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A revision of the genus *Psammogorgia* Verrill, 1868 (Cnidaria, Anthozoa, Octocorallia) in the tropical eastern Pacific Ocean

Odalisca Breedy[1,2], Hector M. Guzman[2]

1 *Centro de Investigación en Estructuras Microscópicas, Centro de Investigación en Ciencias del Mar y Limnología, Escuela de Biología, Universidad de Costa Rica. P.O. Box 11501-2060, Universidad de Costa Rica, San José, Costa Rica* **2** *Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Panama, Republic of Panama*

Corresponding author: Odalisca Breedy (odalisca.breedy@ucr.ac.cr)

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Abstract

The species of the genus *Psammogorgia* Verrill, 1868 from the shallow waters of the tropical eastern Pacific were mainly described from 1846 to 1870. Very few contributions were published subsequently. Recently, the genus was revisited with the addition of two new species. However, a comprehensive generic study is still missing for the eastern Pacific. *Psammogorgia* is characterised by having axes cores without mineralisation, mainly coarse irregular spindles and thorny, leafy or tuberculate clubs coenenchymal sclerites and the anthocodial armature with distinct collaret and points arrangements. Herein a taxonomic revision of the genus is presented based on type material which was morphologically analysed and illustrated using optical and scanning electron microscopy. Comparative character tables are provided for comparison among species in the genus, along with a taxonomic key. Moreover, the taxonomic status of each species was analysed. The genus *Psammogorgia* comprises six valid species and two varieties, and three lectotypes and a new combination are proposed to establish the taxonomic status of these species.

Keywords

Biodiversity, gorgonians, key to plexaurid genera, octocoral, Plexauridae, taxonomic review, taxonomy

Introduction

Seven genera in the family Plexauridae have been reported for the tropical eastern Pacific: *Muricea*, Lamouroux, 1821; *Thesea* Duchassaing & Michelotti, 1860; *Swiftia* Duchassaing & Michelotti, 1864; *Heterogorgia* Verrill, 1868a; *Psammogorgia* Verrill, 1868a; *Adelogorgia* Bayer, 1958 and *Chromoplexaura* Williams, 2013. Previous taxonomic reviews of Plexauridae for the region dealt with *Heterogorgia* Verrill, 1868a and *Muricea* Lamouroux, 1821 (Breedy and Guzman 2011, 2015, 2016).

The genus *Psammogorgia* Verrill, 1868a was established by Verrill to place a species previously assigned to the genus *Echinogorgia* Kölliker, 1865 (*E. arbuscula* Verrill, 1866), which was subsequently named *Psammogorgia arbuscula* (Verrill, 1868a). Later, Verrill (1868b) properly described *P. arbuscula* and two of its varieties: (*Psammogorgia arbuscula* var. *pallida* Verrill, 1868, and *P. arbuscula* var. *dowii* Verrill, 1868), and two other species (*Psammogorgia gracilis* Verrill, 1868 and *Psammogorgia teres* Verrill, 1868). In his review, Verrill (1868b) also included material of *Gorgonia fucosa* Valenciennes, 1846, which was collected during the French expedition 'Voyage autour du monde sur la frégate la Vénus'.

From 1868 to 1951 more species were described within the genus *Psammogorgia* from different regions and bathymetric ranges (Studer 1878; Ridley 1888; Studer 1894; Nutting 1909; Thomson and Simpson 1909; Thomson 1911; Kükenthal 1919; Stiasny 1935, 1951). Some of these species have been studied and placed in different genera, while the taxonomic status of others remains uncertain and in need of revision. Nutting (1909) proposed three species, *Psammogorgia simplex* Nutting, 1909, *Psammogorgia spauldingi* Nutting, 1909, and *Psammogorgia torreyi* Nutting, 1909 from California, which are presently placed in the genus *Swiftia* Duchassaing & Michelotti, 1864. Stiasny (1951) described *Psammogorgia digueti* Stiasny, 1951 from Canal San Lorenzo, Gulf of California, which according to Bayer (1958) is a species of the genus with " the size of sclerites given by Stiasny being exceptionally small."

The status of most species of the genus *Psammogorgia* is uncertain because the previous authors did not designate holotypes and the illustrations of specimens and sclerites in old publications are mostly insufficient for proper species identification. Additionally, some species have been described from one to few specimens or fragments, while their type material is lost to science or their location unknown. According to Bayer (1961) without an accurate knowledge of the type material, no clear concept of genera or species can exist.

Breedy and Guzman (2014, 2020) revisited the genus *Psammogorgia* and described two species: *Psammogorgia hookeri* Breedy & Guzman, 2014 from Perú, and *Psammogorgia pax* Breedy et al., 2020 from Panamá. However, a comprehensive review with the original type material of this genus is necessary to establish the status of the species. Herein, we present a taxonomic revision of the genus *Psammogorgia* in the tropical eastern Pacific based on type material. This research represents the seventh and last review in a series proposed to evaluate the genera of gorgonians historically reported from the shallow eastern Pacific waters.

Acronyms

MCZ	Museum of Comparative Zoology, Harvard University, Boston, USA.
MNHN	Muséum national d'Histoire naturelle, Paris, France.
NMNM / USNM	National Museum of Natural History, Smithsonian Institution, Washington, USA.
YPM	Yale Peabody Museum of Natural History, New Haven, USA.

Material and methods

The type specimens used in this study were analysed during visits to museums or acquired on loan from the **MCZ, MNHN, NMNM,** and **YPM**. For the species *Psammogorgia fucosa* (Valenciennes, 1846), the only type material available is a sclerite slide found in the MCZ. Depth of collection of the type specimens was not recorded; however, most of the types collected by F.M. Bradley were obtained by pearl divers between 8 and 12 m in depth (Verrill 1868b).

The taxonomic identification and description of the octocorals was based on external morphology: shape, size and colour of the colonies, and calyx structures, as well as on internal morphology: sclerites content, dominance, shape, size and arrangement. Terminology used in this study mostly follows Bayer et al. (1983). For microscopic study, fragments of the tips of the colonies were treated with 5% sodium hypochlorite to dissociate sclerites from the tissues. The structures were washed several times in distilled water and dehydrated with 100% ethanol and posteriorly dried in the oven (Breedy and Guzman 2002). For old specimens in bad conditions it was difficult to clean the sclerites. These samples were treated with hydrogen peroxide to remove remains of organic matter, but most sclerites from these samples were still dirty as shown by the Scanning Electron Microscope (**SEM**) micrographs. Notes on the colours of the colonies and sclerites based on dry type material and literature reports were taken, considering that colours are stable and persist after fixation of the *Psammogorgia* specimens.

In order to prepare the sclerome for imaging and measurements, different microscope preparations were made. For optic microscopy, sclerites were mounted in water or glycerine and photographed with an Olympus LX 51 inverted microscope. For SEM, sclerites were mounted on SEM stubs by double stick carbon tape and silver paint bridges between the tape and the stubs were made to increase the electronic conduction. The samples were then sputter-coated with gold, 30–60 nm layer, in an Eiko IB-5 Ion Coater and the pictures were obtained using a Hitachi SEM S-3700N. Unsorted optic microscope micrographs reveal colour details and sclerites composition while the SEM illustrations show details and sculpture of the sclerites. Not all sclerite types of a species are presented in the SEM figures. Measurements of the sclerites were obtained from the SEM images, and for *P. fucosa* from the optical micrographs the length of the sclerites was measured from one tip to the other and

the width was taken from the most distant points across the sclerites, reporting the largest sizes found in the samples. Because type material was generally in bad condition, the anthocodial sclerite arrangement at the base of the polyps was not described in some cases. The diameter of the branches, branchlets, and stems was noted, taking the length of the calyces into account.

Designation of lectotypes was done for three species with unclear identity described by either Verrill or Valenciennes without type designation. Lastly, data on geographical distributions are based on our personal collections (Museo de Zoología, Universidad de Costa Rica, Naos Laboratory, Smithsonian Tropical Research Institut, Panamá, **STRI**), museum catalogues and published monographs.

Taxonomy

Key to plexaurid genera presently reported from the tropical eastern Pacific

1 Coenenchyme contains massive unilateral spinous sclerites. Polyps retract into shelf-like or tubular calyces ..... ***Muricea***

– Coenenchyme does not contain unilateral spinous sclerites. Polyps do not retract into shelf-like or tubular calyces **2**

2 Calyces with lobed rims armed with strongly projecting thorns forming a bristling barricade around calycular apertures. Axis's cores with organic fibres mineralised with carbonate hydroxylapatite ..... ***Heterogorgia***

– Calyces without lobed rims armed with strongly projecting thorns forming a bristling barricade around calycular apertures. Axis's cores with organic fibres non-mineralised with carbonate hydroxylapatite **3**

3 External coenenchyme with characteristic large rugose plates having the inner side with low composite warts, and the outer side with wide lobes..... ***Thesea***

– External coenenchyme without characteristic large rugose plates having the inner side with low composite warts, and the outer side with wide lobes **4**

4 External coenenchyme with conspicuous double disk sclerites with one side expanded in longitudinal crests with various degrees of ornamentation ..... ***Adelogorgia***

– External coenenchyme without conspicuous double disk sclerites, with one side expanded in longitudinal crests with various degrees of ornamentation **5**

5 Coenenchymal sclerites mainly thin, sharp spindles with or without fused tubercles in incomplete disks. Anthocodial armature with a few bar-like rods transversely arranged not forming distinct collaret and points..... ***Swiftia***

– Coenenchymal sclerites without thin, sharp spindles fused in incomplete disks. Anthocodial armature forming distinct collaret and points..... **6**

6 Coenenchymal sclerites mainly coarse, irregular spindles and thorny, foliate or tuberculate clubs..... ***Psammogorgia***

– Coenenchymal sclerites mainly radiates and spindles, without foliate or tuberculate clubs ..... ***Chromoplexaura***

Systematics

Class Anthozoa Ehrenberg, 1834
Subclass Octocorallia Haeckel, 1866
Order Alcyonacea Lamouroux, 1816
Family Plexauridae Gray, 1859

Genus *Psammogorgia* Verrill, 1868

Psammogorgia Verrill, 1868a: 414; Verrill 1868b: 414; Studer 1887: 60; Wright 1889: lix; Nutting 1909: 719; Nutting 1910: 16; Kükenthal 1919: 234–236, 905; Kükenthal 1924: 106; Bayer 1956: F212; Bayer 1958: 43; Harden 1979: 114; Bayer 1981: 925; Breedy and Guzman 2014: 494; Breedy et al. 2020: 171–172.

Type species. *Echinogorgia arbuscula* Verrill, 1866 by subsequent designation (Verrill 1868b).

Diagnosis. Colonies bushy to flabellate. Branching lateral, dichotomous, irregularly dichotomous, or subpinnate. Branches round or slightly flattened. Axis horny, chambered central core filled with organic non-mineralised fibres. Calyces on all sides of branches, flat, slightly raised or prominent. Polyp apertures slit-like or swollen. Anthocodial sclerites mostly large, elongated, warty, spinose or slender spindles, with or without median waist, in collaret and points arrangements at base of tentacles. Sclerites of coenenchyme thick, warty spindles; radiates, and crosses. Clubs warty or foliate-like with variation of those types mostly present at calyx rims and external coenenchyme. Colony colours dark red, red, orange, pink and white. Sclerites colours red, pink, orange, yellow, various hues of these, and/or colourless.

Distribution. The genus has been reported from the eastern Pacific, Californian province, the Indian Ocean and the north Atlantic.

Remarks. Axes analysis of the species of *Psammogorgia* show chambered central cores filled with organic non-mineralised fibres (e.g., Fig. 1).

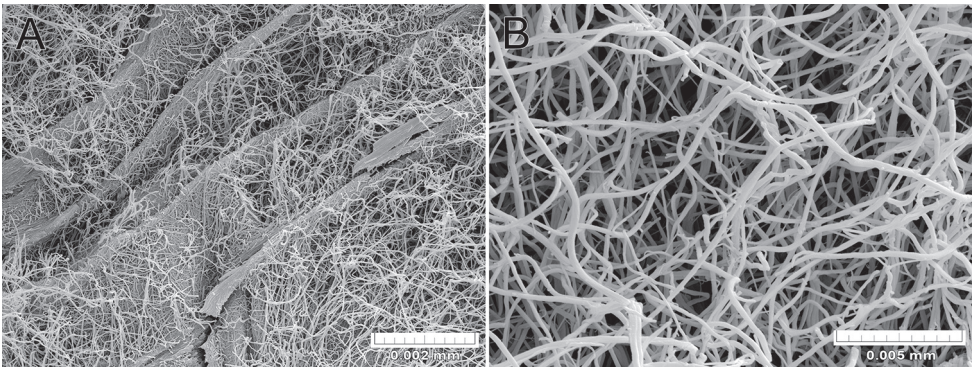

Figure 1. *Psammogorgia arbuscula* (Verrill, 1866) STRI 269 **A** central core chambers filled with organic non-mineralised fibres **B** detail of organic non-mineralised fibres.

***Psammogorgia arbuscula* (Verrill, 1866)**
Figures 2–4

Echinogorgia arbuscula Verrill, 1866: 329.
Psammogorgia arbuscula Verrill, 1868a: 414; 1868b: 414–415; not Nutting 1909: 719–720; Nutting 1910: 16; Kükenthal 1919: 236–237; Kükenthal 1924: 107; Bayer 1958: 44; Harden 1979: 114–116.
Psammogorgia arbuscula typica Kükenthal, 1924: 107.

Type material. ***Lectotype*** (designated herein). YPM 573, dry, Pearl Islands, Gulf of Panamá, Panamá, F.H. Bradley, 1866–1867, no additional data.

Paralectotypes. YPM 573 a-h; MCZ 425B, MCZ 573 (part of YPM 573), MCZ 727, 728A-B (4916=YPM 1577), MCZ 4017–4019, MCZ 4021–4022, MCZ 4024, MCZ 4998 (=MCZ 728) same data as the lectotype. MCZ 7009, dry, Nicoya Gulf, Costa Rica, collected by pearl divers, J.A. Mc. Neil, 1866–1867, no additional data.

Type locality. Pearl Islands, Panamá.

Diagnosis. Colonies bushy, irregularly dichotomous. Stems short, slightly flattened, one to several stems emerging from a common holdfast. Branches and branchlets

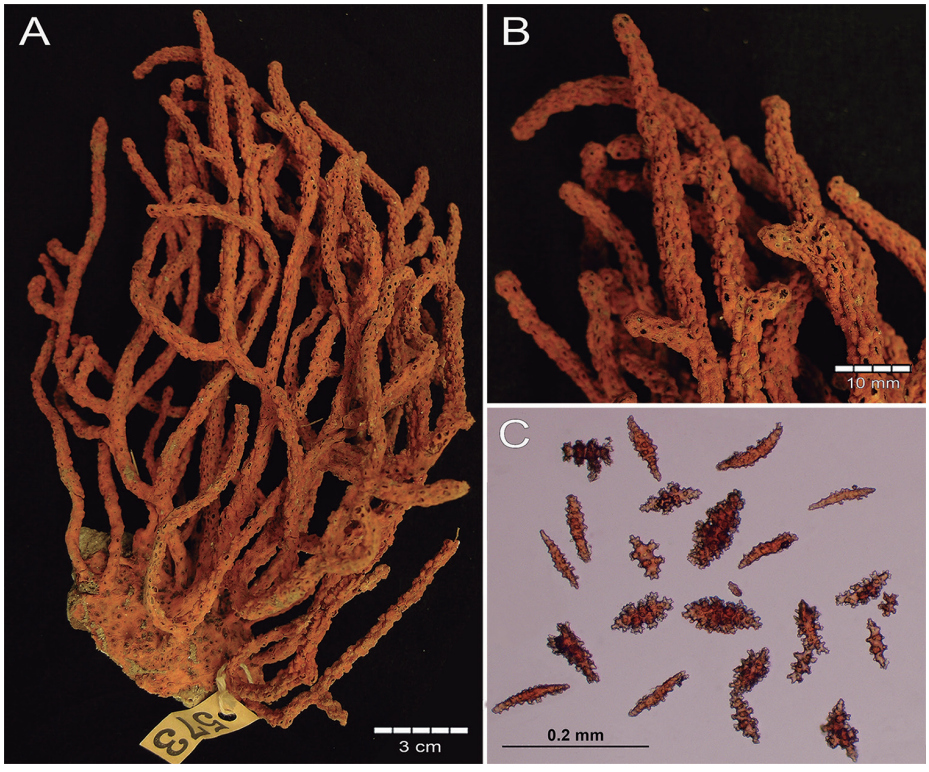

Figure 2. *Psammogorgia arbuscula* (Verrill, 1866) YPM 573 **A** colony **B** detail of branches **C** coenenchymal and anthocodial sclerites.

thin, rounded with long free ends in large colonies. Holdfasts encrusting with a thin layer of coenenchyme often with polyps. Coenenchyme of branches moderately thick and granulose. Coenenchymal sclerites: irregular spindles with acute or bifurcated ends, up to 0.30 mm long; warty and irregular radiates up to 0.13 mm long and some crosses. Calyces prominent and swollen, all around the branches, mostly closely placed in two or three longitudinal rows on each side of the branches. Calyces with thorny and irregular spindles and wart-clubs, up to 0.19 mm long, around the calyx rim. Anthocodial spindles up to 0.26 mm long, in collaret and points arrangements. Sclerites red and orange. Dry colonies red to red-orange, dark red when alive. Polyps bright yellow when alive.

