanc & Doorenweerd **sp. n.**, *B.* (*Parazeugodacus*) *clarifemur* Leblanc & Doorenweerd **sp. n.**, and *B.* (*Bactrocera*) *adamantea* Leblanc & Doorenweerd **sp. n.** In addition to morphological data COI DNA sequence data of both the COI-5P and COI-3P mitochondrial DNA gene regions is provided. Three of the four newly described species are morphologically and genetically easily distinguished from all other members of Dacini. *Bactrocera clarifemur* **sp. n.** is superficially similar to *B. pendleburyi* (Perkins) based on morphology, but there are several apomorphic characters to distinguish the two. Both COI and a segment of the nuclear gene Elongation Factor 1 alpha separate the two species as well.

Keywords

Dacini, *Dacus*, pest, taxonomy, *Zeugodacus*

Introduction

Dacini fruit flies are a species rich group distributed throughout the Old World tropics, including remote Pacific islands. It includes 932 described species, of which 83 are pests of fruit and fleshy vegetables, and new species are continuously being discovered (Vargas et al. 2015, Doorenweerd et al. 2018). Extensive surveys for Dacini fruit flies were carried out in Asia in recent decades (Linder and McLeod 2008). Vietnam was particularly well surveyed, with 78 species, including 19 described as new, reported to occur in the country (Drew and Romig 2013, 2016, Table 1).

Several advances have been made in recent years towards reconstructing the Dacini tree of life based on molecular data, the results of which are often in conflict with interpretations of the morphology of the flies (Krosch et al. 2012, Virgilio et al. 2015, Dupuis et al. 2017, San Jose et al. 2018). At present, there are no reliable apomorphy-based morphological circumscriptions for three of the four genera in the tribe: *Dacus*, *Bactrocera*, *Zeugodacus* (San Jose et al. 2018). Only *Monacrostichus*, which includes just two species, is recognized from its wing venation and is presumed to represent a basal branch, but no representatives have been included in any molecular phylogenetic studies. The genus *Dacus* is often presented as distinct by having 'merged' abdominal tergites (Drew and Romig 2013, 2016) but these are not merged in any physical sense, they just tightly join, hence this is not an absolute character and there are species which display this to a varying extent. The most recent phylogenies based on either a fairly good species coverage (San Jose et al. 2018) or a large amount of genetic data (Dupuis et al. 2017) support a sister relationship between *Dacus* and *Zeugodacus*, with *Bactrocera* as sister to both. Adding more species to these phylogenies will enable further studies of the morphological characters that may be used to recognize members of these genera.

Identifying Dacini flies is of interest not only to taxonomists and systematists, but also to customs officers, pest prevention program employees and farmers. Because of the large size of the group and the high levels of homoplasy between characters and little morphological diversity, morphology-based identifications are currently mostly reserved to specialists. Until we reach a better understanding of the relationships among species that will allow for an assessment of the polarity of morphological characters (San Jose et al. 2018), molecular diagnostics may be a preferred method for identifying potential pest species. Sequencing of the DNA barcoding marker COI (5'P region) has been applied to Dacini for both species identification and determining potential source of invading populations (e.g., Barr et al. 2014, Choudhary et al. 2017, Meeyen et al. 2014). However, the reliability of such approaches heavily depends on the availability of validated reference data (Mutanen et al. 2016). As part of a project to survey the genetic diversity of potential pest species across Asia and further understand phylogenetic relationships globally (Leblanc et al. 2015b, 2016), our team carried out Dacini fruit fly surveys in Vietnam in 2015 and 2017. A number of new country records and undescribed new species were uncovered, greatly aided by the inclusion of the male lure zingerone (Royer 2015, Royer et al. 2017) in the trapping. Four new species, which were also included under temporary species names in a recently published phylogeny (San Jose et al. 2018), are described here.

Table 1. Checklist of Dacine fruit flies of Vietnam, including previously known species, new country occurrence records, and number of specimens collected in the surveys (2015–2017) reported in this paper. A complete list of species of Vietnam and its neighboring countries is available on Suppl. material 1: Table S1 (supplementary online material).

Taxon	Lure	Ba Bể	Mê Linh – Tam Đảo	Bạch Mã	Cát Tiên
Genus *Bactrocera*					
B. abbreviata (Hardy)*	ZN	7	110	1579	74
B. adamantea Leblanc & Doorenweerd*	ZN	0	0	0	4
B. aethriobasis (Hardy)	ME	0	0	0	0
B. bhutaniae Drew & Romig	CL	1	15	5	8
B. bimaculata Drew & Hancock	CL	0	0	0	0
B. binhduongiae Drew & Romig	ME	0	0	0	0
B. bivittata Lin & Wang*	ME	0	0	3	2
B. carambolae Drew & Hancock [1]	ME, ZN	0	0	23	68
B. cibodasae Drew & Hancock	CL	0	0	0	0
B. clarifemur Leblanc & Doorenweerd*	ZN	0	0	4	45
B. connecta Leblanc & Doorenweerd*	ZN	0	0	1	3
B. correcta (Bezzi) [1]	ME	0	0	70	4
B. dongnaiae Drew & Romig	CL	0	0	0	9
B. dorsalis (Hendel) [1]	ME	1136	1369	1603	946
B. ernesti Leblanc & Doorenweerd*	ZN	0	0	6	0
B. eurycosta Drew & Romig	CL	0	0	0	0
B. flavoscutellata Lin & Wang	CL	0	0	5	0
B. fulvifemur Drew & Hancock	CL	0	0	0	0
B. fuscitibia Drew & Hancock	CL	0	0	0	0
B. gombokensis Drew & Hancock	CL	4	0	0	3
B. holtmanni (Hardy)	CL	0	0	0	0
B. illusioscutellaris Drew & Romig	CL, ZN	0	1	2	3
B. jaceobancroftii Drew & Romig	ME	0	0	0	0
B. kanchanaburi Drew & Hancock	ME	0	0	0	193
B. laithieuiae Drew & Romig	CL	0	0	0	0
B. lateritaenia Drew & Hancock	CL	0	0	11	5
B. latifrons (Hendel) [2]	latilure	0	0	0	0
B. limbifera (Bezzi)	CL	0	0	19	0
B. lombokensis Drew & Hancock	CL	0	0	0	0
B. neocognata Drew & Hancock	CL	0	0	0	0
B. nigrita (Hardy)	ME	0	0	0	0
B. nigrotibialis (Perkins)	CL	0	0	29	22
B. osbeckiae Drew & Hancock	CL	0	0	0	0
B. paraarecae Drew & Romig*	ME	0	0	1	9
B. pendleburyi (Perkins)*	ZN	0	0	17	1
B. propinqua Hardy & Adachi	CL	0	0	7	42
B. pruniae Drew & Romig [3]	No lure	0	0	0	0
B. pyrifoliae Drew & Hancock [2]	No lure	0	0	0	0
B. quasiunfulata Drew & Romig	CL	0	0	0	0
B. raiensis Drew & Hancock	ME	0	0	0	0
B. ritsemai (Weyenbergh)	CL	0	0	0	2
B. rubigina (Wang & Zhao)	CL, ZN	16	34	7	3
B. sapaensis Drew & Romig	CL	0	0	0	0
B. syzygii White & Tsuruta*	ZN	1	1	110	400
B. thailandica Drew & Hancock	CL	19	84	2	0
B. tuberculata (Bezzi) [2]	ME	0	0	0	0
B. umbrosa (Fabricius)* [3]	ME	0	0	11	0
B. usitata Drew & Hancock	CL	0	0	2	13
B. verbascifoliae Drew & Hancock	ME	0	0	0	0
B. wuzhishana Li & Wang	ME	0	2	1	0

Taxon	Lure	Ba Bể	Mê Linh – Tam Đảo	Bạch Mã	Cát Tiên
B. zonata (Saunders) [1]	ME	0	0	0	0
B. species 59 (*dorsalis* complex)**	CL	0	0	1	0
B. species 74**	ZN	0	0	0	1
B. species 104 (near *rubigina*) (ms6131)**	CL	0	0	0	3
B. species 105 (near *citima*) (ms6135)**	CL	0	0	0	3
B. species 106 (*dorsalis* complex)**	CL	0	0	9	17
Genus *Dacus*					
D. bannatus Wang	CL	0	0	0	0
D. discretus Drew & Romig	CL	0	0	0	0
D. dorjii Drew & Romig	CL	0	0	0	0
D. longicornis (Wiedemann) [4]	CL	4	0	0	2
D. satanas (Hering)	ZN	12	3	0	2
D. siamensis Drew & Hancock	CL	0	0	0	0
D. sphaeroidalis (Bezzi)	CL	0	0	0	0
D. tenebrosus Drew & Hancock*	CL, ZN	0	0	0	2
D. vijaysegerani Drew & Hancock	CL, ZN	0	0	0	41
Genus *Zeugodacus*					
Z. ablepharus (Bezzi)	CL	4	0	0	0
Z. aithonota (Drew & Romig)	CL	0	0	0	0
Z. apicalis (de Meijere)	CL	0	0	1	253
Z. assamensis White	CL	0	0	0	0
Z. atrifacies (Perkins)	CL	0	0	2	0
Z. baoshanensis (Zhang, Ji, Yang & Chen)	CL	0	0	0	0
Z. caudatus (Fabricius) [5]	CL	0	0	0	3
Z. cilifer (Hendel)	CL	2	1	0	0
Z. cucurbitae (Coquillett) [4]	CL, ZN	1	0	1	66
Z. daclaciae (Drew & Romig)	CL	0	0	0	0
Z. diaphorus (Hendel)	CL	0	0	0	1
Z. diversus (Coquillett) [5]	ME	0	0	0	0
Z. heinrichi (Hering)	CL, ZN	223	0	66	19
Z. hoabinhiae (Drew & Romig)	CL	0	0	0	0
Z. hochii (Zia) [4]	CL, ZN	0	0	0	60
Z. incisus (Walker)	CL	2	0	0	5
Z. infestus (Enderlein)	CL	143	0	0	0
Z. isolatus (Hardy)	CL	0	0	0	0
Z. khaoyaiae (Drew & Romig)*	CL	10	0	0	0
Z. maculifacies (Hardy)	CL	0	0	0	0
Z. melanofacies (Drew & Romig)*	CL	0	0	0	1
Z. mukiae (Drew & Romig)	CL	0	0	0	0
Z. nakhonnayokiae (Drew & Romig)	CL	0	0	0	0
Z. ochrosterna (Drew & Romig)	CL	0	0	0	0
Z. proprescutellatus (Zhang, Che & Gao)*	CL	0	0	2	0
Z. scutellaris (Bezzi) [5]	CL	0	0	0	0
Z. scutellatus (Hendel) [5]	CL	41	13	0	0
Z. sinensis (Yu, Bai & Chen)*	CL	0	0	1	0
Z. sonlaiae (Drew & Romig)	CL	0	0	0	0
Z. tau (Walker)	CL	200	36	5	73
Z. trilineatus (Hardy)	CL	0	0	0	0
Z. vultus (Hardy)	CL	0	0	0	0
Z. yoshimotoi (Hardy)	CL	0	0	0	0
Z. species 72 (near *infestus*)**	CL	0	0	0	1
Z. species 101 (near *tau*)**	CL	0	0	0	2

* New country occurrence records. ** Undescribed new species. [1] Polyphagous fruit pest. [2] Oligophagous fruit pest. [3] Monophagous fruit pest. [4] Cucurbit fruit pest. [5] Cucurbit flower pest. Pest categorizations after Vargas et al. (2015).

Materials and methods

Collecting and curation

To collect fruit flies, we used sets of three traps made of modified urine sample cups (described in Leblanc et al. 2015a), separately baited with the fruit fly lures methyl eugenol, cue-lure and zingerone, with a 10×10mm piece of dichlorvos insecticide strip to kill trapped flies. These traps were maintained for three to five days at each of 220 sites in forest reserves and national parks in 2015 and 2017 (Figure 1). Specimens retrieved from the traps were preserved in 95 % ethanol and stored in a -20 °C freezer when returned to the laboratory. A selection of specimens was dried and pinned. We pinned these specimens fresh out of the ethanol each with a minuten pin through the scutum, then soaked them in ethyl-ether for 3–12 hours to preserve the coloration, and double-mounted them. We photographed specimens using a Nikon D7100 camera attached to an Olympus SZX10 microscope. Pictures from different focal plains were merged using Helicon Focus pro v6.7.1. Initially, we performed identifications based on morphology, using available keys (Drew and Hancock 1994, Drew and Romig 2016). Measurements were taken using an ocular grid mounted on an Olympus SZ30 dissecting microscope. The collecting and taxonomy information for all specimens can be found at BOLD http://dx.doi.org/10.5883/DS-VIETDACI.

Morphological terms

For the morphological terms we generally follow White (1999). We have attempted to avoid comparative terms to describe the size of structures, although this was sometimes necessary to stay consistent with the common practice in Dacini. In particular, two structures that have typically been used to designate subgenera group or genus assignments: the male surstylus posterior lobe size and the concavity of sternum V (Drew and Romig 2013, figure 22; Virgilio et al. 2015, De Meyer et al. 2015). The posterior lobe of the male surstylus is considered 'long' when it is twice as long as the anterior lobe, and the concavity is considered 'deep' when it reaches midway of the tergum. The application of subgenera in their current sense is debatable, as they are mostly not monophyletic (San Jose et al. 2018). However, to allow for easier comparison with existing literature and in the absence of a better alternative, we assign the newly described species to a subgenus that best fits morphologically. For each species we indicate in the notes section how it may be incorporated into the widely used keys for Dacini in Asia (Drew and Romig 2016).

DNA extraction, PCR and sequencing

The new species we describe here have been included in a previously published seven-gene molecular phylogeny under temporary species names (San Jose et al. 2018), where

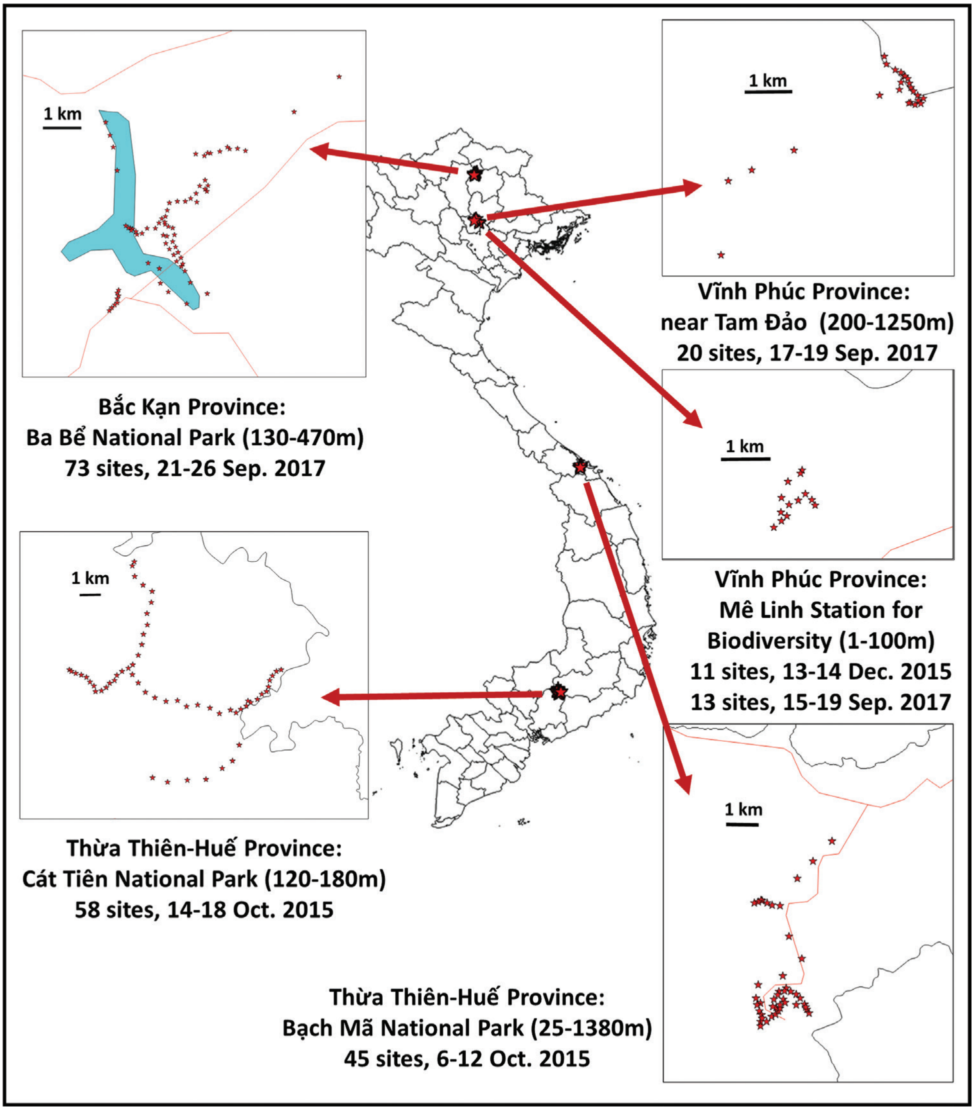

Figure 1. Trapping locations in the Vietnam surveys (2015, 2017).

the methods for DNA extraction, PCR primers and conditions and sequencing methods were extensively described. For all holotypes we extracted DNA from one dissected hind leg and sequenced the seven genes that were used for the molecular phylogeny: the 3'P side of COI, two fragments of CAD, Wingless, White-eye, PGD, EF1-alpha, and Period. For this study we also sequenced the 5'P side of COI, the DNA barcoding fragment, using the primer pair L1-DCHIM (5'-TCGCCTAAACTTCAGCCATT-3') and HCO-2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'). Concatenating the 5'P barcoding side and 3'P side of COI resulted in a 1,535 base-pair (bp) long alignment of fragments. Some additional EF1-alpha sequence data were produced for specimens of *B. clarifemur*, using the primers and sequencing conditions as described in San Jose et al. (2018). All sequences are made available both through BOLD (dx.doi.org/10.5883/DS-VIETDACI) and GenBank (accession numbers cited in the BOLD link and accession numbers MG683030–MG684292, previously published in San Jose et al. (2018), with *B. connecta* referred to as *Bactrocera* sp. 68, *B. adamantea* as sp. 69, *B. clarifemur* as sp. 70 and *B. ernesti* as sp. 71). Maximum likelihood trees were generated using FastTree v2.1.5 (Price et al. 2010), implemented in Geneious R10.2.3, using the General-Times-Reversable (GTR) model of nucleotide evolution. To account for the varying rates of evolution across sites, we used 25 rate categories for each site. Support values were calculated with the Shimodaira-Hasegawa test (Shimodaira and Hasegawa 1999) and are indicated on each respective branch. Sample numbers for the taxa refer to the individual voucher numbers of the flies. For the statistical parsimony (TCS) haplotype network based on COI sequence data for the species pair *B. pendleburyi* and *B. clarifemur*, we trimmed the ends of the alignments with ambiguous bases, and reconstructed a network using PopArt (Clement et al. 2002, Leigh and Bryant 2015). The phylogenies presented on Figures 3, 5, 11 are single gene trees and are interpreted as molecular diagnostic tools, for phylogenetic relationships we refer to the published multi-gene phylogenies (San Jose et al. 2018, Dupuis et al. 2017).

Estimating total diversity

To determine the fraction of the diversity we covered by our sampling, whilst acknowledging the male lure collecting method bias, we used EstimateS (Colwell 2013) to generate species accumulation curves. The estimates are based on the number of species collected, in particular singletons and doubletons, to extrapolate to the diversity with increasing number of samples using the incidence-based Chao 2 algorithm. The Chao 2 indicator was selected because it does not include abundance in its extrapolation, compensating for the abundance bias in our data related to how strongly each species is attracted to the lures that were used, plus, with several species being agricultural pests, the overall diversity abundance likely does not follow a normal distribution. Diversity estimations were done for the overall dataset and for the four broad sampled locations (Figure 1) separately, with 100 randomizations without replacement for confidence intervals.

Abbreviations

UHIM	University of Hawaii Insect Museum
CTAHR	University of Hawaii College of Tropical Agriculture and Human Resources
USDA	United States Department of Agriculture
WFBM	University of Idaho's William F. Barr Entomological Museum
VNMN	Vietnam National Museum of Nature

Results

We collected a total of 9,516 specimens, representing 56 species (Table 1). Eleven previously described species, most of which are known to occur in neighboring countries, are new occurrence records for Vietnam. Another 11 species that were collected are either new to science, four of which are described below, or we were otherwise unable to link them to any described species. Our survey results increase the total number of described species in Vietnam from 78 to 93, 10 % of the globally known diversity of Dacini (Doorenweerd et al. 2018). Potentially, an additional 52 species, known to be present in China, Laos, Cambodia, and Thailand, excluding southern Thailand, may be found in Vietnam (Drew and Romig 2013, Leblanc et al. 2016; listed in Suppl. material 1: Table S1).

Zingerone attraction

Noteworthy is the capture of *B. syzygii*, a species not attracted to the traditional male lures methyl eugenol and cue lure, and previously assumed to be endemic to Sri Lanka. We collected 512 specimens in zingerone-baited traps in all four parks, indicating that it is commonly present. It was also recently collected in Bangladesh (LL, unpublished) and in India (David et al. 2017). A larger distribution for *B. syzygii* could have been expected, considering the common occurrence of *Syzygium* host plants in the region. Zingerone is also a new lure record for multiple species previously not known to be attracted to male lures: *B. abbreviata* (all 1,770 specimens collected in zingerone), *B. illusioscutellaris* (3/6, i.e. 3 of 6 specimens collected in zingerone), *B. pendleburyi* (all specimens), *B. rubigina* (1/60), *D. satanas* (16/17), *D. tenebrosus* (2/2 specimens), *D. vijaysegerani* (all 41 specimens), *Z. heinrichi* (211/308), and *Z. hochii* (15/60). The four new species described in this paper were also drawn to zingerone. Several other species were collected in very small numbers in zingerone traps, and we therefore find it too uncertain to record them as being attracted to zingerone: *B. bhutaniae* (3 specimens), *B. flavoscutellata* (1), *B. gombokensis* (2), *B. kanchanaburi* (1), *B. lateritaenia* (1), *Z. atrifacies* (1), *Z. infestus* (2), *Z. khaoyaiae* (1), and *Z. tau* (4). Even with only a single specimen out of 60 drawn to zingerone, the attraction of *B. rubigina* to that lure was confirmed in surveys carried out in Bangladesh in 2017, with 2,237 specimens collected in cue-lure and 63 collected in zingerone-baited traps (LL, unpublished).

