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Research article

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The new Southeast Asian genus *Cambonilla* gen. nov. (Zodariidae, Araneae): ‘bis repetita placent’

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Abstract. The new genus *Cambonilla* Jocqué gen. nov. is described on the base of two species, each known from both sexes. A cladistic analysis based on morphology, showed that the new genus is the sister-group of *Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012 with which it shares the granulated carapace with branched setae and the marbled ventral abdominal pattern, but differs by the abdominal, tubular sclerotized protrusion around the pedicel in males and the absence of posterior ventral abdominal spines in the female. The type species *Cambonilla securicula* Jocqué gen. et sp. nov. was found in rainforest along the Mekong River in Cambodia and Laos. The second species *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov., provided with conspicuous femoral stridulating organs, was recorded from the same localities but in Cambodia only. An illustrated key to the genera of tropical Asia is presented.

Keywords. Cladistic analysis, key to genera, Mekong River, riverine distribution.

Jocqué R, Jocque M., Stock W., Rin N. & Henrard A. 2019. The new Southeast Asian genus *Cambonilla* gen. nov. (Zodariidae, Araneae): ‘bis repetita placent’. *European Journal of Taxonomy* 501: 1-24. <https://doi.org/10.5852/ejt.2019.501>

Introduction

The genus *Mallinella* Strand, 1906 is with more than 200 species known and many more to be described, by far the largest genus in the Zodariidae (Jocqué 1991; Nzigidahera *et al.* 2011). In a review of the genus from East Asia, Dankittipakul *et al.* (2012) described two genera closely related to *Mallinella*: *Workmania* Dankittipakul, Jocqué & Singtripop, 2012 and *Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012. The latter turned out to be the sister-group of *Mallinella* in an analysis based on 98 morphological characters (Dankittipakul *et al.* 2012). During a recent inventory in lowland forest in Cambodia, two species were found that appear to belong to yet another unknown genus, hence the subtitle of the paper: ‘bis repetita placent’ (nice to have it twice!). Not only because this is the second paper describing new taxa on the generic level in this clade, but also because two species are involved which supports the ‘new genus’ hypothesis. Considering the fact that the forest soil spider fauna of the country is very poorly known, *Asceua septemmaculata* (Simon, 1893) is the only species of zodariids that has been recorded from there (World Spider Catalog 2018), it is not surprising to find novelties in the area, even at the genus level. Apart from the species of the new genus, the collection further contained two species of *Asceua* Thorell, 1887, three of *Mallinella*, one of *Storenomorpha* Simon, 1884 and one of *Tropizodium* Jocqué & Churchill, 2005. We here describe the new genus, provide a cladistic analysis to illustrate its relationships and present a new key to the genera of tropical Asia.

Material and methods

Specimens were observed, drawn and measured with a WILD M 10 stereo microscope. Measurements and photographs of the habitus, details of body parts, detached male palps and female genitalia were taken with a Leica MZ16 using the LAS automontage software (ver. 3.8). The female genitalia were dissected and digested with pancreatin, then immersed in 75% ethanol.

For SEM photographs, specimens were dried overnight in Hexamethyldisilazane, gold coated and examined and photographed with a JEOL 6480 LV scanning electron microscope. All types are deposited in the Royal Belgian Institute of Natural Sciences (RBINS Brussels, Belgium) and vouchers in the Naturmuseum Senckenberg (SMF, Frankfurt, Germany). All measurements are in mm. All palp illustrations are from left palps except the ventral view with SEM. Maps were created with the online tool SimpleMappr (Shorthouse 2010).

Abbreviations

ALE	=	anterior lateral eyes
AME	=	anterior median eyes
ALS	=	anterior lateral spinnerets
AW	=	anterior width
C	=	conductor
Cx	=	coxa
d	=	dorsal
disp	=	dispersed
dw	=	distal whorl
E	=	embolus
EB	=	embolus base
F	=	femur
MA	=	median apophysis
Mt	=	metatarsus
P	=	patella
pl	=	prolateral
PLE	=	posterior lateral eyes

JOCQUE R. *et al.*, *Cambonilla*: a new genus of Zadariidae from Southeast Asia

PLS	=	posterior lateral spinnerets
PME	=	posterior median eyes
PMS	=	posterior median spinnerets
PVS	=	posterior ventral spines
RBINS	=	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
rl	=	retrolateral
RTA	=	retrolateral tibial apophysis
SMF	=	Senckenberg Museum Frankfurt, Germany
t	=	tarsus
T	=	tibia
TM	=	tegular membranous area
Tr	=	trochanter
v	=	ventral

Phylogenetic analysis

The analysis is based upon the data matrix used by Dankittipakul *et al.* (2012). We used the same outgroups *Storenomorpha reinholdae* Jocqué & Bosmans, 1989 and *Cydrela pristina* Dankittipakul & Jocqué, 2004 but also *Asceua dispar* (Kulczynski, 1911) with the same scoring as *Asceua* sp. it replaces. Including these, we made a selection of 44 species, out of the original 84, plus the two new species described in this paper. The selection contained representatives of the different species-groups of *Mallinella* Strand, 1906, of *Heradion* Dankittipakul & Jocqué, 2004, *Euryeidon* Dankittipakul & Jocqué, 2004, *Workmania* Dankittipakul *et al.*, 2012 and eight out of the ten known *Heliconilla* Dankittipakul *et al.*, 2012. The same 98 characters were used. Only two characters were added and for character 22 concerning the presence of PVS, the specification ‘in males’ was added. The new characters are:

99. Female palpal tibia 0. without sinuous modified spine; 1. with short, sinuous modified spine (although uninformative, only one species in the matrix shows this character, it was considered special enough to have a trace of it in the matrix).

100. PVS on abdomen in females. 0. absent; 1. in single row; 2. in more than one row or a group. The score was identical as that of character 22 (now restricted to males), except for *Cambonilla* Jocqué gen. nov. because there are no PVS in the females.

The scoring for the new species is as follows:

Cambonilla securicula 1 0 1 0 1 1 2 0 1 0 0 1 2 0 2 1 1 1 0 3 4 0 1 2 3 2 1 1 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 2
1 0 0 0 0 0 0 0 0 0 2 1 0 0 1 1 0 0 0 1 1 0 0 0 1 0 1 2 0 0 1 0 1 4 0 0 0 0 1 0 0 1 0 1 0 0 0 3 2 1 0 0 0 1 1 0

Cambonilla symphonia 2 0 1 0 1 1 2 0 1 0 0 1 2 0 1 1 1 1 0 3 2 0 1 2 1 2 1 1 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 2
1 0 0 0 0 0 0 1 0 1 0 2 0 0 0 1 1 0 0 0 0 1 0 0 0 1 3 1 2 0 0 1 0 1 4 0 0 0 0 1 0 0 1 0 0 0 0 0 3 2 1 0 0 0 1 0 0

Analyses were carried out with Winclada (version 1.00.08 Nixon 1999–2002) by using ‘the ratchet’ with default settings (200 iterations, 1 tree to be hold, 9 characters to sample). Twelve characters were uninformative, including the new 99, and were deactivated.

Results

The parsimony analysis in Winclada resulted in five equally long trees with length 415, consistency index 45 and retention index 72. The preferred tree is shown in Fig. 1. In three of the five trees, and evidently also in the majority consensus (60%), *Cambonilla* gen. nov. and *Heliconilla* turned out to be sister-groups, forming a clade, which is sister to *Mallinella* including *Workmania*. In the other two,

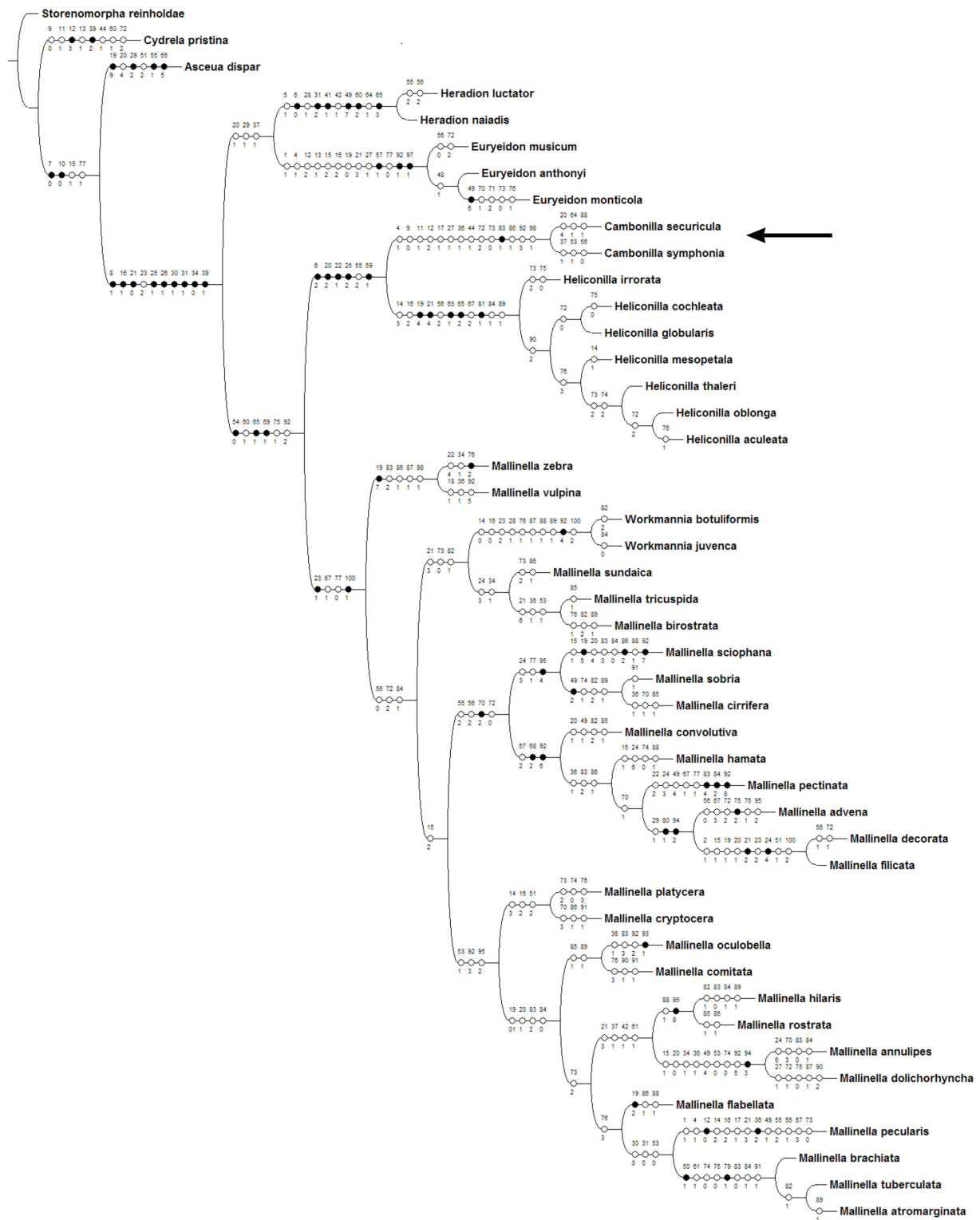


Fig. 1. Preferred tree out of 5 (46 taxa, 100 characters), length 415, CI 45, RI 72. Arrow indicates the position of *Cambonilla* Jocqué gen. nov. Black circles indicate non-homoplastic synapomorphies and white circles indicate homoplastic changes. Character numbers (see Dankittipakul *et al.* 2012) are placed above the circles and the states are shown under the circles.