Description. (see also Verrill 1866, 1868b; Bayer 1956). The lectotype is a bushy, irregularly dichotomous dry colony, 12 cm long and 9.5 cm wide. The colony is of a red orange colour (Fig. 2A, B). Nine stems arise from an oval encrusting holdfast which is ~ 4.5 cm in diameter (Fig. 2A). The holdfast is covered by a thin layer of coenenchyme with polyps. Most of the stems are 3.0–3.2 mm in diameter bifurcating a few mm above the base, two of them raising up to 2 cm before subdividing in several branches 2–4 mm in diameter including calyces. The colony branches up to eight times. The branches emerge at angles of 45–90°, ascending parallel and slightly curved at the end. Terminal branchlets are 2.5–10 mm long (Fig. 2A). The calyces are with rounded somewhat tapered tips. Calyces are closely arranged around the branches, mostly in 2–3 longitudinal rows on each side of the branches; somehow in quincunx (arrangements of five) as Verrill (1868b) mentioned (Fig. 2B). The calyces are prominent, up to 1 mm tall and around 2 mm diameter, composed of eight marginal swollen lobes around the polyp apertures, which is evident when polyps are withdraw or in dry condition (Fig. 2B). Calyces present a concentration of thorny, irregular spindles and wart-clubs around the borders. The coenenchyme is moderately thick, granulose and brittle in the dry lectotype. Coenenchymal sclerites are dark red, red, orange and of lighter hues (Fig. 2C), and of different forms: irregular spindles with acute or bifurcated ends, some being slightly curved (Figs 2C, 3A), 0.14–0.20 mm long and 0.06–0.07 mm wide. Warty radiates are 0.07–0.13 mm long and 0.065–0.085 mm wide (Fig. 3B); and some warty crosses up to 0.11 mm by 0.1 mm. Wart-clubs are 0.09–0.18 mm long and 0.049–0.12 mm wide, variable in form and with a larger end expanded and covered with thorny warts (Fig. 3C). They are concentrated at the calyx rims and the base of the anthocodia. The anthocodial armature is well developed. It is composed of spiny spindles arranged in a collaret and points, 0.13–0.17 mm long (0.20–0.26 mm long according to Verrill (1868b)) and 0.02–0.045 mm wide (Fig. 3D); its flat spindles are with small tubercles and scattered warts.

Variability. Most of the type material of the form typica of *P. arbuscula* is constituted of small colonies 5–15 cm long and 3–7 cm wide or fragments of colonies, the largest specimen being MCZ 7009 (28 cm long and 20 cm wide), with unbranched ends up to 15 cm long. Stems can reach up to 4 mm diameter, branches up to 3.5–3.8 mm in diameter and branchlets up to 2.0–2.6 mm in diameter. The sclerites content is consistent among the types. When alive, the colonies are dark red and the polyps are bright yellow (Verrill 1868b) (Fig. 4).

Distribution. Tropical eastern Pacific: Panamá, Costa Rica, Ecuador, México and El Salvador.

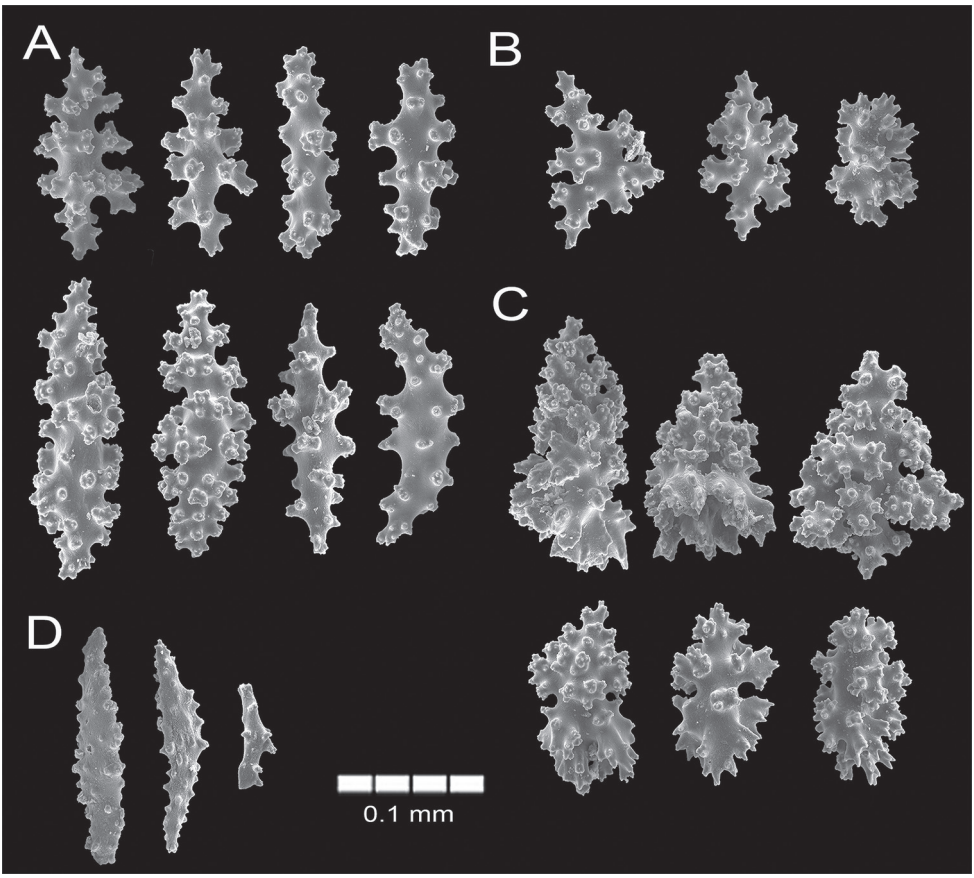

Figure 3. *Psammogorgia arbuscula* (Verrill, 1866) YPM 573 **A** spindles **B** radiates **C** wart clubs **D** anthocodial spindles.

Remarks and comparison. The *Psammogorgia arbuscula typica* is different in calyx structure, size of sclerites and colour from the varieties *P. arbuscula* var. *dowii* and *P. arbuscula* var. *pallida* (see Tables 1, 2). These other varieties lack the prominent and swollen calyces present in *P. arbuscula typica*. *Psammogorgia gracilis* and *Psammogorgia hookeri* have prominent calyces however, there are many other differences that separate them from *P. arbuscula* (Tables 1, 2). *Psammogorgia gracilis* has thinner and longer branchlets as well as shorter spindles, longer wart clubs, and shorter anthocodial sclerites (Tables 1, 2). *Psammogorgia hookeri* has smaller bushy colonies with a typical coral red colour, different from the larger colonies of *P. arbuscula*. In general, *P. hookeri* has star-like sclerites absent in the later, and smaller sclerites than in *P. arbuscula*.

Bayer (1958) treated specimen MCZ 4022 as the holotype for the species however, Verrill did not designate a holotype. Verrill´s 1866 original description of *Echinogorgia arbuscula* is general, and he did not describe specimen MCZ 4022 specifically. We consider specimen YPM 573 more representative of the species and designate this as the lectotype to clearly establish the taxonomic status of *P. arbuscula*.

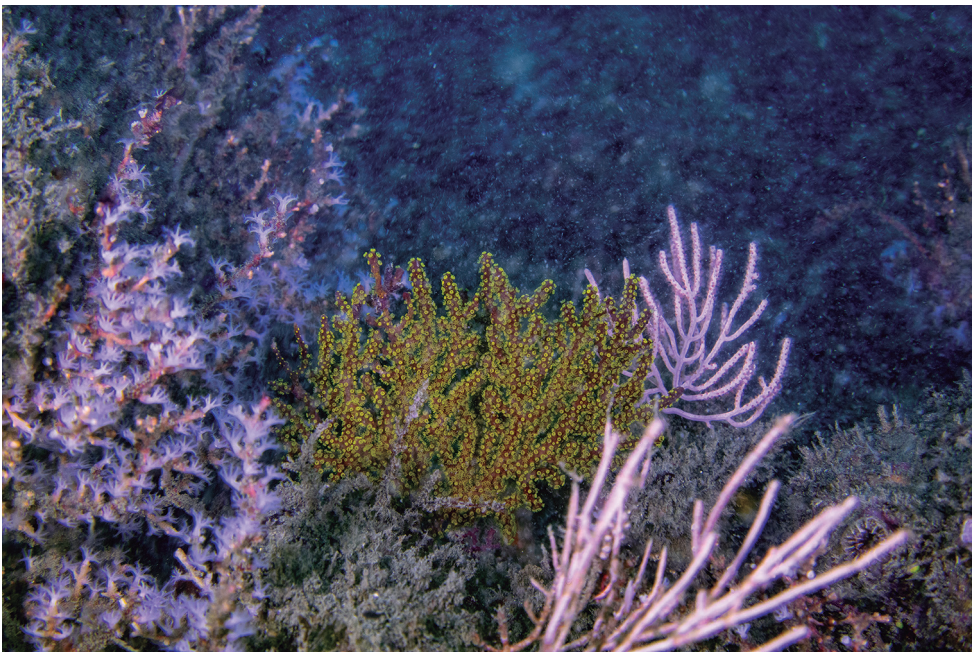

Figure 4. *Psammogorgia arbuscula* (Verrill, 1866). A *In situ* colony, 13 m deep, Rocas Corcovado, Osa Peninsula, Costa Rica. Photograph: Manu San Felix, National Geographic Pristine Seas.

Table 1. Comparative features of *Psammogorgia* colonies from the tropical eastern Pacific, according to analyses of type material from museums (YPM, MCZ, MNHN), and taxonomic descriptions by Verrill (1868b, 1870) and Bayer (1958). Diameter of the branches includes calyces. Measurements in millimetres.

Species	Colony colour	Colony shape and branching pattern	Maximum # branching	Length of terminal branchlets	Diameter of branchlets	Branch anastomosis	Calyx of branchlets	Presence of swollen calyx rims	Calyx arrangement at branchlets
P. arbuscula (Verrill, 1866)	dark red	bushy, irregularly dichotomous	8	2.5–15	2–4	absent	prominent	yes	close
P. arbuscula var. *dowii* Verrill, 1868b	dark red	*flabellate, dichotomous	2	6–35	2	absent	slightly raised	no	sparse
P. arbuscula var. *pallida* Verrill, 1868b	yellowish	flabellate, irregularly dichotomous	15	40	2–3	absent	flat/ slightly raised	no	sparse
P. fucosa Valenciennes, 1846	reddish	bushy, irregularly dichotomous	12	12.7–25.4	3–4.5	absent	flat	no	sparse
P. gracilis Verrill, 1868	red	*flabellate, irregular dichotomous	9	60	1.5–1.6	absent	prominent	yes	close
P. hookeri Breedy & Guzman, 2014	coral red	bushy, irregularly dichotomous	8	10–15	2–2.5	absent	prominent	yes	close
P. pax Breedy et al. 2020	white	flabellate, irregularly dichotomous	20	10–125	3–4	present	slightly raised	no	sparse
P. teres Verrill, 1868	red orange	bushy, irregularly dichotomous	12	5–60	3–5	absent	flat	no	sparse

*Data from Verrill (1868b): syntype colony is small or a fragment.

Table 2. Comparative features of sclerites of *Psammogorgia* species in the tropical eastern Pacific Ocean according to an analysis of type material from museums (YPM, MCZ, MNHN) and taxonomic descriptions by Verrill (1868b, 1870), Bayer (1958), Breedy and Guzman (2014), and Breedy et al. (2020).

Species	Spindle length (mm)	Wart club length (mm)	Radiates length (mm)	Anthocodials length (mm)	Colour of coenenchymal sclerites	Colour of anthocodial sclerites
P. arbuscula (Verrill, 1866)	0.14–0.30	0.09–0.18	0.07–0.13	0.12–0.26	dark red, red, orange	red, orange
P. arbuscula var. *dowii* Verrill, 1868	0.14–0.21	0.11–0.18	0.13–0.15	0.12–0.20	dark red, red, orange	red, orange
P. arbuscula var. *pallida* Verrill, 1868	0.15–0.23	0.11–0.16	0.08–0.16	0.11–0.23	pale pink, colourless	orange red
P. fucosa Valenciennes, 1846	0.10–0.22	0.10–0.18	0.09–0.11	0.10–0.21	red, pink, colourless	red
P. gracilis Verrill, 1868	0.12–0.24	0.11–0.25	0.08–0.10	0.11–0.20	red, orange, yellow	orange, pale yellow
P. hookeri Breedy & Guzman, 2014	0.12–0.19	0.11–0.16	0.09–0.11	0.10–0.18	coral red, reddish	yellowish, pale pink
P. pax Breedy et al. 2020	0.21–0.24	0.13–0.33	not found	0.21–0.26	colourless	orange
P. teres Verrill, 1868	0.11–0.20	0.07–0.16	0.07–0.14	0.13–0.26	red, orange, colourless	pale yellow, colourless

Psammogorgia arbuscula var. *dowii* Verrill, 1868

Figures 5, 6

Psammogorgia arbuscula var. *dowii* Verrill, 1868b: 415; Kükenthal 1919: 237; Harden 1979: 117.

Psammogorgia arbuscula dowii Kükenthal, 1924: 107.

Type material. ***Syntypes:*** YPM 1787, dry, Pearl Islands, Panamá, F.H. Bradley, 1866–1867, no additional data. YPM 8684 (fragments, mixture of species), not *P. arbuscula* var. *dowii*, dry, Pearl Islands, Panamá, F.H. Bradley, 1866–1867, no additional data.

Description. The syntype YPM 1787 is a small, 5.8 cm long dark red colony of two dichotomous branches. A 1.1 cm long stem arises from an oval holdfast ~ 1 cm in diameter (Fig. 5A). The holdfast is covered by a thin layer of coenenchyme without polyps. The stem is 2.0 mm in diameter and bifurcates, subdividing in two branchlets up to 3.5 cm long. The branchlets are of the same diameter as the stem, with rounded tips. The branchlets bifurcate at angles of 45°, ascending parallel and are slightly curved. Terminal branchlets are 6–35 mm long (Fig. 5A). The coenenchyme is granulose and brittle. Coenenchymal sclerites are of different forms: irregular spindles with acute or bifurcated ends, some are slightly curved (Fig. 6A), 0.14–0.21 mm long and 0.05–0.09 mm wide. Warty radiates and crosses are 0.13–0.15 mm long and 0.10–0.11 mm wide (Fig. 6B). Wart-clubs are 0.11–0.18 mm long and 0.05–0.085 mm wide at the expanded head being variable in form with a larger end expanded and covered with thorny warts and leaf-like projections (Fig. 6C). Coenenchymal sclerites are of various colours: orange, red, and darker (Fig. 5C).

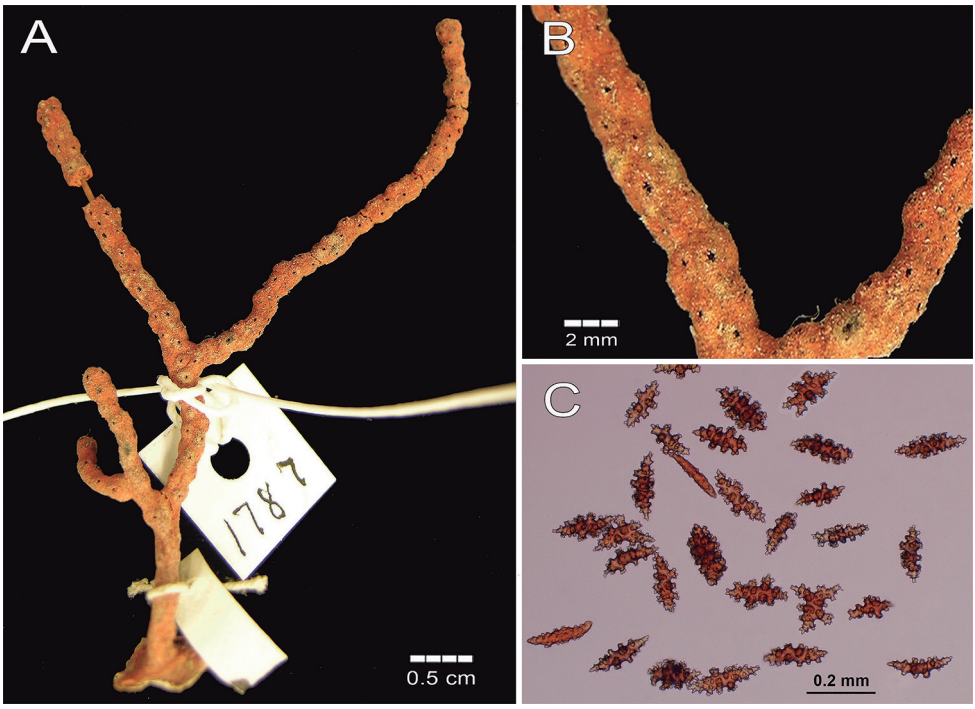

Figure 5. *Psammogorgia arbuscula* var. *dowii* Verrill, 1868. YPM 1787 **A** colony **B** detail of branches **C** coenenchymal and anthocodial sclerites.

The calyces are arranged all around the branches, not very close, slightly raised up to 0.5 mm tall as small mounds composed of eight marginal lobes with small polyp apertures at the summits (Fig. 5B). Thorny, irregular spindles and some wart-clubs appear often, around the calyx aperture. The anthocodial armature is well developed and composed of spiny spindles arranged in a collaret and points, 0.12–0.20 mm long and 0.032–0.056 mm wide (Fig. 6D); its flat rods are with small tubercles and scattered warts. Anthocodial sclerites are red and orange (Fig. 5C).

Remarks and comparison. The calyces in this specimen are more separated and do not have swollen polyp apertures as in *P. arbuscula typica*. Verrill (1868b) mentioned a more flabellate colony but YPM 1787 is not flabellate having only a few branches. Verrill (1868b) did not provide data approximately the size of sclerites of this variety, uniquely pointing out that the sclerites resemble the ones of *P. arbuscula typica*. We found that the sclerites of the only specimen of this variety are smaller and similar to, the ones of *P. arbuscula typica*. Specimen YPM 8684 corresponds to several colony fragments belonging to *P. teres*, *P. arbuscula* and an undetermined species.

Distribution. Tropical eastern Pacific: only reported from the type locality, Pearl Islands, Panamá.