Diversity estimates

A species accumulation curve, generated using all data across the four locations (Figure 2A), suggest that the 56 species collected represent 60–85 % of the local fauna

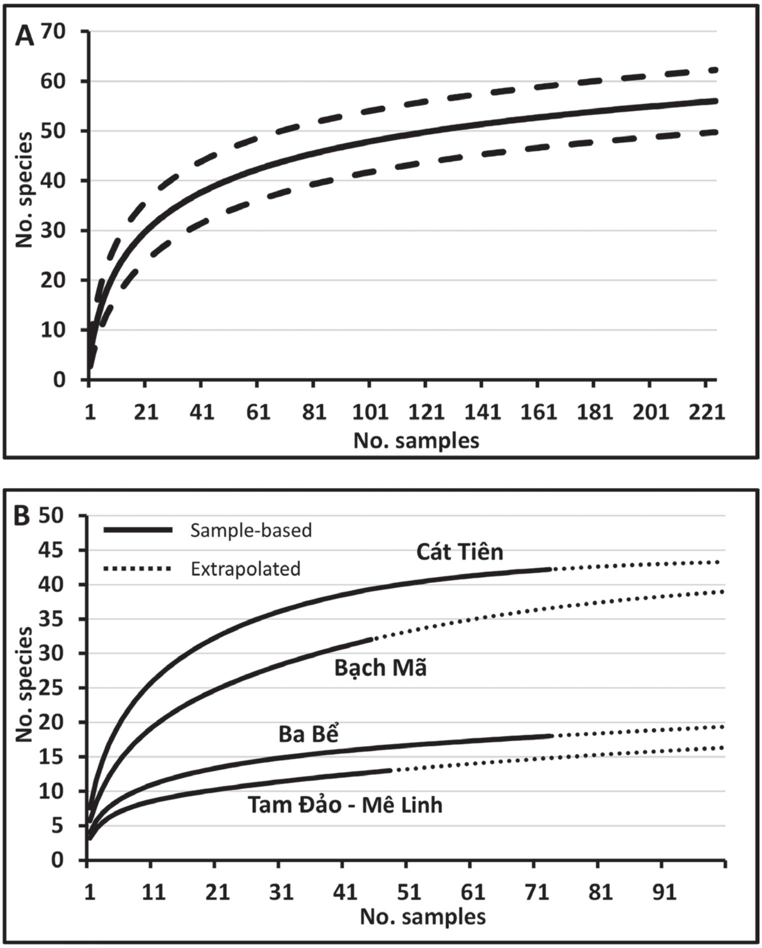

Figure 2. Species accumulation curves for species collected in fruit fly surveys (2015, 2017) across the entire region (**A**), and for the four broad surveyed locations (**B**).

attracted to the three male lures methyl eugenol, cue lure and zingerone, with a Chao 2 mean estimate of 65.0 species (95 % CI = 58.1–93.9). By far the highest species diversity was collected and projected in central and southern Vietnam: Cát Tiên with 41 species and a mean estimate of 43.1 (41.3–54.2), and Bạch Mã with 32 species and a mean estimate of 39.3 (33.7–63.1) (Figure 2B). The northern sites yielded a lower diversity, despite intense sampling effort (117 trapping sites): Ba Bể with 18 species and a mean estimate of 21.0 (18.4–40.7) and Tam Đảo and Mê Linh together with 13 species, with mean estimate of 16.0 (13.4–35.6). These estimates are based on species attracted to male lures. It is likely that a broader diversity will be uncovered with the regular use of zingerone in trapping and through host fruit surveying. The four new species described below were all collected in zingerone-baited traps.

***Bactrocera* (*Tetradacus*) *ernesti* Leblanc & Doorenweerd, sp. n.**
http://zoobank.org/DC201837-F7AE-487B-86C0-D09B903F4CA7

Holotype. Male. Labelled: "Vietnam: Thừa Thiên-Huế Province, Bạch Mã National Park, 16.2297N, 107.8494E, 6–8-x-2015, M. San Jose and D. Rubinoff, FF485, zingerone lure. Molecular voucher ms6192". Deposited in UHIM. **Paratypes**: 5 males. Same data as holotype. All specimens pinned and one specimen is molecular voucher ms6255. Three of the paratypes are deposited at UHIM, one at WFBM and one at VNMN.

Differential diagnosis. *Bactrocera ernesti* is similar to other members of the subgenus *Tetradacus* in having an elongate oval abdomen with a petiolate base [oval in most *Bactrocera*] with separate terga [tightly joined in *Dacus*], and a slight concavity of sternum V and short surstylus lobe in the males. It is most similar to *B. minax* and *B. brachycera*, but differs from both in lacking a lateral yellow band connecting the postpronotal lobes to the notopleural suture, the absence of medial postsutural vitta, the anteriorly convergent lateral postsutural vittae, the lightly infuscate wing, and absence of distinct costal band, and the black bands on every abdominal segment.

Molecular diagnostics. *B. ernesti* sp. n. was referred to as *Bactrocera* species 73, represented by the holotype, in the seven-gene phylogeny presented in San Jose et al. (2018). Based on the sampling therein, its closest relative is *B.* (*Tetradacus*) *tsuneonis* (Miyake). The closest relative we could identify based on COI alone is the Australian species *B. visenda*, at a minimum intraspecific pairwise genetic distance of 13.52 % [14.89 % in COI5P and 12.27 % in COI3P] (Figure 3).

Description of adult. *Head* (Figure 4A). Vertical length 1.82 ± 0.04 (*SE*) (1.75–1.85) mm. Frons, of even width, length 1.16 ± 0.05 (1.10–1.26) times breadth; uniformly fulvous; anteromedial hump and frons covered by short red–brown hairs; orbital and frontal setae, when present, red–brown: orbital setae absent or at most very weak and frontal setae very weak and may be restricted to superior pair; lunule fuscous. Ocellar triangle black. Vertex fulvous. Face fulvous with elongate black spot in lower half of each antennal furrow, connected by a faint narrow fuscous band across mid height of face; length 0.69 ± 0.02 (0.65–0.70) mm. Genae fulvous, with fuscous sub–ocular spot; one large and numerous smaller red–brown setae present. Occiput fulvous with fuscous markings laterally on its lower half; occipital row with 9–13 dark setae and an irregular inner row of finer setae. Antennae with segments 1 (scape) and 2 (pedicel) fulvous, segment 3 (first flagellomere) fulvous with pale fuscous on outer surface; a strong red–brown dorsal seta on segment 2; arista black (fulvous basally); length of segments: 0.19 ± 0.01 (0.18–0.20) mm; 0.26 ± 0.02 (0.23–0.28) mm; 0.76 ± 0.04 (0.70–0.83) mm.

Thorax (Figure 4B, E). Scutum red–brown except a broad light fuscous lanceolate pattern on its posterior third, anteriorly prolonged into three very narrow lines reaching anterior margin, narrow elongate dark fuscous bands adjacent to inner margins of lateral postsutural vittae, broad lateral dark fuscous markings behind postpronotal lobes and two short and narrow parallel dark fuscous bands between postpronotal lobes. Pleural areas dark fuscous except red–brown below postpronotal lobes, anterior

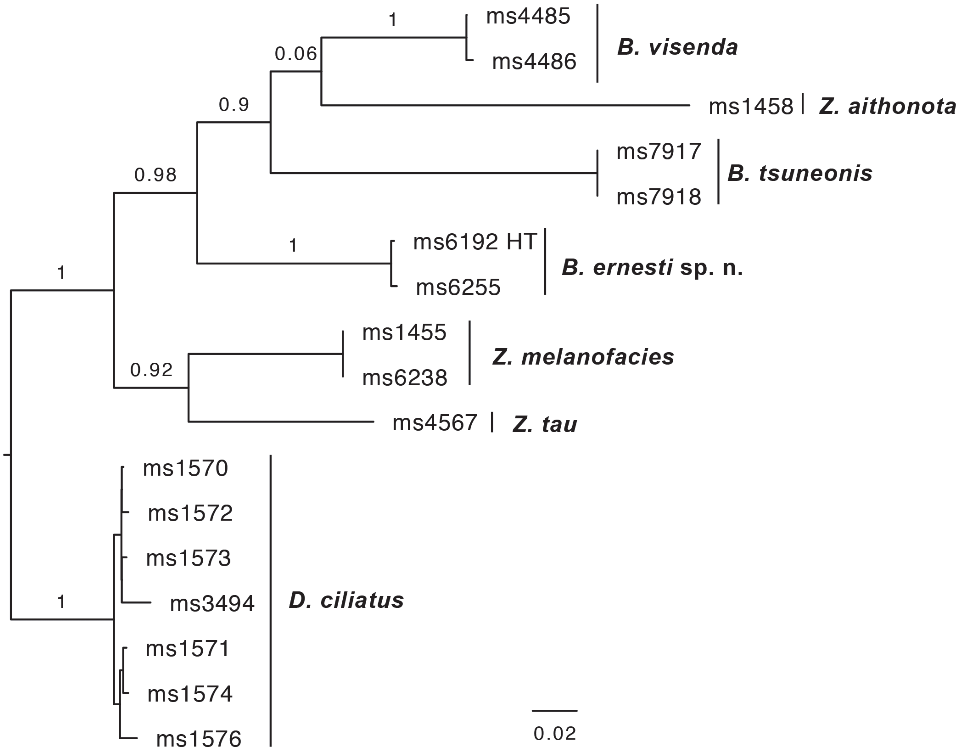

Figure 3. Maximum likelihood tree based on COI sequences of *B. ernesti* sp. n. and several of its genetically closest neighbors, which include *Bactrocera*, *Zeugodacus* and *Dacus* species. Bootstrap branch supports shown for intraspecific relationships. Abbreviations: HT holotype.

half of anepisternum and posterior portion of katepisternum. Yellow markings as follows: postpronotal lobes; notopleura; medium sized and parallel-sided mesopleural (anepisternal) stripe, reaching anterior margin of notopleuron, continuing to katepisternum as a transverse spot, anterior margin straight; entire katatergite except red–brown narrowly along posterior margin; lower quarter to half of anatergite (remainder dark fuscous and red-brown on posterior margin of lower quarter to half); two moderately broad parallel sided lateral postsutural vittae ending shortly before intra-alar setae and curved slightly inwards along notopleural suture. Postnotum medially red–brown and laterally black. Scutellum yellow except for narrow dark fuscous basal band. Setae: 2 scutellar; 1 intra-alar; 1 posterior supra-alar; 1 mesopleural; 4 notopleural; 4 or 6 scapular (often a second pair of median scapular, just behind each bristle); anterior supra-alar and prescutellar bristles absent; all setae well developed and red–brown.

Legs (Figure 4E). Fore coxae yellow with outer face dark fuscous; fore trochanters and mid coxae and trochanters yellow; hind coxae and trochanters dark fuscous. Femora yellow with broadly fuscous outer and inner surfaces. Fore and mid tibiae fulvous with dark fuscous on outer face of fore tibia and around base of mid tibia; hind tibiae dark fuscous. Tarsi fulvous with dark fuscous fore tarsomeres 2–5 and ventral face of fore basitarsus. Mid-tibiae each with an apical black spur.

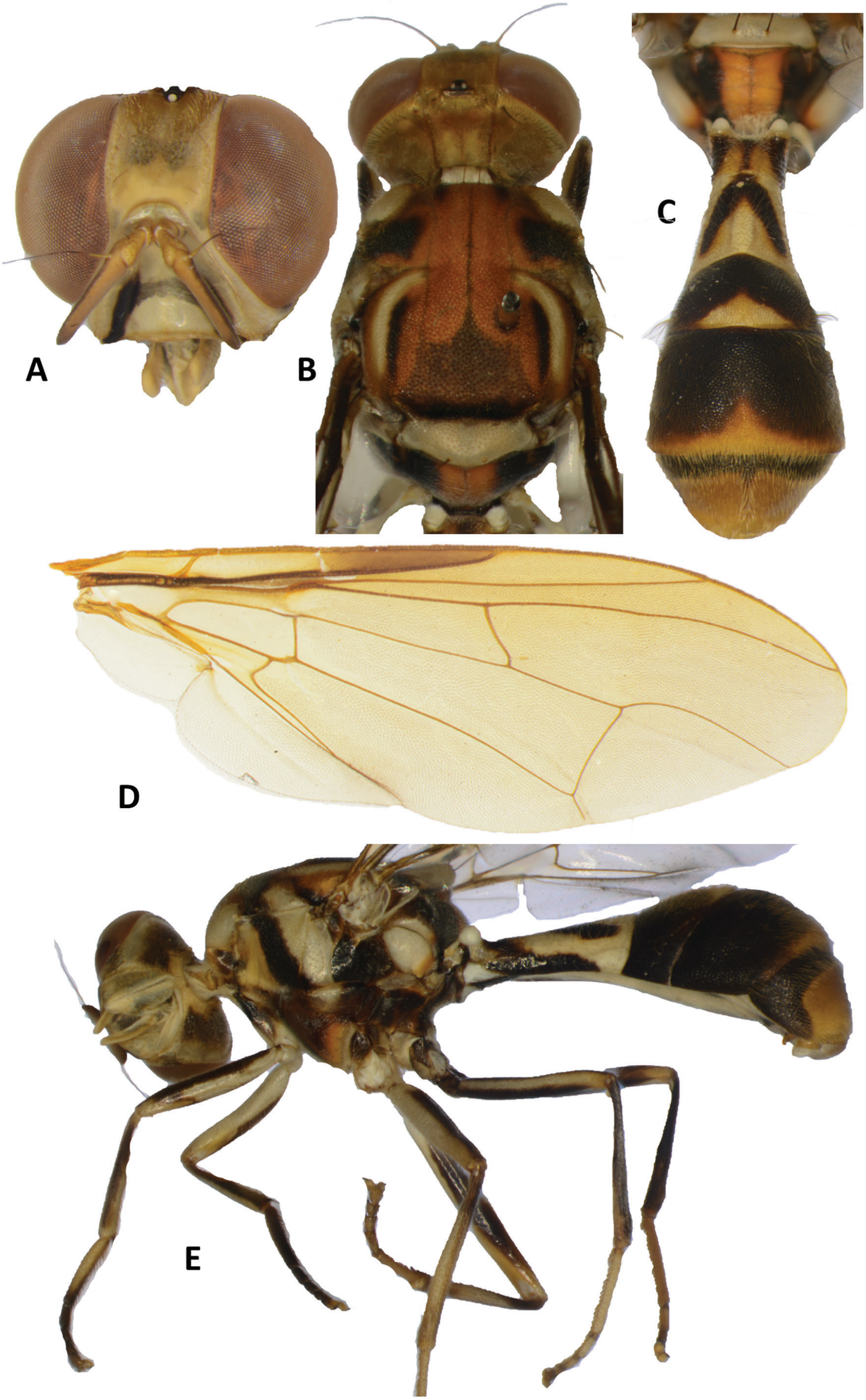

Figure 4. *Bactrocera* (*Tetradacus*) *ernesti*. **A** head **B** head and scutum **C** abdomen **D** wing **E** lateral view.

Wings (Figure 4D). Length 7.56 ± 0.21 (7.22–7.78) mm; basal costal (bc) cell infuscate and costal (c) cells mostly colorless except at apex; microtrichia along costal margin of cell bc and along costal margin and outer corner of cell c; remainder of wings colorless except fuscous subcostal cell, and lightly infuscate membrane between R_1 and R_{4+5}; supernumerary lobe weakly developed.

Abdomen (Fig. 4C, E). Elongate oval and petiolate; terga free; pecten present on tergum III; posterior lobe of surstylus short; abdominal sternum V with a slight concavity on posterior margin. Tergum I as long as wide and tergum II and sterna I and II longer than wide. Tergum I medially fuscous with a faint narrow fuscous medial longitudinal band and laterally black. Tergum II yellow with a large inverted V-shaped medial marking. Tergum III black with large apical triangular yellow marking. Tergum IV black with apical fulvous band with a medial expansion; tergum V fulvous with a narrow basal black band expanded laterally to half the tergum length. Abdominal sterna dark, except yellow sternum II.

Etymology. This species is named after Ernest James Harris (1928–2018), in honor of his long career working as a fruit fly ecologist for the USDA (1962–2006). Some of Dr. Harris's important contributions include the field implementation of the first eradication program against invasive fruit flies in the Mariana Islands, the establishment of Mediterranean fruit fly suppression programs in North Africa and Chile and studies on its ecology and SIT in Hawaii, as a prelude to the initiation of the ongoing SIT program to prevent its establishment in California, and the development of mass rearing techniques of the fruit fly parasitoid *Fopius arisanus* (Sonan). He published over 120 scientific papers and was honored with distinctions by the State of Arkansas Black Hall of Fame (1999), the NAACP Hawaii Chapter (2012), the Alpha Phi Alpha Fraternity National award (2013), the US Congressional Gold Medal (2016), the USDA-ARS Hall of Fame (2017), and as CTAHR Outstanding Alumnus (2017). His emergence as African American from a modest cotton farming family in Arkansas to an internationally respected prominent scientist, through hard work and his love for his research, makes Ernie a true role model for the senior author of this paper. Biographic sketches of Dr. Harris were published by Riddick et al. (2015) and Leblanc and Vargas (2018, in press).

Notes. *Bactrocera ernesti* keys to couplet 2, page 314, in Drew and Romig (2016), where it can be differentiated from *B. minax* and *B. brachycera* based on the characters mentioned in the differential diagnosis.

***Bactrocera* (*Asiadacus*) *connecta* Leblanc & Doorenweerd, sp. n.**

http://zoobank.org/E534D6C5-300A-4A64-95C7-FE8EAF1AA134

Holotype. Male. Labelled: "Vietnam: Thừa Thiên–Huế Province, Bạch Mã National Park, 16.2098N, 107.8632E, 6-12-x-2015, M. San Jose and D. Rubinoff, FF494, zingerone trap." ms6195 Deposited in UHIM. **Paratypes**: 3 males. Vietnam, Lâm Đồng Province, Cát Tiên National Park, 16–18-x-2015, at the following sites, identified by their geographical coordinates: 11.4485N, 107.4416E, (1 pinned, molecular voucher ms6105), 11.4447N, 107.4372E, (2 pinned, one molecular voucher ms6239). All specimens collected by Michael San Jose and Dan Rubinoff in zingerone baited traps. One paratype deposited at UHIM, one at WFBM and one at VNMN.

Differential diagnosis. *Bactrocera connecta* shares morphological features common to all members of *Asiadacus* (absence of prescutellar and anterior supra-alar setae, scutellum with one pair of setae, and males with long posterior lobe on surstylus, slight concavity of sternum V and pecten of cilia present on the abdominal tergum III). It is distinguished from other members of *Asiadacus* by the elongate facial spots along antennal furrows and the small to extensive fuscous transverse band on face (Fig. 6A, B), the broad, apically expanded costal band (Figure 6H, I), and the absence of a medial longitudinal band and presence of extensive lateral black markings on the abdomen (Figure 6D–G).

Molecular diagnostics. *Bactrocera connecta* was referred to as *Bactrocera* species 68, sister to *B.* (*Apodacus*) *visenda* (Hardy), in the seven-gene phylogeny presented in San Jose et al. (2018). The nearest neighbor we could identify based on COI sequence data is *Zeugodacus melanofacies*, at 15.34 % minimum pairwise intraspecific genetic distance [16.18 % in COI5P and 14.47 % in COI3P] (Figure 5).

Description of adult. *Head* (Figure 6A, B). Vertical length 1.64 ± 0.23 (*SE*) (1.45–1.88) mm. Frons, of even width, length 1.13 ± 0.07 (1.07–1.22) times as long as broad; fulvous with fuscous around orbital setae and on anteromedial hump; latter covered by short red–brown hairs; orbital setae black: one pair of superior and two pairs of inferior fronto-orbital setae present; lunule yellow. Ocellar triangle black. Vertex fuscous. Face fulvous with elongate black spots in each antennal furrow and a fuscous band across lower half of face varying from a small medial spot (Figure 6A) to an entire band across face (Figure 6B); length 0.63 ± 0.09 (0.53–0.75) mm. Genae fulvous, with dark fuscous sub-ocular spot; black seta present. Occiput light to dark fuscous (fulvous laterally in one specimen) and yellow along eye margins; occipital row with 9–11 dark setae. Antennae with segment 1 (scape) fulvous, segments 2 (pedicel) fulvous and fuscous on outer surface, and segment 3 (first flagellomere) fuscous and narrowly fulvous on inner surface; strong red–brown dorsal seta on segment 2; arista black (fulvous basally); length of segments: 0.23 ± 0.02 (0.20–0.25) mm; 0.34 ± 0.02 (0.33–0.38) mm; 0.76 ± 0.07 (0.70–0.83) mm.