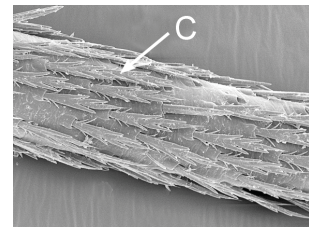
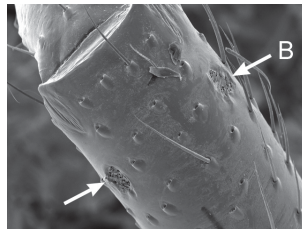
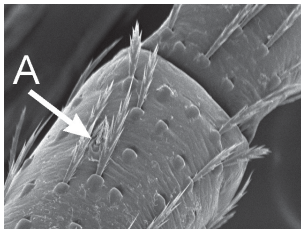
Cambonilla gen. nov. is sister to the majority of the ingroup containing *Mallinella*, *Heliconilla* and *Workmania*.

Affinities

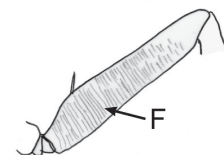
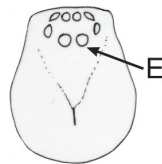
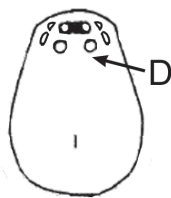
From the phylogenetic analysis it is clear that *Cambonilla* gen. nov. and *Heliconilla* are closely related. They share a granulated domed carapace with a cover of branched setae, the strongly procurved eye rows, the abdomen with a characteristic ventral marbled pattern, the PVS have rows of denticles and are set in an unclear arrangement at least in males, absent in females, and the cymbium of the male palps provided with a short lateral fold and long field of chemosensitive setae. *Cambonilla* gen. nov. is distinct by the absence of PVS in the female, the protrusion of the frontal scutum around the pedicel in the male.

Key to the genera of Zodariidae from tropical Asia

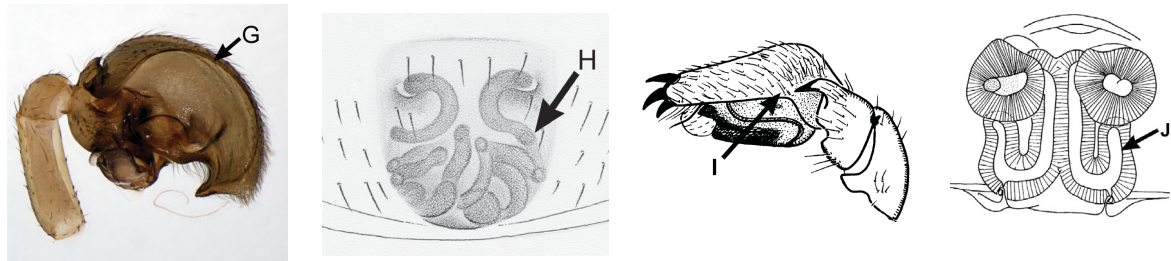
1. Femoral organ present on all legs, or at least legs II-IV (A) 2
 - Femoral organ absent 5
2. Legs with dense cover of flattened incised setae (C); femoral organ single, on retro-lateral side (A) *Tropizodium* Jocqué & Churchill, 2005
 - Legs not covered with flattened incised setae; femoral organ double, on pro- and retrolateral side (B) 3



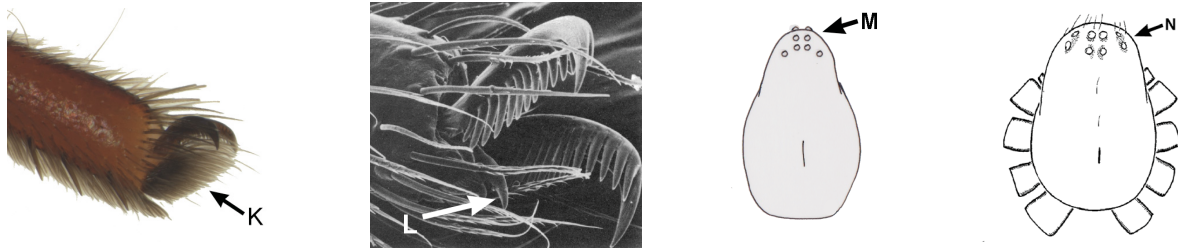
3. AME less than half their diameter apart (E); anterior femora with prolateral wrinkles (F); chilum faint (females unknown) *Malayozodarium* Ono & Hashim, 2008
 - AME their diameter or slightly less apart (D); femora without wrinkles; chilum well developed ... 4



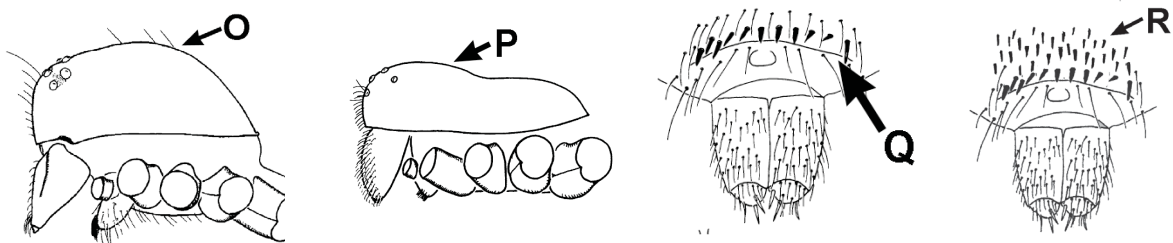
4. Cymbium narrow, with strong retrolateral fold (G); ducts in epigyne intricately wound (H) *Asceua* Thorell, 1887
 - Cymbium wide, without retrolateral fold (I) but sometimes with pit; epigyne with few loops (J) *Suffasia* Jocqué, 1991
5. Tarsi with two claws and claw tuft (K) *Hermippus* Simon, 1893
 - Tarsi with three claws (L), unpaired claw may be hidden by thick scopula in *Storenomorpha* 6



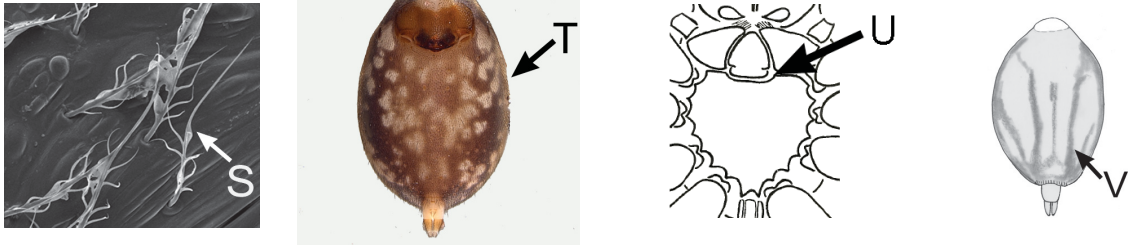
6. Eyes in three rows, 2-2-4 (M)..... 7
 – Eyes in two rows 4-4 (N)..... 8
7. Highest part of carapace near fovea (O); body covered with sticky setae, covered with mud and soil debris..... *Cryptothele* L. Koch, 1872
 – Highest part of carapace in eye region (P); without sticky setae *Cydrela* Thorell, 1873
8. Posterior eye row strongly recurved (M); tarsal claws strongly curved and in alveolus; tarsi with well-developed scopulae..... *Storenomorpha* Simon, 1884
 – Posterior eye row straight or procurved (N); tarsal claws as usual; tarsi without scopulae 9



9. Posterior ventral spines (PVS) in front of spinnerets absent (females only).....
 *Cambonilla* Jocqué gen. et sp. nov.
 – Posterior ventral spines in front of spinnerets present (Q) 10
10. Posterior ventral spines arranged in a single row (Q), normally situated on weakly sclerotized area..... *Mallinella* Strand, 1906
 – Posterior ventral spines arranged in a group or more than one row (R)..... 11



11. Carapace granulated with tiny branched setae; venter of abdomen with marbled pattern (T); anterior margin of sternum straight; apical surface of PVS serrated, consisting of two rows of minute denticles (visible in SEM only)..... 12
 – Carapace smooth or when granulated with simple setae; venter abdomen with pattern of longitudinal dark stripes (V); anterior margin of sternum with central concavity accommodating labium (U); apical surface of PVS smooth (visible in SEM only) (W)..... 13



12. Carapace with thick longitudinal band of setae (S); without sclerotized protrusion around the pedicel..... *Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012
 – Carapace without longitudinal band of setae; with sclerotized protrusion around pedicel (X) (males only) *Cambonilla* Jocqué gen. et sp. nov.
13. Chelicerae with two small teeth on promargin; PLE more than three times their diameter from PME (Y); AER strongly pro-curved; carapace strongly domed and strongly granulated; dorsal scutum on opisthosoma large and ovoid, heavily sclerotized *Euryeidon* Dankittipakul & Jocqué, 2004
 – Chelicerae without teeth; distance between PLE and PME not so wide (< 2 times diameter); AER slightly procurved or straight; carapace not elevated and not strongly granulated; dorsal scutum on opisthosoma longitudinal, weakly sclerotized or absent; legs elongated 14



14. Carapace smooth and shiny; setae, if present, restricted to margins; F with basal, dorsal, tipped swelling bearing a spine (Z); dorsal scutum on opisthosoma longitudinal, weakly sclerotized *Heradion* Dankittipakul & Jocqué, 2004
 – Carapace reticulated or rugose and provided with dispersed setae; F without basal swelling; dorsal scutum on abdomen indistinct *Workmania* Dankittipakul, Jocqué & Singtripop, 2012

Taxonomy

Class Arachnida Cuvier, 1812
 Order Araneae Clerck, 1757
 Family Zodariidae Thorell, 1881

Genus *Cambonilla* Jocqué gen. nov.