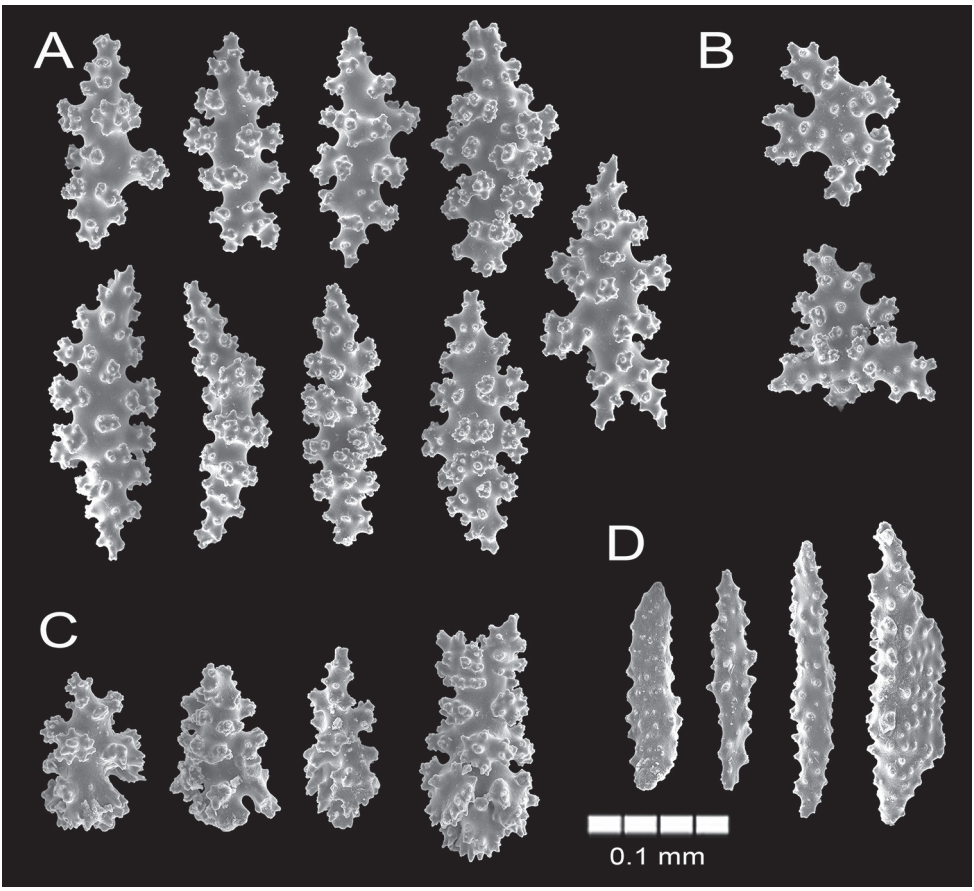

Figure 6. *Psammogorgia arbuscula* var. *dowii* Verrill, 1868. YPM 1787 **A** spindles **B** radiate and cross **C** wart clubs **D** anthocodial spindles.

Psammogorgia arbuscula var. *pallida* Verrill, 1868

Figures 7–9

Psammogorgia arbuscula var. *pallida* Verrill, 1868b: 415–416; Kükenthal 1919: 237; Harden 1979: 119.
Psammogorgia arbuscula pallida Kükenthal, 1924: 107.

Type material. ***Syntypes:*** MCZ 729 (4916), YPM 1785a-b, dry, Pearl Islands, Panamá, F.H. Bradley, 1866–1867, no additional data.

Description. The syntype MCZ 729 is a yellowish flabellate, 10.5 cm long and ~ 9 cm wide colony. Two main stems arise from a holdfast that is 1.6 cm in diameter nd devoid of polyps (Fig. 7A). The stems are less than 1 cm tall and 2.5 mm in diameter, subdividing irregularly in secondary branchlets of 2–3 mm diameter with rounded tips (Fig. 7A). The branchlets emerge at angles of 45–180° and spread irregularly in one plane. The colony branches up to 15 times. Terminal branchlets are up to 40 mm

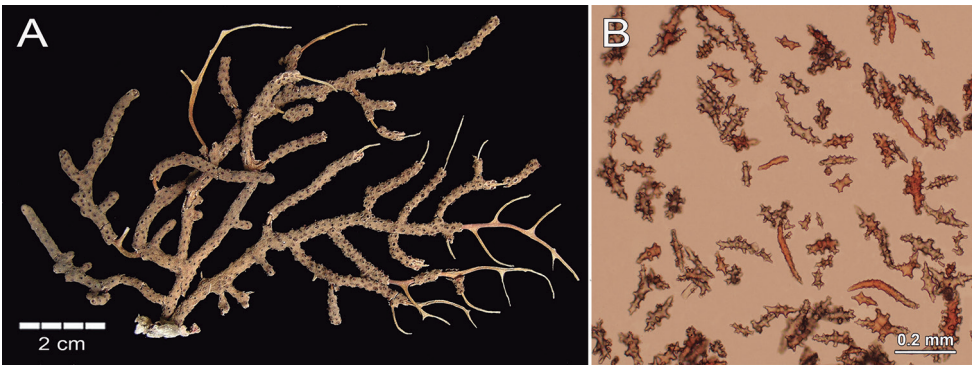

Figure 7. *Psammogorgia arbuscula* var. *pallida* Verrill, 1868. MCZ 729 (4916). **A** Colony **B** coenenchymal and anthocodial sclerites.

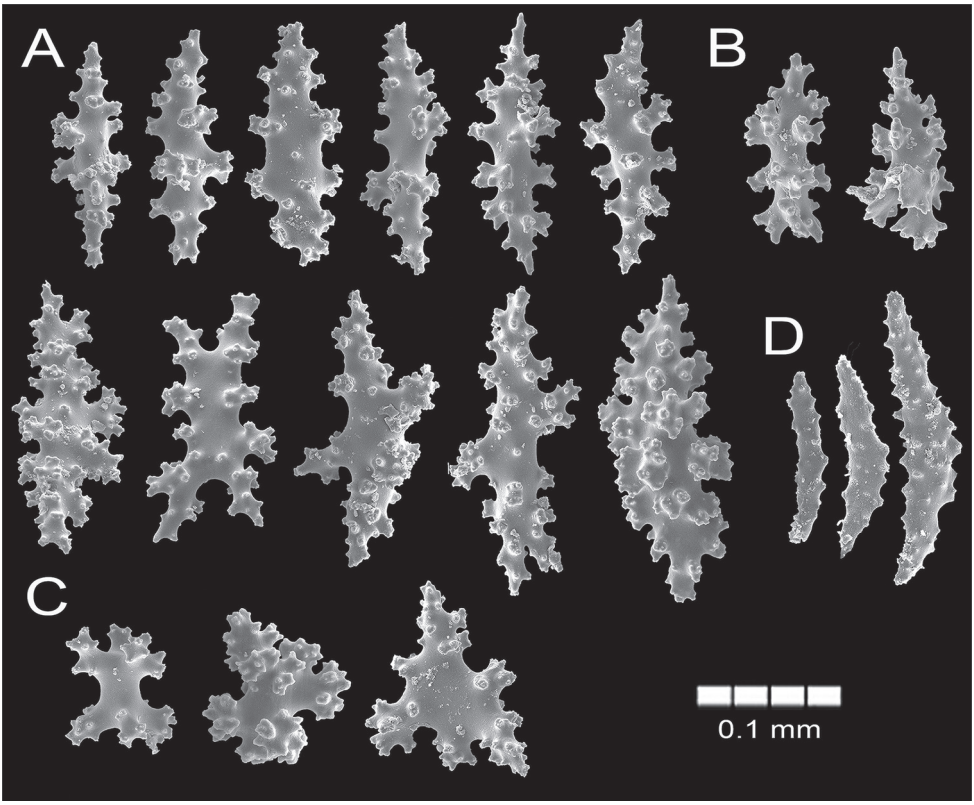

Figure 8. *Psammogorgia arbuscula* var. *pallida* Verrill, 1868. MCZ 729 (4916) **A** spindles **B** wart clubs **C** radiates and crosses **D** anthocodial spindles.

long (Fig. 7A). The polyps occur all around the branches, 1–1.5 mm apart on branchlets and 1.5–2.5 mm apart on the branches. The calyces are almost flat with a few being ~ 0.02 mm tall with oval or round polyp-apertures. Thorny, irregular spindles

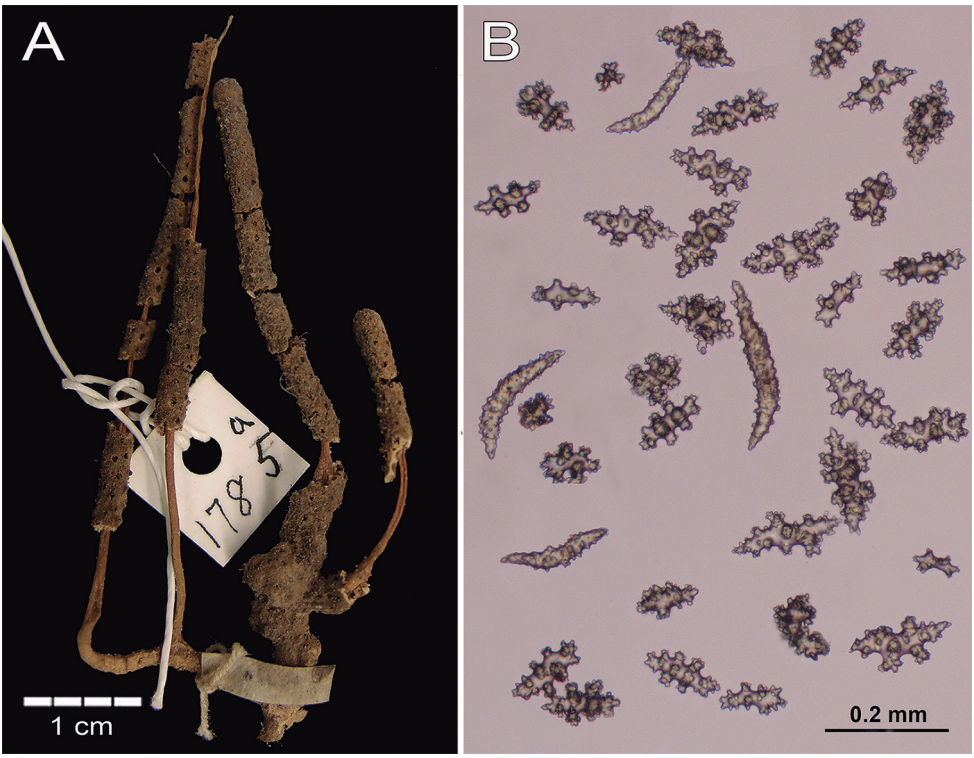

Figure 9. *Psammogorgia arbuscula* var. *pallida* Verrill, 1868. YPM 1785 **A** colony **B** coenenchymal and anthocodial sclerites.

and wart-clubs occur around the calyx rim (Fig. 7B). The coenenchymal sclerites are mostly irregular tuberculate spindles (Figs 7B, 8A) with acute or bifurcated ends or combinations of both (Fig. 8A) with colours varying from pale pink to mostly colourless (Fig. 7B). These sclerites are 0.15–0.23 mm long and 0.04–0.09 mm wide. Wart clubs are 0.11–0.14 mm long and 0.05–0.06 mm wide with warts or with wide tubercles (Fig. 8B). Crosses various intermediate forms and radiates are 0.08–0.16 mm long and 0.07–0.12 mm wide with tubercles (Fig. 8C). The anthocodial armature is composed of slightly bent spiny orange-red sclerites arranged in a collaret and points, 0.11–0.23 mm long and 0.02–0.045 mm wide (Figs 7B, 8D).

The syntypes YPM 1785a, b are two fragments of a lighter colour than MCZ 729 (Fig. 9B). The largest fragment is 5.6 cm long and composed of four branchlets with 2–3 mm in diameter; flat calyces all around the branches (Fig. 9A). All sclerites, including the anthocodials, are pale yellow to colourless. Sclerites from the syntypes are more ornamented than in specimen MCZ 729 but mostly colourless (Fig. 9B). The coenenchymal sclerites are mostly irregular, tuberculate warty spindles with acute or bifurcated ends or combinations of both; being 0.13–0.18 mm long and 0.035–0.08 mm wide. Clubs have a few warts or with wide tubercles being 0.11–0.16 mm long and

0.05–0.60 mm wide. Radiates have tubercles appearing in various intermediate forms, being 0.07–0.10 mm long and 0.05–0.08 mm wide. The anthocodial armature is composed of slightly bent spiny spindles arranged in collaret and points, 0.12–0.22 mm long and 0.025–0.043 mm wide.

Remarks and comparison. Verrill´s material at MCZ includes two specimens, MCZ 729 (4916) and YPM 1785, both with similar sclerites but different in external morphology. One is a small colony and the other is a small fragment in bad condition. According to Verrill´s description (Verrill 1868b) the type material has a "corallum more or less flabelliform, branching dichotomously, branchlets round, sometimes as large as the main stem, usually smaller. Cells a little raised forming low verrucae". However, Verrill did not measure the specimens. YPM 1785 is different from Verrill's description while MCZ 729 (4916) matches some details of his description. Orange-red anthocodial sclerites are present in MCZ 729, as well as at the *P. arbuscula* var. *pallida* description by Verrill (1868b), in contrast with the colourless rods in specimen YPM 1785. Also, pale pink, colourless, and transparent coenenchymal sclerites match his description (Fig. 7B). In terms of sclerite sizes, Verrill's description better matches MCZ 729 with larger sclerite sizes than the smaller YPM 1785 ones. As Verrill suggested, with this and *dowii* variety, we opt to keep *P. arbuscula* var. *pallida* as a variety.

Distribution. Tropical eastern Pacific: only reported from the type locality at Pearl Islands, Panamá.

Psammogorgia fucosa (Valenciennes, 1846), nomen dubium

Figures 10, 11

Gorgonia fucosa Valenciennes, 1846: pl. 15
Plexaura fucosa Milne-Edwards & Haime, 1857: 154; Valenciennes 1855: 12.
Psammogorgia fucosa Verrill, 1868b: 417; 1870: 556–557; 1869: 427; Kükenthal 1919: 237; Kükenthal 1924: 107; Harden 1979: 118–119.

Type locality. Mazatlán, México, Pacific coast (Valenciennes 1855).

Type material. Plate 15, figured specimen (Valenciennes 1846). MCZ ¨spicules du *Gorgonia fucosa* sclerite slide from MNHN. Holotype figured. Valenciennes material from 'Voyage autour du monde sur la frégate la Vénus, pendant les années 1836–1839' expedition was deposited in the MNHN; however, the specimen was not found in the museum (M. Castelin, MNHN, pers. comm. March 2018). The description below is based on Verrill (1868b), Bayer (1958), the figured specimen of Valenciennes (1846: plate 15), and MNHN sclerite slide (Fig. 10B).

Diagnosis. Colony dull reddish. Colonies bushy and irregularly dichotomous. Stems short and up to 12.5 mm in diameter. Branchlets up to 4.5 mm in diameter. Calyces flat, sparsely distributed all around the branches. Coenenchymal sclerites red, pink or colourless, mostly spindles up to 0.22 mm long; wart-clubs, up to 0.18 mm long; and warty radiates. Anthocodial spindles red, up to 0.21 mm long.

Figure 10. *Psammogorgia fucosa* Valenciennes, 1846 **A** original figure of the holotype, Valenciennes 1846: plate15 **B** microscopic slide with sclerites deposited at MNHN.

Description. Valenciennes´ figured type was originally presented in natural size (Fig. 10A). Verrill (1868b) reported this dull reddish specimen to be 25.4 cm long and 22.8 cm wide, with the branches ~ 3.8 mm wide. Approximately five stems arise from the holdfast, the thicker being around 12.5 mm in diameter. The colony branches up to 12 times. The branches are irregularly dichotomous, emerging at angles of 45–120°, mostly ascending in parallel and bifurcating at distances of 12.5 to 50.8 mm. The end branchlets are mostly crooked, scarcely tapering and obtuse or clavate at the tips with a diameter of 3–4.5 mm. Branchlets tips are ~ 12.7 to 25.4 mm long (Fig. 10A). The calyces occur all around the branches but not close to each other (Fig. 10A).

The coenenchymal sclerites vary remarkably in diversity of colour, size and form as Verrill has pointed out. Verrill found white, yellowish, light red, deep red and amethystine intermingled sclerites while we observed transparent, red and pink sclerites in the MNHN slide. The MNHN sclerites show a diversity of sclerites that is typical of the genus: mostly irregular warty spindles with acute, blunt or bifurcated ends, and several irregular forms (Figs 10B, 11). These sclerites measure 0.10–0.19 mm in length (reaching 0.22 mm according to Bayer (1858)) and 0.04–0.095 mm in width. Spindles commonly lack the naked median space as they are densely covered with warts. Few wart-clubs are found in the sample, 0.10–0.18 mm long and 0.04–0.06 mm wide at the expanded head. Radiates are densely covered by warts measuring 0.09–0.11 mm in length and 0.055–0.07 mm in width (Fig. 11). Anthocodial spindles are red, long, slender, and covered with small warts measuring 0.10–0.21 mm long and 0.01–0.02 mm wide (Fig. 11).

Remarks and comparison. Verrill´s description of sclerites was based on the MNHN sclerite slide that was sent to him at the MCZ for analysis, probably by R.A. Kölliker (Bayer 1958). We have also analysed sclerites from the slide, showing details that are difficult to compare with those of other species. Though, we found larger sizes of the sclerites than sizes given by Verrill (1870), as also observed by Bayer (1958). This species is similar to *P. teres*, in many aspects (see analysis below). It is indeed possible that *P. fucosa* is a synonym of *P. teres*; however, without a specimen to examine we prefer to keep the status of *P. fucosa* as dubious.

Distribution. Tropical eastern Pacific: only reported from the type locality at Mazatlán, México.

***Psammogorgia gracilis* Verrill, 1868**

Figures 12–13

Psammogorgia gracilis Verrill, 1868b: 417–418; Kükenthal 1919: 238; Kükenthal 1924: 108; Breedy & Guzman 2011: 29.
Heterogorgia gracilis Harden, 1979: 112–113.

Type material. ***Lectotype*** (designated herein): YPM 813a, dry, Pearl Islands, Panamá, F.H. Bradley, 1866–1867, no additional data.