Thorax (Figs 6C, 7). Scutum black except sometimes with red–brown as limited markings behind postpronotal lobes and anterior to lateral postsutural vittae and area below postsutural vittae. Pleural areas black except usually red–brown anterior portion of anepisternum. Yellow markings as follows: postpronotal lobes and notopleura (notopleural callus), usually connected by a lateral longitudinal band; medium sized mesopleural (anepisternal) stripe, reaching midway between anterior margin of notopleura and anterior notopleural seta dorsally, continuing to katepisternum as a transverse spot, anterior margin convex; anatergite (posterior apex black); anterior 75 % of katatergite (remainder black); moderately broad medial postsutural vitta beginning at level of or slightly anterior of prescutellar setae and ending at or slightly beyond the

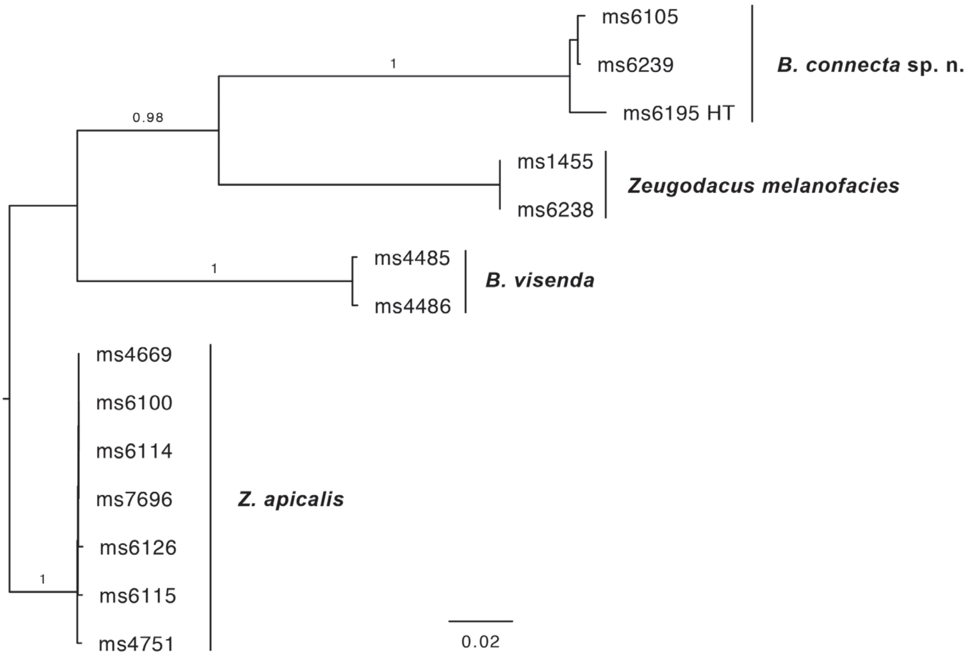

Figure 5. Maximum likelihood tree based on COI sequences of *B. connecta* sp. n. and several of its genetically closest neighbors, which include both *Bactrocera* and *Zeugodacus* species. Bootstrap branch supports shown for intraspecific relationships. HT = holotype.

level of notopleural suture; two moderately broad parallel sided lateral postsutural vittae ending at or shortly before intra-alar setae and curved inwards along notopleural suture. Postnotum black with apical median red–brown spot. Scutellum yellow except for narrow black basal band. Setae (number of pairs): 1 scutellar; prescutellar absent; 1 intra-alar; 1 posterior supra-alar; anterior supra-alar absent; 1 mesopleural; 2 notopleural; 4 scapular; all setae well developed and red–brown.

Legs (Figure 7). Femora fulvous, except for dark fuscous ventral faces of basal three quarters of fore femur, apical three quarters of mid femur and apical two–fifths of hind femur, and yellow basal quarter of mid femur and basal three–fifths of hind femur; tibiae dark fuscous, with or without ventral faces narrowly fulvous; mid-tibiae each with an apical black spur; tarsi fulvous.

Wings (Figure 6H, I). Length 5.75 ± 0.67 (5.11–6.67) mm; basal costal (bc) and costal (c) cells fuscous and both covered with microtrichia; remainder of wings colorless except broad fuscous costal band nearly confluent with R_{4+5} and broadly expanded apically; anal streak absent; dense aggregation of microtrichia around A_1 + CuA_2; supernumerary lobe of medium development.

Abdomen (Figs 6D–G, 7). Elongate oval; terga free; pecten present on tergum III; posterior lobe of surstylus long; abdominal sternum V with a slight concavity on posterior margin. Tergum I and sterna I and II wider than long. Tergum I black. Tergum II yellow with sub-basal or basal broad medial transverse black band that may be extend-

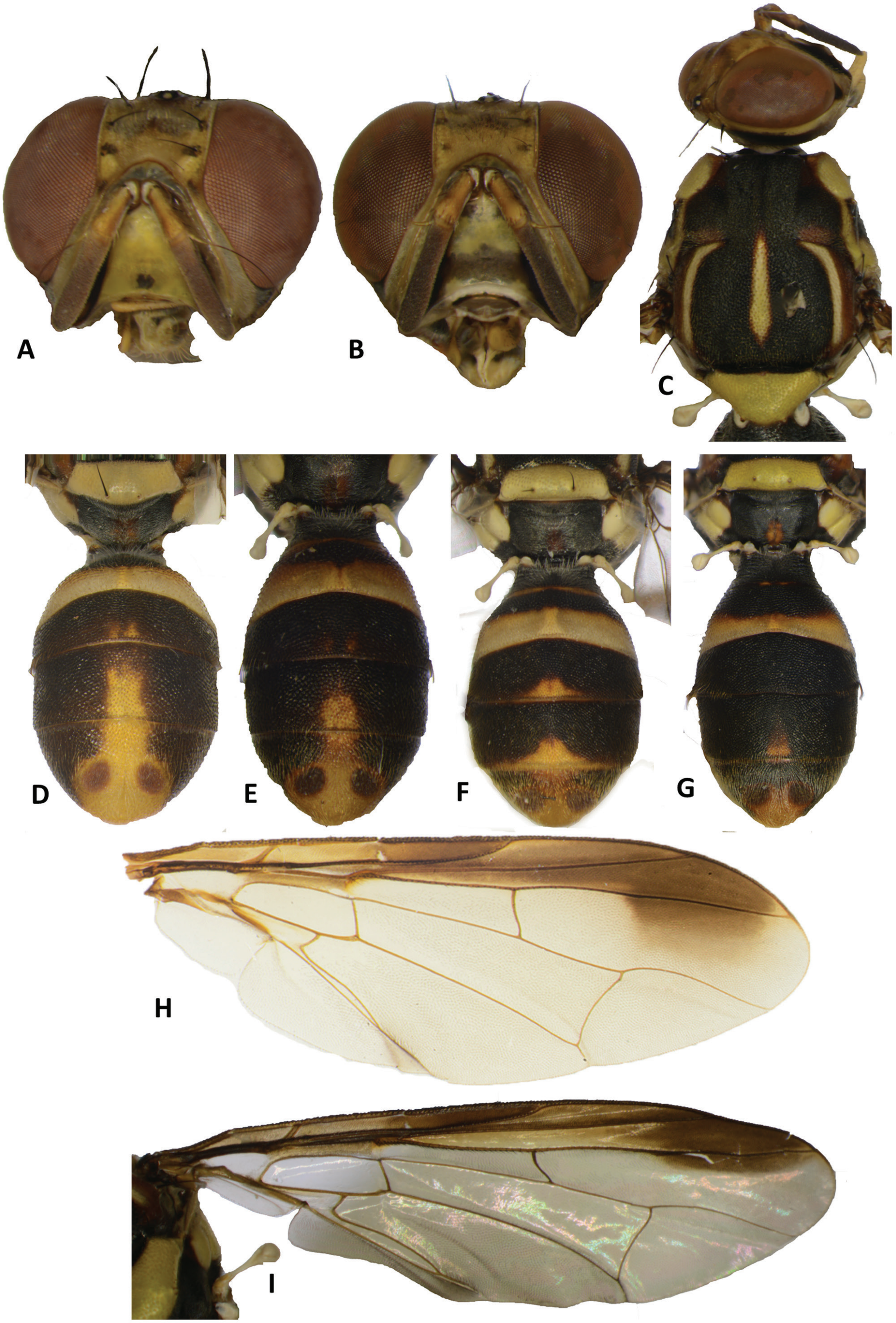

Figure 6. *Bactrocera* (*Asiadacus*) *connecta*. **A, B** head **C** head and scutum **D, E, F, G** abdomen variation **H, I** wing.

Figure 7. *Bactrocera* (*Asiadacus*) *connecta*: lateral view.

ed to cover entire basal half of tergum. Terga III–V black with fulvous areas as small markings on apex of tergum III and narrow median area on tergum IV (or restricted to small apical median marking), continued on base of tergum V and expanded around ceromata. A pair of dark fuscous ceromata (shining spots) on tergum V. Abdominal sterna black, except fulvous sternite II.

Etymology. The species name is an adjective that refers to the longitudinal yellow band connecting the postpronotal lobes and notopleura.

Note. We have tentatively assigned *B. connecta* to *Asiadacus* based on the following combination of characters: absence of prescutellar and anterior supra-alar setae, scutellum with one pair of setae, a long posterior lobe of the male surstylus, slight concavity of sternum V and pecten of cilia present on the abdomen (Drew 1989, Drew and Romig 2016). All known species of *Asiadacus* were transferred to *Zeugodacus*, based on the surstylus and sternum V concavity characters which made them part of the *Zeugodacus* group of subgenera (de Meyer et al. 2015). Only more recently was one species, *B.* (*Asiadacus*) *apicalis*, genetically confirmed to belong to *Zeugodacus* (San Jose et al. 2018). In that same molecular phylogeny, however, *B. connecta* is only distantly related to *B. apicalis* and is placed in the basal grade of subgenera in *Bactrocera*. Recently, Hancock and Drew (2017, 2018) transferred all but two species of *Asiadacus* to the subgenera *Parasinodacus*, *Sinodacus* and *Zeugodacus*, leaving in *Asiadacus* the two species with a large, oval apical wing spot that reaches but does not cross vein M. Because *B. connecta* falls within *Bactrocera* in the recently published phylogeny (San Jose et al. 2018), it cannot be assigned to any of these three subgenera. Moreover, in *B. connecta* the lateral postsutural vittae are not extended as yellow markings beyond the notopleural suture, a character shared by the *Zeugodacus* group of subgenera and genus *Dacus*, referred to as "small notopleural xanthines" by White (2006) and "lateral yellow triangles that reach the notopleural lobes" by Hancock and Drew (2018). Because *B. connecta* cannot be fitted in existing subgenera and to avoid creating a new subgenus, we arbitrarily assign this species to the subgenus *Asiadacus* sensu Drew and Romig (2016), until the subgeneric relationships within *Bactrocera* are more clearly elucidated. It cannot be keyed beyond couplet 4, page 48, in Drew and Romig (2016), where it can be singled out by the costal band on the wing overlapping R_{2+3} and expanding apically (Figs 6H, I).

***Bactrocera* (*Parazeugodacus*) *clarifemur* Leblanc & Doorenweerd, sp. n.**

http://zoobank.org/22A6F281-868E-4FC5-9959-545E5F8BCBCE

Holotype. Male. Labelled: "Vietnam: Thừa Thiên–Huế Province, Cát Tiên NP, 11.4480N, 107.3826E, 14-18-x-2015, M. San Jose and D. Rubinoff, FF540, zingerone lure, molecular voucher ms6176". Deposited in UHIM. **Paratypes**: 48 males. Vietnam, Thừa Thiên-Huế Province, Bạch Mã National Park, 6–8-x-2015, at the following sites, identified by their geographical coordinates: 16.2279N, 107.8557E, (1 in ethanol, molecular voucher ms6191), 16.1943N, 107.8490E, (2 in ethanol, including molecular voucher ms6194), 16.2006N, 107.8481E, (1 pinned). Vietnam, Lâm Đồng Province, Cát Tiên National Park, 14–18-x-2015, at the following sites, identified by their geographical coordinates: 11.4920N, 107.3855E, (7 pinned), 11.4867N, 107.3834E, (1 in ethanol, molecular voucher ms6175), 11.4764N, 107.3817E, (2 in ethanol, including molecular voucher ms6249), 11.4715N, 107.3809E, (2 in ethanol), 11.4480N, 107.3826E, (1 in ethanol, molecular voucher ms6176), 11.4436N, 107.3925E, (8 in ethanol), 11.4412N, 107.4026E, (3 pinned), 11.4419N, 107.4080E, (1 in ethanol, molecular voucher ms6177), 11.4394N, 107.4241E, (5 pinned and 2 in ethanol, including molecular vouchers ms6094 and ms6095, in ethanol), 11.4531N, 107.3557E, (1 in ethanol), 11.4486N, 107.3584E, (1 in ethanol), 11.4564N, 107.3686E, (1 in ethanol), 11.4381N, 107.4267E, (1 in ethanol), 11.4398N, 107.4290E, (1 in ethanol), 11.4539N, 107.4430E, (4 pinned), 11.4485N, 107.4416E, (3 pinned); 11.4472N, 107.4392E, (1 pinned). All specimens collected by Michael San Jose and Daniel Rubinoff in zingerone baited traps. All paratypes are deposited at UHIM, except five at WFBM and three at VNMN.

Differential diagnosis. *Bactrocera clarifemur* (Figure 9A–G) is genetically and morphologically closely related to *B. pendleburyi* (Perkins) (Figure 10A–E). Both share the defining characters of subgenus *Parazeugodacus* (two pairs of scutellar setae; male with lateral pecten on tergum III (though present or absent in different species of *Parazeugodacus* according to Hancock and Drew 2015), a slight concavity on posterior margin of abdominal sternum V, and posterior lobe of male surstylus short), as well as the absence of medial postsutural vitta and the entirely yellow scutellum. *Bactrocera clarifemur* differs from *B. pendleburyi* in that all femora are entirely fulvous (Figure 9G), whereas apices of all femora in *B. pendleburyi* are apically broadly dark (Figure 10E).

Molecular diagnostics. This species was referred to as *Bactrocera* sp 70 and is a close relative yet distinctly monophyletic sister to *B.* (*Parazeugodacus*) *pendleburyi*, in the San Jose et al. (2018) seven-gene phylogeny. Based on COI sequence data the two species are in two monophyletic clusters, with one exception. We found an aberrant COI haplotype from specimen (ms6095) that groups with *B. pendleburyi* in ML analysis, though at a minimum of 2.66 % pairwise genetic distance from any of the other specimens (Figure 8). Morphologically, specimen ms6095 fits with *B. clarifemur* (Figure 9A–G). We sequenced an additional nuclear gene to confirm the genetic distinction. Based on EF1a sequences, both species, with specimens from the same localities, were separated in monophyletic groups with a minimum pairwise distance of 1.35 %. A haplotype network of COI sequences further shows that specimen ms6095 is relatively distantly related to both and may eventually be found to represent a cryptic species. The nearest neighbor to both *B. pendleburyi* and *B. clarifemur* is *B. abbreviata* at 6.91 % minimum intraspecific pairwise distance in COI.

Description of adult. *Head* (Figure 9A). Vertical length 1.40 ± 0.13 (*SE*) (1.20–1.55) mm. Frons, of even width, length 1.32 ± 0.06 (1.22–1.43) times as long as broad; fulvous with usually fuscous spot around orbital setae and on anteromedial hump; latter covered by short red–brown hairs; orbital setae dark fuscous: one pair of superior and two pairs of inferior fronto-orbital setae present; lunule yellow. Ocellar triangle black. Vertex fuscous. Face fulvous with medium sized oval black spots in each antennal furrow; length 0.47 ± 0.04 (0.40–0.53) mm. Genae fulvous, with fuscous sub-ocular spot; red–brown seta present. Occiput dark fuscous and yellow along eye margins; occipital row with 5–7 dark setae. Antennae with segments 1 (scape) and 2 (pedicel) fulvous and segment 3 (first flagellomere) fulvous with pale fuscous on outer surface; a strong red–brown dorsal seta on segment 2; arista black (fulvous basally); length of segments: 0.21 ± 0.02 (0.18–0.23) mm; 0.24 ± 0.01 (0.23–0.25) mm; 0.62 ± 0.05 (0.53–0.68) mm.

Thorax (Figure 9B, G). Scutum black and frequently red–brown below lateral postsutural vittae. Pleural areas black and usually narrowly red–brown on anterior corner and frequently posterior corner of proepisternum anterior to postpronotal lobes. Yellow markings as follows: postpronotal lobes; notopleura (notopleural callus); medium sized mesopleural (anepisternal) stripe, reaching anterior margin of notopleura dorsally, continuing to katepisternum as a transverse spot, anterior margin slightly convex; anatergite (posterior apex black); anterior 60 % of katatergite (remainder black); two moderately broad and short postsutural vittae, tapering posteriorly and ending a short distance behind anterior intra-alar setae. Postnotum black. Scutellum yellow except for narrow black basal band. Setae (number of pairs): 2 scutellar; 1 prescutellar; 1 intra-alar; 1 posterior supra-alar; 1 anterior supra-alar; 1 mesopleural; 1 notopleural; 4 scapular; all setae well developed and black.

Legs (Figure 9G). Femora entirely fulvous; fore and hind tibiae dark fuscous, mid tibia basally dark fuscous and apically becoming fulvous; mid-tibiae each with an apical black spur; tarsi fulvous.

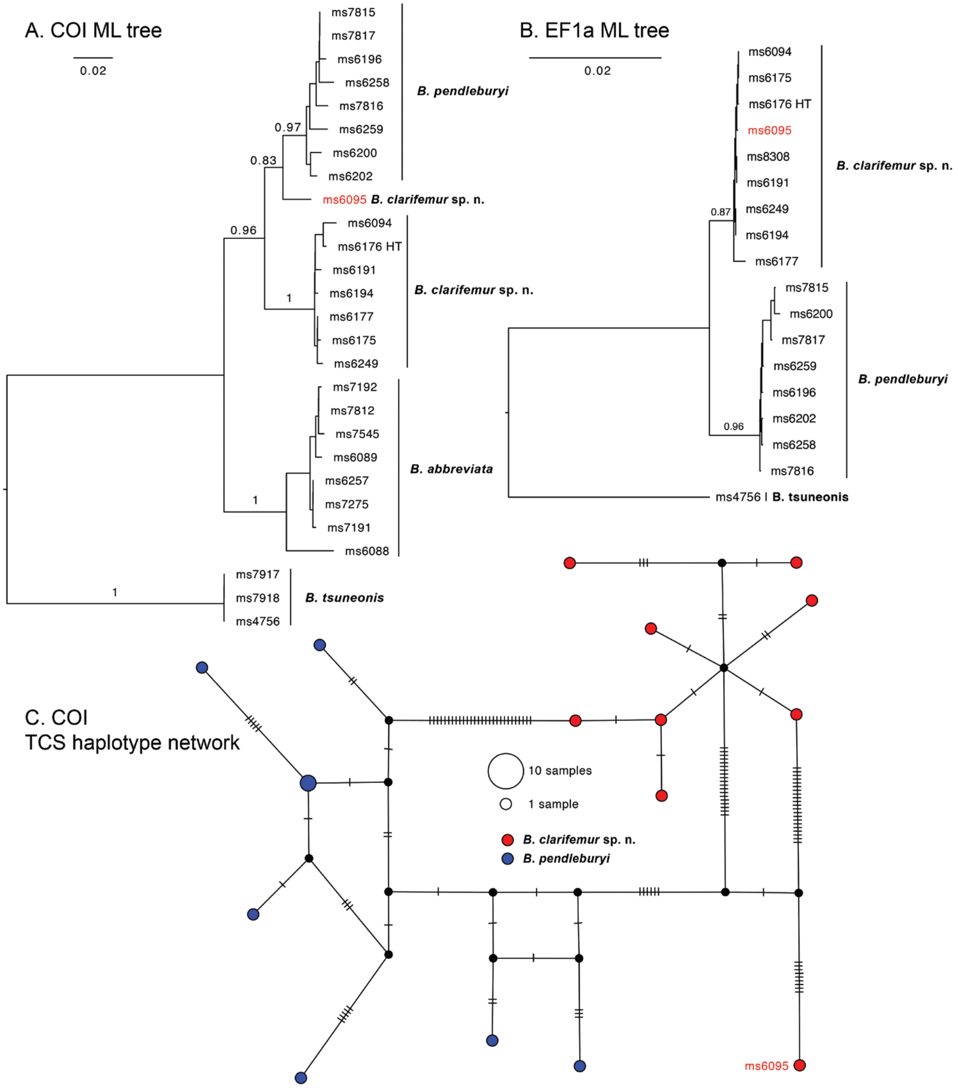

Figure 8. Maximum likelihood trees and haplotype network based on COI (A) and EF1a (B) sequences of *B. clarifemur* sp. n. and several of its genetically closest neighbors. C displays a TCS haplotype network, with notches on the connections to indicate mutations, based on COI data of *B. clarifemur* and *B. pendleburyi* and shows that specimen ms6095 is relatively distantly related from all others. Bootstrap branch supports shown for intraspecific relationships. Abbreviation: HT holotype.

Wings (Figure 9F). Length 4.68 ± 0.35 (4.22–5.00) mm; basal costal (bc) and costal (c) cells colorless; microtrichia in outer corner of cell c only; remainder of wings colorless except fuscous subcostal cell, very narrow light fuscous costal band confluent with R$_{2+3,}$ not widened apically and ending just slightly past the extremity of R$_{4+5}$; anal streak absent; dense aggregation of microtrichia around A$_1$ + CuA$_2$; supernumerary lobe of medium development.