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Type species

Cambonilla securicula Jocqué gen. et sp. nov.

Diagnosis

Species of *Cambonilla* gen. nov. are recognized by the tubular protrusion around the pedicel and dispersed PVS, with rows of tiny denticles in males, absence of PVS in females; both sexes have a marbled pattern of the abdominal venter, strongly recurved PER and granulate carapace teguments.

Etymology

The genus name is derived from the country of the type locality Cambodia, in combination with the ending of its sister genus *Heliconilla*. The gender is feminine.

Description

MEDIUM SIZE SPIDERS (7.5–7.3 mm). With granulate teguments of carapace (Fig. 2A), sternum and basal leg segments. Carapace longer than wide ($L/W < 1.29–1.65$) with sparse cover of split pale setae (Fig. 2B); widest at level of coxae II, narrowed to about 0.63 times maximum width in males (Figs 2A, 5A) and 0.66–0.80 times maximum width in females (Fig. 6A) (cephalic width measured on posterior tangent of PME); domed (Fig. 2C), without cervical grooves, profile highest at fovea.

COLOUR (Fig. 5A–D). Carapace dark brown; chelicerae, legs, mouthparts and sternum medium to orange brown; abdomen dorsum dark with pattern of numerous white spots without apodemes, in males anteriorly overlaid by transparent reddish orange oval scutum; venter with sepia pattern on dark background; sclerotized in front of epigastric fold, in males extended into short tubular extension around pedicel.

EYES. In two strongly procurved rows: PLE at level of AME (Fig. 2D). All eyes pale and subequal. Clypeus straight, height 2.8 to 4.2 times diameter of ALE (Figs 2D, 5C).

CHILUM. Single, well developed and delimited, protruding in the middle. Chelicerae conical with many evenly dispersed setae; without teeth; fangs about three times longer than wide at base (Fig. 2E). Labium triangular. Endites roughly triangular, converging (Fig. 5B). Sternum shield-shaped, almost as wide as long, with rounded precoxal depressions (Fig. 4A–B); anterior margin straight, lateral margins with inter- and intracoxal triangular extensions; posterior tip slightly indented in males, rounded or truncate in females.

LEGS. Slender. Formula 4123 or 4132. Tibial process well developed in all legs. Spination reduced on legs I and II, well developed on III and IV. Most spines short and slender. Bothria with three ridges (Fig. 1F). Superior tarsal claws with up to 15 teeth on leg I and II (Fig. 3A), with up to 8 teeth on legs III and IV (Fig. 3B). One dorsal hinged hair on tibiae I and II (Fig. 3C). Mt II–IV with preening brush of chisel-shaped setae (Fig. 3D).

FEMALE PALPAL TARSUS. With claw turned inward over $\pm 30^\circ$, provided with four or five small, basal, prolateral teeth; with several spines; without distal patch of chemosensitive setae.

ABDOMEN. Oval; tracheal spiracle fairly small, provided with small rectangular scutellum. Both sexes with six spinnerets. ALS large, conical, biarticulate. PLS and PMS provided with 1 and 4 cylindrical gland spigots respectively. Colulus represented by haired field. Venter with dispersed thick setae in posterior half (Figs 5B, D, 8B, D) and with short PVS provided with rows of tiny denticles (Fig. 3E–F), in ill-defined row and/or group in males; both absent in females; hinged hairs sparse (Fig. 6B–C).

MALE PALP. Tibia with strong RTA (Figs 4D, 5E). Cymbium with a few small distal spines; without distal claw; with patch of chemosensitive setae (Figs 4C–D, 5E), short lateral fold opening ventrad, reaching middle of cymbium; tegulum with large central membranous area (Figs 5F, 7A); MA situated

near retrolateral distal part of tegulum; C relatively small; embolus with massive well delimited base, originating on posterior part of tegulum, long, bifid (Fig. 4E).

EPIGYNE. With central plate wider than long (Figs 6D, 7C, 9D, 10C). Spermathecae poorly delimited smoothly fused to copulatory ducts (Fig. 6E).

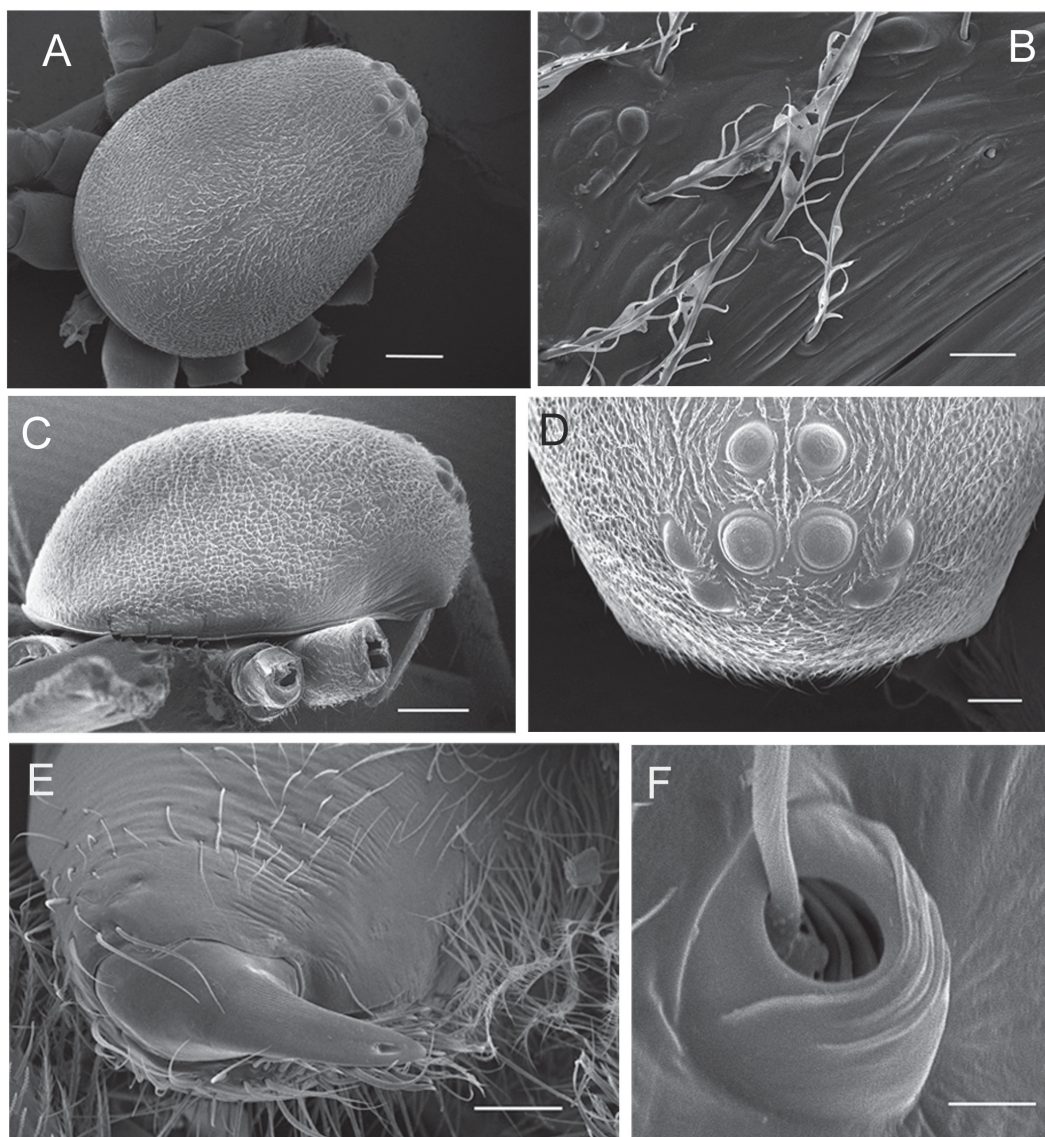


Fig. 2. *Cambonilla securicula* Jocqué gen. et sp. nov., male paratype (RBINS IG 33.889/002), scanning electron micrographs. **A.** Carapace, dorsal view. **B.** Branched setae near fovea. **C.** Carapace, lateral view. **D.** Eye region, frontal view. **E.** Chelicerae, ventral view. **F.** Trichobothrium on male palp, dorsal view. Scale bars A, C = 0.5 mm; B = 20 μ m; D = 0.2 mm; E = 0.1 mm; F = 5 μ m.