***Paralectotype*:** YPM 813b, dry small fragment, same data as the lectotype.

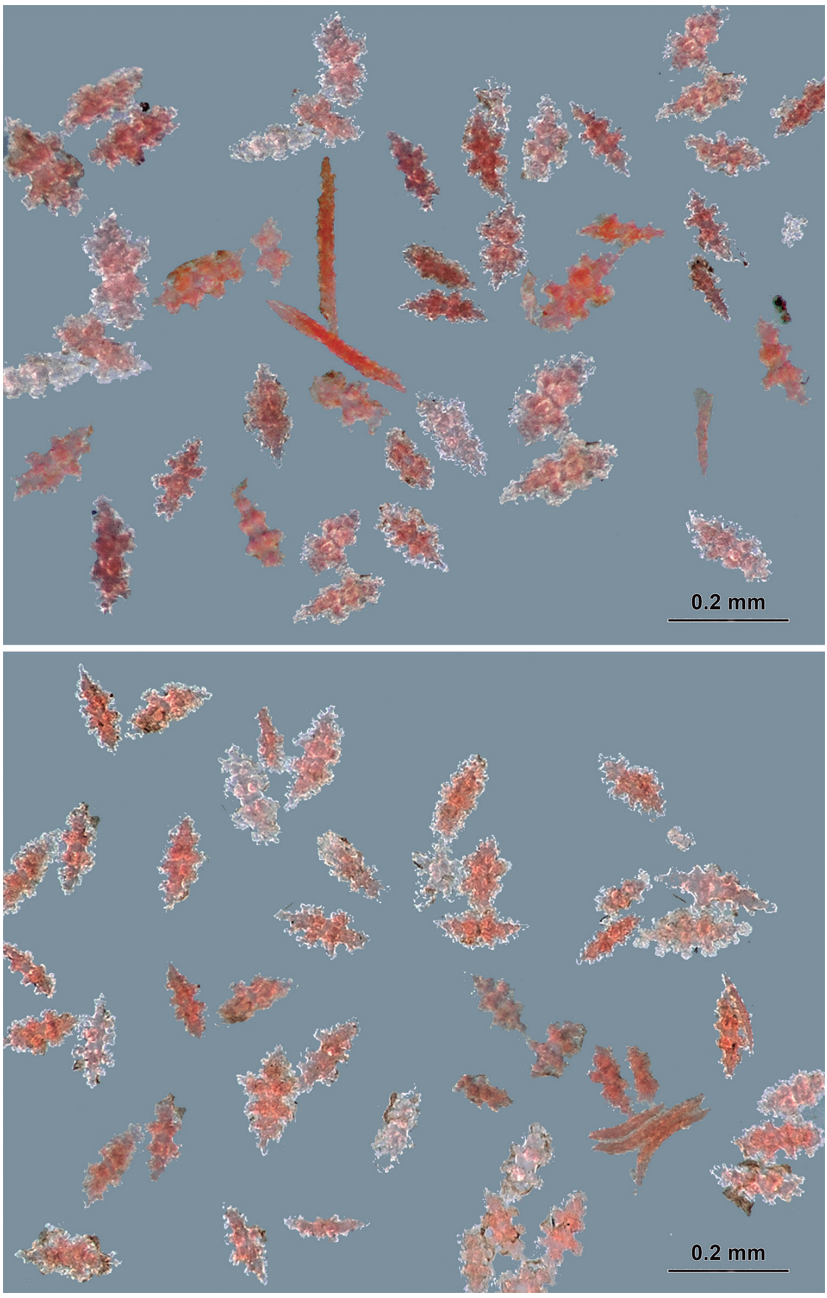

Figure 11. *Psammogorgia fucosa* Valenciennes, 1846. Coenenchymal and anthocodial sclerites, in stereomicroscope. Photographs: Jennifer Winifred Trimble IZ Curatorial Assistant, MCZ, 2018.

Type locality. Pearl Islands, Panamá.

Diagnosis. Colonies red, tall, flabelliform, branches subparallel and elongated. Stem a few centimetres long. Calyces close together and all around the branches. Caly-

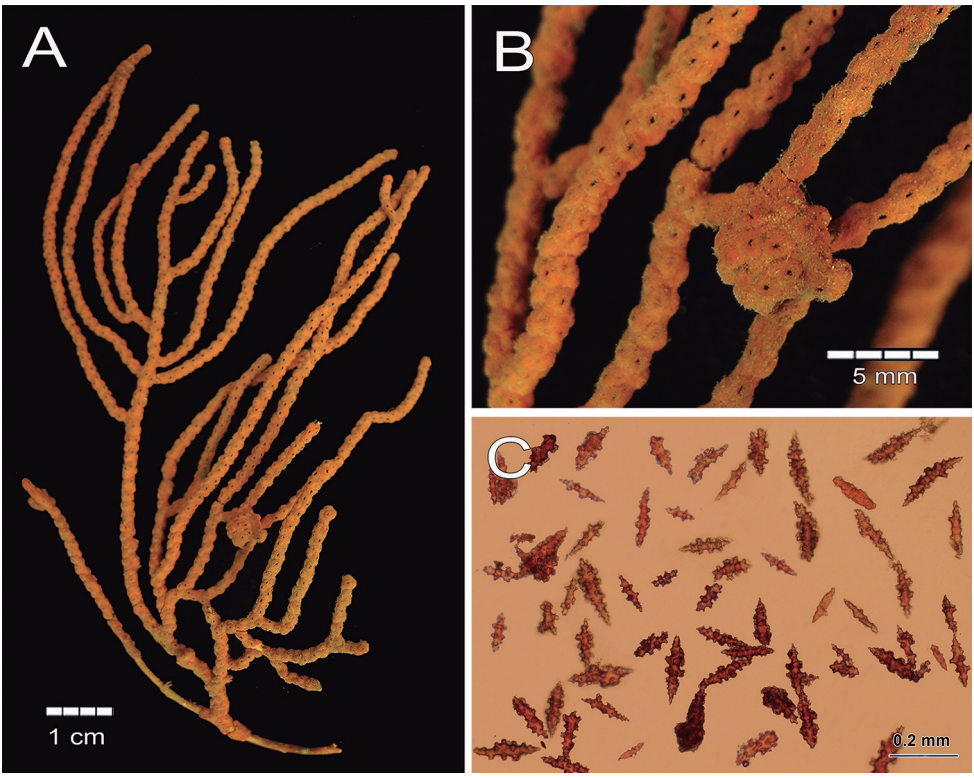

Figure 12. *Psammogorgia gracilis* Verrill, 1868. YPM 813a **A** colony **B** detail of branches showing a tumor **C** coenenchymal and anthocodial sclerites.

ces slightly raised and swollen with concentration of wart-clubs up to 0.25 mm long, and acute spindles around the calyx rim. Coenenchymal sclerites: irregular spindles with acute or bifurcated ends up to 0.20 mm long; warty and irregular radiates and some crosses. Anthocodial spindles up to 0.24 mm long in collaret and points arrangements. Sclerites red and orange or of lighter hues.

Description. The lectotype colony is red and 10 cm long and ~ 6 cm wide. Branching is irregularly dichotomous. The holdfast is absent. The branches emerge at angles of 45–90°, ascend parallel and slightly curve. The main branch of the colony is 2.5 mm in diameter subdividing into long, slender, ascending branchlets, 1.5–1.6 mm in diameter. Branches are round, slender, some extending up to 6.3 cm, undivided or bifurcating at the ends. Branches subdivide up to nine times while terminal branchlets are up to 60 mm long with rounded slightly tapered tips. (Fig. 12A). The calyces are densely arranged around the branches, slightly raised, swollen and are around 0.3 mm tall and 1 mm in diameter (Fig. 12B). The calyces have wart-clubs and some irregular spindles around the calyx rim and the base of the anthocodiae. Coenenchymal sclerites are red, orange or of lighter hues (Fig. 12A–C); including slim spindles with acute ends that may bifurcate (Figs 12C, 13A). Spindles are 0.12–0.24 mm long and 0.04–0.07 mm wide. Wart-clubs are 0.11–0.25 mm long and 0.04–0.08 mm wide at

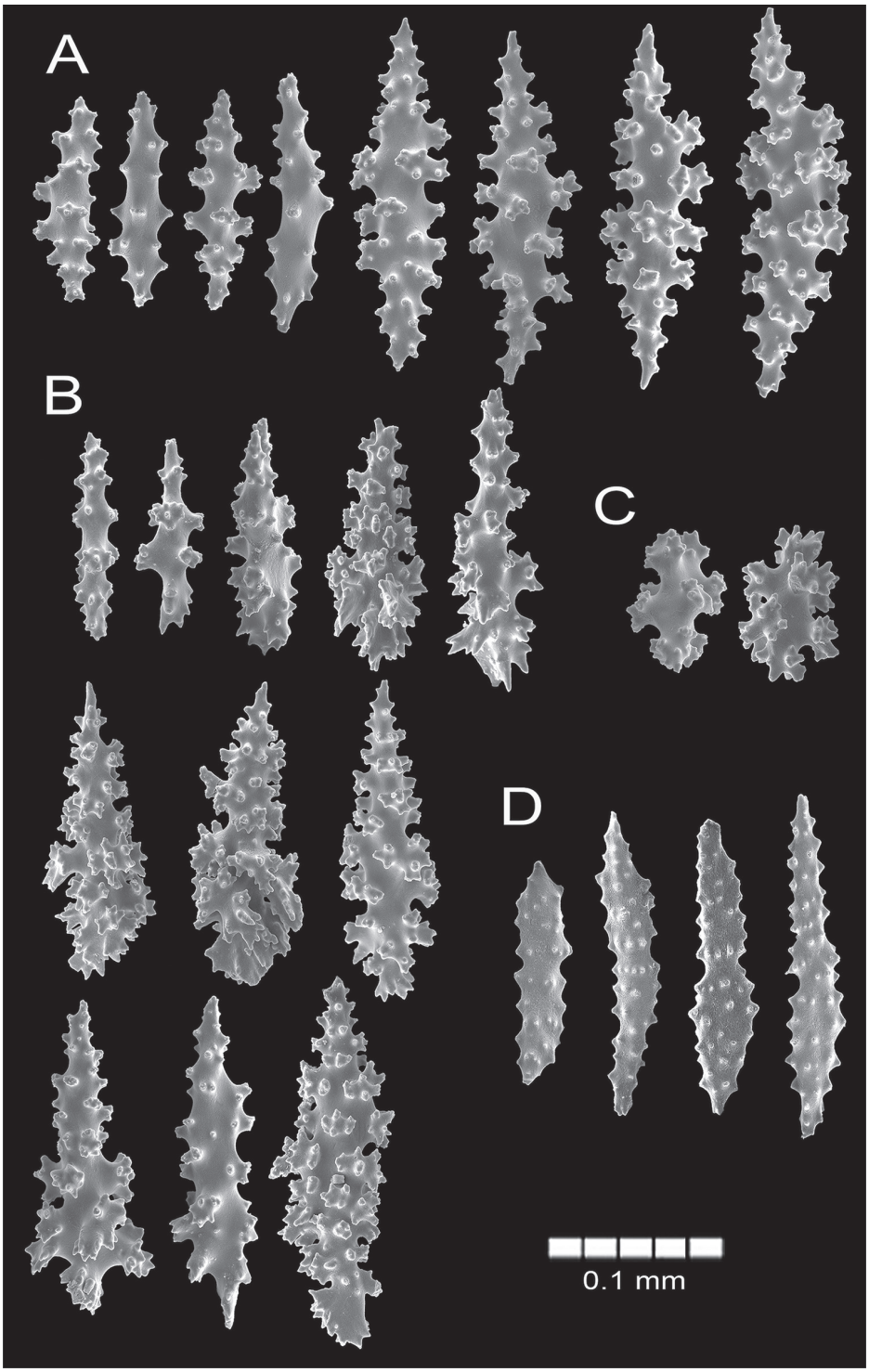

Figure 13. *Psammogorgia gracilis* Verrill, 1868. YPM 813a **A** spindles **B** wart clubs **C** radiates **D** anthocodial spindles.

the expanded head (Fig. 13B). Warty radiates and crosses are 0.08–0.10 mm long and 0.055–0.07 mm wide (Fig. 13C); and some warty crosses up to 0.10 mm by 0.09 mm. Anthocodial armature is well developed with orange and pale yellow spiny spindles arranged in collaret and points (Fig. 12A–C), measuring 0.11–0.20 mm long and 0.03–0.04 mm wide (Fig. 13D) and flat spindles with small tubercles and scattered warts.

Remarks and comparison. This species differs from the others by having long, slender and ascending branchlets, which are thinner than in the other species of the genus (Table 1). Verrill (1868b) pointed out the abundance of wart-clubs in this species when compared to *P. arbuscula* and *P. teres*. According to Verrill, the specimen he described was slender, flabelliform with subparallel and elongated branchlets, measuring12.7 cm long and 10.2 cm wide. The material left (YPM 813a) matches Verrill´s description and illustration. Therefore, we designate this specimen, YPM 813a, as the lectotype of *P. gracilis*.

Distribution. Tropical eastern Pacific: only recorded at the type locality Pearl Islands, Panamá.

Psammogorgia hookeri Breedy & Guzman, 2014

Figure 14

Psammogorgia hookeri Breedy & Guzman, 2014: 2–5.

Type locality. Isla Gallán, Paracas National Reserve, Perú.

Diagnosis. Colonies coral red, small, bushy, multiplanar and irregularly dichotomous. Coenenchyme granular. Coenenchymal sclerites: wide, irregular spindles with acute or bifurcated ends, and combinations of both; warty and irregular radiates, crosses and conspicuous star-like radiates. Colours of coenenchymal sclerites reddish, coral red, and lighter. Calyces prominent, swollen and closely placed. Thorny, irregular spindles, and wart-clubs around the calyx rim up to 0.16 mm long. Anthocodial spindles, thin and spiny, in collaret and points arrangements, yellowish, and pale pink in colour. We refer to Breedy and Guzman (2014) for a full description of the species.

Distribution. This species has only been reported for Perú, Isla Gallán, Paracas National Reserve at 25 m depth, and from Bahía Independencia at unknown depth (Fig. 14).

Psammogorgia pax Breedy, Guzman, Murillo & Vargas, 2020

Psammogorgia pax Breedy et al., 2020: 5–7.

Type locality. Hannibal Bank, Gulf of Chiriquí, Pacific Panamá.

Diagnosis. Colonies white, flabellate and branching in one plane, profuse irregularly dichotomous with occasional anastomosis. Calyces slightly raised, not close together with spiny lobes around polyp apertures. Thorny, irregularly-shaped spindles, and wart clubs around the calyx rims; wart clubs up to 0.26 mm long. Coenenchyme granular. Coenenchymal sclerites white, irregular spindles with acute or bifurcated

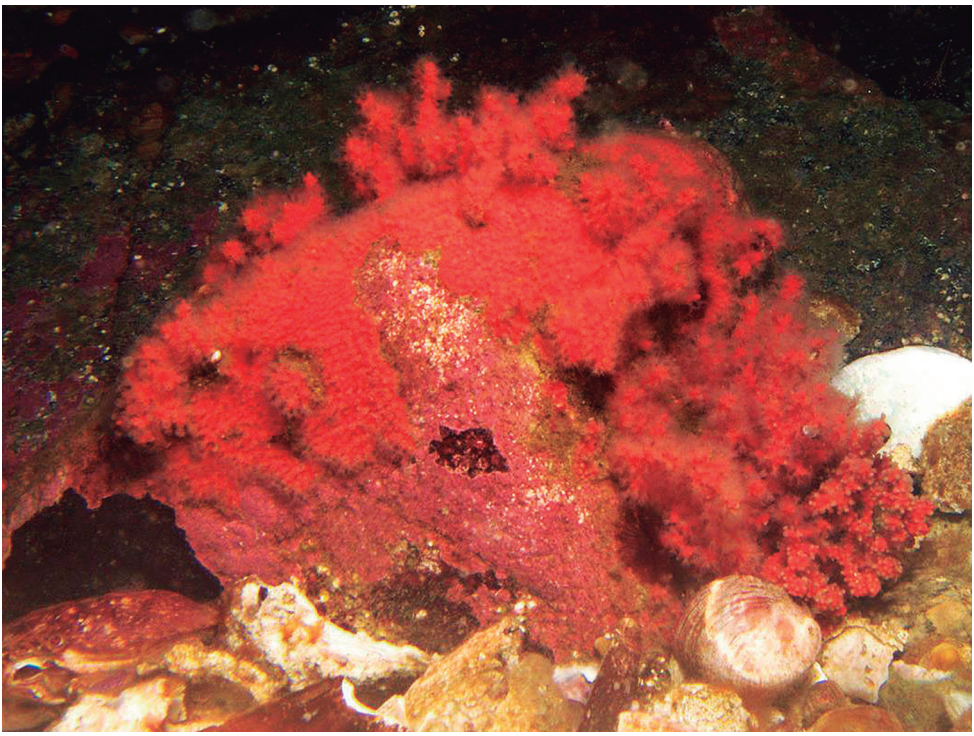

Figure 14. *Psammogorgia hookeri* Breedy & Guzman, 2014. *In situ* colonies at Isla San Gallán, Paracas National Reserve, 25 m deep. Photograph: Yuri Hooker (UPCH).

ends or combinations of both as well as warty and irregular radiates. Anthocodial spindles orange, thin and spiny, in collaret and points arrangements. We refer to Breedy et al. (2020) for a full description of the species.

Distribution. This species has only been reported from its type locality in the upper mesophotic habitats of the Hannibal Bank at 63 m depth.

Psammogorgia teres Verrill, 1868

Figures 15, 16

Psammogorgia teres Verrill, 1868b: 416–417; Hickson 1915: 554; Kükenthal 1919: 237–238; Kükenthal 1924: 108; Harden 1979: 120.

Type material. ***Lectotype*** (designated herein). YPM 1556b, dry, Pearl Islands, Gulf of Panamá, Panamá, F.H. Bradley, 1866–1867, no additional data.