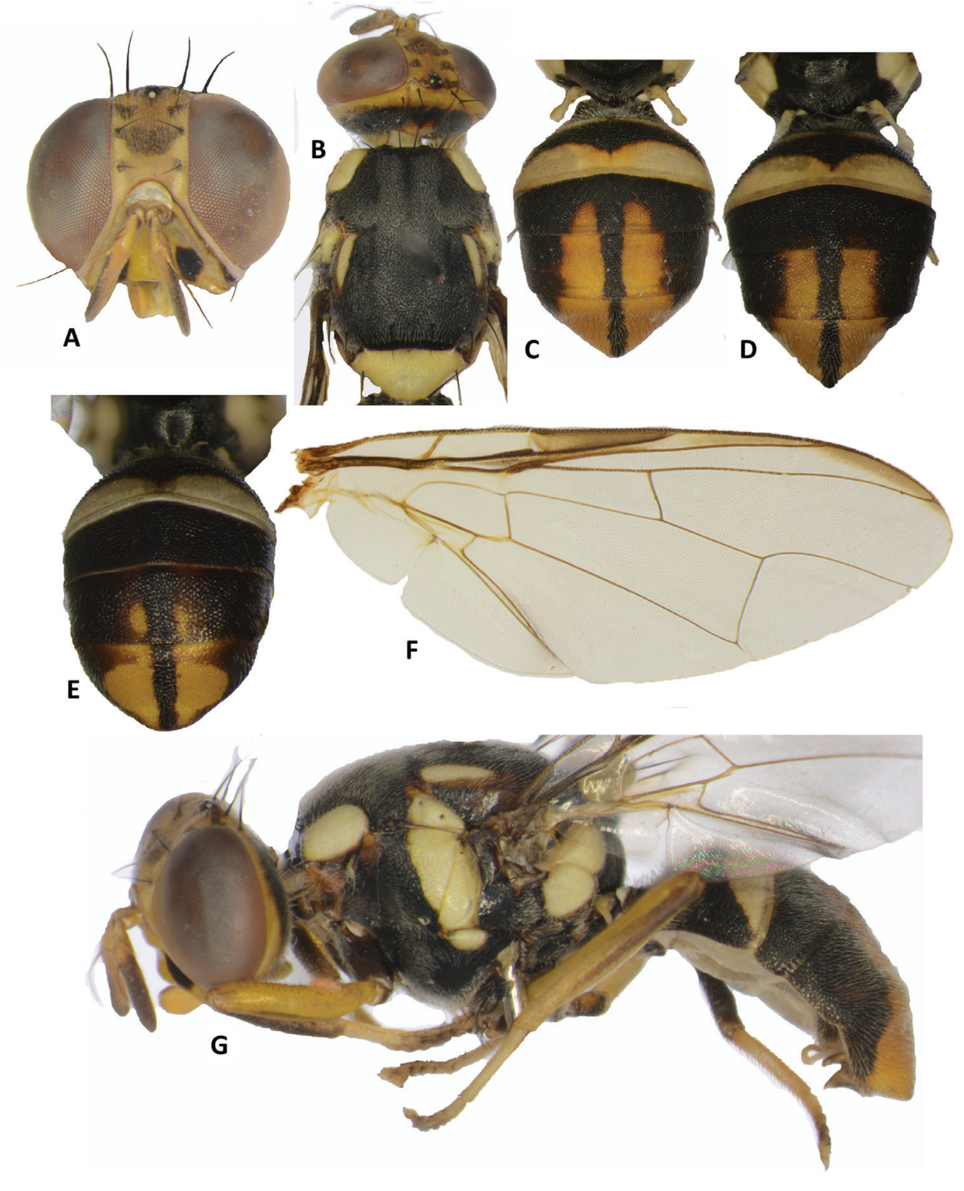

Figure 9. *Bactrocera* (*Hemigymnodacus*) *clarifemur*. **A** head **B** head and scutum **C, D, E** abdomen variation **F** wing **G** lateral view.

Abdomen (Figure 9C–E). Oval; terga free; pecten present on tergum III; posterior lobe of surstylus short; abdominal sternum V with a slight concavity on posterior margin. Tergum I and sterna I and II wider than long. Tergum I dark fuscous with a narrow transverse fulvous band across posterior margin but not reaching lateral margins; tergum II dark fuscous with a transverse posterior fulvous band which just reaches the narrow black posterolateral corners; tergum III dark fuscous; terga IV–V orange–brown with broad

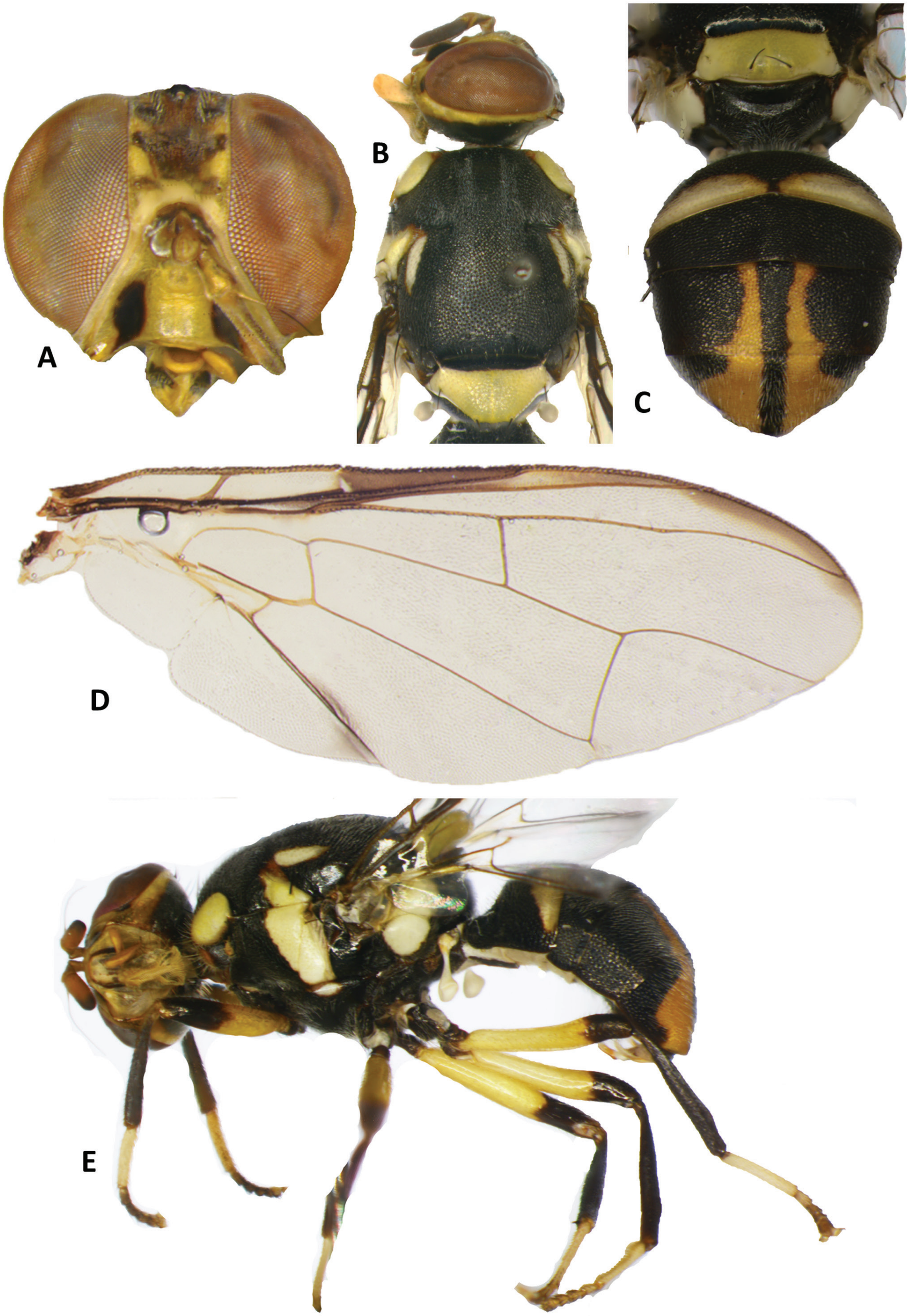

Figure 10. *Bactrocera* (*Hemigymnodacus*) *pendleburyi*. **A** head **B** head and scutum **C** abdomen **D** wing **E** lateral view.

medial dark fuscous band reaching the apex of abdomen and broad lateral dark fuscous bands narrowed in apical half of tergum V. Orange–brown markings and medial band frequently extended to apical portion of tergum III. Ceromata (shining spots) on tergum V orange–brown and indistinct. Abdominal sterna dark, except for fuscous sternite II.

Etymology. The name is an adjective that refers to the absence of dark markings on the femora.

Notes. The characters distinguishing *B. clarifemur* and *B. pendleburyi* were noted as variation of *B. pendleburyi* by Drew and Romig (2013), genetic evidence hereby confirms that they indicate distinct species.

Bactrocera (*Bactrocera*) *adamantea* Leblanc & Doorenweerd, sp. n.

http://zoobank.org/9813AF40-899B-4DFE-A80C-A839B3474860

Holotype. Male. Labelled: "Vietnam: Lâm Đồng Province, Cát Tiên National Park, Ranger station Road, 11.4485N, 107.4416E, 16–18-x-2015, M. San Jose and D. Rubinoff, FF581, Zingerone trap. Molecular voucher ms6092". Deposited in UHIM. **Paratypes**: 3 males. Vietnam, Lâm Đồng Province, Cát Tiên National Park, 16–18-x-2015, at the following sites, identified by their geographical coordinates: 11.4539N, 107.4430E, (1 pinned, molecular voucher ms6093), 11.4485N, 107.4416E, (1 pinned, molecular voucher ms6236), 11.4472N, 107.4392E, (1 in ethanol). All specimens collected by Michael San Jose and Daniel Rubinoff, in zingerone-baited traps. One paratype deposited in UHIM, one in WFBM and one in VNMN.

Differential diagnosis. *Bactrocera adamantea* belongs to the (polyphagous) *B. dorsalis* complex of notoriously difficult to identify species (Leblanc et al. 2015c), defined by having a mostly dark scutum, a costal band that does not expand apically, and a black T shaped pattern on the abdomen. It can easily be differentiated from all congeners however by the yellow diamond shaped medial vitta on the scutum (Figure 12B).

Molecular diagnostics. *Bactrocera adamantea* is easily distinguished from all other *Bactrocera* using either section of COI. The closest species is *B. nigrita*, with a minimum intraspecific pairwise distance of 7.82 % in 1,496 bp of COI [8.66 % in COI5P, 7.18 % in COI3P] (Figure 11).

Description of adult. *Head* (Figure 12A). Vertical length 1.66 ± 0.09 (*SE*) (1.55–1.73) mm. Frons, of even width, length 1.38 ± 0.02 (1.36–1.40) times as long as broad; fulvous with light fuscous (may be absent) around orbital setae and on anteromedial hump; latter covered by short red–brown hairs; orbital setae dark fuscous: one pair of superior and two pairs of inferior fronto-orbital setae present; lunule yellow. Ocellar triangle black. Vertex light fuscous. Face fulvous with medium sized oval black spots in each antennal furrow; length 0.58 ± 0.04 (0.55–0.63) mm. Genae fulvous, with fuscous sub-ocular spot; red–brown seta present. Occiput fulvous to light fuscous and yellow along eye margins; occipital row with 6–8 dark setae. Antennae with segments 1 (scape) and 2 (pedicel) fulvous and segment 3 (first flagellomere) fulvous with fuscous outer surface; a strong

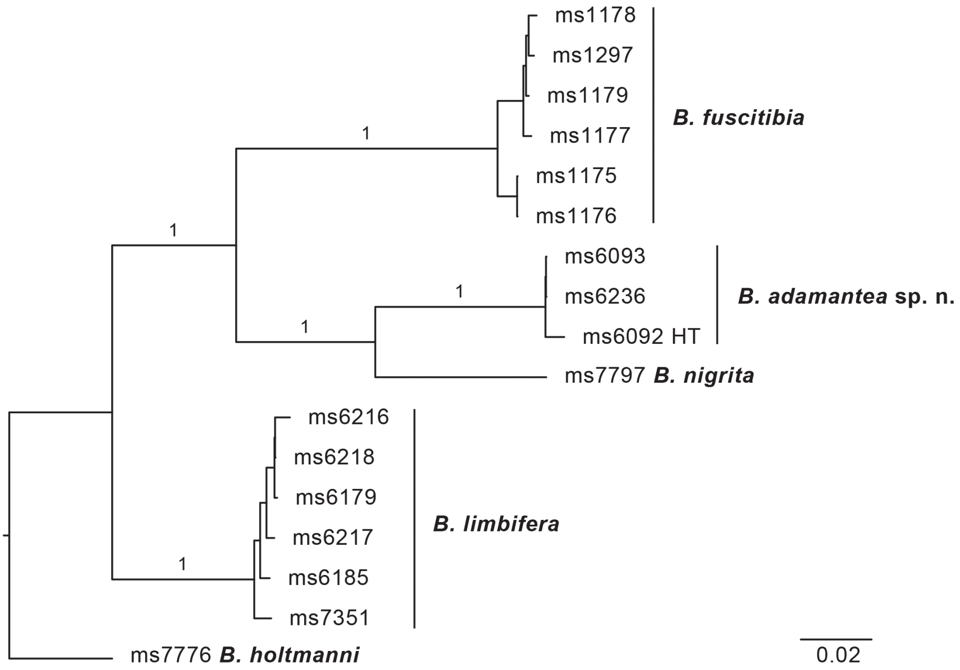

Figure 11. Maximum likelihood tree based on COI sequences of *B. adamantea* sp. n. and several of its genetically closest congeners. Bootstrap branch supports shown for intraspecific relationships. HT = holotype.

fulvous dorsal seta on segment 2; arista black (fulvous basally); length of segments: 0.23 ± 0.01 (0.23–0.25) mm; 0.28 ± 0.03 (0.25–0.30) mm; 0.82 ± 0.01 (0.80–0.83) mm.

Thorax (Fig. 12B, F). Scutum black except red–brown as two parallel bands running from anterior margin to mid-length and as markings around notopleural suture and medial to postpronotal lobes. Pleural areas black except red–brown proepisternum and anterior portion of anepisternum below postpronotal lobes. Yellow markings as follows: postpronotal lobes; notopleura (notopleural callus); broad mesopleural (anepisternal) stripe, reaching level of anterior notopleural seta dorsally, continuing to katepisternum as a transverse spot, anterior margin slightly convex; anatergite (posterior apex black); anterior 80 % of katatergite (remainder black); two broad parallel-sided lateral postsutural vittae ending at level of intra-alar setae; large diamond-shaped medial marking on posterior end of scutum. Postnotum red–brown medially and black laterally. Scutellum yellow except for narrow black basal band. Setae (number of pairs): 1 scutellar; 1 prescutellar; 1 intra-alar; 1 posterior supra-alar; 1 anterior supra-alar; 1 mesopleural; 2 notopleural; 4 scapular; all setae well developed and red–brown.

Legs (Figure 12F). Femora fulvous, except for small fuscous subapical spot on outer surface of fore femur; tibiae dark fuscous; mid-tibiae each with an apical black spur; tarsi fulvous.

Wings (Figure 12E). Length 5.78 ± 0.11 (5.67–5.89) mm; basal costal (bc) and costal (c) cells colorless; microtrichia in outer corner of cell c only; remainder of

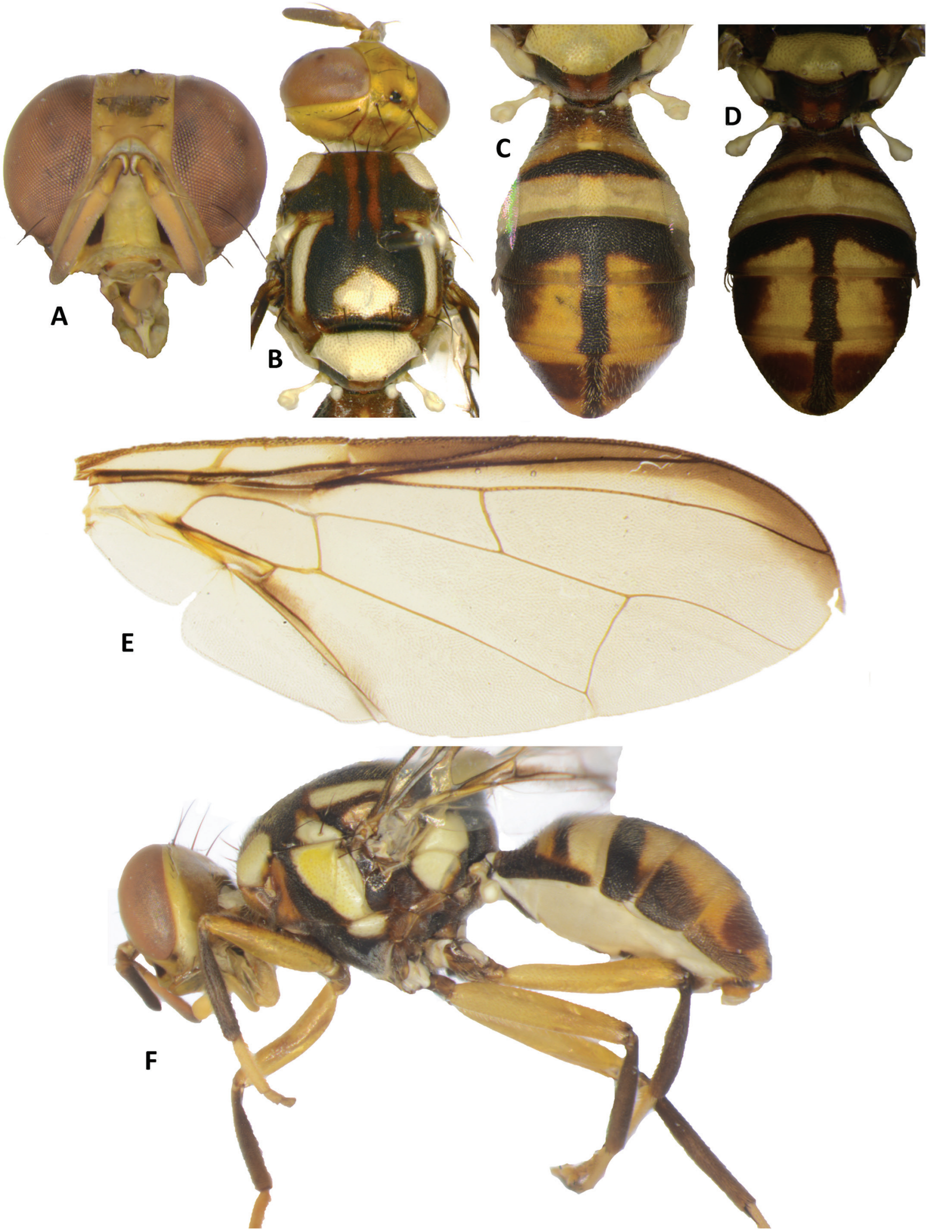

Figure 12. *Bactrocera* (*Bactrocera*) *adamantea*. **A** head **B** head and scutum **C, D** abdomen **E** wing **F** lateral view.

wings colorless except fuscous subcostal cell, moderately broad fuscous costal band overlapping with R_{2+3} and widening slightly as it crosses apex of R_{2+3} to end between extremities of R_{4+5} and M, a narrow fuscous anal streak ending at apex of posterior cubital cell; dense aggregation of microtrichia around A_1 + CuA_2; supernumerary lobe of medium development.

Abdomen (Figure 12C, D, F). Elongate oval; terga free; pecten present on tergum III; posterior lobe of surstylus short; abdominal sternum V with a deep concavity on posterior margin. Tergum I and sterna I and II wider than long. Tergum I fulvous with dark fuscous along base medially and black along lateral margins; tergum II fulvous except for a narrow transverse black band across anterior margin which extends to cover narrow lateral margins. Terga III–V orange–brown with a dark T-shaped pattern consisting of a broad transverse black band across anterior margin of tergum III expanding broadly over lateral margins and a broad medial longitudinal black band over all three terga, broad black lateral markings on tergum IV and narrowly black along lateral margins of tergum V. A pair of dark fuscous ceromata (shining spots) on tergum V. Abdominal sterna dark fuscous except for fulvous sternite II.

Etymology. The name *adamantea* is an adjective that refers to the diamond-shaped marking on the scutum, uniquely distinctive to this species.

Notes. It was referred to as *Bactrocera* species 69, sister to *B.* (*Bactrocera*) *fuscitibia* Drew and Hancock, in the phylogeny presented in San Jose et al. (2018). It keys as far as couplet 80, page 240, in Drew and Romig (2016), and differs from *B. lateritaenia* by the presence of the conspicuous diamond-shaped marking on the scutum (Figure 12B), which is also uniquely distinctive among Dacine fruit flies.

Acknowledgements

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Supplementary material 1

Table S1. Species of Dacine fruit flies recorded in Vietnam and neighboring countries, with references to published records

Authors: Luc Leblanc, Camiel Doorenweerd, Michael San Jose, Hong Thai Pham, Daniel Rubinoff

Data type: occurence

Link: https://doi.org/10.3897/zookeys.797.29138.suppl1

ZooKeys 797: 117–160 (2018)
doi: 10.3897/zookeys.797.24549
http://zookeys.pensoft.net

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Composition and natural history of the snakes from the Parque Estadual da Serra do Papagaio, southern Minas Gerais, Serra da Mantiqueira, Brazil

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Abstract

The Serra da Mantiqueira is one of the least inventoried physiographic areas of southeastern Brazil. There is great potential for detection of endemic species for which little or nothing is known about basic aspects of natural history. The Parque Estadual da Serra do Papagaio (PESP) within the Serra da Mantiqueira is an area of extreme biological importance because it houses mixed formations of grasslands, ombrophilous forests, and enclaves of Araucaria forests (mixed ombrophilous forest). Currently, the mixed ombrophilous forest covers less than 5% of its original range and areas occupied by this forest type, and associated ecosystems constitute refuges, housing several endemic, high altitude species. Between September 2015 and April 2016, field samplings were performed in the PESP using four distinct methods. The objective was to determine the composition and natural history of snakes from an isolated, high altitude area of the Serra da Mantiqueira. In PESP and surrounding areas, 80 individuals representing 24 species, 19 genera, and three families were recorded. Data are presented on abundance, habitat, daily activity, diet, reproduction, and defense. Comparison of the PESP snake assemblage with 30 other Atlantic Forest areas in southeastern Brazil indicate the Serra da Mantiqueira presents particular characteristics regarding snake composition.