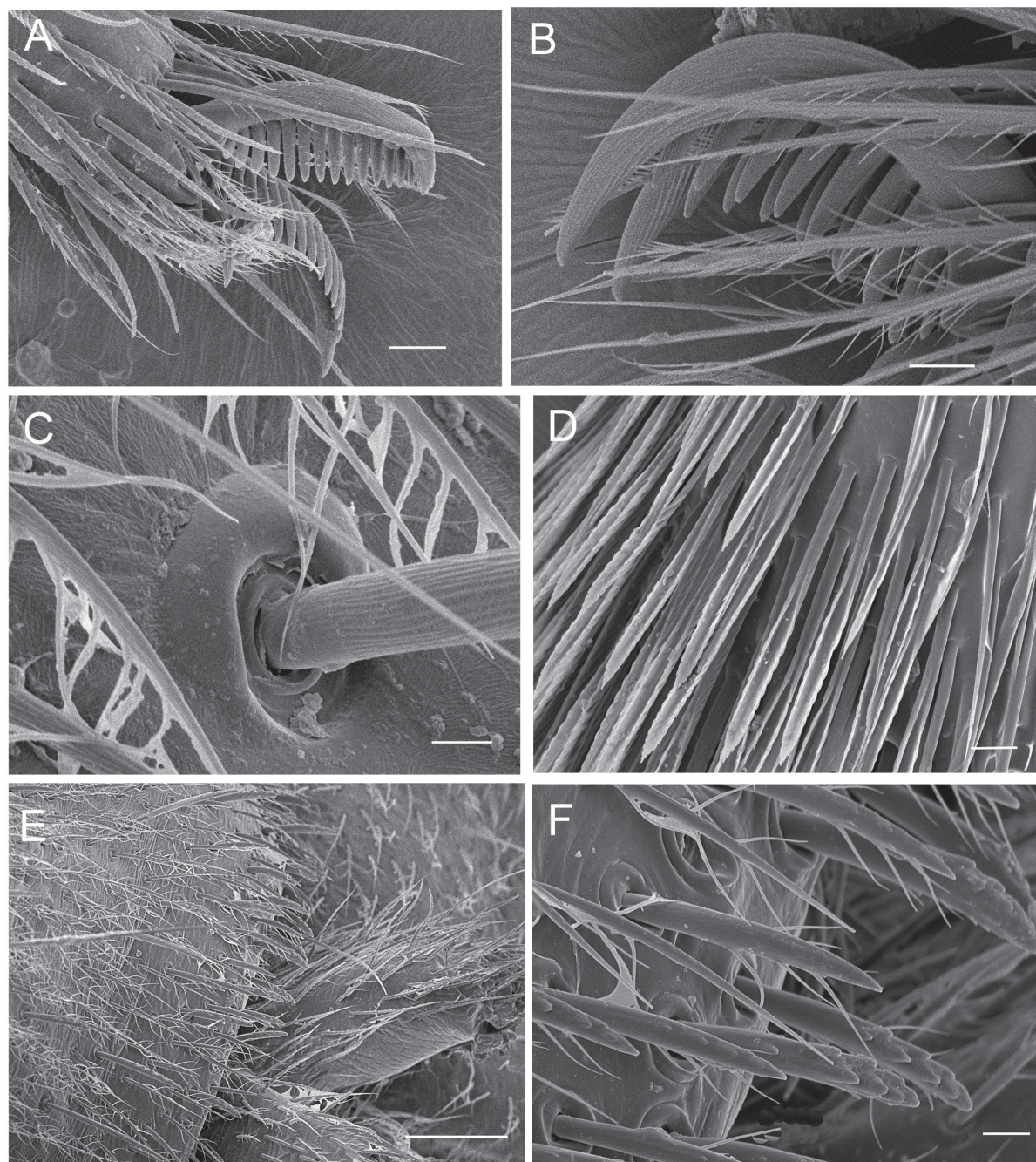


Fig. 3. Scanning electron micrographs. **A.** *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov., male paratype (RBINS IG 33.889/009). **B–F.** *Cambonilla securicula* Jocqué gen. et sp. nov. male paratype (RBINS IG 33.889/005) **A.** Tarsal claws of leg I, pro-lateral view. **B.** Tarsal claws of leg III, retro-lateral view. **C.** Hinged hair on T I. **D.** Chisel shaped setae on Mt III. **E.** PVS, ventral view. **F.** As preceding, detail. Scale bars: A–B, D = 20 μ m; C = 5 μ m; E = 100 μ m; F = 10 μ m.

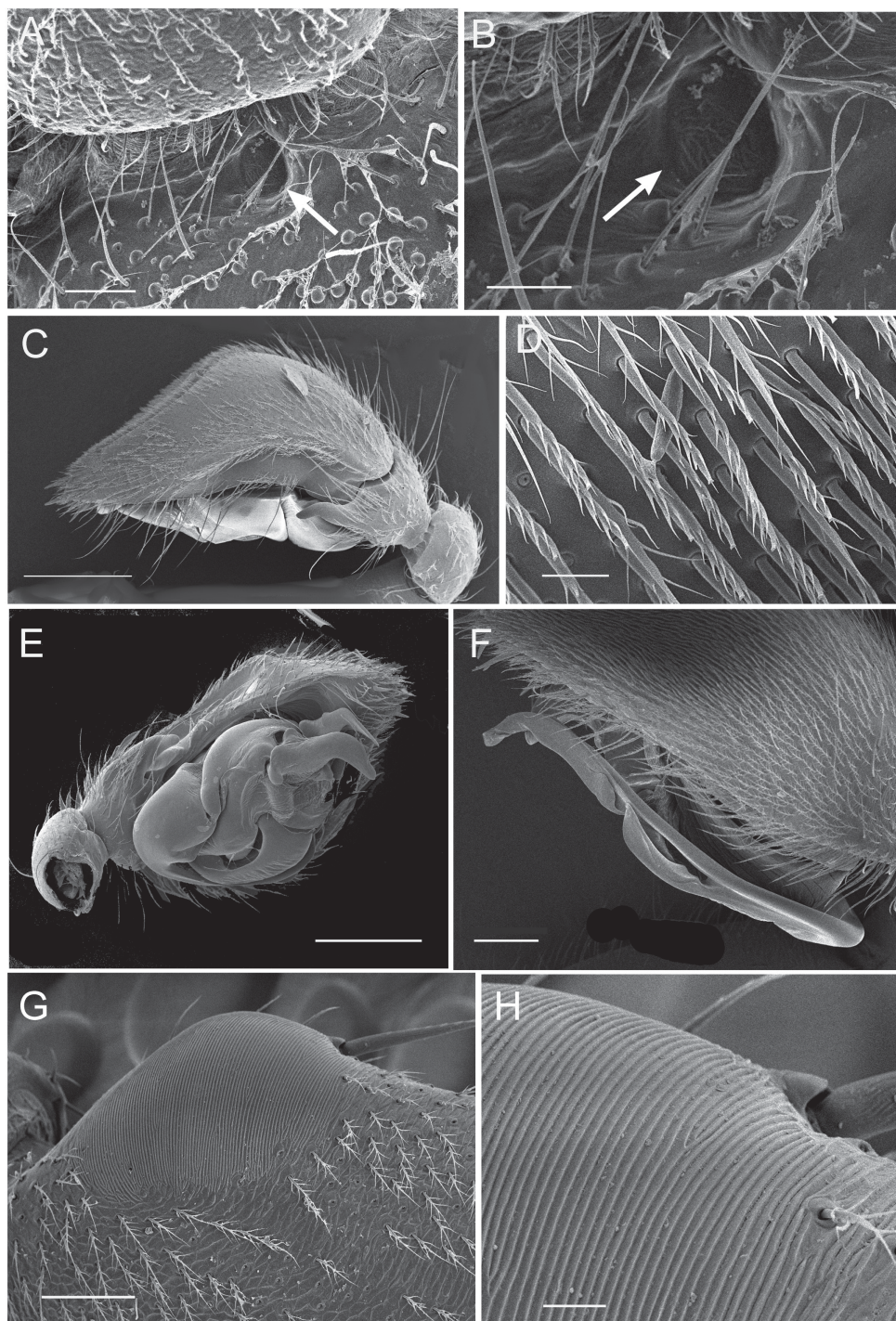


Fig. 4. Scanning electron micrographs. **A–F.** *Cambonilla securicula* Jocqué gen. et sp. nov., male paratype (RBINS IG 33.889/005). **G–I.** *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov., male paratype (RBINS IG 33.889/009). Scanning electron micrographs. **A.** Sternal depression. **B.** As preceding, detail. **C.** Male palp, lateral view. **D.** Chemosensitive setae on cymbium, lateral view. **E.** Male palp, ventral view. **F.** Embolus with bifurcation, prolateral view. **G.** Stridulating file on base of F I, prolateral view. **H.** As preceding, detail. Scale bars: A, G = 0.1 mm; B = 50 μ m; C, E = 0.5 mm; D, H = 20 μ m; F = 0.2 mm; G = 0.1 mm; H = 20 μ m.

Species included

Cambonilla securicula gen et sp. nov. (♂♀)

Cambonilla symphonia gen et sp. nov. (♂♀)

Distribution

Cambonilla is known from lowland forest in the vicinity of the Mekong River in Cambodia and Laos.

Cambonilla securicula Jocqué gen. et sp. nov.

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Figs 2, 3B–F, 4A, 5, 6, 7, 11

Diagnosis

The male of *Cambonilla securicula* sp. nov. is recognized by the presence of small lateral scuta behind the epigastric fold and by the male palp in which both the MA and the C are hatchet shaped. The female has a remarkable, small, modified spine on the tibia of the palp and a characteristic epigyne in which the central plate has a concave anterior and a straight posterior margin.

Etymology

The species name ‘*securicula*’ meaning hatchet, is a noun in apposition referring to the shape of both the MA and the C.

Material examined

Holotype

CAMBODIA • ♂; Kratie Province, Base Camp; 13.00986° N, 106.0640° E; 16 May 2018; M. Jocque & W. Stock leg.; Herpetology pitfall in forest; RBINS IG 33.889/001.

Paratypes

CAMBODIA • 3 ♂♂; same data as for holotype; RBINS IG 33.889/002(=CA3) • 2 ♂♂, 1 ♀; 17 May 2018; same data as preceding; RBINS IG 33.889/003 • 4 ♂♂ 2 ♀♀; 13 May 2015; same data as preceding; RBINS IG 33.889/004 • 4 ♂♂; Kratie Province, Base Camp 4; 13.0198° N, 105.9268° E; 5 May 2018; M. Jocque and W. Stock leg.; pitfall set 1; RBINS IG 33.889/005 • 1 ♂; Kratie Province; 13.00986° N, 106.06395° E; 10 May 2018; M. Jocque and W. Stock leg; pitfall set 3; RBINS IG 33.889/006.