Paralectotype. YPM 1556a, c, same data as the lectotype.

Type locality. Pearl Islands, Panamá.

Diagnosis. Colonies red or orange when preserved but brighter when alive. Colonies bushy and branch laterally and irregularly dichotomous. Stems vary from few mil-

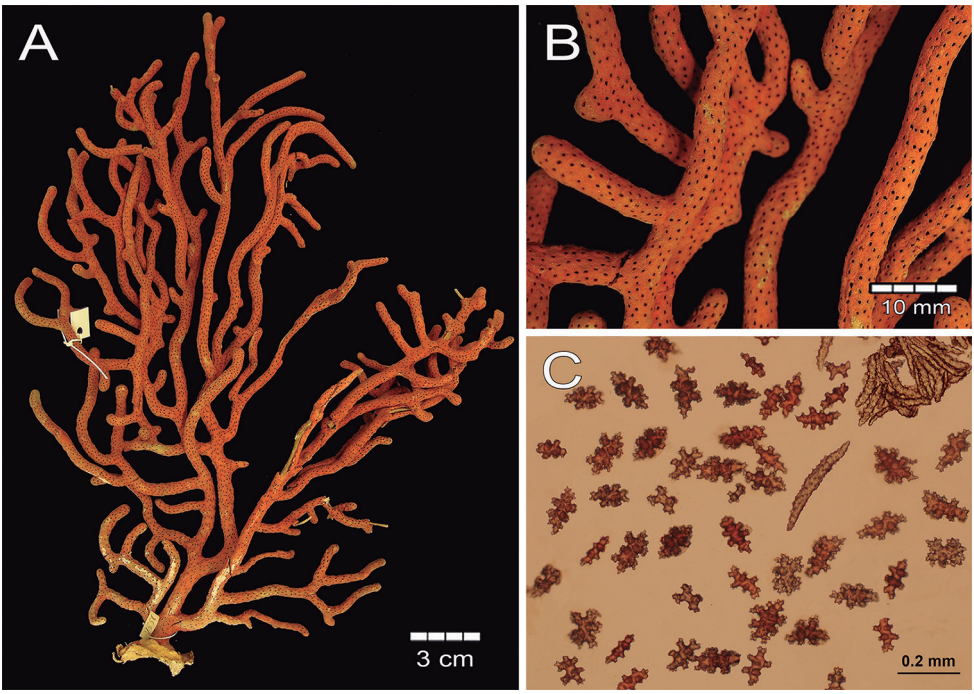

Figure 15. *Psammogorgia teres* Verrill, 1868. YPM1556b **A** colony **B** detail of branches **C** Coenenchymal and anthocodial sclerites.

limetres up to 5 cm long, and 6 mm in diameter. Holdfasts encrusting with thin coenenchyme, often with polyps. Calyces flat, sparsely distributed all around the branches. Calyces with thorny, irregular spindles and wart-clubs around the calyx rim. Coenenchyme compact. Coenenchymal sclerites red, orange or colourless, mostly irregular warty spindles with acute or bifurcated ends and asymmetrical forms with prominent warty tubercles up to 0.20 mm long; wart-clubs with wide heads, up to 0.16 mm long; warty radiates and crosses. Anthocodial spindles pale yellow or colourless, flat or spiny, up to 0.26 mm long and in collaret and points arrangements. Coenenchymal sclerites red, orange and colourless, anthocodial rods pale yellow and colourless.

Description. The lectotype is a red orange dry colony, which was brighter when alive (Verrill 1868b), with 25 cm long and 20 cm wide (Fig. 15A, B). The colony is bushy and laterally branched with an irregularly dichotomous pattern which branches up to 12 times (Fig. 15A, B). The stem is 5 mm long and is 6 mm in diameter, arising from an oval holdfast with around 3.1 cm in diameter that bifurcates in two main branches. These branches are 5–6 mm thick at the base diminishing toward the tips to branchlets of around 3 mm in diameter (Fig. 15A). The branches emerge at angles of 45–90°, ascending mostly parallel to each other and bifurcating the same way. Branchlets are mostly perpendicular to the branch of origin and slightly curved. Terminal branchlets are 5 to 60 mm in length (Fig. 15A). Calyces occur all around the branches, being flat and with a polyp rim 0.4–1.0 mm in diameter and, mostly separated be-

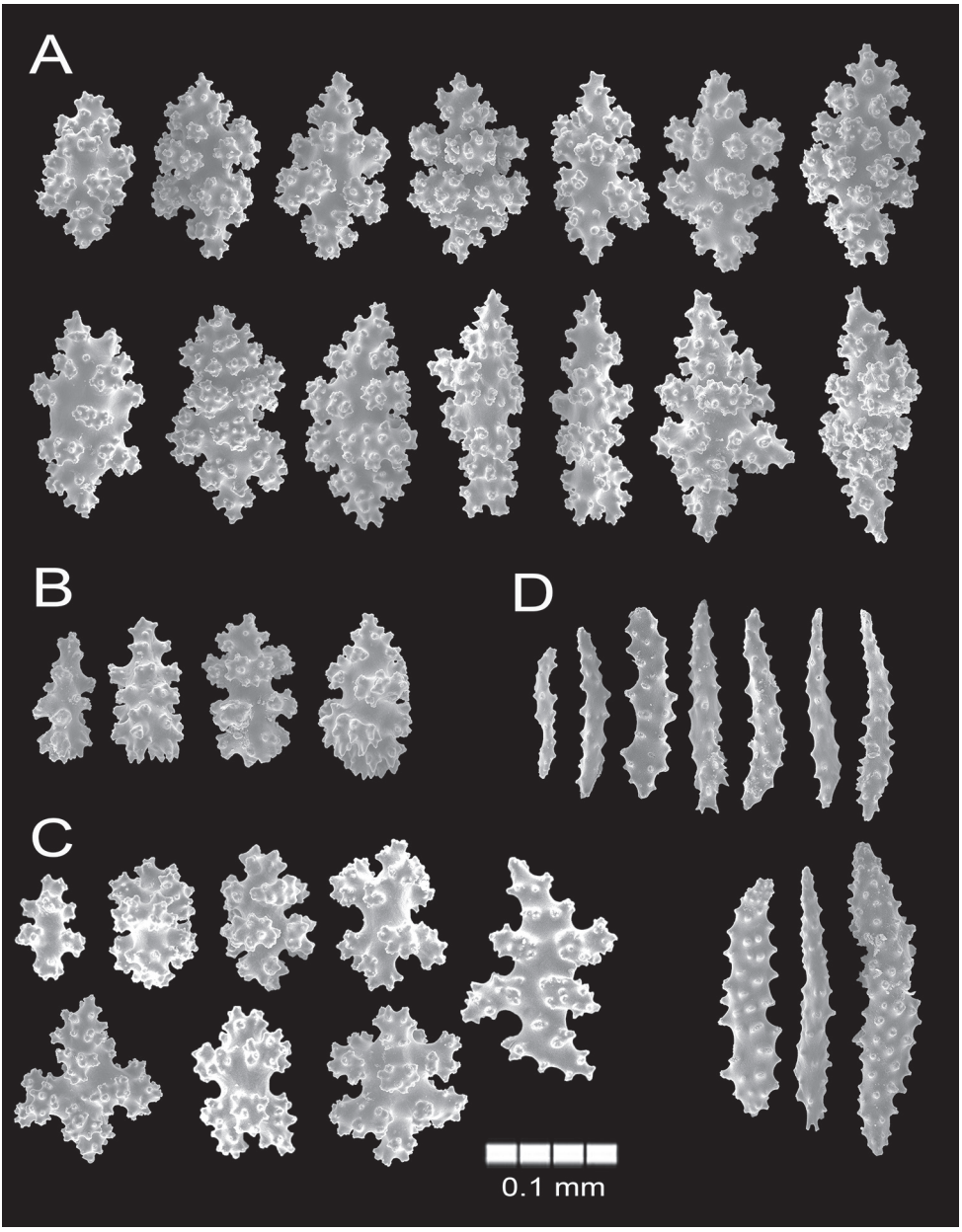

Figure 16. *Psammogorgia teres* Verrill, 1868. YPM1556b **A** spindles **B** Wart clubs **C** Radiates and crosses **D** anthocodial spindles.

tween each other by 0.5–4.0 mm with an average of 3.5 mm (Fig. 15B). Calyces have concentration of thorny, irregular spindles and wart-clubs appearing usually around the calyx rim. The coenenchyme is compact with a finely granulated surface. The coenenchymal sclerites are very variable in size and form, being red, orange or colourless and mostly composed of irregular warty spindles with acute or bifurcated ends, and

some asymmetrical forms with prominent warty tubercles (Figs 15C, 16A). Spindles are 0.11–0.20 mm long and 0.07–0.12 mm wide. Wart-clubs have wide leafy heads and are 0.07–0.16 mm long and 0.045–0.10 mm wide (Fig. 16B). Warty radiates are 0.07–0.13 mm long and 0.06–0.09 mm wide (Fig. 16C); and some crosses, 0.95–0.11 mm by 0.08–0.11 mm (Fig. 16C). The anthocodial armature is well developed and composed of pale-yellow to colourless spiny spindles and flat warty sclerites arranged in collaret and points, measuring 0.13–0.24 mm in length and 0.02–0.04 mm in width (Figs 15C, 16D).

Remarks and comparison. While the largest anthocodial sclerite measured in the lectotype was 0.24 mm long, Verrill (1886b) mentioned a slightly larger length of 0.26 mm. This is in accordance to the anthocodials of other specimens revised in this study. The syntype YPM1556b closely fits Verrill´s (1868b) description of the colony and the sclerites. For this reason, we designate this as the lectotype to clearly establish the species identity.

Psammogorgia teres has a colony morphology similar to that of *P. fucosa* (Table 1), but it has different sclerite sizes and colours in comparison with the type's sclerite slide (Table 2). In *P. teres*, spindles and wart-clubs are shorter while anthocodials and radiates are larger than in *P. fucosa* (Table 2). Anthocodials of *P. fucosa* are red but colourless in *P. teres*, which is a diagnostic feature of this species.

In comparison with *P. arbuscula* and *P. gracilis*, *P. teres* differs in the external morphology represented by colonies with thicker branches and flat calyces; and relative abundance and sizes of sclerites (Tables 1, 2).

Distribution. The species occurs in Pearl Islands, Panamá (type locality) and also in in the Chiriquí Gulf, Panamá. However, the species presents a wider regional distribution in the tropical eastern Pacific. It was sampled by us, along the Pacific coast of Costa Rica, El Salvador, Nicaragua, and Ecuador, and encountered in collections from the Pacific coasts of México and Colombia.

Conclusions

The genus *Psammogorgia* comprises six species and two varieties belonging to two morphological species-groups: *Psammogorgia arbuscula* group consisting of *P. arbuscula*, *P. gracilis*, *P. hookeri* and *P. pax*. and the *Psammogorgia teres* group consisting of *P. teres* and *P. fucosa*. We have explored and collected *Psammogorgia* species in Costa Rica, El Salvador, Nicaragua and Panamá, and have revised collections from Colombia, Ecuador, México and Perú. We found *P. arbuscula* and *P. teres* from these localities; nonetheless, *P. gracilis* and the two varieties of *P. arbuscula* were not found as additional records. Regarding *P. digueti*, after our analysis of a specimen in the MNHN we conclude that it belongs to a different genus and its status has to be revised. Lastly, *P. hookeri* and *P. pax* seem to be endemic to their regions, the first one from Perú and the other from mesophotic habitats off the Pacific coast of Panamá. However, without more explorations and further records, the geographic distribution and species richness of *Psammogorgia* is incomplete.

Key to the valid species of the genus *Psammogorgia* Verrill, 1868 reported from the tropical eastern Pacific

1 Colony white. Calyces slightly raised. Deep water species (> 60 m) ..... ***P. pax***
– Colony red or of different hues of red. Calyces prominent to flat. Shallow water species (< 40 m) **2**
2 Calyces prominent with swollen polyp apertures..... **3**
– Calyces flat without swollen polyp apertures..... **5**
3 Colony coral red. Wart clubs < 0.16 mm in length. Star-like radiates present in coenenchyme..... ***P. hookeri***
– Colony red or dark red. Wart clubs > 0.16 mm in length. Star-like radiates absent from coenenchyme..... **4**
4 Branch diameter > 2 mm. Anthocodial spindles > 0.20 mm in length .... ***P. arbuscula***
– Branch diameter < 2 mm. Anthocodial spindles < 0.20 mm in length ....***P. gracilis***
5 Terminal branchlets long (> 25 mm). Anthocodial spindles pale yellow to colourless and >0.20 mm in length..... ***P. teres***
– Terminal branchlets long (< 25 mm). Anthocodial spindles red and < 0.20 mm in length..... ***P. fucosa***

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RESEARCH ARTICLE

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A new Caribbean species of *Hylaeanura* Arlé, 1966 (Collembola, Neanuridae, Pseudachorutinae)

Claudia M. Ospina-Sánchez[1], José G. Palacios-Vargas[2], Grizelle González[1]

1 *USDA-FS, International Institute of Tropical Forestry, Río Piedras, 00926-1119, Puerto Rico* **2** *Laboratorio de Ecología y Sistemática de Microartrópodos, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 México, D.F., México*

Corresponding author: Claudia M. Ospina-Sánchez (cmarcela.ospinas@gmail.com)

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Abstract

We here describe a new Collembola species, *Hylaeanura emiliae* **sp. nov.**, from the Luquillo Experimental Forest in Puerto Rico. We describe *H. emiliae* **sp. nov.** as a distinct species based on the enlarged sensilla s3 in antennal segment IV, the absence of modified sensorial setae in abdominal segment IV and the presence of four setae on each dens. An updated key with illustrations for the identification of worldwide species of the genus is included.

Keywords

Island, Luquillo Experimental Forest, Puerto Rico, subtropical forest, taxonomy

Introduction

In Puerto Rico, most studies of arthropod community dynamics have been performed in the Luquillo Mountains (Richardson 1999; González and Barberena 2017; Quiñones et al. 2018). The Luquillo Experimental Forest (LEF) contains four forest types defined by elevation and distinct tree species composition (Gould et al. 2006; Weaver and Gould 2013). The present study focuses on three of them: (1) The Tabonuco (*Dacryodes excelsa* Vahl) forest occupies areas below 600 m, (2) the mid-elevation, Palo Colorado (*Cyrilla racemiflora* L.) forest occurs in areas above the cloud conden-

sation level from 600–900 m, and (3) the Elfin forest (*Tabebuia rigida* Urban), with stunted vegetation and waterlogged anoxic soils, is located only on the highest peaks above 900 m (Gould et al. 2006). These forests represent the subtropical wet and subtropical rain forest life zones in Puerto Rico (Ewel and Whitmore 1973).

In most studies of litter and soil fauna in the LEF, Collembola are an important group for ecosystem functioning because of their dominant abundance and their key responses to changes in disturbance, altitude and vegetation type (Schowalter and Ganio 1999; Schowalter et al. 2003; Richardson et al. 2005; Richardson et al. 2010; Schowalter et al. 2014). In Puerto Rico, collembolans are well known in comparison to other groups of soil arthropods. However, not all Collembola species from LEF have been identified (González and Barberena 2017). In a recent survey made between 2014 and 2015, 16 families 37 genera and 60 species/morphospecies were identified, and among these, 15 are new species to science (Ospina-Sánchez 2019). The purpose of this paper is to describe a new species of *Hylaeanura* Arlé, 1966.

The genus *Hylaeanura* was conceived by Arlé (1966) to place *Paranurella infima* described by himself in 1959. So far only four species are known: *Hylaeanura nepalensis* (Yosii, 1966), originally described as *Paranura nepalensis* from the Himalayas; *H. nohbecana* Vázquez, Cutz-Pool & Palacios-Vargas, 1998, from Mexico; *H. mendoncae* Zeppelini & Palacios-Vargas, 2013, from Brazil and *H. infima* from Brazil, French Guiana and Peru (Najt et al. 1990). The first taxonomic report of the genus from Puerto Rico was *H. infima* (Ospina-Sánchez et al. 2020) and it now includes the new species *Hylaeanura emiliae*.

Materials and methods

The material used to describe the new *Hylaeanura* species came from the survey of the Collembola microhabitats in the Luquillo Mountains conducted in 2014 and 2015 along three forest types (Tabonuco, *Dacryodes excelsa*; Palo Colorado, *Cyrilla racemiflora* and Elfin forest, *Tabebuia rigida*). Collembola were extracted from soil and litter samples using a Berlese-Tullgren funnel and stored in 95% ethanol. They were cleared using Nesbitt solution and fixed in slides using Mac André II solution (Mari Mutt 1976). To harden the solution, the slides were dried in a slide warmer at 45 to 50 °C for seven days. Finally, each specimen was labeled with its collecting data. Specimens were examined with a Leica DM500 phase-contrast microscope. The drawings were made with the aid of a drawing tube.

Abbreviations:

a.s.l.	above sea level	**Sgd**	dorsal guard sensillum of Ant III
Abd	abdominal segment	**Sgv**	ventral guard sensillum of Ant III
Ant	antennal segment	**ss**	sensorial setae
PAO	Postantennal Organ	**Tita**	tibiotarsi
S	sensilla	**Th**	thoracic segment

Taxonomy

Poduromorpha
Neanuridae
Pseudachorutinae

Hylaeanura Arlé, 1966

Diagnosis (modified from Zeppelini and Palacios-Vargas 2013). Habitus of *Paranurella* or *Kenyura*, i.e., reduced appendices and without pigment; less than 1.0 mm in size; without eyes or at most 2 eyes per side; antennae shorter than half the cephalic diagonal, Ant. IV with 7 sensilla, S8 hypertrophied; mandible with one to three teeth, maxilla styliform; legs very short, ungues without teeth and unguiculus, tenent hairs not developed. Ventral tube with 3+3 setae; tenaculum 2+2 to 3+3, furcula very reduced, each dens with 3 setae, mucro minute or lacking. Body chaetotaxy reduced and with very small setae.