Keywords
Araucaria Forests, Atlantic Rainforest, cluster analysis, Serpentes, southeastern Brazil

Introduction

The structure of a snake community can be influenced by historical factors, such as biogeography (Cadle and Greene 1993, Martins and Oliveira 1998, Marques 1998, Sawaya et al. 2008), and ecological factors, such as competition (Inger and Colwell 1977, Henderson et al. 1979, Vitt and Vangilder 1983, Pianka 1989, Krebs 2001), predation (Connel 1975, Krebs 2001), and the influence of species natural history on the assemblage evolution (Schoener 1968, 1983, Wiens 1977). However, the basic natural history and biology for many snake species remains unknown. This is compounded by loss of such information with the reduction of habitat (Marques 1998). Description of snake communities with the intention of understanding interactions between species, patterns of diversity (e.g., species richness, dominance and relative abundance), and the processes that influence community structure is becoming increasingly important.

Snake fauna of tropical areas is typically characterized by high species richness, low abundance, and complex ecological interactions (Duellman 1978, Henderson et al. 1979). These features pose challenges to quantitative and comprehensive study of these populations. There have been several efforts to describe the ecology and natural history of snakes in Brazil (e.g., Amazon Forest: Cunha and Nascimento 1978, Martins and Oliveira 1998, Pantanal: Strüsmann and Sazima 1993, Cerrado: Nogueira 2001, Sawaya et al. 2008, Caatinga: Mesquita et al. 2013, Guedes et al. 2014; Atlantic Forest: Marques 1998, Cicchi et al. 2007, Centeno 2008, Cicchi et al. 2009, Hartmann et al. 2009a, b, Trevine et al. 2014). Although these studies have advanced our understanding of snake fauna in various ecosystems, studies focusing on snake communities in high altitude areas and the Araucaria forests remain scarce. Studies with this focus are mainly concentrated in the Serra do Mar of São Paulo State (e. g., Parque Estadual da Serra do Mar: Hartmann et al. 2009b; Parque Natural Municipal Nascentes de Paranapiacaba: Trevine et al. 2014; Parque Nacional da Serra da Bocaina: Ortiz et al. (2017) and southern Brazil (e.g., Centro de Pesquisas e Conservação da Natureza Pró-Mata: Di-Bernardo 1998; Parque Nacional de Aparados da Serra: Deiques 2009). However, there is a lack of knowledge about the Serra da Mantiqueira snake fauna.

The Serra da Mantiqueira is one of the least well-understood physiographic areas of southeastern Brazil. There is considerable potential for the record of remarkable and endemic species, for which basic natural history has yet to be described. To date only a single study reports on a snake assemblage in this region (Cardoso 2011). This work presented the ecological aspects of a snake community in Munhoz (southern Minas Gerais) and provided the first insight into the composition and natural history of snakes in this region. Here we report on the snake composition of the Parque Estadual da Serra do Papagaio (PESP), Minas Gerais, Southeastern Brazil, a high altitude area of the Serra da Mantiqueira. We describe the species observed, natural history data, altitudinal distribution, as well as an identification key for the recognition of snake species in the area. Finally, we compare the snake fauna composition of PESP with those of 30 other Atlantic forest areas in southeastern Brazil, including the states of Minas Gerais (MG), Rio de Janeiro (RJ) and São Paulo (SP).

Materials and methods

Study area

This study was conducted in the Parque Estadual da Serra do Papagaio (PESP) (22°8'33"S, 44°43'43"W, ca. 22.900 ha) located at Serra da Mantiqueira, southern Minas Gerais State, southeastern Brazil. The PESP overlaps the municipalities of Aiuruoca, Alagoa, Baependi, Itamonte and Pouso Alto within MG, and has an altitudinal range from 1200–2359 m above sea level (Silva et al. 2008). Southward, the PESP contacts the Itatiaia National Park, forming an ecological corridor between the forests of southern Minas Gerais with those of the coastal mountain ridges (= Serra do Mar) in Rio de Janeiro and São Paulo States. The park presents little-disturbed vegetation, within five vegetation zones: 1 - Ombrophilous Dense High Montane Forest (nebular forest), covering altitudes above 1800 m a.s.l.; 2 - Ombrophilous Dense Montane Forest, covering altitudes below 1800 m a.s.l.; 3 - Mixed Ombrophilous Forest, concentrated in valleys along watercourses at 1600 m a.s.l.; 4 – High altitude grasslands, covering parts with altitudinal heights between 1300 and 1800 m a.s.l. and 5 - Rocky Fields, associated with rocky outcrops above 2000 m a.s.l. (Silva et al. 2008). According to Köppen`s classification, the predominant climate is mesothermal tropical of altitude, with a cold and dry winter, and high rainfall levels in the summer. The average annual precipitation exceeds 1500 mm, with 80% occurring from October to March. Winter temperatures range from 0 °C to 10 °C and frost and drought can occur during in this period. Summer is mild with temperatures ranging up to 30 °C (Silva et al. 2008).

Sampling design

Snake sampling lasted eight months, from September 2015 to April 2016. We sampled between altitudes 1600 and 2359 m a.s.l. across all of the available vegetation types. Field trips of four to seven days at a time were made monthly for a total of 40 days of field observation. Four different sampling methods were used to capture snakes:

1) Pitfall traps with drift fences (Greenberg et al. 1994, Cechin and Martins 2000) were installed in three types of vegetation: Ombrophilous Dense Montane Forest, Mixed Ombrophilous Forest, and High Altitude Grasslands. Two sets of traps were used, each comprised of two 50-meter lines, separated from each other by 100 m. Each line consisted of five 60-L buckets, joined by an approximately 50 cm

high drift fence. The buckets were drilled in the bottom to avoid accumulation of rainwater. Inside each bucket, we also put foliage together with a styrofoam plate to serve as a refuge for the fallen animals (Mesquita et al. 2013). The drift fence was buried 20 cm below the ground and held upright by wood stakes. These traps were opened for the four to seven days of each monthly field trip, except for May, June, July, and August. They were inspected daily, totaling 40 days of open traps (2400 bucket days).

2) Time-constrained search was also employed (Campbell and Christman 1982, Martins and Oliveira 1998). Trails were covered on foot, searching all possible shelters and microhabitats that might be used by snakes. In total, 360 hours of visual searching was performed in the study area vegetation types.
3) Accidental encounter (Sawaya et al. 2008) of live or dead specimens sampled opportunistically, with no methodology like pitfall traps or time-constrained search. Here we included individuals found in the PESP and the surrounding areas. Snakes found in the surroundings were included in the list only when recorded above 1600 m (lower altitude of our sampling site) and if they presented literature records at equal to or higher elevations. This methodology was used primarily on roads BR 354, LMG 881, and an unpaved road that links Itamonte, MG, to the PESP headquarters.
4) Records made by local people (Martins and Nogueira 2012). Snakes found by local people from the PESP area and surroundings were also incorporated in the sampling. To get more information about the specimens found, we delivered record sheets for registering information on snakes, such as time and site of the encounter (open area, forest edge, and forest interior), behavior and posture (moving, stationary, coiled or stretched).

For each specimen, we recorded: date and time of observation, habitat, microhabitat, mass (g), sex, diet, reproduction, activity, and defensive behavior. Snake size was categorized according to Marques et al. (2001). Diet was characterized in two different ways. Collected snakes had their stomach examined through a ventral incision along the posterior two-thirds of the body (Martins and Gordo 1993). However, most individuals were not collected and so they were submitted to regurgitation through soft palpation on the abdomen in an antiperistaltic movement (Shine 1995). These animals were subsequently released at the site of capture. Whenever diet items were found, they were identified to the lowest possible taxonomic level using identification keys, comparison with other specimens from zoological collections, and expert assistance. To describe the reproductive condition, we recorded the number of follicles in secondary vitellogenesis or eggs/embryos present in females (Almeida-Santos et al. 2014). The specimens collected during this study were deposited in two zoological collections: Coleção Herpetológica Alphonse Richard Hoge of Instituto Butantan (IBSP), São Paulo, SP, Brazil and in Museu de Zoologia João Moojen (MZUFV), Viçosa, MG, Brazil.

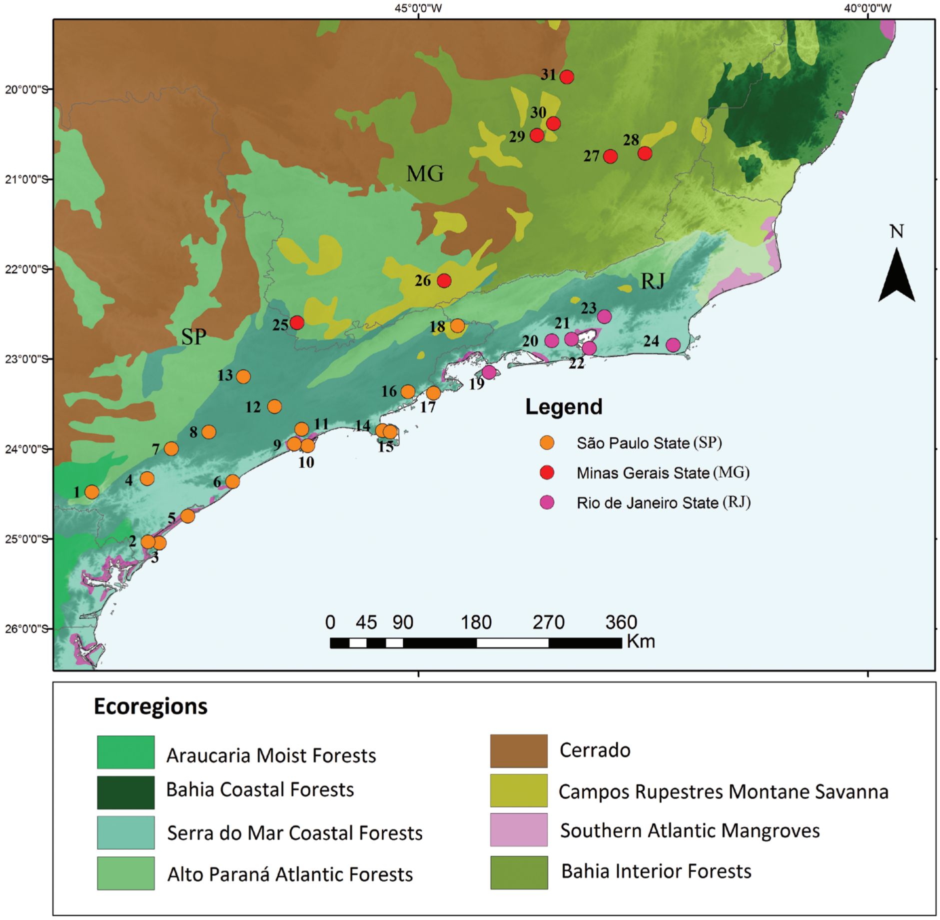

Figure 1. Areas used for the analysis of similarity between snake assemblages. The following snake assemblages were included in the analyzes: São Paulo State: **1** Parque Estadual Turístico do Alto Ribeira (Araújo et al. 2010) **2** Ilha da Cananéia (Cicchi et al. 2007) **3** Parque Estadual Ilha do Cardoso (Rocha et al. 2008) **4** Fazenda Etá (Fiorillo 2016) **5** Ilha Comprida (Cicchi et al. 2007) **6** Estação Ecológica Juréia-Itatins (Marques and Sazima 2004) **7** Parque Estadual Carlos Botelho (Forlani et al. 2010) **8** Municipalities of Tapiraí and Piedade (Condez et al. 2009) **9** São Sebastião (Centeno et al. 2008) **10** Ilhabela (Centeno et al. 2008) **11** Parque Municipal de Paranapiacaba (Trevine et al. 2014) **12** São Paulo (Barbo et al. 2011) **13** Parque Estadual da Serra do Japi (Sazima and Haddad 1992) **14** São Vicente Island (Cicchi et al. 2007) **15** Santo Amaro Island (Cicchi et al. 2007) **16** Parque Estadual da Serra do Mar (Núcleo Santa Virgínia) (Hartmann et al. 2009a) **17** Parque Estadual da Serra do Mar (Núcleo Picinguaba) (Hartmann et al. 2009b) **18** São José do Barreiro (Ortiz et al. 2017); Rio de Janeiro State **19** Ilha Grande (Rocha and Van-Sluys 2006) **20** Parque Natural Municipal da Serra do Mendanha (Pontes et al. 2009) **21** Duque de Caxias (Salles and Silva-Soares 2010) **22** Niterói (Citeli et al. 2016) **23** Estação Ecológica do Paraíso (Vrcibradic et al. 2011) **24** Núcleo Experimental de Iguaba Grande (Martins et al. 2012) Minas Gerais State **25** Munhoz (Cardoso 2011) **26** Parque Estadual da Serra do Papagaio (This study) **27** Parque Estadual da Serra do Brigadeiro (Moura et al. 2012) **28** Viçosa (Costa et al. 2010) **29** Ouro Branco (São-Pedro and Pires 2009) **30** Ouro Preto and surroundings (Silveira et al. 2010) **31** Estação Ambiental de Peti (Bertoluci et al. 2009).

Data analysis

We compared the snake assemblage from Parque Estadual da Serra do Papagaio with those of 30 other localities in the Atlantic forest, in southeastern Brazil (Fig. 1).

With this data set, we generated a binary presence/absence matrix of 120 species. To compare snake assemblages, we used this matrix to run a Cluster Analysis, using the Jaccard's similarity index, and the Pair Group Average Method (UPGMA) as the grouping method. We also calculated the cophenetic correlation coefficient to indicate the similarity matrix degree of representation in the dendrogram. In this index, values greater than or equal to 0.8 allow considering the dendrogram as adequate to the similarity matrix (Rohlf 2000). The result of this analysis was visually compared, allowing the identification of groups clustered together by the similarities of species composition from different localities.

Finally, a Nonmetric Multidimensional Scaling (NMDS) was used for another view of the Jaccard index clusters. The stress value was used as a representative measure of the groupings, and values <0.20 were considered acceptable (Clarke and Warnick 1994). Multivariate analyzes were performed in R software (R Core Team 2014), using the *vegan* package (Oksanen et al. 2015).

Taxonomic accounts

Several nomenclature changes have been proposed to the taxonomy of Neotropical snakes in recent years. To provide consistency during similarity analysis we present a brief list of species that have had names changes and identify the name used in this report. The name "*Taeniophallus* gr. *occipitalis*" was used for specimens traditionally referred to as *Taeniophallus occipitalis* (Jan, 1863) because more than one species often fall under this designation (Santos-Jr. 2008). Specimens identified as *Mussurana montana* (Franco, Marques & Puorto, 1997) by Hartmann et al. (2009b) belong to *Pseudoboa serrana* Morato, Moura-Leite, Prudente & Bérnils, 1995 (Francísco Luís Franco pers. obs.). Specimens identified as *Atractus* sp. by Hartmann et al. (2009b) were described as *Atractus francoi* Passos, Fernandes, Bérnils and Moura-Leite, 2010. Specimens referred to as *Dipsas* sp. by Hartmann et al. (2009a) were described as *Dipsas sazimai* Fernandes, Marques & Argôlo, 2010. Specimens identified as *Dipsas indica* Laurenti, 1768 by Hartmann et al. (2009a) were considered *Dipsas petersi* Hoge & Romano, 1975, according to Harvey and Embert (2008). The specimen referred to as *Helicops* sp. by Costa et al. (2010) was described as *Helicops nentur* Costa, Santana, Leal, Koroiva and Garcia 2016. The specimen identified as *Tropidophis* cf. *paucisquamis* by Silveira et al. (2010) was described as *Tropidophis preciosus* Curcio, Nunes, Argôlo, Skuk & Rodrigues, 2012. The specimen identified as *Philodryas oligolepis* Gomes *in* Amaral, 1921 by Silveira et al. (2010) belongs to *Philodryas laticeps* Werner, 1900 (Zaher et al. 2008). Specimens identified as *Thamnodynastes* sp. by Salles and Silva-Soares (2010) belong to *Thamnodynastes nattereri* (Mikan, 1820) (Franco and Ferreira 2002), as well as the specimens cited as *Thamnodynastes* cf. *nattereri* by Marques and Sazima (2004), Centeno et al. (2008), Pontes et al. (2008), Bertoluci et al. (2009), Hartmann et al.

(2009b), Silveira et al. (2010), Vrcibradic et al. (2011), Moura et al. (2012) and Citeli et al. (2016). Specimens considered as *Chironius flavolineatus* (Jan, 1863) by Condez et al. (2009), São Pedro and Pires (2009), Forlani et al. (2010) and Silveira et al. (2010) were described as *Chironius brazili* Hamdan & Fernandes, 2015 (Hamdan and Fernandes 2015). The specimen considered *Micrurus ibiboboca* (Merrem, 1820) by Martins et al. (2012) corresponds to a new species which is being described (Francisco Luís Franco, unpubl. data). The specimen regarded as *Dipsas incerta* (Jan, 1863) by Citeli et al. (2016) corresponds to *Dipsas alternans* (Fischer, 1885) (Passos et al. 2004). The specimen cited as *Epicrates* sp. by Moura et al. (2012) was considered *Epicrates cenchria* (Linnaeus, 1758) according to the own comments on Moura et al. (2012). Specimens addressed as *Dipsas neivai* Amaral, 1926 by Centeno et al. (2008) correspond to *Dipsas variegata* (Duméril, Bibron & Duméril, 1854) (Harvey and Embert 2008). The specimens cited as *Chironius* cf. *quadricarinatus* and *Liophis* cf. *almadensis* by Bertoluci et al. (2009) were considered *Chironius quadricarinatus* (Boie, 1827) and *Erythrolamprus almadensis* (Wagler, 1824), respectively. Specimens identified as *Tantilla* cf. *melanocephala* by Barbo et al. (2011) are here considered *Tantilla melanocephala* (Linnaeus 1758). The specimen "IBSP 30496" regarded as *Clelia rustica* (Cope, 1878) by Franco et al. (1997), corresponds to a new species that is being described (Francisco Luís Franco, unpubl. data). Taxonomy on family level follows Grazziotin et al. (2012).

Results

Species composition

We recorded 80 snakes during the eight month period of fieldwork through all sampling methods. In this group we separated 24 species of 19 genera, of which 67% are dipsadids, 19% viperids, and 14% colubrids (Table 1). The five most abundant species in the study area were dipsadids *Atractus zebrinus* and *Thamnodynastes strigatus* (each 18.5% of the records), followed by *Philodryas patagoniensis* (11.2%), *Gomsesophis brasiliensis* (10%), and the viperid *Bothrops fonsecai* (8.7%). Among viperid records, the most abundant species was *B. fonsecai* (*n* = 7; 63%), followed by *B. jararaca* (*n* = 2; 18%), and *B. neuwiedi* and *Crotalus durissus* (*n* = 1; 9% each).

Comparison with other snake assemblages from the Atlantic Forest of southeastern Brazil

The cluster analysis (cophenetic correlation coefficient = 0.8381) based on 120 snake species recorded at 31 localities, including Parque Estadual da Serra do Papagaio, resulted in three main groupings (Fig. 2).

Group 1 was composed generally by localities of mid to high altitudes (> 600 m): the coastal forests of Serra do Mar and Bahia Interior Forests (Olson et al. 2001), covering the Paranapiacaba, Cantareira and Bocaina Mountains in São Paulo, and the Mantique-

Table 1. List of species found in the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil. Abbreviations: abundance (N), relative frequency of each species (f%), environment (1 - High altitude grassland, 2 - Rocky Field, 3 - Dense Montane Ombrophilous Forest, 4 - Mixed Ombrophilous Forest), habitat (aa - open area, bf - forest edge, da – disturbed areas, fl - forest, lo - lotic environment, le - lentic environment), and habits (F-fossorial, C-cryptozoic, SAQ-sub-aquatic, T-terrestrial, SA-sub-arboreal, and A-arboreal). Species registered outside the park area (*).

Family/ Species	N	F%	Environments	Habitat	Habit	Altitudinal variation (m)	New record altitudinal (m)
COLUBRIDAE							
Chironius bicarinatus (Wied, 1820)	1	1.2	1,3	bf, at	SA	0–1850	–
Chironius brazili Hamdan & Fernandes, 2015	1	1,2	1,3	Bf, fl, at	SA	200–2030	–
Spilotes pullatus (Linnaeus, 1758)	2	2.5	3	fl	SA	0–1100	1630
DIPSADIDAE							
Apostolepis assimilis (Reinhardt, 1861)*	1	1.2	1	Aa, at	F, T	170–1610	–
Atractus zebrinus (Jan, 1962)	15	18.7	1,2,3	Aa, fl, at	F, T	20–1610	1730
Boiruna maculata (Boulenger, 1896)	1	1.2	3	fl	T	0–1880	–
Echinanthera cephalostriata Di-Bernardo, 1996	2	2.5	3	Bf, fl	C, T	0–1610	1730
Erythrolamprus miliaris (Linnaeus, 1758)	1	1.2	3	Fl, le	SAQ	–	1643
Gomesophis brasiliensis (Gomes, 1918)	8	10	1	Aa, lo, le, at	SAQ	430–1650	1750
Mussurana montana (Franco, Marques & Puorto, 1997)*	1	1.2	4	fl	T	750–1610	1740
Oxyrhopus clathratus Duméril, Bibron & Duméril, 1854*	1	1.2	1	Aa, at	T	0–1610	–
Oxyrhopus rhombifer Duméril, Bibron & Duméril, 1854	1	1.2	1	Aa, at	T	0–1330	1730
Philodryas aestiva (Duméril, Bibron & Duméril, 1854)	2	2.5	1,2	aa	T	0–1730	1800
Philodryas patagoniensis (Girard, 1858)	9	11.2	1,2	Aa, at	T	0–1600	2200
Sibynomorphus mikanii (Schlegel, 1837)	1	1.2	1	Aa, at	T	110–1350	1630
Taeniophallus affinis (Günther, 1858)	3	3.7	1,3	aa	T, C	0–1600	1760
Taeniophallus gr. *occipitalis**	1	1.2	1	bf	T, C	–	1600
Thamnodynastes strigatus (Günther, 1858)	15	18.7	1,3,4	Aa, fl, bf, at	SAQ	0–2450	–
Tomodon dorsatus Duméril, Bibron & Duméril, 1854	2	2.5	3,4	fl	T	0–1610	1730
Xenodon merremii (Wagler *in* Spix, 1824)	1	1.2	1,2	aa	T	0–1300	1610
VIPERIDAE							
Bothrops fonsecai Hoge & Belluomini, 1959	7	8.7	1,2,3,4	Aa, bf, fl	T	440–1730	2175
Bothrops jararaca (Wied, 1824)	2	2.5	1,2,3,4	Bf, fl	T	0–1640	2150
Bothrops neuwiedi Wagler *in* Spix, 1824	1	1.2	1,2	Aa, bf	T	0–1600	2150
Crotalus durissus Linnaeus, 1758	1	1.2	1,2	Aa, bf	T	0–1400	1950
Total	80	100					

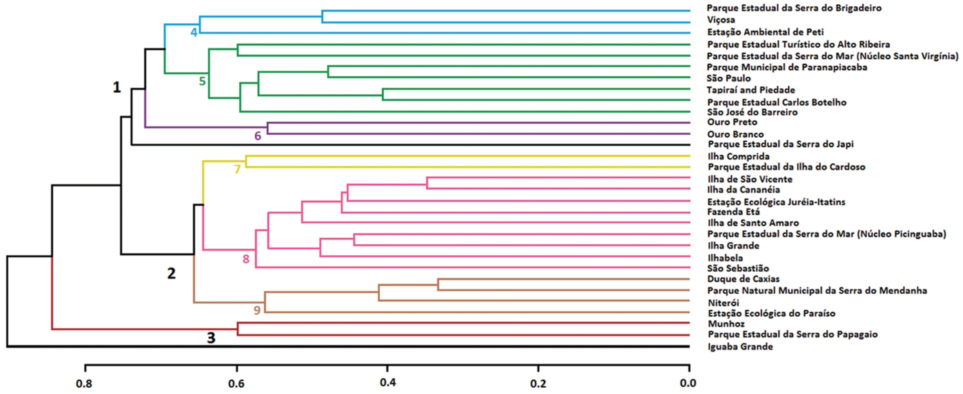

Figure 2. Cluster analysis based on snake species composition from 31 localities of the Atlantic Forest, southeastern Brazil.