Other material

CAMBODIA • 1 ♂, 1 ♀; Kratie Province, Base Camp; 13.00986° N, 106.0650° E; 6–11 May 2018; M. Jocque and W. Stock leg.; forest, by hand; RBINS IG 33.889/010 • 2 ♂♂; Kratie Province, Base Camp 1; 12.61788° N, 106.00296° E; 10 Apr. 2018; M. Jocque and W. Stock leg.; flooded forest on sand, Malaise trap, by hand; RBINS IG 33.889/011.

LAOS – **Vientiane Province** • 1 ♀; Vientiane, Ban Don Ma Khay; 18.08384° N, 102.1713° E; 13 Jun. 2013; P. Jäger leg.; 186 m, secondary forest, at night by hand; SMF – **Champasak Province** • 1 ♀; Muang Bachieng, That Paxuam; 15.17653° N, 105.9225° E; 3 Aug. 2016; P. Jäger and S. Munnich leg.; 197 m, secondary forest with single primary trees, by night, by hand; SMF – **Khammouan Province** • 1 ♀; Ban Tathot; 17.62361° N, 105.1466° E; 18–19 Feb. 2003; P. Jäger leg.; ca 180 asl, village and neighbourhood, shrubs and rocks, night and evening; SMF.

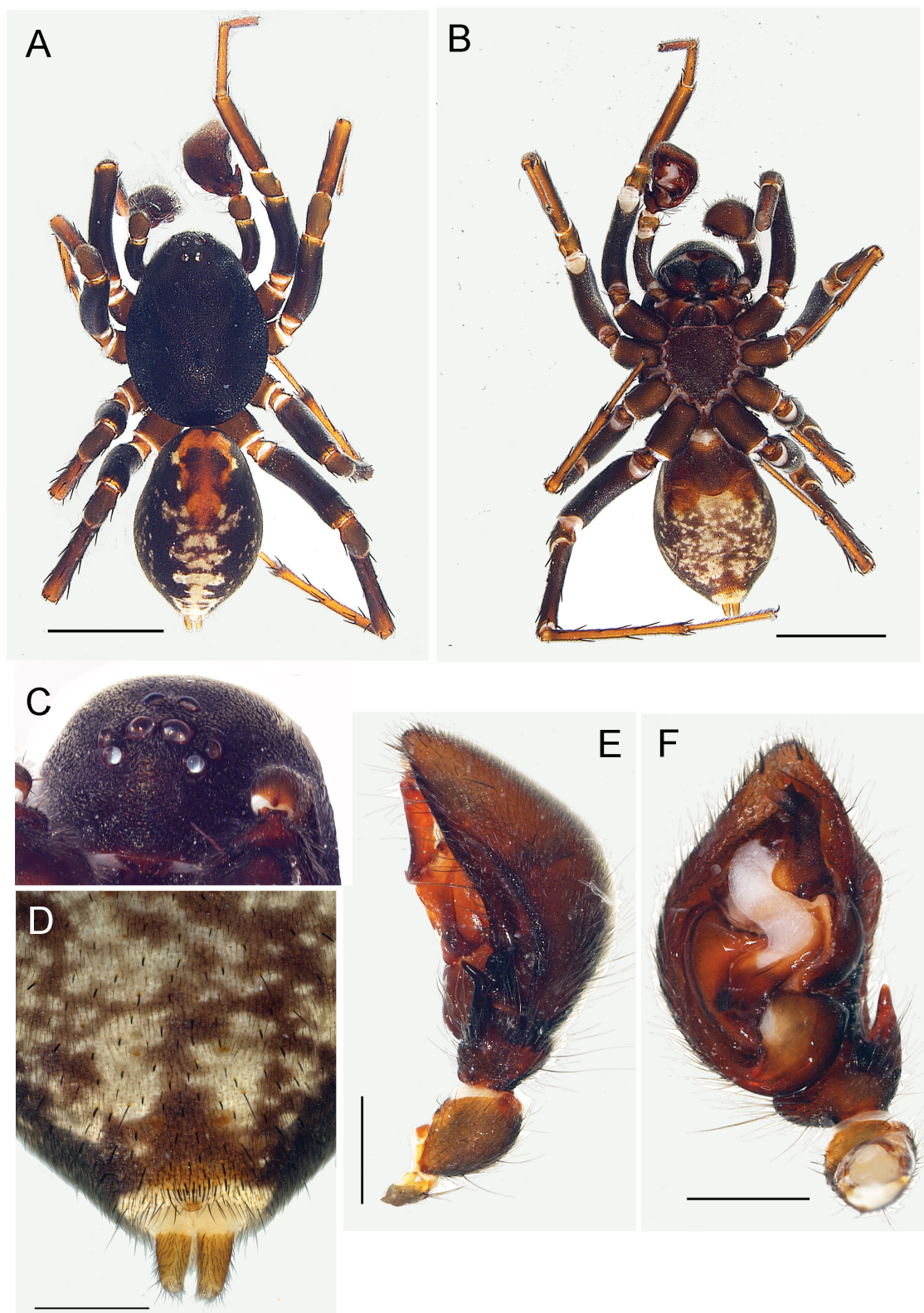


Fig. 5. *Cambonilla securicula* Jocqué gen. et sp. nov., male holotype. **A.** Habitus, dorsal view. **B.** Habitus, ventral view. **C.** Carapace, frontal view. **D.** Abdomen, posterior part, ventral view. **E.** Male palp, retrolateral view. **F.** Male palp, ventral view. Scale bars: A–B = 2 mm; C = 1 mm; D–F = 0.5 mm.

Description**Male holotype**

TOTAL LENGTH. 6.96. Carapace: length 3.48, width 2.70, height 2.00.

COLOUR (Fig. 5A–D). Carapace uniform dark chestnut brown; chelicerae dark brown with orange extremity and white tip; chilum medium brown; sternum medium brown; labium and endites medium brown, paler towards anterior white tip; legs: Cx and Tr medium brown, Fe dark brown, P and T greyish brown, Mt and t pale brown. Abdomen: dorsum with pale reniform patches fused in front and at posterior end, overlaid by reddish orange, translucent oval scutum; further backward with five transverse bands and pale patch above spinnerets on dark background; venter sclerotized in front of epigastric furrow and yellow sclerotized area on either side behind epigastric furrow; remainder marbled with sepia on pale background; spinnerets pale brown.

CARAPACE GRANULATED. With sparse cover of thin, pale, branched setae.

EYES. ALE 0.16; AME 0.20; PLE 0.13; PME 0.13; ALE-AME 0.10; AME-AME 0.07; PLE-PME 0.12; PME-PME 0.12. Clypeus 0.66 high.

CHILUM. 0.21 high, 0.43 wide, with slightly concave inferior side, centre protruding.

STERNUM (Fig. 5B). Shield shaped, granular; 1.42 wide, 1.49 long. Posterior tip shallowly indented; with rounded depressions in front of coxae; no precoxal sclerites.

LEGS. Trochanters III and IV with anterior ventral indentation; dorsal hinged hair on base of T I and II. Cx and ventral side of F granular.

LEG MEASUREMENTS.

	Fe	P	T	Mt	t	Total
I	2.31	0.84	1.75	1.89	1.61	8.40
II	2.03	0.84	1.40	1.75	1.40	7.42
III	2.03	0.84	1.26	1.61	0.98	6.72
IV	2.59	0.91	1.96	2.87	1.89	10.22

SPINATION.

	F	P	T	Mt
I	pl1d2	-	v1-1-2	disp3 dw4
II	pl1d3	pl2	v1-1-2	disp5 dw4
III	pl1d3r1	pl2r1	pl3d3r1v1-2-2	disp6 dw4
IV	pl1d4r1	pl2r1	pl4d3r1v2-2-2	disp8 dw4

ABDOMEN. With PVS in ill-defined group and dispersed thick setae in posterior half (Fig. 5D); with short tubular extension around pedicel, its anterior margin ventrally indented (Fig. 5B).

MALE PALP (Figs 4C–F, 5E–F, 7A–B). T with strong, slightly sinuous, downcurved, blunt RTA; cymbial fold as long as half the cymbium's length; embolus with large base, originating at an angle of 270° to longitudinal axis, halfway with short, flat bifurcation, distal end corkscrew shaped; MA hatchet-shaped with short ventral tooth at base; C with short, sharp, flat, distal protrusion, pointing prolaterad.