Hylaeanura emiliae sp. nov.

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Figures 1–9, Table 1

Type material. ***Holotype.*** Female on slide. ***Paratypes:*** 1 female and 1 juvenile on slide. All the type material kept at corresponding author's institution.

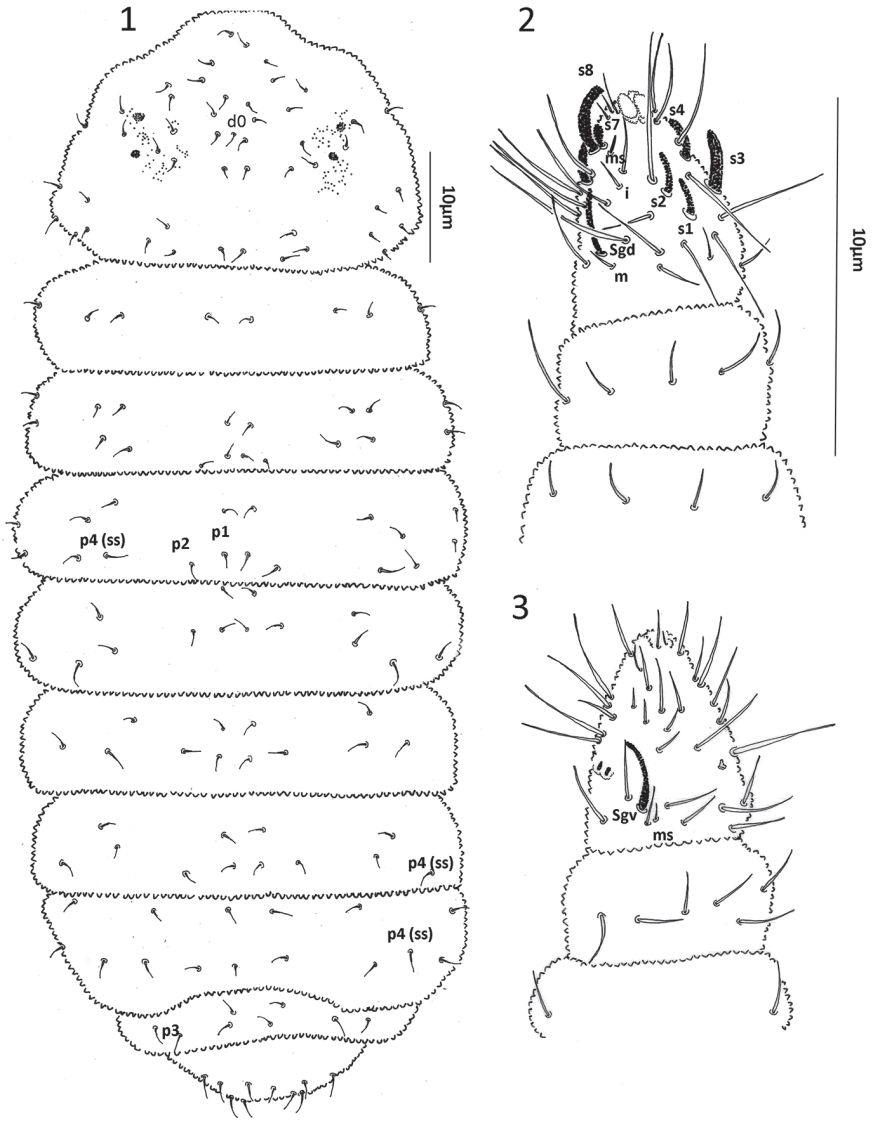
Type locality. Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1,18°16'40"N, 65°50'53"W; 815 m a.s.l.; ex soil, *Cyrilla racemiflora* forest type, 18 November 2014. All specimens were extracted using Berlese-Tullgren funnels from samples collected in leaf litter and soil at the Luquillo Mountains. C. M. Ospina and M. Rivera leg.

Other material. Female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 2, 18°16'40.3"N, 65°51'01"W, *Cyrilla racemiflora* forest type, leaf litter, 795 m a.s.l., 18 November 2014, C.M.Ospina leg. One (1) juvenile on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, 18°16'40"N, 65°50'53"W, *Cyrilla racemiflora* forest type, leaf litter, 815 m a.s.l., 18 February 2015, C. M. Ospina leg.

Diagnosis. *Hylaeanura emiliae* sp. nov. has an enlarged sensillas S3 and S8 on Ant IV, Abd IV without modified setae, and four setae on each dens.

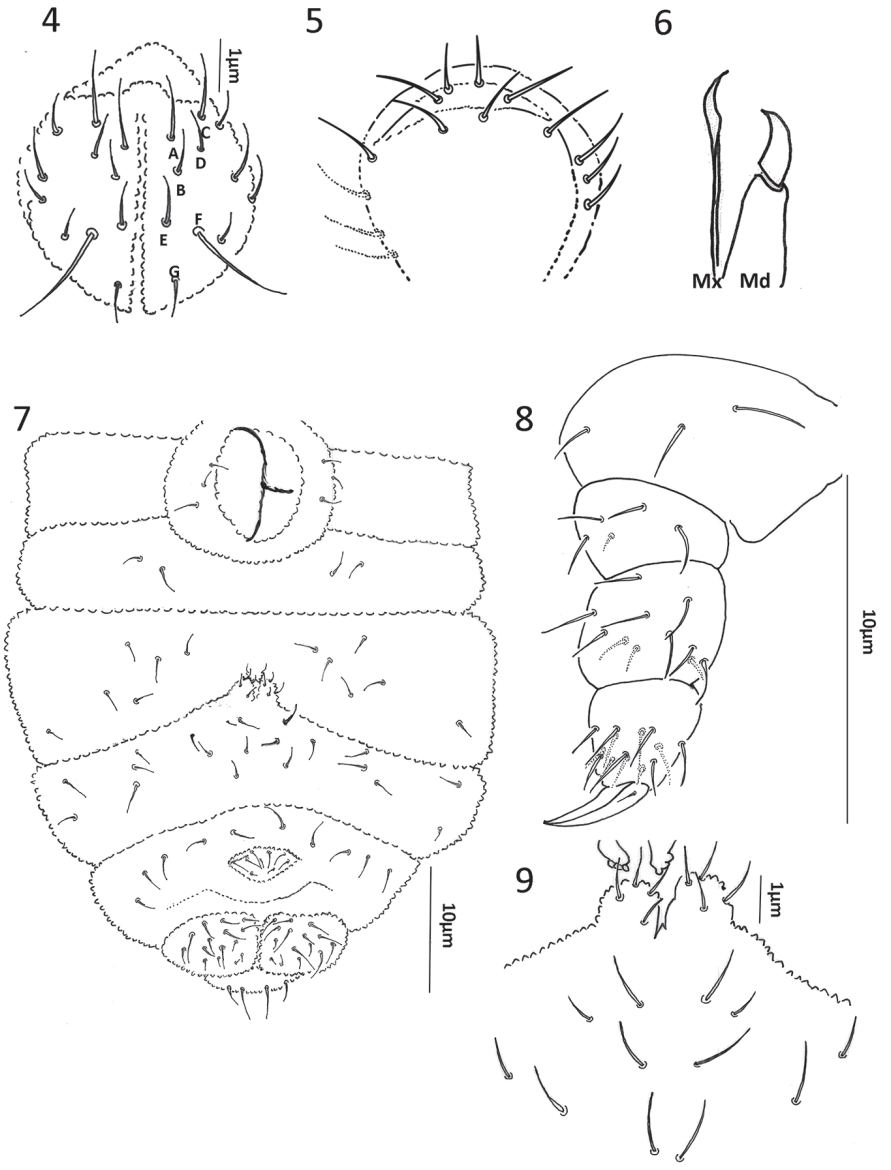
Description. Length of the holotype 1050 µm (female paratype 653 µm and juvenile paratype 550 µm). Specimens in ethanol without color, body with coarse granulation and without tubercles. Body setae short and smooth, the sensorial setae longer than ordinary setae, both acuminate (Fig. 1).

Head: Antenna smaller (0.47×) than cephalic diagonal. Ant III and IV fused dorsally. Ant IV dorsally with a trilobed apical vesicle; subapical organite absent and dorsoexternal microsensillum, 7 subcylindrical sensilla, S8 hypertrophied, S7



Figures 1–3. *Hylaeanura emiliae* sp. nov. **1** Dorsal chaetotaxy **2** Ant. I–IV dorsal view **3** Ant. I–IV ventral view.

smaller and S3 large; 12 long setae plus i (Fig. 2); Ant III sense organ with two small internal straight sensilla and two subequal subcylindrical guard sensilla; ventral microsensillum present (Fig. 3); Ant II with 11 setae; Ant I with six setae. Eyes 2+2 in a pigmented patch. PAO absent. Head dorsal quetotaxy as in Fig. 1, unpaired setae d0 present. Labium with a total of 11 setae per side with setae A to G, setae C and D slightly displaced apically (Fig. 4). Labral chaetotaxy 4, 2, 2 (Fig. 5). Mandible with one tooth, maxilla styliform (Fig. 6).



Figures 4–9. *Hylaeanura emiliae* sp. nov. **4** Labium **5** Labrum **6** Mandible (Md) and Maxillae (Mx) **7** Ventral abdominal chaetotaxy **8** leg I **9** reduced furcula and tenaculum.

Body: Ordinary body setae smooth, distributed as in Fig. 1. Th I with 3+3 setae. Sensory setae (ss) similar to body setae, in position p4 in all segments and distributed on Th. II-Abd V as 11/11111. Ventral chaetotaxy as in Fig. 7. Female genital plate with 3+3 pregenital setae, 7 circumgenital and 2 eugenital (Fig. 7). Male genital plate not seen. Each anal ventral lobe with 14 setae.

Table 1. Summary of main characters of described species of *Hylaeanura* Arlé, 1966.

Species	Total length (µ)	Ventral guard sensillum	Dorsal guard sensillum	Mandible teeth	Eyes per side of head	Shape Abd IV sensillum	Tenaculum teeth	Setae in dens	Setae in manubrium	Mucro
H. infima	500	st	st	2	0	ss	?	3	2	–
H. nohbecana	1000	st	st	3	0	cf	3+3	3	2	+
H. nepalensis	700	st	st	3	2	ss	2+2	3	2	–
H. mendoncae	600	si	si	2	2	ss	2+2	3	0 (6)	–
H. emiliae sp. nov.	850	st	st	1	2	ss	3+3	4	0 (6)	–

st, straight
si, sinuous
cf, candle-flame shaped
ss, sensillum acuminated
?, no information included in the original description
-, absent
+, present

Legs: Chaetotaxy of legs I–III as follow: Coxae with 3, 5, 7 trochanter with 5, 5, 4; femora 11, 11, 10 and tita with 16, 16, 14 setae (Fig. 8). Tenent hair not developed and unguiculus absent; claws without teeth.

Collophore with 3+3 setae; tenaculum with 3+3 teeth and without setae; furcula reduced, manubrium reduce with 6+6 setae in Abd III ventrally; dens with four setae, mucro absent (Fig. 9).

Etymology. This species is dedicated to the daughter of the senior author, Emilia, who was born while this research was being conducted.

Distribution. *Hylaeanura emiliae* sp. nov. is only known from the Luquillo Mountains in the *Cyrilla racemiflora* forest type, on the Toro Trail between 795–815 m a.s.l.

Fenology. *Hylaeanura emiliae* sp. nov. was extracted from leaf litter and soil in both dry and rainy seasons during November 2014 and May and August 2015.

Identification key to the species of *Hylaeanura* Arlé, 1966

(updated from Zeppelini and Palacios-Vargas 2013)

1 Without eyes **2**
– With 2 eyes per side **3**
2 Sensorial seta on Abd IV candle-flame shaped. Dens with a minute mucro present ..... ***H. nohbecana*** **Vázquez, Cutz-Pool & Palacios-Vargas, 1998**
– Sensorial seta on Abd IV sensillum shaped. Dens without mucro ..... ***H. infima*** **(Arlé, 1959)**
3 Dorsal and ventral guard sensilla sinuous (Sensorial organ Ant Ill). Mandible with two teeth..... ***H. mendoncae*** **Zeppelini & Palacios-Vargas, 2013**
– Dorsal and ventral guard sensilla straight, Mandible with 1 or 3 teeth **4**
4 Tenaculum with 2+2 teeth. Mandible with 3 teeth ..... ***H. nepalensis*** **(Yosii, 1966)**
– Tenaculum with 3+3 teeth. Mandible with 1 tooth..... ***H. emiliae*** **sp. nov.**

Discussion

The description of *Hylaeanura emiliae* sp. nov. fits with the most recent genus diagnosis proposed by Zeppelini and Palacios-Vargas (2013). Although in the diagnosis of the genus, the dens each have three setae and *H. emiliae* sp. nov. has four setae in each, the number of setae on the dens, as well as the shape of the mucro, are variable characters among the species (D'Haese 2003). The similar genus *Kenyura* includes species having numerous teeth on the mandible, S8 is normal and the presence of pigmentation (Arlé 1966, Vázquez et al. 1998).

Hylaeanura emiliae sp. nov. is different from other *Hylaeanura* due to the enlargement of the sensilla s3 in Ant IV, the absence of modified S setae in Abd IV and the presence of four setae in the dens. Additionally, it has an unpaired seta d0 in the head. This setae is absent in other described species of the genus, but defines a unique difference within head chaetotaxy.

Using the comparative morphology of *Hylaeanura* presented by Zeppelini and Palacios-Vargas (2013), the character combination of the new species is different from all others previously described. According to their descriptions the most similar is *Hylaeanura nepalensis*, but it differs in size, the presence of 2+2 tenacular teeth and three mandibular teeth (Yosii 1966).

Hylaeanura infima is the smallest species and has a sensillum of Abd IV of setae shape. It differs from the new species by the absence of eyes and the presence of two teeth in the mandible and the presence of three setae in dens (Arlé 1966, Thibaud and Massoud 1983).

Hylaeanura nohbecana is the biggest *Hylaeanura*, and is similar to the new species in the straight shape of the guard sensillum of Ant IV, the differences appearing in the chaetotaxy: the absence of unpaired setae d0 in the head, the presence of setae a3 in Abd II-IV and the position of the ss in p3 in Abd I. Additionally, *H. nohbecana* has no eyes, the furcula has two small dens each bearing 3 setae and a small vestigial mucro (Vázquez et al. 1998).

The most recently described species, *H. mendoncae* differs from *H. emiliae* sp. nov. in the position of ss in Abd I to III in p3. In Abd IV, ss is also in position p3 but in the shape of a candle-flame setae. In Abd V ss is in position p2. The furcula is reduced and dens have 3 setae each without a mucro (Zeppelini and Palacios-Vargas 2013). Similar to *H. emiliae* sp. nov., *H. mendoncae* has 6 + 6 setae present ventrally in Abd III as vestigial manubrium. The differences between described *Hylaeanura* species are described in Table 1.

Acknowledgements

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RESEARCH ARTICLE

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Twenty-eight new species of the spider genus *Merizocera* Fage, 1912 (Araneae, Psilodercidae) from South and Southeast Asia

Wan-Jin Chang[1,2,4*], Zhiyuan Yao[3*], Shuqiang Li[1,4]

1 *Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China* **2** *Southeast Asia Biological Diversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw 05282, Myanmar* **3** *College of Life Science, Shenyang Normal University, Shenyang 110034, Liaoning, China* **4** *University of Chinese Academy of Sciences, Beijing 100049, China*

Corresponding author: Shuqiang Li (lisq@ioz.ac.cn)

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Abstract

Previously, the genus *Merizocera* Fage, 1912 comprised only seven species from Indonesia, Malaysia, Sri Lanka, and Thailand. In this study, 28 new species are described from South and Southeast Asia: *M. baoshan* Li, **sp. nov.** (♂♀), *M. betong* Li, **sp. nov.** (♂♀), *M. colombo* Li, **sp. nov.** (♂♀), *M. galle* Li, **sp. nov.** (♂♀), *M. hponkanrazi* Li, **sp. nov.** (♂), *M. kachin* Li, **sp. nov.** (♂♀), *M. kandy* Li, **sp. nov.** (♂♀), *M. mandai* Li, **sp. nov.** (♂♀), *M. krabi* Li, **sp. nov.** (♂♀), *M. kurunegala* Li, **sp. nov.** (♂♀), *M. lincang* Li, **sp. nov.** (♀), *M. mainling* Li, **sp. nov.** (♂♀), *M. nyingchi* Li, **sp. nov.** (♀), *M. peraderiya* Li, **sp. nov.** (♂♀), *M. phuket* Li, **sp. nov.** (♂♀), *M. putao* Li, **sp. nov.** (♂♀), *M. ranong* Li, **sp. nov.** (♂♀), *M. ratnapura* Li, **sp. nov.** (♂♀), *M. salawa* Li, **sp. nov.** (♂), *M. tak* Li, **sp. nov.** (♀), *M. tanintharyi* Li, **sp. nov.** (♂♀), *M. tengchong* Li, **sp. nov.** (♂), *M. thenna* Li, **sp. nov.** (♂♀), *M. uva* Li, **sp. nov.** (♀), *M. wenshan* Li, **sp. nov.** (♂♀), *M. wui* Li, **sp. nov.** (♂♀), *M. yala* Li, **sp. nov.** (♀), and *M. yuxi* Li, **sp. nov.** (♂♀). Among them the genus *Merizocera* is reported for the first time from China, Myanmar, and Singapore.

Keywords

biodiversity, morphology, Ochyroceratidae, taxonomy, tropics

* Both authors contributed equally to this work.

Introduction

The spider family Psilodercidae was proposed as Psilodercinae by Machado (1951) under the family Ochyroceratidae Fage, 1912. Deeleman-Reinhold (1995) studied the Indo-Pacific ochyroceratids and erected two subfamilies, Theotiminae and Psilodercinae: Psilodercidae was elevated to family rank by Wunderlich (2008), and Pérez-González et al. (2016) formally confirmed that Psilodercinae Machado, 1951, has priority over Psilodercinae Deeleman-Reinhold, 1995.