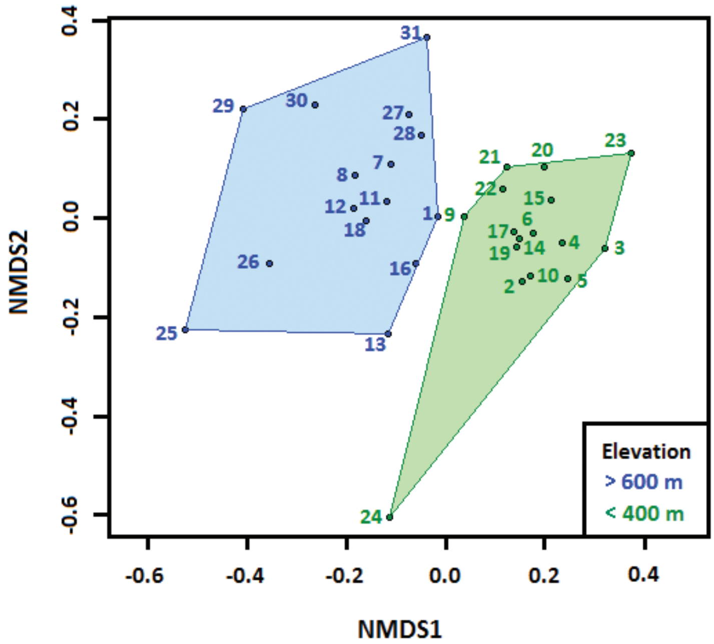

Figure 3. Groupings formed through NMDS analysis (stress 0.1547). The relationship between altitude and the composition of snake species in the Atlantic Forest of southeastern Brazil is shown. The numbers correspond to the same localities as in figure 1.

ira and extreme south of Espinhaço mountains in Minas Gerais. An exception was the Parque Estadual da Serra do Japi, which has remained isolated from the other localities. Three subgroups can be visualized in this grouping. The first (4) is formed by areas in the northern portion of Serra da Mantiqueira and surroundings (Parque Estadual da Serra do Brigadeiro and Viçosa), in Minas Gerais state, as well as a locality in southern Espinhaço

Mountains (Estação Ambiental de Peti). The second (5) is comprised of the mountains in São Paulo State. The third (6) is composed of two localities in the southern region of Serra do Espinhaço (Municipalities of Ouro Branco and Ouro Preto and surroundings).

Group 2 consisted of low areas (< 400 m a.s.l.) of the Coastal Forests of Serra do Mar, comprising island and continental regions in the coastal strip of São Paulo and Rio de Janeiro states. In this group, three subgroups can also be observed. The first (7) consists of two continental islands on the south coast of São Paulo state (Ilha do Cardoso and Ilha Comprida). The second (8) composed by the other insular and lowland locations of the Atlantic Forest in São Paulo state, in addition to an island in Rio de Janeiro State (Ilha Grande). Geographically, this subgroup is close to the Parque Estadual da Serra do Mar (Picinguaba, São Paulo State), with which it shares several snake species. The third (9) is composed of lowland locations in the state of Rio de Janeiro, east of Serra dos Órgãos, for which similarities have already been described by Citeli et al. (2016).

Group 3 is composed of only two high altitude localities (> 1100 m a.s.l.) in the southern Mantiqueira Mountains: the Parque Estadual da Serra do Papagaio and Munhoz.

The NMDS ordering analysis (stress 0.1547) graphically depicts the relative position of localities in a two-dimensional space (Fig. 3). It suggests the clustering pattern found between the locations is associated with the spatial distribution, mainly altitudinal, in the study area and corroborates the results of the cluster analysis.

Natural history information about the species

Colubridae Oppel, 1811

Chironius bicarinatus (Wied, 1820)

Natural history notes. Medium-sized snake (*n* = 1), diurnal and semi-arboreal (Marques et al. 2001). An individual was observed on the ground during the day (12:00 h) in March, next to a small fragment of disturbed forest. Upon detecting the observer's approach, the snake fled into the forest. Sazima and Haddad (1992) also mention the presence of *C. bicarinatus* in fragments of disturbed forests. The diet is specialized in anurans, composed mainly of hylids and leptodactylids (Dixon et al. 1993). Reproduction is seasonal, with copulation in early autumn and between 4 – 14 eggs laid at the end of winter (Marques et al. 2009, Pontes and Rocha 2008).

Altitudinal variation. From sea level, from the northern coast of Rio Grande do Sul to Bahia, to a maximum altitude of 1610 m in Campos do Jordão, SP (Bérnils 2009). In this study, the maximum altitudinal record was 1730 m, in Baependi, MG. Dixon et al. (1993) cited the species in "*Brazil, Rio de Janeiro, Marombe* [sic], *Itatiaia*," at 1850 m a.s.l.. The Maromba region encompasses altitudes from 500 to 2000 m. Despite several records of this species in elevated areas (above 800 m a.s.l.) (Bérnils 2009), *Chironius bicarinatus* is thought to occupy predominantly plains (Dixon et al. 1993, Carreira et al. 2005).

Distribution and habitat. Northeast, central-west, southeast and south of Brazil (Bahia, Goiás, Mato Grosso do Sul, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul), Argentina, and Uruguay (Bérnils 2009, Wallach et al. 2014). This species inhabits all forest formations and open areas such as pampas, cerrado, restingas (Sazima and Haddad 1992, Dixon et al. 1993, Carreira et al. 2005) and rocky fields.

Chironius brazili Hamdan & Fernandes, 2015

Figure 4A

Natural history notes. Medium-size species (*n* = 1), diurnal and semi-arboreal (Dixon et al. 1993, Marques et al 2015). Five observations of *C. brazili* were made (one during fieldwork and four outside the sampling period). Three individuals were observed between the stones of a waterfall (10:00 – 15:00 h). A recently road-killed adult male was found during the day (11:00 h) in a forest area. Additionally, we observed an individual at rest, coiled over the vegetation at 1.30 m above the ground during the day (16:30 h). All records occurred near watercourses. Abegg et al. (2016) also mention the occurrence of *C. brazili* in riparian forests. No data on the diet was obtained from the examined specimen. However, as in the other species of the genus, it is likely that *C. brazili* preys primarily on anurans, mainly hylids (Dixon et al. 1993). We could observe the following defensive behaviors for *C. brazili*: head elevation and neck S-coil.

Altitudinal variation. The maximum altitudinal record for the species was at 2030 m a.s.l. at Pico do Inficionado, Catas Altas, MG (Bérnils 2009). In the present study, the maximum altitudinal record was at 1600 m a.s.l., in Baependi, MG.

Distribution and habitat. Central-west, southeast and south of Brazil (Federal District, Goiás, Minas Gerais, São Paulo and Rio Grande do Sul) (Hamdan and Fernandes 2015). This species is thought to live in habitats similar to those of *C. flavolineatus* and inhabits riverine forests and forest borders near open areas (Hamdan and Fernandes 2015).

Spilotes pullatus (Linnaeus, 1758)

Natural history notes. A large species (*n* = 1), with semi-arboreal habits, and diurnal activity (Marques et al. 2001, Marques and Sazima 2004). Both of our records were made in the same place, during the day (12:00 and 12:10 h), in September and October, respectively, indicating that it may be the same individual. On both occasions, the individuals were on the ground, in a forest area. The diet is mainly composed of mammals (Marques et al. 2014), but *S. pullatus* also feeds on lizards, birds and their eggs, and anurans (Martins and Oliveira 1998, Marques and Sazima 2004, Bernarde and Abe 2006). This species lays five to twelve eggs (Amaral 1930, Marques et al. 2014). No defensive behavior was observed for this species.

Figure 4. Snakes from the Serra do Papagaio. **A** *Chironius brazili* **B** *Apostolepis assimilis* **C** *Gomesophis brasiliensis* **D** *Philodryas aestiva* **E** *Philodryas patagoniensis* **F** *Thamnodynastes strigatus* **G** *Tomodon dorsatus* **H** *Xenodon merremii* **I** *Bothrops fonsecai* **J** *Bothrops jararaca* **K** *Bothrops neuwiedi* **L** *Crotalus durissus*. Photographs by Mário Sacramento, Frederico de Alcântara Menezes, Arthur Diesel Abegg, and Leonardo Chaves.

Altitudinal variation. In Brazil, range spans at minimum of sea level from the coast of Santa Catarina to Bahia to a maximum of 1100 m a.s.l., Brasília, Federal District (Bérnils 2009). The maximum altitudinal record of this species for Brazil is expanded here by our observations at 1630 m a.s.l.. From the toponyms surveyed, Bérnils (2009) recorded only 8% in areas higher than 800 m a.s.l. and 57% between the range of sea level and 400 m a.s.l.

Distribution and habitat. This species can be found in all Brazilian states, and in Argentina and Paraguay (Wallach et al. 2014). It lives in open formations associated with riparian, dense and seasonal ombrophilous forests (Bérnils 2009).

Dipsadidae Bonaparte, 1838

Apostolepis assimilis (Reinhardt, 1861)

Figure 4B

Natural history notes. Species of small size (*n* = 1), with nocturnal activity and cryptozoic or fossorial habits (Ferrarezzi et al. 2005, Marques et al. 2015). In December, an adult was seen at 07:30 h. moving in an open area. The record occurred in Aiuruoca-MG, near the PESP. The diet is composed of amphisbaenids and other elongate vertebrates (Ferrarezzi et al. 2005). Barbo (2011) mentions two females with four and six vitellogenic follicles in November and March. No defensive behavior was observed for this species.

Altitudinal variation. This species was found at a minimum of 170 m a.s.l., in Cuiabá, Mato Grosso and maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). In this study, the record occurred outside the park limits at 1100 m a.s.l., in Aiuruoca, MG.

Distribution and habitat. Northeast, central-west, southeast and southern Brazil (Bahia, Mato Grosso, Mato Grosso do Sul, Goiás, Distrito Federal, Minas Gerais, São Paulo and Paraná), southeast Paraguay, northern Argentina, and Bolivia (Bérnils 2009; Wallach et al. 2014). This species is typical of the Cerrado morphoclimatic domain, also occurring in adjacent forested areas (Ferrarezzi et al. 2005).

Atractus zebrinus (Jan, 1862)

Natural history notes. Species of small size (*n* = 15), nocturnal, with fossorial habits (Marques et al. 2001). Data on *A. zebrinu* activity and habitat use are available from sparse records and inferred from ecological attributes of other species of the genus (e.g., *Atractus pantostictus* and *A. reticulatus*). The species was considered abundant in the study area and was found in all the sampled vegetation types. The exception was mixed ombrophilous forest, which are located in valleys along water courses and undergo seasonal flooding in the rainy season. This species was often captured in pitfall traps (open area = 7, forest area = 8, pitfall = 8). Seven individuals were found during the day (09:30–18:00 h.), all at rest; three under trunks, three were buried and came up when a tractor revolved the soil, and one was basking. An adult female was observed at 20:00 h. crossing the road in a forest area. This information reinforces the conclusion that this species is nocturnal and a generalist for vegetation use, because it was found in both open and forested areas. Similar to other *Atractus* species, the diet is composed of annelids (Marques et al. 2001). Of the seven individuals examined, two had earthworms in their stomachs. This species was found in all sampling months at similar numbers. There is no information in the literature regarding reproduction. A female collected in October (SVL = 425 mm; TL = 34 mm) presented four vitellogenic follicles and another female was found in December (SVL = 480 mm; TL = 40 mm) with 12 undeveloped follicles. In June, two young individuals (approx SVL = 200 mm) were found together when a tractor revolved the earth. Passos et al. (2016) observed aggregation of juveniles after parturition in *Atractus potschi*. As defensive tactics, we observed cloacal discharge and head hiding.

Altitudinal variation. Found at a minimum of 20 m a.s.l. in Itaboraí, RJ and maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). The maximum altitude of the species is expanded here by individuals we observed at 1730 m a.s.l.

Distribution and habitat. South and southeast of Brazil (Santa Catarina, Paraná, São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo) (Bérnils 2009, Wallach et al. 2014). The toponyms occupied by this species are concentrated in the coastal mountain ranges of Paraná and São Paulo States: Paranapiacaba, Órgaos, Mantiqueira, and Espinhaço mountain ranges. The species is found in areas with predominantly dense ombrophilous forests, mixed ombrophilous forest, seasonal forest (Bérnils 2009), and high altitude grasslands.

Boiruna maculata (Boulenger, 1896)

Natural history notes. A large species (*n* = 1), terrestrial (Marques et al. 2015), although there is one record of arboreal substrate (Gallardo et al. 2006). In October, a juvenile was collected at 07:30 h. while crossing an unpaved road in a forested area. Data on daily activity are scarce. In the literature, there are two observations of activity at night, one during twilight, and one during the day (Gallardo et al. 2006, Hartmann and Giasson 2008, Gaiarsa et al. 2013). Although the specimen was found active in the early hours of the day, it is thought that the species is predominantly nocturnal, similar to other Pseudoboine species (Marques 1998, Sawaya et al. 2008). A recently ingested lizard (*Ophiodes* sp.), swallowed head-first, was found in the digestive tract of this specimen. Previous studies indicate this species is a generalist, feeding primarily on snakes, but also birds, small mammals, anurans, and lizards (Lema et al. 1983, Carreira 2002, Gallardo et al. 2006, Hartmann and Giasson 2008, Gaiarsa et al. 2013). This is the first record of an *Ophiodes* as prey for *B. maculata*. No reproductive data were obtained from the examined specimen. However, the species is known to lay from four to 15 eggs (Sawaya et al. 2008). No defensive behavior was observed for this species.

Altitudinal variation. Species records indicate a minimum of sea level in Rio Grande do Sul and maximum of 1240 m a.s.l. in Serra do Salitre, MG (Bérnils 2009). In Brazil, the maximum altitudinal record of the species is for the study area (at 1600 m a.s.l.). Observations at toponyms below 400 m a.s.l. were recorded only on the coast, from Uruguay to Rio Grande do Sul, and in the western and southernmost parts of its distribution (Negro, Jacuí, Uruguay, Paraguay, and Paraná basins) (Bérnils 2009). Quinteros-Muñoz (2006) collected an individual at 1880 m a.s.l. in the National Park La Yunga, Bolivia in a region that encompasses altitudes ranging from 1000 to 4000 m a.s.l.

Distribution and habitat. North, central-west, southeast and south of Brazil (Amazonas, Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, Rio Grande do Sul, São Paulo), Argentina, Paraguay, and Uruguay (Bérnils 2009, Wallach et al.

2014). Typically, this is a species of open areas (cerrados, savannas, chacos, and pampas) with records near adjacent forests (Bérnils et al. 2007).

Echinanthera cephalostriata Di-Bernardo, 1996

Natural history notes. Species of small size (*n* = 2), predominantly diurnal, terrestrial and cryptozoic (Marques et al. 2001). Feeds on anurans (Marques et al. 2001, Forlani et al. 2010). In September, a female was found in the early afternoon (12:00 h), inside a bromeliad (*Aechmea aiuruocensis* Leme) on the forest floor. In its digestive tract, we found a *Physalaemus olfersii* (Lichtenstein & Martens, 1856) (ingested by the leg), and three anuran eggs. Moura-Leite et al. (2003) recorded a specimen with 32 anuran eggs in the stomach. The second individual, another female, was found resting during the day. The record was made in November, at the forest edge, near a swamp area. This individual had ingested three *Physalaemus jordanensis* Bokermann, 1967 (two were ingested head-first and the last by the leg). Pontes et al. (2008) found *E. cephalostriata* only in primary and secondary forests. The presence of *P. jordanensis* (found in PESP just in open area marshes, F. Menezes pers. obs.) as prey of *E. cephalostriata*, indicates this snake also forages in open areas and lentic environments. Reproduction data of the species are scarce. The female collected in September (SVL = 490 mm; TL = 210 mm) presented nine vitellogenic follicles. Fiorillo (2016) refers to a female from Iguape, with eight vitellogenic follicles in November. No defensive behavior was observed for this species.

Altitudinal variation. Found at altitude minimum of sea level from Santa Catarina coast to Rio de Janeiro and maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). The maximum altitude for this species is recorded here, with two individuals found at 1730 m a.s.l.. Bérnils (2009) mentioned that more than 80% of the toponyms come from hill and plateau areas. Although the distribution range is concentrated in mountains and plateau areas, this species is also frequent in lower altitudes (see Hartmann 2005, Fiorillo 2016).

Distribution and habitat. Northeast, southeast, and southern Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina and São Paulo) (Wallach et al. 2014). Occurs in dense and mixed ombrophilous forest formations, as well as in semi-deciduous forests (Di-Bernardo 1996, Bérnils 2009).

Erythrolamprus miliaris (Linnaeus, 1758)

Natural history notes. Species of medium size (*n* = 1), predominantly diurnal and semi-aquatic (Marques et al. 2001), although there are reports of activity at night (Sazima and Haddad 1992). In September, an individual was found standing still on the forest floor during the day (15:00 h) at a swamp border. This species feeds mainly on amphibians, fish, and tadpoles (Marques and Souza 1993, Marques and Sazima 2004), although it can occasionally feed on other reptiles (Marques and Sazima 2004, Bonfiglio and Lema 2007, Hartmann et al. 2009a). Pizzatto and Marques (2006) reported a continuous reproductive cycle in a population of southern Bahia state coast (northern distribution) and seasonal reproductive cycles in populations of both inland and coastal São Paulo and Paraná states (southern distribution). Fecundity is six to seventeen eggs, with individuals reaching sexual maturity at twelve months (Vitt 1992, Pizzatto and Marques 2006). No defensive behavior was observed for this species.

Altitudinal variation. We found no information in the literature regarding the altitudinal variation of the species. In this study, the maximum altitudinal record was at 1643 m a.s.l., in Baependi-MG.

Distribution and habitat. Northern, northeast, central-west, southeast and southern Brazil (Alagoas, Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Norte, Rio Grande Do Sul, Rondônia, Santa Catarina, São Paulo, Sergipe) (Wallach et al. 2014). This species occurs in semi-deciduous, dense, and mixed ombrophilous forests, as well as in adjacent open areas, from the Amazon to the Atlantic Forest (Gans 1964).

Gomesophis brasiliensis (Gomes, 1918)
Figure 4C

Natural history notes. Species of small size (*n* = 8). This species is considered nocturnal and aquatic, associating with lentic watercourses (Gomes 1918, Marques et al. 2001, Gonzalez et al. 2014). During our fieldwork, it was found during all months of sampling in similar numbers and all observations occurred during the day in open areas. Five individuals were found active: four were moving from a river edge towards a swamp (10:00 h, 16:00 h, 17:00 h, 17:30 h) and one towards a creek (14:00 h). Three individuals were found at rest; one on a creek edge (9:00 h.), one in a muddy area (15:00 h) and another in a swamp (16:00 h). Fortes et al. (2010) recorded two active individuals at 21:00 h swimming on the surface of an 80-cm-deep turbid water lagoon. A male (SVL = 420 mm; TL = 75 mm) was kept in a 70cm × 30cm × 45cm terrarium for 10 consecutive days. During this period, it was monitored by camera 24 hours/day, to study its activity. It presented a unimodal activity pattern, with 96.4% of activity records during the day and peak activity from 9:30 to 17:00 h. Data obtained in the laboratory and field observations indicate this species is predominantly diurnal and semi-aquatic. *G. brasiliensis* frequently uses the ground (instead of the water), mainly during the day, to move between lentic and lotic environments. Of the three specimens examined, one had an earthworm in its stomach. Our results are consistent with the study by Oliveira et al. (2003) who also found traces of earthworm in the digestive tract of *G. brasiliensis*. Earthworms are sensitive to light and ultraviolet radiation (Edwards and Lofty 1977), so they are predominantly nocturnal, coming to the surface at night or during periods of very low light intensity during the day (Lee 1985). The diurnal activity of *G. brasiliensis* does not match its prey activity period. *G. brasiliensis* may hunt and capture its prey underground, during the day, possibly on the borders of marshes where the concentration of earthworms is higher (Frederico Menezes, pers. obs.). No information about reproduction of the examined specimens was recorded, except for a pregnant female in February. The species has seasonal reproduction associated with the rainy season, with juvenile recruitment between February and March (Oliveira et al. 2003). The defensive repertoire is described in Menezes et al. (2017).