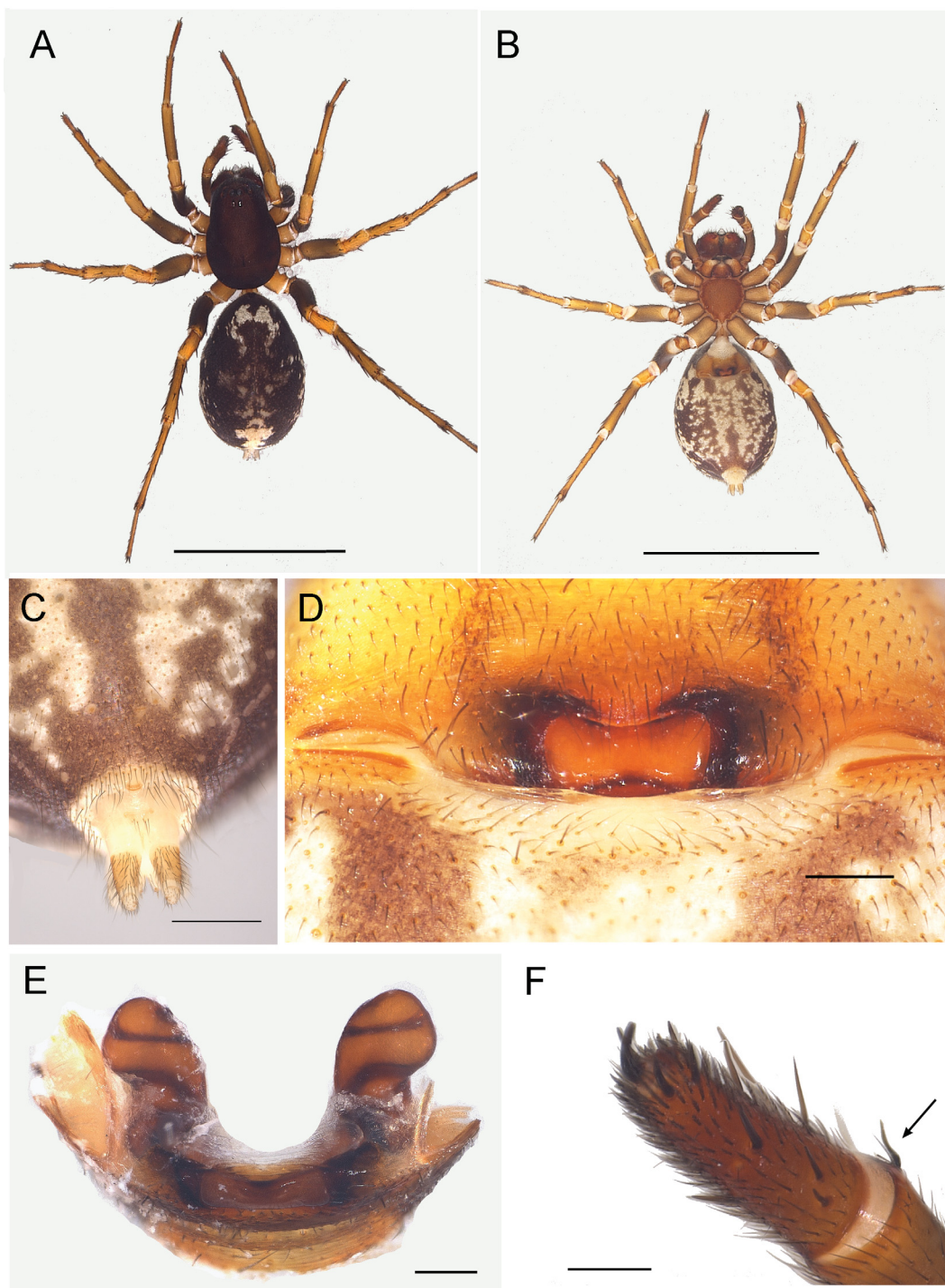


Fig. 6. *Cambonilla securicula* Jocqué gen. et sp. nov., female paratype (RBINS IG 33.889/003). **A.** Habitus, dorsal view. **B.** Habitus ventral view. **C.** Abdomen, posterior part, ventral view. **D.** Epigyne, ventral view. **E.** Epigyne, digested, dorsal view. **F.** Palp, dorsal view, arrow indicates modified prolateral spine on tibia. Scale bars: A–B = 5 mm; C = 1 mm; D–F = 0.2 mm.

Female (RBINS IG 33.889/003)

TOTAL LENGTH. 7.31. Carapace: length 3.05, width 2.06, height 1.42.

COLOUR (Fig. 6A–C). Carapace uniform dark brown; chelicerae medium brown with pale tip; chilum medium brown. Endites and labium medium brown with pale frontal margin. Sternum uniform medium brown. Legs I: Cx medium brown, Tr pale brown, F dark brown, remainder yellowish orange; palp medium brown except T yellowish orange. Abdomen: dorsum with two ill-defined reniform spots touching in front, without scutum overlay, followed by small, faint, pale patches and large patch in front of spinnerets; venter with sclerotized band in front of epigastric furrow, without tubular extension, remainder marbled with sepia on pale background, spinnerets pale yellow.

CARAPACE. Rugose with sparse cover of branched setae.

EYES. ALE 0.18; AME 0.18; PLE 0.15; PME 0.13; ALE-AME 0.15; AME-AME 0.07; PLE-PME 0.23; PME-PME 0.08. Clypeus 0.51 high.

CHILUM. A single sclerite 0.12 high, 0.33 wide, with central protrusion.

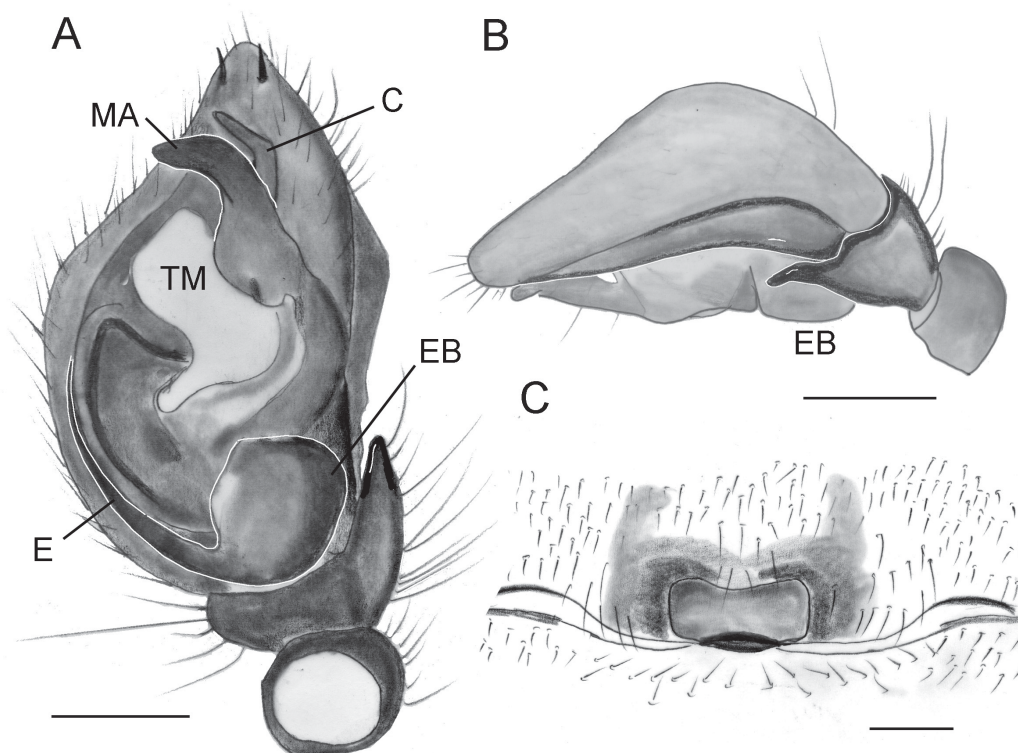


Fig. 7. *Cambonilla securicula* Jocqué gen. et sp. nov. **A–B.** Male holotype. **C.** Female paratype (RBINS IG 33.889/003). **A.** Male palp, ventral view. **B.** As preceding, retrolateral view. **C.** Epigyne, ventral view. Abbreviations: C = conductor; E = embolus; EB = embolus base; MA = median apophysis; TM = tegular membranous area. Scale bars: A–B = 0.5 mm; C = 0.2 mm.

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STERNUM (Fig. 6B). Shield shaped; 1.28 wide, 1.35 long. Posterior tip rounded; with rounded depressions in front of coxae; no precoxal sclerites.

LEGS. Tr III and IV posteriorly indented. Hinged hair on T I and II.

SPINATION.

	F	P	T	Mt
I	pl1d3	-	v1-1-1-2	disp3 dw4
II	pl1d3	pl2	v1-1-1-2	disp5 dw4
III	pl1d3r1l	pl2r1l	pl4d3r13v1-2-2	disp5 dw4
IV	pl1d3r1l	pl2r1l	pl4d3r14v1-2-2	disp8 dw4

LEG MEASUREMENTS.

	Fe	P	T	Mt	t	Total
I	1.89	0.77	1.47	1.40	1.26	6.79
II	1.61	0.77	1.12	1.33	1.05	5.88
III	1.68	0.70	0.91	1.61	1.05	5.95
IV	2.10	0.91	1.75	2.45	1.40	8.61

FEMALE PALP. Tarsus with toothed claw turned inward over 30°, eight dispersed spines; tibia with short, sinuous prolateral spine (Fig. 6F).

ABDOMEN. Venter without PVS or thick setae (Fig. 6C).

EPIGYNE (Figs 6D-E, 9D). With wide rectangular plate, concave in front, posterior margin convex and thickened in the middle. Copulatory ducts with few whorls, ending in poorly delimited spermathecae near posterior end.

Variation

The abdominal venter of the female specimen from Ban Tathot (17.62361 °N, 105.1466 °E) is not marbled but has three dark, faint longitudinal lines.

Distribution

Known from lowland forest in Cambodia and Laos; all localities are along the Mekong river (Fig. 11).

Cambonilla symphonia Jocqué & Henrard gen. et sp. nov.

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Figs 3A, 4G–I, 8, 9, 10, 11

Diagnosis

The male of *Cambonilla symphonia* gen. et sp. nov. is recognized by the presence of stridulating organs on Fe I and II, and by the strong tapered RTA on the palp, the female by the epigyne with very deeply incised central plate.