The family is restricted to tropical South Asia, southern China, and Southeast Asia (WSC 2020). It currently includes eleven genera and 196 species, of which *Luzonacera*, *Qiongocera*, *Relictocera*, *Sinoderces,* and *Thaiderces*, all authored by Li & Li, 2017, and *Priscaleclercera* Wunderlich, 2017, were described only recently (Liu et al. 2017; Li 2020; WSC 2020). Currently, the genus *Merizocera* contains only seven species: *M. brincki* Brignoli, 1975, *M. cruciata* (Simon, 1893), *M. oryzae* Brignoli, 1975, and *M. picturata* (Simon, 1893) from Sri Lanka; *M. pygmaea* Deeleman-Reinhold, 1995 from Thailand; *M. crinita* (Fage, 1929) from Malaysia; and *M. stellata* (Simon, 1905) from Indonesia (Simon 1893a, b; WSC 2020). Of these seven known species, four were described from only a single male or female specimen.

In this paper, 28 new species of *Merizocera* collected in southern China, Myanmar, Singapore, Sri Lanka, and Thailand are described and illustrated. This is the first record of the genus in China, Myanmar, and Singapore.

Materials and methods

Types are deposited in the Institute of Zoology, Chinese Academy of Sciences (**IZ-CAS**) in Beijing. All specimens collected were studied and preserved in 75% ethanol. The specimens were measured and examined with a Leica M205 C stereomicroscope and further morphological details were observed with an Olympus BX41 compound microscope. Male palps were detached from the left side of the animal for further examination. Carapace length was measured excluding the clypeus. Internal genitalia of the female and palpal bulbs were dissected and immersed in lactic acid. An Olympus C7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus SZX12 stereomicroscope was used to take photos at different focal planes. The photos were then transferred to the image stacking software Helicon Focus 6.7.1 to generate photos with a greater depth of field before further processing with Adobe Photoshop CC 2014. Leg measurements are shown as total length: femur, patella, tibia, metatarsus and tarsus. Leg segments were measured from their retrolateral side. All measurements are given in millimetres (mm). All terminology follows that of Li et al (2014). The distribution map was generated with Google Earth Pro 7.3.2 (Google Limited Liability Company).

Taxonomy

Family Psilodercidae Machado, 1951

Genus *Merizocera* Fage, 1912

Type species. *Ochyrocera cruciata* Simon 1893a: 282, fig. 245, from Sri Lanka.

Diagnosis. *Merizocera* can be recognised by the following combination of characters: 1) presence of cymbial protrusion (except *M. mainling* sp. nov. and *M. tanintharyi* sp. nov.); 2) bulb and cymbium almost similar in length or bulb longer than cymbium; 3) absence of clypeal protrusion (except *M. mainling* sp. nov. and *M. putao* sp. nov.); 4) presence or absence of conductor, if present, connected basally with embolus; 5) elongated pyriform bulb with embolus and conductor (if present) arising distally; 6) cheliceral promargin with lamina having three triangular extensions, retromargin with two small teeth.

Composition. *Merizocera cruciata* (♂♀) (the type species), *M. baoshan* sp. nov. (♂♀), *M. betong* sp. nov. (♂♀), *M. brincki* (♂), *M. colombo* sp. nov. (♂♀), *M. crinita* (♂♀), *M. galle* sp. nov. (♂♀), *M. hponkanrazi* sp. nov. (♂), *M. kachin* sp. nov. (♂♀), *M. kandy* sp. nov. (♂♀), *M. mandai* sp. nov. (♂♀), *M. krabi* sp. nov. (♂♀), *M. kurunegala* sp. nov. (♂♀), *M. lincang* sp. nov. (♀), *M. mainling* sp. nov. (♂♀), *M. nyingchi* sp. nov. (♀), *M. oryzae* (♀), *M. peraderiya* sp. nov. (♂♀), *M. phuket* sp. nov. (♂♀), *M. picturata* (♂♀), *M. putao* sp. nov. (♂♀), *M. pygmaea* (♀), *M. ranong* sp. nov. (♂♀), *M. ratnapura* sp. nov. (♂♀), *M. salawa* sp. nov. (♂), *M. stellata* (♀), *M. tak* sp. nov. (♀), *M. tanintharyi* sp. nov. (♂♀), *M. tengchong* sp. nov. (♂), *M. thenna* sp. nov. (♂♀), *M. uva* sp. nov. (♀), *M. wenshan* sp. nov. (♂♀), *M. wui* sp. nov. (♂♀), *M. yala* sp. nov. (♀) and *M. yuxi* sp. nov. (♂♀).

Remarks. Although the genus *Merizocera* cannot be sufficiently delineated by features of their female genitalia, the somatic morphology and male palp structures are consistent with those of *Merizocera* sensu Li & Li, 2018.

Distribution. The genus is represented by species ranging from Sri Lanka to China's western and southern provinces and to parts of mainland Southeast Asia and beyond, with Java in Indonesia as its currently known southern limit.

Merizocera baoshan Li, sp. nov.

http://zoobank.org/6B67BB8B-DDA0-419D-BCD6-675144ECB22E
Figures 1, 2, 53

Type material. ***Holotype*:** male (IZCAS), Luoshui Cave (25°20.35'N, 98°32.28'E, elevation 1937 m), Jiangdong Mountain, Jiangdong Village, Gudong Town, Tengchong

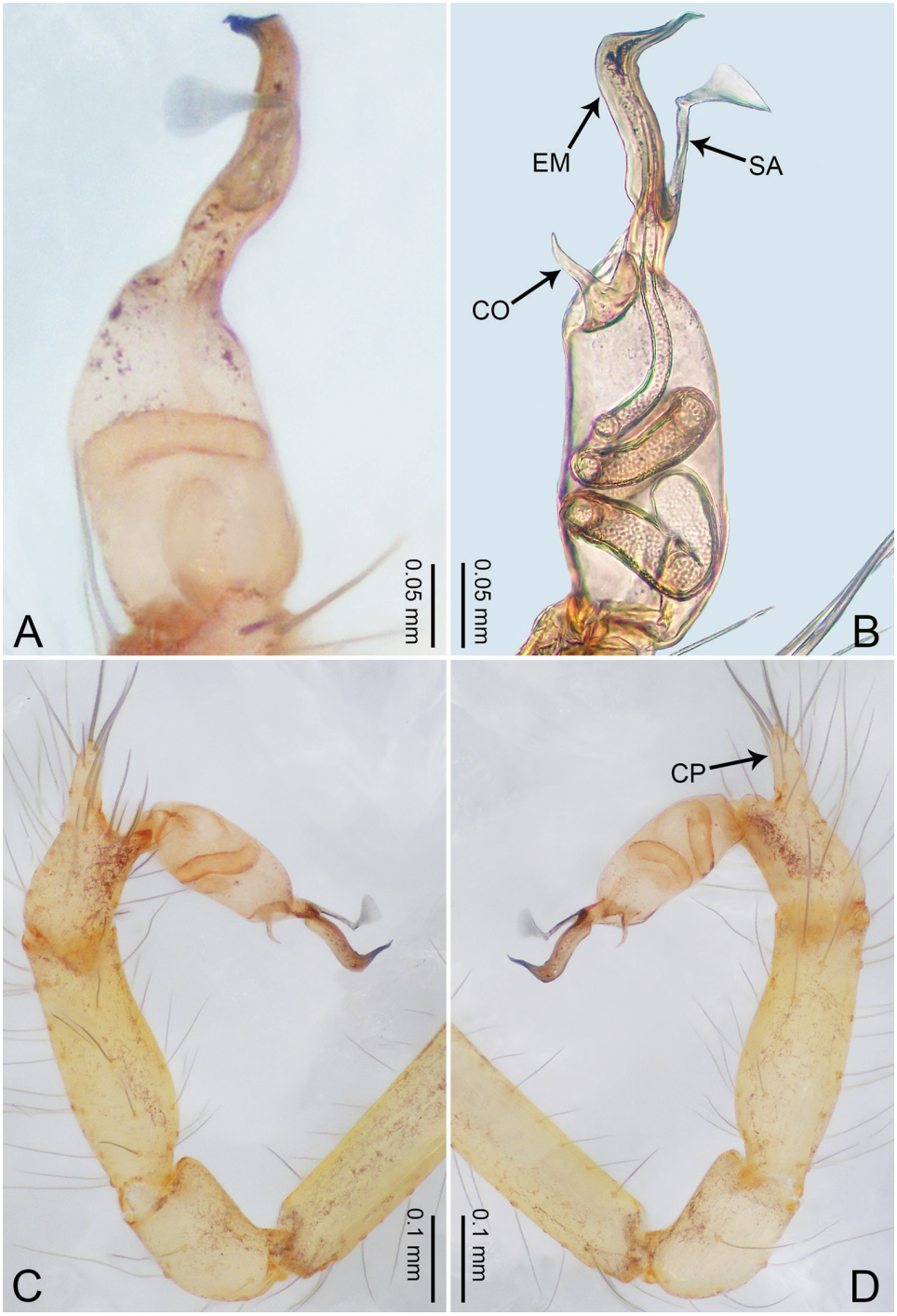

Figure 1. *Merizocera baoshan* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus, SA = stalked apophysis.

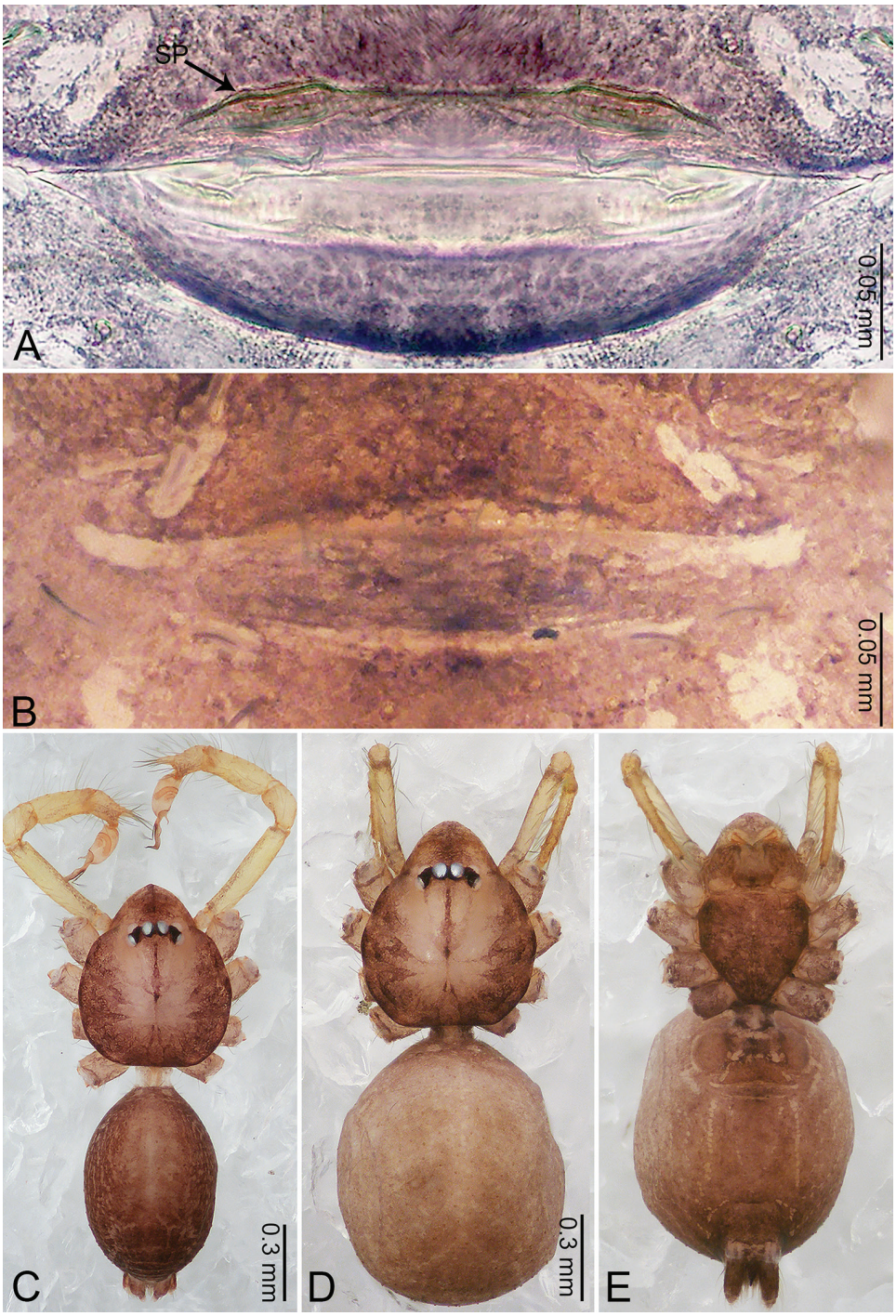

Figure 2. *Merizocera baoshan* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

County, Baoshan, **Yunnan**, **China**, 15 July 2016, Y. Li leg. ***Paratypes*****:** 3 males and 3 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males of *M. baoshan* sp. nov. resemble those of *M. tengchong* sp. nov., but can be distinguished by the pointed and bent tip of the embolus (Fig. 1B) (vs. blunt and upright tip of embolus (Fig. 40B)); a distinct stalked apophysis bearing a pointed distal tip adjacent to the embolus (Fig. 1B) (vs. stalked apophysis bearing globose distal tip (Fig. 40B)); a cymbial protrusion half the length of the tegular (Fig. 1D) (vs. cymbial protrusion 1/4 the length of tegular (Fig. 40D)). The female can be distinguished from congeners by a pair of flattened ovoid spermathecae.

Description. Male (holotype). Total length 1.65; carapace 0.75 long, 0.61 wide; abdomen 0.80 long, 0.55 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median line on anterior half (Fig. 2C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium and sternum dark brown. Abdomen ovoid, dark brown (Fig. 2C). Legs light brown; measurements: I and II missing, III 4.02 (1.13, 0.22, 1.13, 0.98, 0.56), IV 5.70 (1.48, 0.25, 1.70, 1.44, 0.83). Palp (Fig. 1A–D): femur slender, three times longer than patella; patella not swollen; tibia 2/3 length of femur; cymbium with distal protrusion, 1/3 length of femur, length ratio of dorsal protrusion and cymbium 0.57; bulb light brown, elongated pyriform with embolus, conductor and stalked apophysis emerging distally; embolus similar in length and 1/3 the width of tegular, with darkened pointed tip and bent at right angle; conductor tentacle-like, basally attached with embolus; stalked apophysis basally attached with embolus, bearing triangular pointed distal part.

Female (paratype). General features and colouration similar to those of male (Fig. 2D, E). Measurements: total length 1.68; carapace 0.71 long, 0.61 wide; abdomen 0.94 long, 0.80 wide. Leg measurements: I 4.75 (1.24, 0.25, 1.42, 1.14, 0.70), II 3.92 (1.04, 0.25, 1.10, 0.82, 0.61), III 3.27 (0.87, 0.22, 0.88, 0.80, 0.50), IV 4.76 (1.24, 0.24, 1.39, 1.13, 0.76). Epigastric area (Fig. 2B): brown, with a pair of slanting, short, pale brown bands anteriorly, posterior spanned with pale brown horizontal band. Endogyne (Fig. 2A) with pair of connected, flattened, ovoid spermathecae.

Distribution. Known only from the type locality (China; Fig. 53).

Merizocera betong Li, sp. nov.

http://zoobank.org/AC63AF3E-1F1B-4A27-BBE4-0AF87A7D831E
Figures 3, 4, 54

Type material. ***Holotype*****:** male (IZCAS), Ban Bo Nam Ron Village (5°49.96'N, 101°4.08'E, elevation 384 m), Betong District, **Yala**, **Thailand**, 24 October 2015, P. Wongprom leg. ***Paratypes*****:** 1 male and 3 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males of *M. betong* sp. nov. resemble those of *M. ranong* sp. nov. and *M. yuxi* sp. nov., but can be distinguished by the smooth distally arising embolus

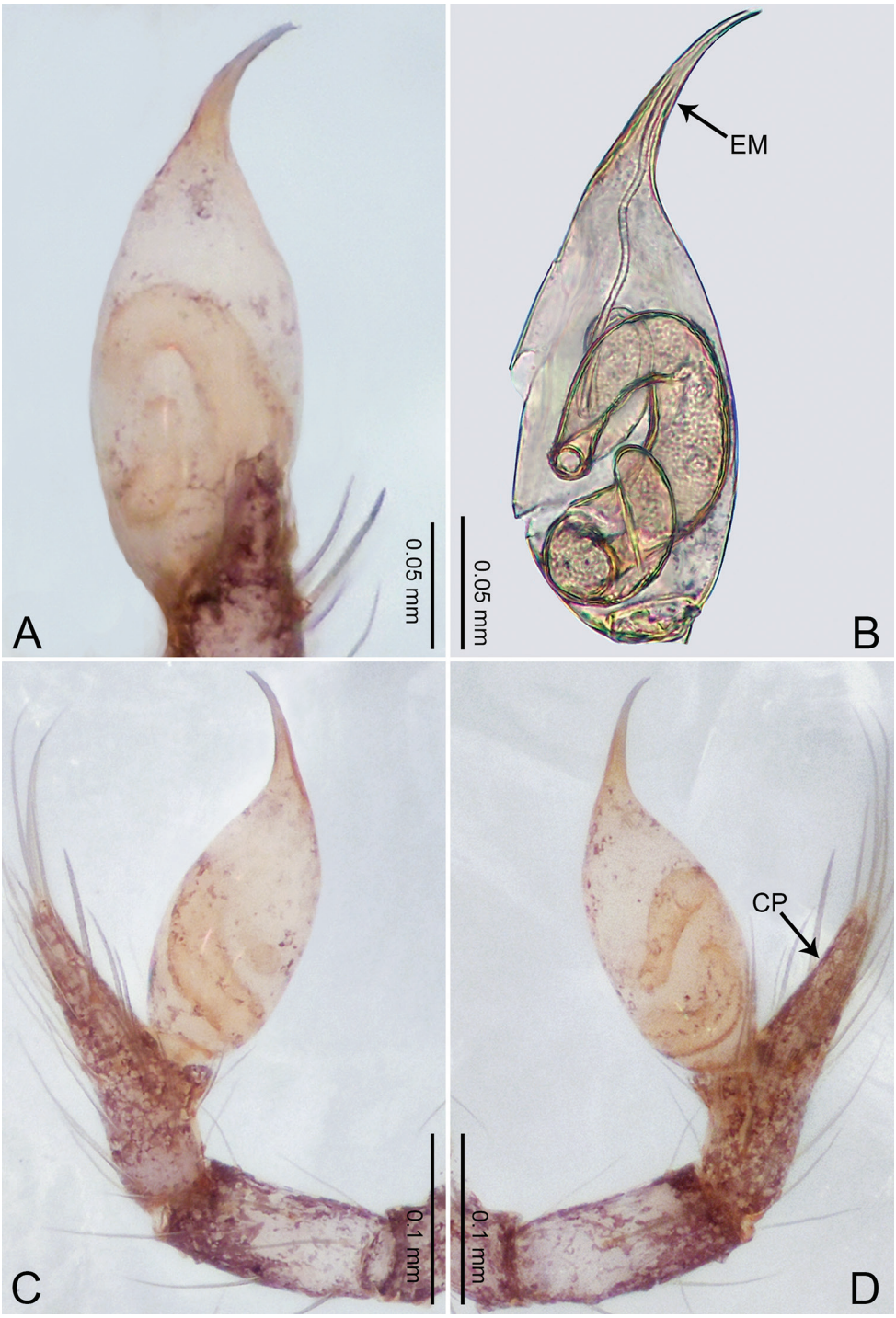

Figure 3. *Merizocera betong* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolatero-dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CP = cymbial protrusion, EM = embolus.