Altitudinal variation. Found at a minimum of 430 m a.s.l. in Encruzilhada do Sul, RS and maximum of 1650 m a.s.l. in the Parque Estadual da Serra do Papagaio, Alagoa, MG. The maximum altitudinal record derives from the same are in this study, where most individuals were recorded at 1750 m altitude, in the PESP, Baependi, MG. The toponyms obtained for this species occur in two altitudinal ranges: 51% are located between 430 and 800 meters and 49% above this range (Bérnils 2009).

Distribution and habitat. This species occurs in natural field areas (Amaral 1977, Ghizoni-Jr et al. 2009) in southern and southeastern Brazil (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, and São Paulo) (Gonzalez et al. 2014).

Mussurana montana (Franco, Marques & Puorto, 1997)

Natural history notes. A large species (*n* = 1), terrestrial (Marques et al. 2001, Gaiarsa et al. 2013). There is no information on the time of activity for this species (Gaiarsa et al. 2013). In October, an adult was seen resting at 11:20 h, coiled in the middle of plant litter, in a forested area. The record occurred in an adjacent conservation area: RPP Alto Montana, Itamonte-MG. Literature data indicate its diet is composed of snakes and lizards (Franco et al. 1997). Regarding the reproduction, Franco et al. (1997) recorded two females: one with seven and the other with 11 eggs. No defensive behavior was observed for this species.

Altitudinal variation. This species was found at a minimum of 750 m a.s.l. in Guaratinguetá, SP and maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). The maximum altitudinal record of the species was 1740 m a.s.l., at RPPN Alto Montana, Itamonte, MG. Bérnils (2009) stated all toponyms found to occur in areas above 750 m a.s.l..

Distribution and habitat. Southeast Brazil (Minas Gerais, Rio de Janeiro, and São Paulo) (Wallach et al. 2014). This species occurs in fields, close to ombrophilous and seasonal forests (Bérnils 2009).

Oxyrhopus clathratus Duméril, Bibron & Duméril, 1854

Natural history notes. Species of medium size (*n* = 1), terrestrial and nocturnal (Marques et al. 2001). A recently road-killed adult male was found in an open area near the PESP, during the morning. There was no evidence of diet or reproduction of the examined specimen. The available information in the literature indicates a diet composed mainly of mammals, although lizards and birds can also be prey (Hartmann et al. 2009b, Gaiarsa et al. 2013). Reproduction is seasonal, with a reproductive peak in the summer (Marques and Sazima 2004). Fecundity varies from four to 16 eggs (Gaiarsa et al. 2013). No defensive behavior was observed for this species.

Altitudinal variation. The species is found at a minimum of sea level from the coast of Rio Grande do Sul to Rio de Janeiro, and a maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). In this study, we found this species outside the PESP limits, at 1000 m a.s.l. in the Aiuruoca, MG. Total altitudinal range is broad with 31.7% of toponyms found from the sea level up to 400 m a.s.l., 36.6% between 401 and 800 m a.s.l. and 31.7% above 801 m a.s.l. (Bérnils 2009).

Distribution and habitat. Northeast and southeast Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo), and Argentina (Wallach et al. 2014, Bernardo et al. 2012). It occurs in dense, mixed ombrophilous and seasonal semidecidual forests (Bernardo et al. 2012).

Oxyrhopus rhombifer Duméril, Bibron & Duméril, 1854

Natural history notes. Species of medium size (*n* = 1), nocturnal and terrestrial (Marques et al. 2001). An individual was found resting during the day (9:30 h) in a pasture area. This species occurs mainly in open areas (Cechin 1999, Sawaya et al. 2008), but may be found in forested areas near fields (Lema 1994, Cardoso 2011). It is a generalist species, feeding mainly on lizards, but also small mammals and snakes (Cechin 1999, Carreira 2002, Maschio et al. 2003, Sawaya et al. 2008). It is oviparous, with litter varying from two to 12 eggs (Gaiarsa et al. 2013). No defensive behavior was observed for this species.

Altitudinal variation. This species is found at a minimum of sea level in Argentina, Uruguay, Rio Grande do Sul, and south of Santa Catarina, and at a maximum of 1330 m a.s.l. in Liberdade, MG (Bérnils 2009). This study provides a new maximum altitudinal record of the species with an individual found at 1730 m a.s.l., Baependi, MG. The records located below 400 m a.s.l. occurred only from the Prata Basin to Santa Catarina (Bérnils 2009).

Distribution and habitat. Northeast, central-west, southeast and southern Brazil (Bahia, Ceará, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, Santa Catarina and São Paulo), Argentina, Bolivia, Paraguay and Uruguay (Wallach et al. 2014). The species was predominantly found in areas with open formations of Pampa, plateau fields, rupestrian fields, restingas, and at the southern portions of the cerrado (Bérnils 2009, Ghizoni-Jr et al. 2009).

Philodryas aestiva (Duméril, Bibron & Duméril, 1854)

Figure 4D

Natural history notes. Species of medium size (*n* = 2), diurnal, often found on the ground in open areas (Di-Bernardo 1998, Marques et al. 2001, Sawaya et al. 2008). A recently road-killed adult male was found in an open field during the morning. The other record is of an adult's shed skin, located at the grassland, in a rock outcrop, at 1800 m a.s.l.. There is no information on diet and reproduction of the examined specimen. Machado-Filho (2015) describes this species as generalist, feeding on mammals (40%), birds (25%), lizards (20%) and anurans (15%). Vitellogenesis occurs between April and December and ovulation between July and December (Fowler et al. 1998). There is a record of a captive female with eleven eggs (Fowler et al. 1998). No defensive behavior was observed for this species.

Altitudinal variation. This species was found at a minimum of sea level from the coast of Uruguay to Santa Catarina and maximum of 1730 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). The maximum altitudinal record for this species is presented here, with a specimen recorded at 1800 m a.s.l.. Bérnils (2009) mentioned the species occurs at sea level only from Uruguay to Santa Catarina. All other localities where this species was found are plateau areas.

Distribution and habitat. Northeast, central-west, southeast and southern Brazil (Bahia, Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo), Argentina, Bolivia, Paraguay and Uruguay (Wallach et al. 2014). This species was predominantly found in open areas of pampas, plateau fields, cerrados, and restingas, with records to adjacent forests (Giraudo and Scrocchi 2002, Bérnils 2009).

***Philodryas patagoniensis* (Girard, 1858)**

Figure 4E

Natural history notes. Species of medium size (*n* = 9), diurnal and terrestrial (Marques et al. 2001, Hartmann and Marques 2005). All observations occurred in open areas during the day. Seven individuals were found between 14:00 and 17:00 h, and two were found in the morning. According to Sazima and Haddad (1992), and Hartmann and Marques (2005), this species is active mainly during the hottest hours of the day. In December, during the day (14:00 h), we found two adults (male and female) about two meters away from each other. Both were coiled at rest and showed evidence of being in the shedding process.

In September, an adult was observed at 14:00 h near a ravine, while it was being attacked by two different birds (*Poospiza* sp. and an unidentified Passeriformes), possibly in defense of a nearby nest. In July, an adult was observed at 15:00 h, while it was ingesting a rodent. Out of the four examined specimens, two presented rodents in their stomach. Machado-Filho (2015) suggest this species is generalist, feeding on anurans (27%), lizards (25.8%), mammals (19.4%), snakes (10.9%), birds (8%), spiders (4%), fish (0.4%) and amphibians (0.4%). *P. patagoniensis* was found during all seasons of the year with higher frequency in December (*n* = 4). There is no information on reproduction of the examined individuals. Previous records indicate reproduction is seasonal, with three to nine eggs, secondary vitellogenesis between August and December, and ovulation between October and December (Fowler et al. 1998, Sawaya et al. 2008). As defensive tactics of this species, we observed cloacal discharge, head elevation, head triangulation, and neck S-coiling.

Altitudinal variation. This species was found at a minimum of sea level from the coast of Argentina to the state of Espírito Santo and maximum of 1660 m a.s.l. in Umuarama, Campos do Jordão, SP (Bérnils 2009). The maximum altitudinal record for this species is from the area in this study, where an individual was recorded at 2200 m a.s.l. altitude, in the Alagoa, MG.

Distribution and habitat. North, northeast, central-west, southeast and southern Brazil (Bahia, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Rio de Janeiro, Rio Grande do Norte, Rio Grande do Sul, Rondônia, and São Paulo), Argentina, Bolivia, Chile, Paraguay and Uruguay (Wallach et al. 2014). This species can be found in open mountain areas, pampas, plateau fields, chacos, cerrados, restingas and deforested areas (Giraudo and Scrocchi 2002, Bérnils et al. 2007).

Sibynomorphus mikanii (Schlegel, 1837)

Natural history notes. Species of small size (*n* = 1), nocturnal and terrestrial (Marques et al. 2001). A recently road-killed individual was found in an open area during the day. No diet or reproduction data was recovered for the examined specimen. Available information indicates this species is a specialist in mollusks (Marques et al. 2001). Fecundity varies from three to 10 eggs, which may be laid in communal spawning (Albuquerque and Ferrarezzi 2004, Pizzatto et al. 2008a). No defensive behavior was observed for this species.

Altitudinal variation. This species was found at a minimum of 110 m a.s.l., in Puerto Bemberg, Iguazú, Argentina and maximum of 1350 m a.s.l. in the Serra do Ouro Branco, Ouro Branco, MG (Bérnils 2009). The maximum altitude for the species is expanded in this work, where a record occurred at 1630 m a.s.l., in the Baependi, MG. Total altitudinal range is broad with 12.3% of toponyms found below 400 m a.s.l., 30.5% above 801 m a.s.l., and 57.2% in the range between 401 and 800 m a.s.l. (Bérnils 2009).

Distribution and habitat. Northeast, central-west, southeast and southern Brazil (Bahia, Goiás, Maranhão, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Norte and São Paulo), Argentina and Paraguay (Bérnils 2009, Wallach et al. 2014). The species is common in forested formations from the Amazon Forest to the Atlantic Forest, in semidecidual and riverine forests and savannah formations of cerrado (Bérnils 2009, Freitas et al. 2014).

Taeniophallus affinis (Günther, 1858)

Natural history notes. Species of small size (*n* = 3), diurnal, terrestrial and cryptozoic (Marques et al. 2001). Two recently road-killed individuals were found during the day at 9:00 h and 14:00 h: one in an open area and the other in a forested area. A third individual was also found during the day in an open area, apparently at rest, near a watercourse. Of the three examined specimens, one presented fragments of anurans in its digestive tract. Available information indicates the diet is composed of anurans primarily, but also by lizards and amphisbaenians (Marques et al. 2001, Barbo and

Marques 2003). There is no information in the literature regarding the reproduction of the species. A female (SVL = 397 mm TL = 125 mm) presented five vitellogenic follicles in September. No defensive behavior was observed for this species.

Altitudinal variation. This species is found at a minimum of sea level from the coast of Rio Grande do Sul to Rio de Janeiro and maximum at 1600 m a.s.l. in Parque Estadual Ibitipoca, Lima Duarte, MG (Bérnils 2009). The maximum altitude for the species is increased, where individuals were observed at 1760 m a.s.l., in Baependi, MG. Bérnils (2009) points out that more than 80% of the toponyms are located in mountains and plateaus above 800 m.

Distribution and habitat. Northeast, southeast and southern Brazil (Alagoas, Bahia, Ceará, Espírito Santo, SE Minas Gerais, Paraná, Rio de Janeiro and Rio Grande do Sul, Santa Catarina, São Paulo) (Wallach et al. 2014). This species was reported in areas with predominantly dense and mixed ombrophilous forests (Bérnils 2009).

Taeniophallus gr. *occipitalis*

Natural history notes. Species of small size (*n* = 1), diurnal and cryptozoic (Sawaya et al. 2008). This individual was killed during the day by a domestic cat, near a forested area. There is no information on diet or reproduction for the examined specimen. There are no records of reproduction or altitudinal variation in *T.* gr. *occipitalis*. Prior reports are limited on diet, indicating only lizards as prey (Cechin 1999). No defensive behavior was observed for this species.

Altitudinal variation. In this study, the maximum record was at 1600 m a.s.l., in the Aiuruoca, MG.

Distribution and habitat. North, northeast, central-west, southeast and southern Brazil (Bahia, Ceará, Distrito Federal, Goiás, Pará, Paraíba, Paraná, Piauí, Rio Grande do Sul, Rondônia, São Paulo and Sergipe), Argentina, Bolivia, Paraguay, Peru and Uruguay (Wallach et al. 2014, Santos-Jr et al. 2008). *Taeniophallus* gr. *occipitalis* occurs in open (cerrados, amazon savannas, plateau fields and pampas) and forested areas (western Amazon Forest and northeastern Atlantic Forest, in Brazil) (Santos-Jr et al. 2008).

Thamnodynastes strigatus (Günther, 1858)

Figure 4F

Natural history notes. Species of medium size (*n* = 15), nocturnal and terrestrial (Marques et al. 2001, Barbo et al. 2011). The species was frequently found in November, December, and January. Ten individuals were observed resting during the day between 9:00 and 15:00 h; nine were in open areas and one on a forest border. Three individuals were found active at 22:00 h, foraging on the margin of a marsh with intense anuran vocal activity. Bernarde et al. (2000a) also observed this aggregation in *T. strigatus* in a permanent pond in Parque Estadual da Mata dos Godoy, Londrina, Paraná

State. A juvenile was collected at 15:00 h while crossing an unpaved road after heavy rain. An adult was observed, also during the day (9:00 h), as it had captured by the leg and was attempting to prey on a *Leptodactylus* sp. Histological features of the retina of *T. strigatus* (i.e., presence of cones, but absence of rods) (Hauzman et al. 2014) along with activity data obtained in captivity (Torello-Vieira and Marques 2017) reinforce the idea this snake exhibits significant activity during the day. Of the seven individuals examined, three presented stomach contents: lizard scales (in a young individual), a *Physalaemus* sp., and a *Rhinella* sp. (this last one also showed traces of an unidentified exoskeleton - possibly a secondary prey). Bernarde et al. (2000b) suggested *T. strigatus* is a generalist, feeding primarily on anurans (71.4%), but also rodents (14.3%), fish (3.6%), and lizards (3.6%). In regard to reproduction, one female (SVL = 585 mm; TL = 155 mm, collected in December) possessed 14 vitellogenic follicles and a young individual (SVL = 200mm; TL = 65 mm) was recorded in January. Barbo et al. (2011) mentioned observations of two females: one with 15 vitellogenic follicles in February and another one in November with 24 embryos. We could observe the following defensive behaviors for this species: cloacal discharge, head triangulation, body flattening, strike, and biting.

Altitudinal variation. This species was found at a minimum of sea level and maximum of 2450 a.s.l. in Itatiaia National Park, state of Rio de Janeiro, Brazil (Winkler et al. 2011). In this study, the maximum altitudinal record of the species was at 1730 m a.s.l., in the Baependi, MG.

Distribution and environment. Southern, southeast, and northern Brazil (Espírito Santo, Minas Gerais, Pará, Paraná, Rio de Janeiro, Santa Catarina, Rio Grande do Sul, Roraima and São Paulo), Paraguay, Uruguay and Argentina (Franco and Ferreira 2003).

Tomodon dorsatus Duméril, Bibron & Duméril, 1854

Figure 4G

Natural history notes. Species of medium size (*n* = 2), diurnal and terrestrial (Marques et al. 2001). Two individuals were found in forested areas during the day, one active at 12:30 h and the other a recently road-kill found at 10:30 h. These records were observed in September and October. We found no data on diet or reproduction of the examined specimens. Prior literature accounts suggest feeding exclusively on slugs. The reproductive cycle is seasonal, with births occurring from January to June (Bizerra et al. 2005). We observed the following defensive behaviors for *T. dorsatus*: cloacal discharge, head triangulation, body flattening, strike and biting.

Altitudinal variation. This species is found at a minimum of sea level from the coast of Rio Grande do Sul to Rio de Janeiro, and a maximum of 1610 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). We contribute a new maximum altitudinal record for our study area, where an individual was observed at 1730 m a.s.l., in Baependi, MG.

Distribution and habitat. Central-west, southeast and southern Brazil (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, and São Paulo), Argentina, Paraguay and Uruguay (Bérnils 2009, Wallach et al. 2014). This species is common in the Atlantic forest areas, with some records to open adjacent areas (Bérnils 2009).

Xenodon merremii (Wagler, 1824)

Figure 4H

Natural history notes. Species of medium size (*n* = 1), diurnal and terrestrial (Marques et al. 2001). In January, an individual was found at 14:00 h crossing an unpaved road in an open area. Prior records indicate this species specialize in anurans, mainly the toxic *Rhinella* spp. (Vitt and Vangilder 1983, Jordão 1997). *X. merremii* has a long reproductive cycle, from the beginning of the dry season to the middle of the rainy season. Fecundity varies between six and 44 eggs with recruitment between January and May (Pizzatto et al. 2008). As a defensive tactic of *X. merremii*, we observed the following behavior: body flattening.

Altitudinal variation. This species is found at a minimum of sea level from the northern coast of Rio Grande do Sul to the extreme south of Santa Catarina, São Paulo, Rio de Janeiro, Espírito Santo, and Bahia. Maximum altitude recorded is 1300 m a.s.l. in the Parque Estadual de Itacolomi, Ouro Preto, MG (Bérnils 2009). This study expands the maximum altitudinal record for this species with an individual registered at 1610 m a.s.l. from the Aiuruoca, MG. This species occupies a large variety of habitats, both vegetal and altitudinal. The recorded toponyms corresponds to the altitudinal gradient with 35.3% of toponyms between sea level and 400 m a.s.l., 33.2% between 401 and 800 m a.s.l. and 31.5% above 801 m a.s.l. (Bérnils 2009).

Distribution and habitat. North, northeast, central-west, southeast, and southern Brazil (Bahia, Brasília, Ceará, Goiás, Mato Grosso, Pará, Paraiba, Paraná, Pernambuco, Rondônia, São Paulo, and Tocantins), Bolivia and Paraguay (Wallach et al. 2014). This species occurs mainly in open areas (e.g., Cerrado, Chaco, plateau fields, rocky fields and Caatinga), but is also present in arboreal formations, such as seasonal forests, secondary forests, riverine forests and restingas (Bérnils 2009).

Viperidae Oppel, 1811

Bothrops fonsecai Hoge & Belluomini, 1959

Figure 4 I

Natural history notes. Species of medium size (*n* = 7), nocturnal and terrestrial (Marques et al. 2001). We collected twelve specimens of *B. fonsecai*, (seven during fieldwork and five outside of designated fieldwork periods. Individuals were more frequently observed in February and March. All observations occurred during the day. Ten adults were observed. Seven were at rest, five in open areas (at 9:00, 9:30, 10:00, 14:00, 14:10 h) and two at a forest edge (9:00 and 11:30 h). Three were found moving, two in open areas (10:00 and 14:00 h) and one entering a forested area (14:50 h). In November, we found an adult female, at rest at 9:00 h, 50 m away from a forested area. This female was about to shed. We found the same individual again at 14:00 h at the same place, with the skin-shed next to it. At 17:00 h, it had already retreated under the bush (goat's beard), remaining coiled in a stalking position. All individuals found in open areas were at most 100 m from a forested area. Two juveniles were found in forested areas, one coiled on the ground in the light-shade mosaics made by the sunlight (12:40 h) and another stretched over the first branches of a bromeliad (*Vriesea sceptrum* Mez)(9:30 h). This individual (SVL = 263 mm; TL = 38 mm; M = 18 g) was collected and contained a freshly ingested rodent (M = 6 g). *B. fonsecai* preys exclusively on rodents (Martins et al. 2001). In PESP, *B. fonsecai* can often be found among ferns (*Pteridium arachnoides* (Kaulf.)) growing near forested areas (Frederico Menezes, pers. obs.), and occasionally in swamp areas. Only juveniles were found within a forest (about 150 m inside). This difference in habitat use may be related to milder temperatures and protection against visually oriented predators. The reproductive cycle has been described by Menezes et al. (in press). We observed the following defensive tactic behaviors: tail vibrating (against the substrate and its own body), cloacal discharge, hiding the head under the body coils and striking.

Altitudinal variation. This species is found at a minimum of 400 m a.s.l. in Barra Mansa, RJ and a maximum of 1730 m a.s.l. in Campos do Jordão, SP (Bérnils 2009). The maximum altitudinal record for this study area is 2175 m a.s.l. in Itamonte, MG. Most of the toponyms where this species can be found (about 65%) are located at altitudes above 800 m a.s.l.

Distribution and habitat. Southeastern Brazil (Minas Gerais, Rio de Janeiro, and São Paulo) (Peters and Orejas-Miranda 1970, Wallach et al. 2014). It occurs in mixed ombrophilous forests and adjacent natural fields (Campbell and Lamar 2004, Bérnils 2009).

Bothrops jararaca (Wied, 1824)

Figure 4J

Natural history notes. A species of medium size (*n* = 2), semi-arboreal and mainly nocturnal (Sazima 1992, Marques et al. 2001). In January, a recently road-killed adult male was found in the morning in a forested area. In March, an adult was seen at 10:40 h. above a rock outcrop at 2150 m a.s.l. near a forested area. When the observer approached, it fled into the forest. We did not obtain information on diet or reproduction from the observed specimen. Available information on diet from prior studies indicates that *B. jararaca* is a specialist, with ontogenetic variation. When juvenile, it often feeds on ectothermic prey (amphibians). This shifts to endothermic prey during adulthood (Sazima 1992). The reproductive cycle is seasonal and biennial. Pregnant females can be found from November to March (Almeida-Santos and Salomão 2002). Gestation ranges from 152 to 239 days, with fecundity from three to 36 snakelets (Alves et al. 2000, Almeida-Santos and Salomão 2002).