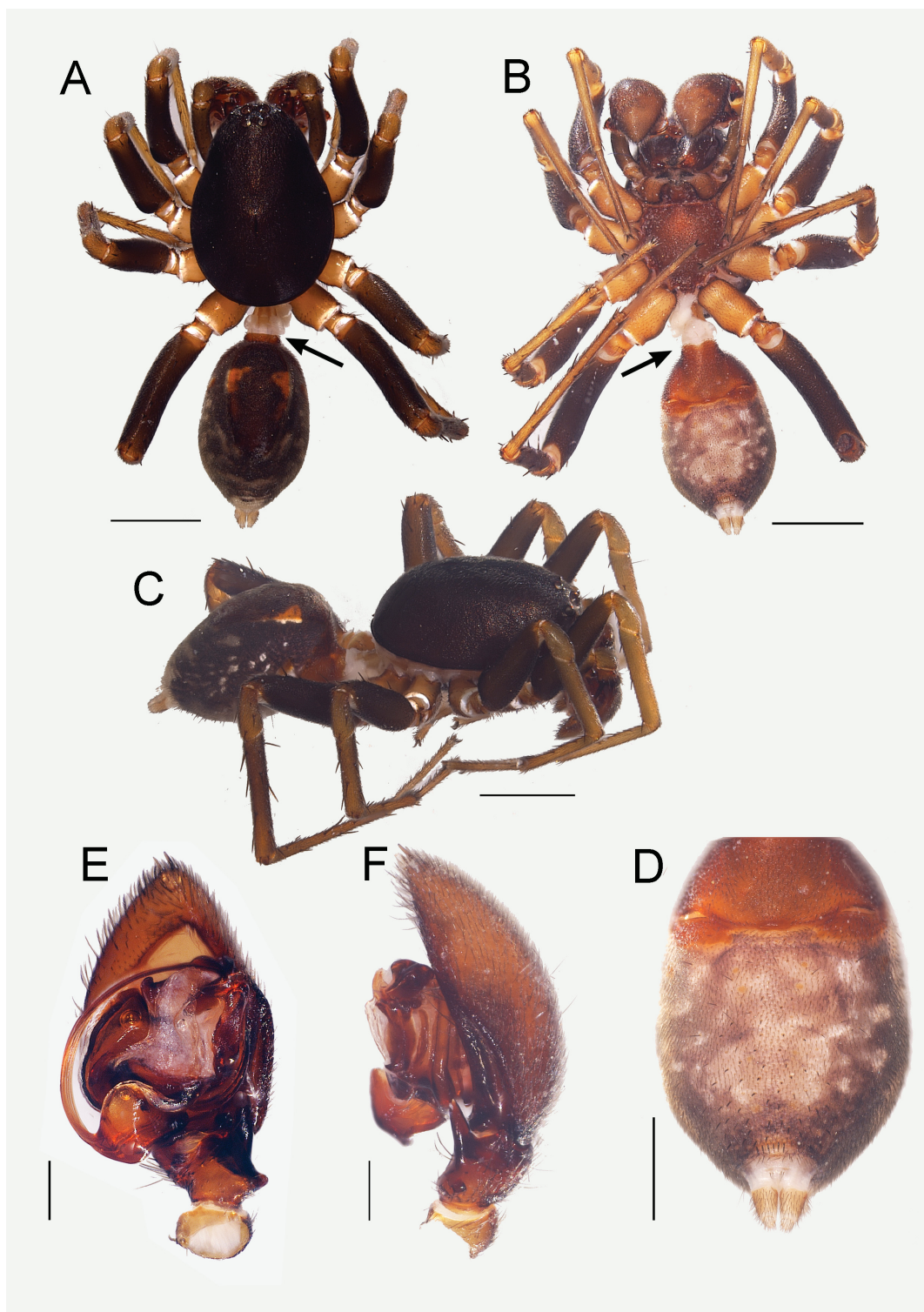


Fig. 8. *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov., male holotype **A.** Habitus, dorsal view. **B.** Habitus, ventral view. **C.** Habitus, lateral view. **D.** Abdomen, ventral view. **E.** Male palp, ventral view. **F.** Male palp, retrolateral view. Arrows indicate tubular extension. Scale bars: A–C = 2 mm; D = 1 mm; E–F = 0.5 mm.

Etymology

The species name '*symphonia*' is a noun in apposition meaning 'orchestra' and refers to the four stridulating organs on the femora of the male.

Material examined

Holotype

CAMBODIA • ♂; Kratie province, Base Camp 4; 12.5460° N, 105.9881° E; 5 May 2018; M. Jocque and W. Stock leg.; pitfall set 1; RBINS IG 33.889/007 (=CA15).

Paratypes

CAMBODIA • 1 ♀; Kratie province, Base Camp 3; 13.0199° N, 106.0395° E; 10 May 2018; M. Jocque and W. Stock leg.; rainforest, pitfall set 3; RBINS IG 33.889/008 • 2 ♂♂; Kratie province, Base Camp 4; 13.0198° N, 105.9268° E; 5 May 2018; M. Jocque and W. Stock leg.; rainforest, pitfall set 1; RBINS IG 33.889/009.

Description

Male holotype

TOTAL LENGTH. 4.83. Carapace: length 2.13, width 1.63, height 0.85.

COLOUR (Fig. 8A–D). Carapace uniform chestnut brown; chelicerae, chilum and sternum brownish orange; endites and labium pale brown with whitish distal margin; legs: Cx and Tr pale brown; Fe dark brown; remainder yellow except T IV medium greyish brown; abdomen: dorsum with two reniform pale patches in front overlaid by translucent pale reddish brown, oval scutum followed by numerous small white spots on dark background, venter sclerotized orange in front of epigastric furrow with short tubular extension around pedicel; remainder with sepia marbling on pale background; spinnerets whitish; sides with dark grey marbling.

CARAPACE. Rugose, with sparse, thin, pale, branched setae; one large seta between AME.

STERNUM (Fig. 8B). Shield shaped; 0.92 wide, 0.85 long. Posterior tip shallowly indented; with rounded depressions in front of coxae; no precoxal sclerites.

CHILUM. A single sclerite 0.12 high, 0.25 wide, with central protrusion.

EYES. ALE 0.12; AME 0.13; PLE 0.10; PME 0.13; ALE-AME 0.10; AME-AME 0.07; PLE-PME 0.13; PME-PME 0.08. Clypeus 0.41 high.

LEGS. Trochanters III and IV with anterior ventral indentation; Fe I and II with basal dorsal stridulation file (Fig. 4G–H); without hinged setae.

LEG MEASUREMENTS.

	Fe	P	T	Mt	t	tot
I	1.47	0.56	1.33	1.26	1.05	5.67
II	1.19	0.49	0.84	1.19	0.98	4.69
III	1.40	0.49	0.84	1.40	0.98	5.11
IV	1.75	0.63	1.40	1.82	1.19	6.79

SPINATION.

	F	P	T	Mt
I	pl1d2rl1	pl1	v1-1-2	v1-1dw4
II	pl1d3	pl1	v1-1-2	v1-1-1dw4
III	pl2d3rl1	pl1d1rl1	pl2d3rl2v1-1-1-2	disp7 dw4
IV	pl2d3rl1	pl1d1rl1	pl3d5rl3v1-1-1-1-2	disp7 dw4

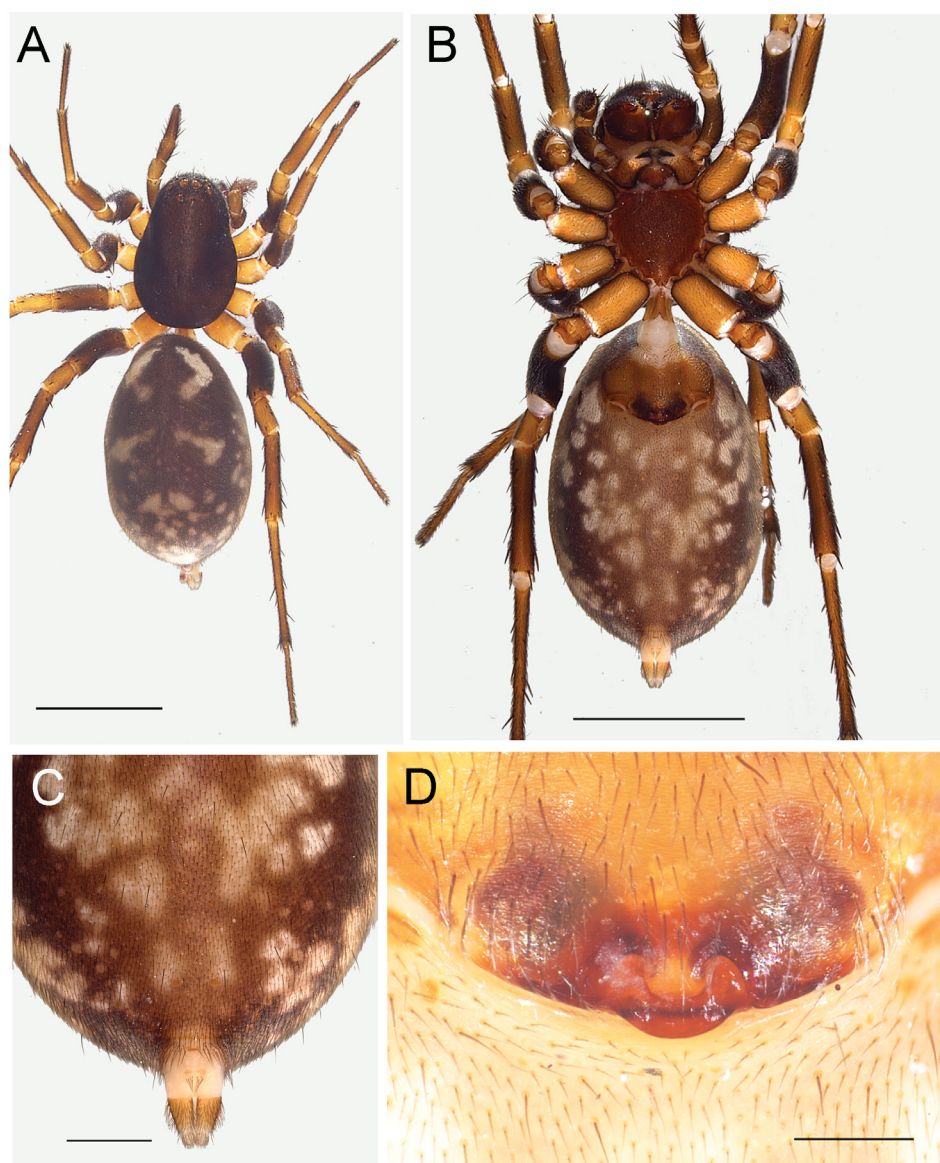


Fig. 9. *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov., female paratype (RBINS IG 33.889/008) **A.** Habitus, dorsal view. **B.** Habitus, ventral view. **C.** Abdomen, posterior part, ventral view. **D.** Epigyne, ventral view. Scale bars A–B = 5 mm; C = 0.5 mm; D–F = 0.2 mm.

ABDOMEN. Venter with dispersed thick setae in posterior half (Fig. 8D); with short tubular extension around pedicel, ventral margin slightly indented (Fig. 8A–B).

MALE PALP (Figs 8E–F, 10A–B). T with a strong, straight, tapered RTA and retrobasal triangular swelling; cymbial fold slightly shorter than half the cymbium's length; embolus with large base, originating at an angle of 270° to longitudinal axis; bifid from base onwards; MA with basal tooth and beak shaped distal extremity pointing prolaterad; C short, tapered, grooved.

Female (RBINS IG 33.889/008)

TOTAL LENGTH. 6.60. Carapace: length 2.56, width 1.56, height 1.14.

COLOUR (Fig. 9A–C). Carapace uniform dark brown; chelicerae medium brown without pale tip; chilum medium brown. Endites and labium medium brown with pale frontal margin. Sternum uniform medium brown. Legs: Cx yellowish brown, with white sital margin; Tr yellowish brown, F dark brown, remainder medium brown; palp medium brown, F slightly darker. Abdomen: dorsum anteriorly with two well separated reniform spots, without scutum overlay, followed by pale transverse band, small, pale patches and large patch in front of spinnerets; venter with sclerotized band in front of epigastric furrow, remainder with sepia marbling on pale background, spinnerets yellow.

CARAPACE. Rugose, with sparse, thin, pale, branched setae; a few large setae between eye region and fovea.

EYES. ALE 0.12; AME 0.15; PLE 0.13; PME 0.15; ALE-AME 0.10; AME-AME 0.05; PLE-PME 0.23; PME-PME 0.08. Clypeus 0.51 high.

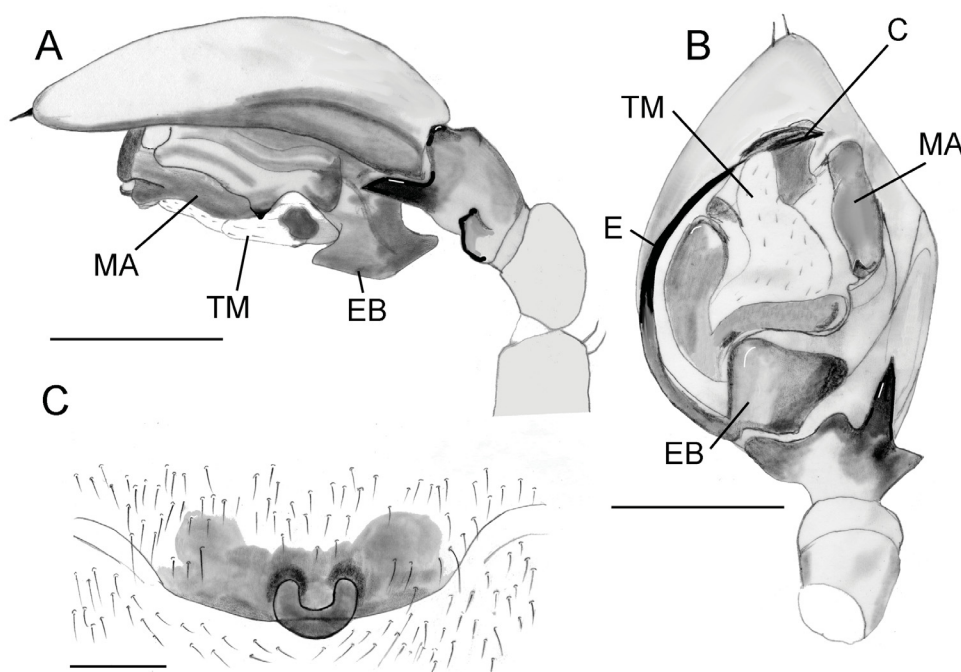


Fig. 10. *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov. **A–B.** Male holotype. **C.** Female paratype (RBINS IG 33.889/008). **A.** Male palp, retrolateral view. **B.** As preceding, ventral view. **C.** Epigyne, ventral view. Abbreviations: C = conductor; E = embolus; EB = embolus base; MA = median apophysis; TM = tegular membranous area. Scale bars: A–B = 0.5 mm; C = 1 mm; D–F = 0.2 mm.

CHILUM. A single sclerite 0.12 high, 0.33 wide, with central protrusion.

STERNUM (Fig. 9B) Shield shaped; 1.14 wide, 1.21 long. Posterior tip truncate; with rounded depressions in front of coxae; no precoxal sclerites.

LEGS. Tr III and IV posteriorly concave. Hinged hair on T I and II.

SPINATION.

	F	P	T	Mt
I	pl1d3	-	v1-1-2	v2 dw2
II	pl1d3	pl1	v1-1-2	v2 dw2
III	pl13r1l	pl2d1r1l	pld3rlv1-1-2	disp6 dw3
IV	pl2d4l1	pl2d1r1l	pl1d3r1l v1-1-2	disp8 dw4

LEG MEASUREMENTS.

	Fe	P	T	Mt	t	Total
I	1.68	0.56	1.26	1.12	1.05	5.67
II	1.54	0.49	1.12	1.05	1.05	5.25
III	1.40	0.56	0.91	0.91	0.91	4.69
IV	1.75	0.70	1.54	1.12	1.12	6.23

PALPAL TARSUS. With toothed claw turned inward over 30°, eight dispersed spines.

ABDOMEN. Without frontal tubular extension. Venter of abdomen without PVS or thick setae (Fig. 9C).

EPIGYNE (Figs 9D, 10C). A broad sclerotized area with narrow, horseshoe shaped plate, delimiting central pit.

Distribution

Known from two localities along the Mekong River in Cambodia (Fig. 11).

Discussion

The discovery of a new genus in the large clade containing *Mallinella* is not particularly surprising mainly because it comes from an area that has hardly been surveyed for spiders (see introduction). It is remarkable though, that the type species has a very vast distribution, which appears to be linked with rainforest along the Mekong River. The adjacent regions in Thailand have been well inventoried (Dankittipakul *et al.* 2012) and the taxon is most likely absent from there. As far as we know, this is the first case of a riverine forest distribution in the Zodariidae.

Cambonilla gen. nov. appears more closely related to *Heliconilla* than to the other genera in the group and is easily recognized as such by the marbled venter of the abdomen, which they share, together with several other characters. However, one of the specimens of *C. securicula* gen. et sp. nov. has an abdominal ventral pattern that is aberrant in this respect (see variation above): it has three longitudinal faint dark lines on a pale background, a pattern that is common in species of *Mallinella*. This suggests that some of the characters in this group might be the result of epigenetic gene expression, a phenomenon that has been recognized as a source of variation in phenotypes (Vogt 2015; Gawne *et al.* 2018). Even at the species level, characters may pop up at several places in a clade: this is the case for

femoral stridulating organs in our ingroup: they are present in *Cambonilla symphonia* gen. et sp. nov., in *Mallinella annulipes* (Thorell, 1892) (see Jocqué 2005) and in several species of *Euryeidon* (e. g. *Euryeidon musicum* Dankittipakul & Jocqué, 2004) (Dankittipakul & Jocqué 2004). This phenomenon evidently puts the value of a purely morphological analysis in perspective, but it would be surprising if a molecular analysis contradicts the hypothesis that the *Cambonilla* gen. nov. species represent a separate genus, considering the number of characters that define it on the preferred tree (Fig. 1).

Acknowledgements

The expedition was supported by WWF Belgium and WWF Cambodia. We thank Isabelle Vertriest, Jerome Laycock, Chandet Horm, Samnang Keo, Kao Sokhon, Kim Høeun and So Ko for help with the project and in the field. Thank you to Heng Neathmony, Somany Phay, Chandet Horm, Heng Neatmony, Teak Seng and Vong Puthkanha for help with the research and export permits. Material was exported under permit number 509, issued 4 June 2018 by the Ministry of Environment of Cambodia. We are indebted to Peter Jäger for the loan of material from Laos and Wouter Dekoninck for the care with the type specimens in this study. Thank you to Dmitri Logunov and an anonymous reviewer who provided helpful comments to improve the manuscript.

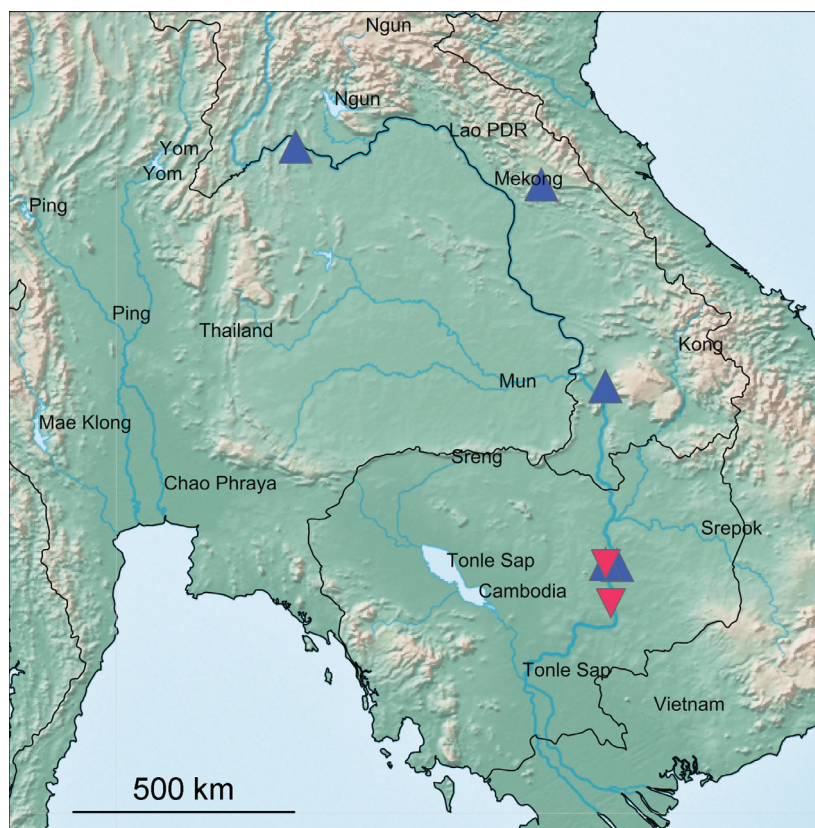


Fig. 11. Distribution of *Cambonilla securicula* Jocqué gen. et sp. nov. (▲) and *Cambonilla symphonia* Jocqué & Henrard gen. et sp. nov. (▼).

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Manuscript received: 29 October 2018

Manuscript accepted: 11 January 2019

Published on: 26 February 2019

Topic editor: Koen Martens

Desk editor: Marianne Salaiün

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Autor(en)/Author(s): Jocque Rudy, Jocque Merlijn, Stock Willem, Rin Naroeun, Henrard Arnaud

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