Altitudinal variation. This species was found at a minimum of sea level between Rio Grande do Sul and Bahia with a maximum of 1640 m a.s.l. in Parque Nacional da Serra da Bocaina, SP (Bérnils 2009). The maximum altitudinal record for this species from this study area is an individual recorded at 2150 m a.s.l., in Baependi-MG. Of the surveyed toponyms, 33% occur at low elevations (0–400 m a.s.l.) and 41.5% at intermediate altitudes (400–800 m a.s.l.) (Bérnils 2009).

Distribution and habitat. Central-west, northeast, southeast, and southern Brazil (Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, São Paulo, and Santa Catarina), Paraguay and Argentina (Wallach et al. 2014). This species is common in ombrophilous and seasonal forests, although it can also be found in secondary forests and disturbed areas (Bérnils 2009).

Bothrops neuwiedi Wagler in Spix, 1824

Fig. 4 K

Natural history notes. Medium-sized snake (*n* = 1), terrestrial and nocturnal (Marques et al. 2016). We spotted an adult during the day (12:50 h) in March, in a rocky field area. It was basking near a forest fragment at 2150 m a.s.l. When the observer approached, it fled into the forest. The available data in the literature indicates it was found mainly in fields and other open formations (Borges and Araújo 1998, Valdujo et al. 2002, Bérnils 2009). Diet is composed primarily of mammals (Martins et al. 2001, Valdujo et al. 2002).

Altitudinal variation. The *neuwiedi* complex species was found at a minimum of sea level in the coast of Rio de Janeiro State, and a maximum of 1600 m a.s.l. in Parque Estadual do Ibitipoca, MG (Bérnils 2009). The maximum altitudinal record for this species is extended here, with an individual observed at 2150 m a.s.l. in the PESP, Baependi, MG. Bérnils (2009) states more than 80% of the surveyed toponyms are located in mountain and plateau areas, and only five toponyms have been recorded at sea level.

Distribution and habitat. Northeast, central-west, southeast and southern Brazil (Bahia, Goiás, Minas Gerais, Paraiba, Paraná, Rio de Janeiro, São Paulo and Santa Catarina) (Wallach et al. 2014). Like other taxa of the *neuwiedi* complex, this species occurs in open formations, such as savannas, rocky fields, and steppes (Bérnils 2009).

Crotalus durissus Linnaeus, 1758

Figure 4L

Natural history notes. Species of medium size (*n* = 1), with terrestrial and nocturnal habits (Marques et al. 2001). In January, an adult male was found during the day (13:00 h) in a high altitude grassland area. It was moving from the edge of a small forested area, towards an open field. Diurnal habits of this species have been described in reports by Sawaya et al. (2008) and Tozetti and Martins (2013) as well. No information of diet or reproduction was obtained from the specimen we observed. Available data indicates *Crotalus* has specialized in mammals, but may also ingest lizards (Sant'Anna 1999, Almeida-Santos and Germano 1996, Hoyos 2006). Interestingly, we found feces from an unidentified feline near the site of observation (at 2000 m a.s.l.) that contained a rattle and rattlesnake's scales, indicating feline predation. Reproduction is viviparous, with a biennial reproductive cycle. Vitellogenesis starts in March and gestation goes through October and January and recruitment happens between January and March (Almeida-Santos and Salomão 1997, Almeida-Santos and Orsi 2002). This specimen presented the following defensive behaviors: cloacal discharge, rattle vibration, s-coil formation, and strike.

Altitudinal variation. This species is found at a minimum of sea level for the coasts of Argentina, Uruguay, Rio Grande do Sul and Bahia and maximum of 1400 m a.s.l. at Taquaral Farm, Paraty, RJ (Bérnils 2009). The maximum altitudinal record for this species in this study area is an individual recorded at 1950 m a.s.l., in the Baependi, MG. Most of the surveyed toponyms occur at intermediate altitudes. Only 21% were found between 0–400 m a.s.l.; 51% between 401 and 800 m a.s.l. and 28% above 801 m a.s.l. (Bérnils 2009).

Distribution and habitat. Southern and southeastern Brazil (Amapá, Amazonas, Bahia, Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Maranhão, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Norte, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo), Netherlands Antilles (Aruba), Guyana, Suriname, French Guiana, Peru, Colombia, Venezuela, Uruguay, Bolivia and Paraguay (Bérnils 2009, Wallach et al. 2014). This species is typically found in open formations, with little vegetation, such as savannas and steppes (Campbell and Lamar 2004).

Discussion

Species composition

The 24 snake species recorded in this study correspond to approximately 11% of the 219 species known from the phytogeographical domain of the Atlantic Forest (Moura et al. 2016). In general, the observed richness to the PESP is similar than that of other sites in the low-elevated Southeast Atlantic Forest (e.g., Marques and Sazima 2004, Centeno et al. 2008, Pontes and Rocha 2008, Hartmann et al. 2009a,b, São Pedro and Pires 2009, Moura et al. 2012, Trevine et al. 2014). Given the altitude increments of this sampling effort, several high-altitude species are expected to be found in the area, such as *Ditaxodon taeniatus* (Peters *in* Hensel, 1868), with a record to the Campos do Jordão - SP, approximately 100 km from the study area (see Thomas et al. 2006); *Philodryas arnaldoi* (Amaral, 1933), with two records for the Franca - SP, approximately 330 km away from the study site (Bérnils 2009). Despite the distance, Franca is directly connected to the extreme west of Serra da Mantiqueira (Bérnils 2009), so both places may present common elements in their faunas (R.S. Bérnils pers. comm.). Other possible species are (for details, see Bérnils 2009): *Micrurus decoratus* (Jan, 1858) with a record for Caxambu – MG (ca. 27 km) (Gonzalez et al. 2014b); *Ptychophis flavovirgatus* Gomes, 1915, with a record for Liberdade - MG (ca. 45 km) (Gonzalez et al. 2014a); *Siphlophis longicaudatus* (Andersson, 1901), with a record for Munhoz - MG (ca 55 km); *Phalotris reticulatus* (Perters, 1960), also for Munhoz - MG; *Erythrolamprus jaegeri*

(Günther, 1858), recorded for Campos do Jordão – SP (ca. 100 km); *Pseudoboa serrana* Morato, Moura-Leite, Prudente & Bérnils, 1995, recorded for Bocaina de Minas – MG (ca. 35 km); *Echinanthera amoena* (Jan, 1863), recorded for Baependi – MG (ca. 25 km); *E. melanostigma* (Wagler 1824), recorded for Lambari - MG (ca. 65 km); *E. undulata* (Wied-Neuwied, 1824), recorded for Campos do Jordão - SP (ca. 100 km); *Taeniophallus bilineatus* (Fischer, 1885), recorded for Campos do Jordão - SP (ca. 100 km) and *T. persimilis* (Cope, 1869), recorded for Bananal - SP (ca. 70 km) (Bérnils 2009).

In any study, the relative frequency of snakes may be influenced by the sampling method (Marques 1998; Martins and Oliveira 1998). Here, the high frequency of *Atractus zebrinus* may be related to the use of pitfall traps, which accounted for 53% of records for that species. Nevertheless, disregarding pitfall trap records, *A. zebrinus* remains among the four most frequently observed species in the study area with seven records. Despite the considerable sample effort (2002 to 2007), Cardoso (2011) did not record *A. zebrinus* in a neighboring area (Farm Santa Elisa, Munhoz, MG, at 1320–1640 m a.s.l.). A possible explanation for this discrepancy is a lack of pitfall trappin method in that study effort. However, *A. zebrinus* has a confirmed voucher in the same farm in the Butantan Institute Collection (Frederico Menezes, pers. obs.). We propose this species simply may not be abundant in the study area covered by Cardoso (2011). In a similar discrepancy at Núcleo Curucutu, SP, Parque Estadual da Serra do Mar, Batista (2017) did not register *A. zebrinus* for this locality despite the use of pitfall traps. While, in an earlier study, Barbo et al. (2008) collected a specimen in the area. It is possible the altitudinal gradient influences species abundance, as noted by Lawton et al. (1987). *Atractus zebrinus* was the most abundant species in two inventories which were carried out at 1500 meters above the sea level: Ortiz et al. (2017), in Serra da Bocaina, with seven individuals (none captured by pitfall traps), and the present study, in Serra da Mantiqueira, with 15 individuals. However, this interpretation remains speculative and we suggest further tests, with a larger data set, to investigate this possibility.

In contrast to other Neotropical snake community studies (Cardoso 2011, Fiorillo 2016, Hartmann 2009a, b, Marques 1998, Cechin 1999, Sawaya et al. 2008, Costa et al. 2010), the family Viperidae was not the most abundant in this study. Our findins are more similar to the observations from temperate areas of Araucaria Forests and associated ecosystems (Di-Bernardo 2007, Deiques 2009). This may reflect a pattern for elevated areas. In this context, several factors may account for the predominance of *B. fonsecai* over other viperids (*B. jararaca*, *B. neuwiedi*, and *C. durissus*), which are somewhat common and easy to find (see Sazima 1988, Sazima 1992, Marques and Sazima 2004, Sawaya et al. 2008, Hartmann 2009a,b). Climatic factors, especially temperature, can act directly on the abundance of species that coexist in a given locality (Vitt 1987). We hypothesize that *B. fonsecai* is more tolerant of lower average temperatures, and as a result predominates in this study area where temperature may be a limiting factor for abundance of other vipers. For example, *B. jararaca* is very abundant in sites between 0 - 800 m altitude and yet rare in higher localities of Serra da Mantiqueira and Araucaria Plateau (Bérnils 2009). Altitude also seems to influence the population density of species *Chironius bicarinatus*, *E. miliaris*, *O. clathratus*, *S. mikanii*, and *S. pullatus*. These species are well-represented in inventories carried out at lower altitudes (e.g., Hartmann et al. 2009a,b, Marques 1998, Fiorillo 2016, Trevine et al. 2014), but are rare in the study area, with only one record each. Regarding viperids *Bothrops fonsecai* and *B. alternatus* specifically, the later was not recorded in the PESP (1600 to 2359 m als). Hoge and Belluomini (1964) have discussed allopatry between these two species for the state of São Paulo and in areas near Minas Gerais State. Bérnils (2009) affirmed the allopatry proposed by these authors was not accurate, since, in these states some areas where *B. fonsecai* occur within areas where *B. alternatus* is dominant. However, sympatry could not be confirmed for these locations primarily because the specimens, housed in zoological collections, do not contain precise georeferences (Bérnils 2009). *Bothrops alternatus* is confirmed for Aiuruoca (IBSP data), at Ponte Coberta Farm (between 900 and 1000 m a.s.l.). In the same municipality, we recorded a *B. fonsecai* at approximately 1900 m a.s.l., which indicates sympatry between these species in the area. *B. fonsecai* is likely to be restricted to the higher altitudes, with different microclimatic conditions, and where there are still well-preserved forest fragments (Frederico Menezes pers. obs.). As for *B. alternatus*, this species is concentrated in lower open areas (Bérnils 2009).

The high species richness registered for the PESP might be related to environmental heterogeneity and the mix of habitats allowing more species of reptiles to coexist (Pianka 1969). However, comparing abundance data across altitude suggests this might have the greater effect on the number of individuals found. The frequency of individuals obtained in the PESP was at least 5.7 times lower than in Marques (1998), 3.5 times lower than Hartmann (2009a), 3.3 times lower than Fiorillo (2016), and only larger than Trevine et al. (2014). It is necessary to consider that these inventories were not performed uniformly and this could be a bias in comparing the abundance of snakes between these localities. Though decrease in abundance and species richness as altitude increases has been observed in other animal groups (Lawton et al. 1987, Moraes et al. 2017), it remains to be explored for snakes (Marques 1998). Undoubtedly, factors influencing species abundance across altitude are complex and differ for species and altitudinal transects. Although this hypothesis is speculative, we encourage further research to test this relationship in Brazilian snakes through systematic samplings at different altitudinal gradients.

Comparison with other snake assemblages from the Atlantic Forest of southeastern Brazil

The species composition of the Parque Estadual da Serra do Papagaio is very similar to the Munhoz, which is also in southern Serra da Mantiqueira. These areas have very similar vegetation types. Both are present in the Alto Paraná Atlantic Forest, which contains rocky fields, savannahs, and montane forests (sensu Olson et al. 2001). The only other locality with similar vegetation to PESP and Munhoz is the São José do Barreiro, in São Paulo State (Ortiz et al. 2017). However, this locality belongs to another topographical complex: the Serra da Bocaina, which is separated from the Serra da Mantiqueira by the Paranapiacaba valley. This valley may pose a geographical barrier to the dispersal of the snake fauna (Ortiz et al. 2017, this study). Thus, the Serra da Mantiqueira seems to contain a *sui generis* composition of snake species, resulting in group 3 of our cluster analysis.

The other two main groups are composed of plateau areas (1) in the states of São Paulo and Minas Gerais (except localities in southern Serra da Mantiqueira); and (2) lowland areas and in São Paulo and Rio de Janeiro states. The formation of a cluster containing low coastal localities has already been described for anurans (Pombal Jr et al. 2004, Bertoluci et al. 2007, Forlani et al. 2010). Coastal climatic conditions and other environmental characteristics may be the primary factors acting on formation of a particular fauna. These are certainly different between different areas of the Atlantic Forest (Dixo and Verdade 2006, Forlani et al. 2010). The presence of snake species found only in higher areas of the Atlantic Forest had already been highlighted by previous studies (e.g., Bérnils 2009). Thus, a more significant similarity was expected between these highlands. This is especially true of the Planalto Paulista, due to the number of localities inserted in the Ecological Continuous of Serra de Paranapiacaba, one of the largest preserved fragments of Atlantic Forest in São Paulo State (Pisciotta 2002).

Conservation

The Serra da Mantiqueria is defined as an area of particular biological importance, and it stands out in the region as one of the most important areas for biodiversity conservation in the state of Minas Gerais. This status is justified by the high abundance of rare and threatened species (Drummond et al. 2005). The Parque Estadual da Serra do Papagaio is located within the Serra da Mantiqueiria and carries many different types of vegetation, including fields, forests, and ombrophilous mixed forest (Olson et al. 2001, Silva et al. 2001). As it is one of the few areas in Minas Gerais protecting this variety of vegetation, it is regarded as an area of extreme biological importance (Silva et al. 2008). Currently, the mixed ombrophilous forest has been reduced to less than 5% of its original size (SOS Mata Atlântica and INPE, 2014). These remaining areas constitute the last refuges, sheltering several high altitude species (Backes 2009, Cardoso 2011). *Bothrops fonsecai* is endemic to an area that covers approximately 120,000 km^2, in the mountainous portions of São Paulo, Minas Gerais, and Rio de Janeiro States (Barbo 2012). Of the viper species found in this study, *B. fonsecai* was the only one which was not located outside the PESP limits. It appears to be relatively common in protected areas, but rare in unprotected areas. The absence of this species in disturbed areas suggests it may be sensitive to environmental degradation and/or may benefit from the protection. Either of these contributes to a critical situation that demands immediate efforts for conservation. Additionally, little is known about the ecology of *B. fonsecai*. Although we have collected field data about its natural history, a detailed study is still necessary to describe its displacements, home range, habitat use, and reproduction (e. g. Hartmann et al. 2003, Tozetti and Martins 2008).

The dipsadid *Mussurana montana* is another species of interest found in this area. This species is endemic to a region that covers about 16,000 km^2 in the mountainous portions of São Paulo, Minas Gerais, and Rio de Janeiro states (Barbo 2012). According to Costa et al. (2015), it is susceptible to habitat disturbance. In the national assessment of the Brazilian fauna risk of extinction, *M. Montana* was classified as "least concern" (MMA 2014). Regional classification of *M. montana* is "vulnerable" and "near threatened" in the states of São Paulo and Minas Gerais, respectively (Biodiversitas 2007, Bérnils et al. 2009). Recently, Costa et al. (2015) presented three new records of this species in protected areas of the State of Minas Gerais, increasing its known range considerably and supporting the lower conservation status in Minas Gerais. *M. montana* is known only to inhabit tropical ombrophilous or seasonal forest formations of montain ranges from Bocaina, Mantiqueira and Órgãos, between 750–1,610 m a.s.l. (Bérnils 2009, Costa et al. 2015). However, sampling in potentially suitable areas for the species did not yield encounters (Costa et al. 2015). This may mean that *M. montana* is present over a smaller range and more specific habitat than was previously expected. If true, this reinforces the need for conservation in areas where it occurs.

The present study provides data on the occurrence and natural history of snakes in the Parque Estadual da Serra do Papagaio. However, additional field research is encouraged. New inventories could contribute additional knowledge about the natural history of the species of this region, especially those of which ecological, biological, and morphological data are scarce, such as *Mussurana montana*. Our ordination analysis shows a remarkable difference between the compositions of snake faunas between different altitudinal gradients in the Brazilian Atlantic Rainforest. The Serra da Mantiqueira, where the Parque Estadual da Serra do Papagaio is located, seems to present a very unique composition of snake species, most of which are not shared with others localities from the southeast of Brazil. The diverse vegetation types found in this region permits the existence and maintenance of diverse species of animals. Additionally, the protected areas belonging to the Atlantic Forest affords greater potential to find rare and endemic species. These facts together make an argument for prioritizing the conservation of this park. Nevertheless, even if recognized as a conservation unit, the park continues to suffer depredation of its flora and fauna, mainly through illegal hunting. Regrettably, this alarming scenario is widely observable in Brazil due to the scientific scrapping and the neglect of the Brazilian government to control its natural resources (Bockmann et al. 2018).

Key to the snake species from Serra do Papagaio State Park – MG

1 Loreal pit present; solenoglyphous dentition .... **Viperidae**
– Loreal pit absent, aglyphous or opisthoglyphous **2**
2 Aglyphous dentition; even number of dorsal scale rows ....**Colubridae**
– Aglyphous or opisthoglyphous dentition; odd number of dorsal scale rows... .... **Dipsadidae**

Viperidae

1 Rattle at the tip of the tail; with some enlarged shields on top of the head .... ***Crotalus durissus***
– No rattle at the tip of the tail; tiny shields on top of the head **2**
2 Inverted v-shaped spots along the dorsum; second supralabial fusioned with the prelacular .... ***Bothrops jararaca***
– Trapezoid spots along the dorsum; second supralabial not fused with the prelacular **3**
3 Non-fragmented trapezoid spots along the dorsum; black venter .... ***Bothrops fonsecai***
– Trapezoid spots are fragmented at the midline to ventrals; venter cream, with several tiny brown spots .... ***Bothrops neuwiedi***

Colubridae

1 12 scale rows at mid-body........................ **2**
– More than 12 scale rows at mid-body .... ***Spilotes pullatus***
2 2–4 rows of keeled dorsal scales; first third of body black or dark gray, vertebral stripe yellowish or cream; top of the head tan to brown (distinct from the background color of the body); venter cream, with black bordered scales........................ ***Chironius brazili***
– Two rows of keeled dorsal; olive green at the first third of the body; head color similar to the body; venter yellow, without black bordered scales .... ***Chironius bicarinatus***

Dipsadidae

1 17 or fewer scale rows at mid-body **2**
– 19 scale rows at mid-body........................ **10**
2 15 scale rows at mid-body........................ **3**
– 17 scale rows at mid-body........................ **5**
3 Internasal shields absent; body almost uniformly red, with black tail .... ***Apostolepis assimilis***
– Internasal shields present; without red color on the dorsum........................ **4**
4 Black eyes, indistinguishable pupil; venter white, with black spots .... ***Sibynomorphus mikanii***
– Eyes with brown background color and round pupil, easily distinguishable; venter immaculate yellow........................ ***Taeniophallus* gr. *occipitalis***
5 Dark lining, loreal shield absent........................ ***Tomodon dorsatus***
– Light lining, loreal shield present **6**

6 Dorsal color brown, with a lighter longitudinal line on each side; three supralabials in contact with the eyeball .... ***Gomesophis brasiliensis***
– Coloration not as above; two supralabials in contact with the eyeball **7**
7 Dorsal scales with black borders and light centers; venter cream yellow, base of ventral scales with black edges .... ***Erythrolamprus miliaris***
– Coloration not as above **8**
8 Stout and short body; small eyes .... ***Atractus zebrinus***
– Slender and elongate body; large eyes **9**
9 Fourth row of dorsal scales with white dots that, together, form a continuous line along the body; brown top of the head and body; ventral scales with transverse band .... ***Echinanthera cephalostriata***
– The fourth row of dorsals without white dots; top of the head black, contrasting with the brown body; ventral scales without transverse band .... ***Taeniophallus affinis***
10 Two apical pits **11**
– Single apical pit **14**
11 Red iris **12**
– Black or dark brown irish, never red **13**
12 Juveniles are brick red, with a dark brown longitudinal vertebral stripe; adults are entirely dark brown .... ***Mussurana montana***
– Coral color pattern, with black triangular spots, bordered with white, background color red .... ***Oxyrhopus rhombifer***
13 Loreal shield usually absent; contact between frontal and preocular absent... .... ***Oxyrhopus clathratus***
– Loreal shield present; contact between frontal and preocular present............ .... ***Boiruna maculata***
14 Keeled dorsal scales; dorsum uniform green .... ***Philodryas aestiva***
– Smooth dorsal scales; dorsum never green **15**
15 *Canthus rostralis* very evident; without postocular stripe .... ***Philodryas patagoniensis***
– *Canthus rostralis* not evident; conspicuous postocular stripe **16**
16 With two large post-diastemal fangs, aglyphous; venter cream, without longitudinal lines .... ***Xenodon merremii***
– Without two large post-diastemal fangs, but opisthoglyphous; venter cream, with two to four longitudinal lines .... ***Thamnodynastes strigatus***

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