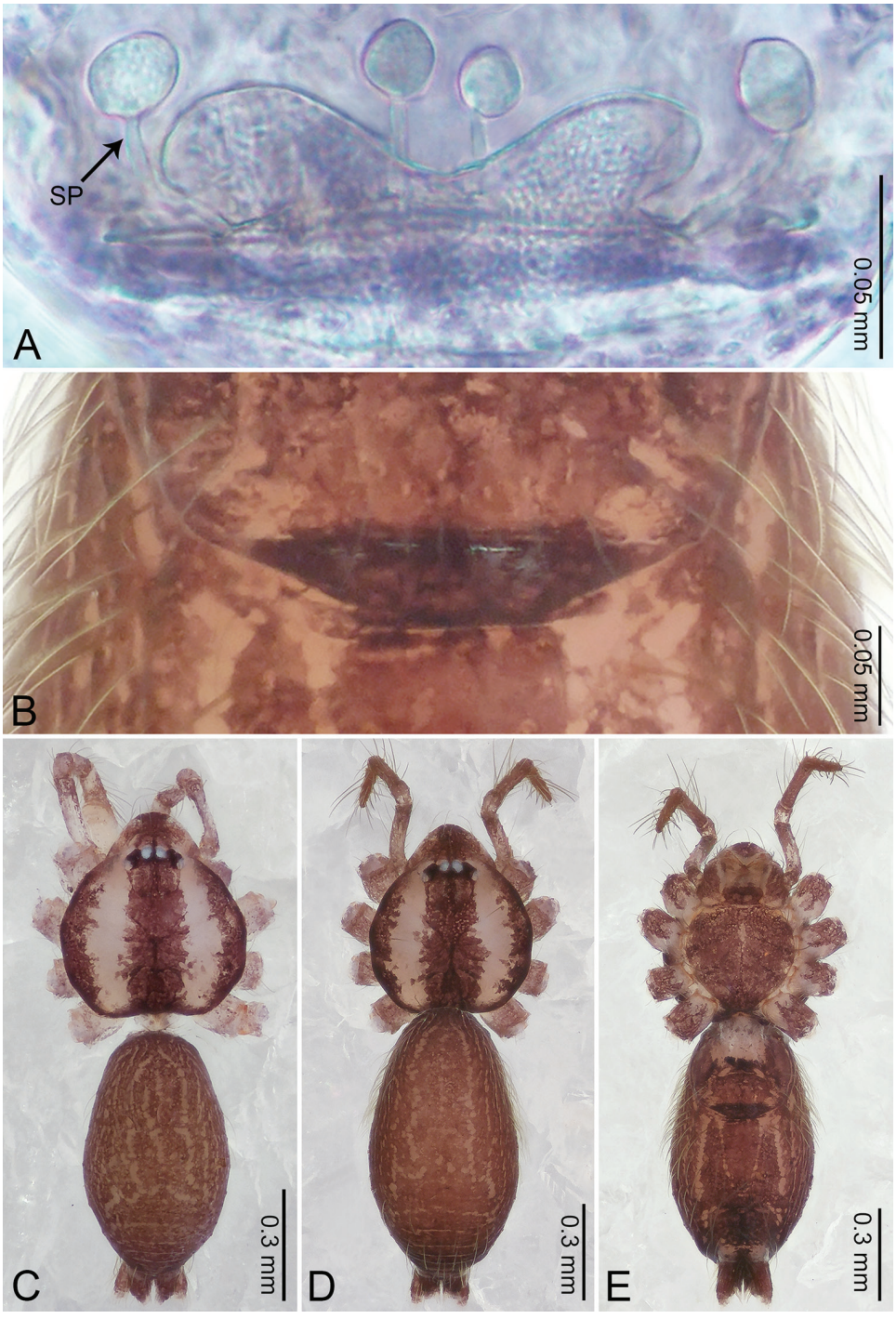

Figure 4. *Merizocera betong* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

(Fig 3B) (vs. the crinkly distally arising embolus in *M. ranong* sp. nov. (Fig. 31B) and *M. yuxi* sp. nov. (Fig. 50B)), slender pyriform bulb (Fig. 3B) (vs. swollen pyriform bulb in *M. ranong* sp. nov. (Fig. 31B) and *M. yuxi* sp. nov. (Fig. 50B)), pointed embolus tip (Fig. 3B) (vs. lamina-like embolus tip in *M. ranong* sp. nov. (Fig. 31B) and flattened tip in *M. yuxi* sp. nov. (Fig. 50B)), embolus stalk 1/2 the length of tegular (Fig. 3B) (vs. embolus stalk 1/3 length of tegular in *M. ranong* sp. nov. (Fig. 31B), and similar in length in *M. yuxi* sp. nov. (Fig. 50B)), cymbial protrusion half the length of tegular in *M. betong* sp. nov. (Fig. 3D) and *M. ranong* sp. nov. (Fig. 31D) (vs. cymbial protrusion similar length with tegular in *M. yuxi* sp. nov. (Fig. 50D)). These species appear similar to those in the *septentrionalis* group of the genus *Psiloderces*, but can be distinguished by the more distinct cymbial protrusion (longer than the bulb or at least half the bulb's length) (vs. cymbial protrusion inconspicuous or shorter than half the length of bulb in *Psiloderces*). The female can be distinguished by having two pairs of stalked spermathecae each bearing a globose distal part (Fig. 4A) (vs. one pair of posteriorly directed tubular spermathecae in *M. ranong* sp. nov. (Fig. 32A) and two pairs of tubular spermathecae in *M. yuxi* sp. nov. (Fig. 51A)).

Description. Male (holotype). Total length 1.33; carapace 0.56 long, 0.51 wide; abdomen 0.71 long, 0.40 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe (Fig. 4C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium, and sternum dark brown. Abdomen slightly elongated, dark brown (Fig. 4E). Legs brown; measurements: I 6.85 (1.84, 0.19, 2.13, 1.86, 0.83), II 5.05 (1.38, 0.19, 1.53, 1.28, 0.67), III 3.79 (1.04, 0.18, 1.11, 0.94, 0.52), IV 5.50 (1.48, 0.18, 1.74, 1.42, 0.68). Palp (Fig. 3A–D): femur slender, three times longer than patella; patella not swollen; tibia half as long as femur; cymbium with distal protrusion, half as long as femur, length ratio of dorsal protrusion and cymbium 1.45; bulb pale yellow, pyriform with embolus arising distally; embolus stalk slightly bent with pointed embolus tip, embolus approx. half the length of tegular.

Female (paratype). General features and colouration similar to those of the male (Fig. 4D, E). Measurements: total length 1.52; carapace 0.61 long, 0.51 wide; abdomen 0.92 long, 0.48 wide. Leg measurements: I 5.09 (1.33, 0.17, 1.60, 1.28, 0.71), II 4.54 (1.23, 0.18, 1.34, 1.13, 0.66), III 3.46 (0.93, 0.18, 0.98, 0.86, 0.51), IV 5.11 (1.31, 0.19, 1.62, 1.28, 0.71). Epigastric area (Fig. 4B) with oval dark brown patch. Endogyne (Fig. 4A) with two pairs of stalked spermathecae, globose distally with medially curved receptacle.

Distribution. Known only from the type locality (Thailand; Fig. 54).

***Merizocera colombo* Li, sp. nov.**

http://zoobank.org/77AD96FF-8BBD-4474-AF0A-0681EB037B41

Figures 5, 6, 52

Type material. *Holotype*: male (IZCAS), Mahawafa Hill (6°55.92'N, 80°14.68'E, elevation 38 m), Mahawafa Village, Avissawella Town, Maniyangama, Colombo District,

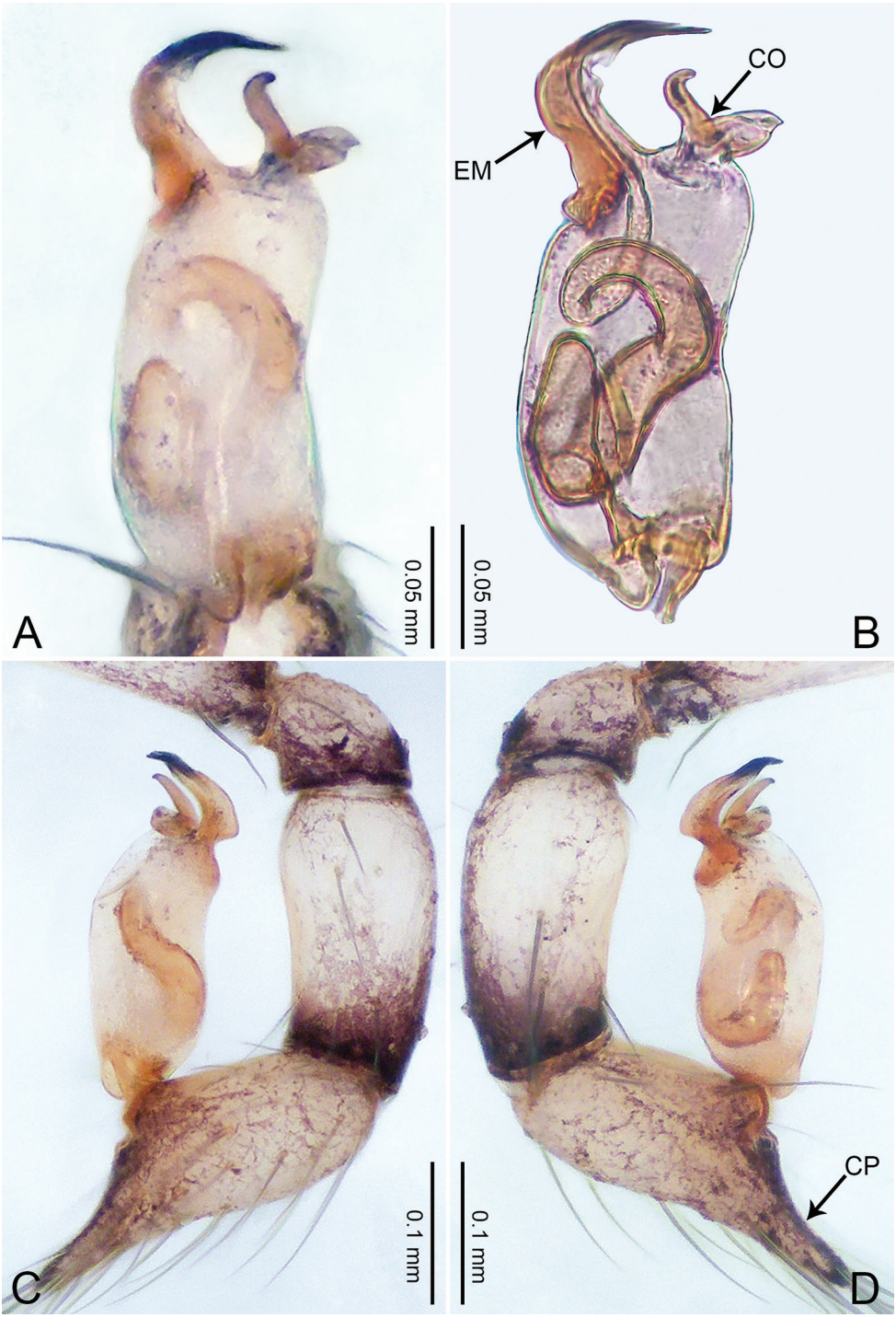

Figure 5. *Merizocera colombo* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

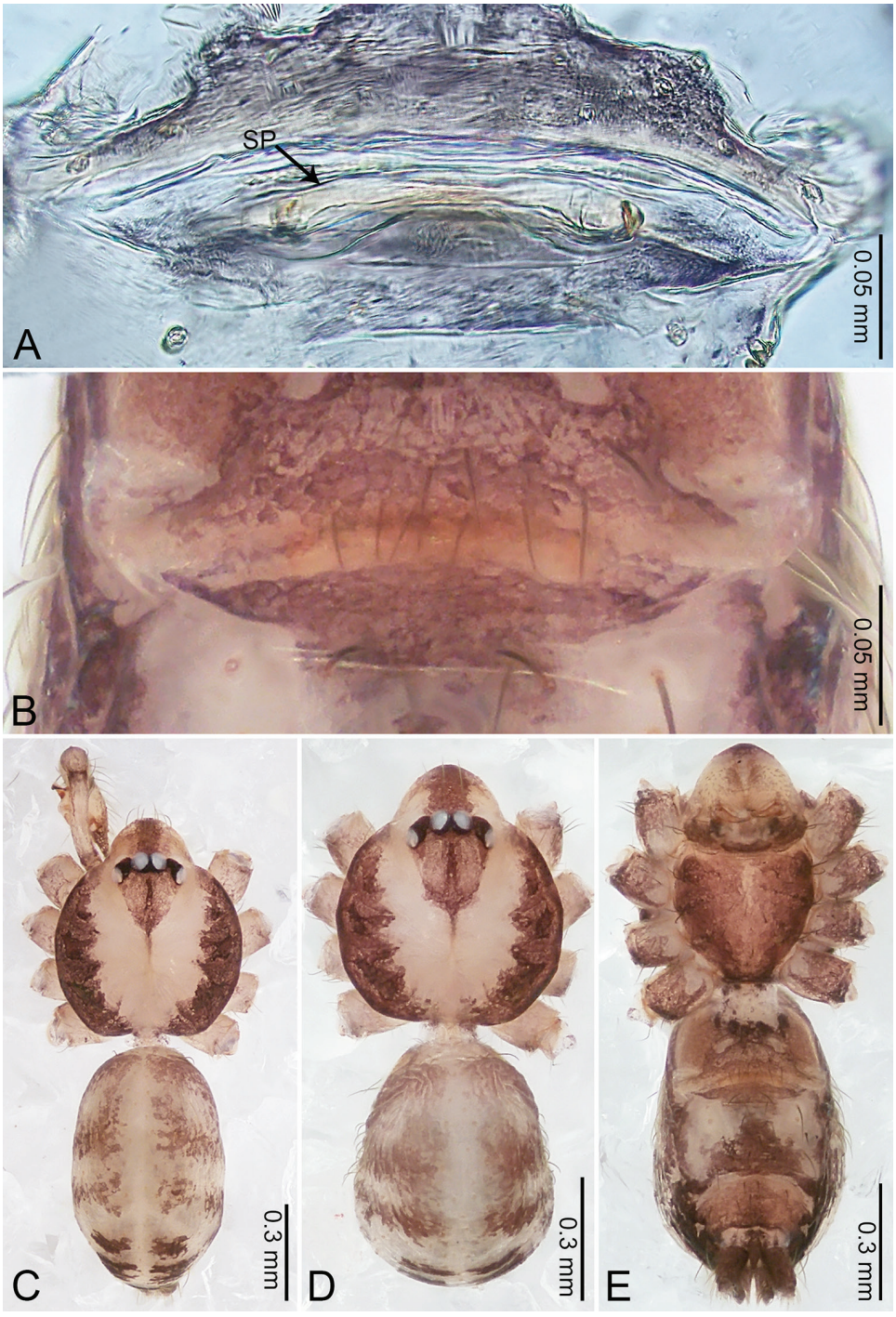

Figure 6. *Merizocera colombo* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

Western Province, **Sri Lanka**, 26 September 2014, S. Kosala leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males of *M. colombo* sp. nov. resemble *M. oryzae*, but can be distinguished by a distinct cymbial protrusion approx. 1/2 length of bulb (Fig. 5D) (vs. inconspicuous cymbial protrusion approx. 1/3 the length of bulb), conductor bifurcate and distinctly shorter than embolus (Fid. 5B) (vs. conductor not bifurcate and almost similar length with embolus). Females can be distinguished by having a pair of elongated spermathecae concaving posteriorly (Fig. 6A).

Description. Male (holotype). Total length 1.48; carapace 0.69 long, 0.59 wide; abdomen 0.75 long, 0.49 wide. Carapace circular, brownish, with dark brown marks laterally and dark median stripe on anterior half (Fig. 6C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium and sternum dark brown. Abdomen slightly elongated, brownish, with dark brown marks dorsally and ventrally (Fig. 6E). Legs light brown; measurements: I 6.07 (1.62, 0.23, 1.80, 1.60, 0.82), II 4.46 (1.20, 0.21, 1.31, 1.13, 0.61), III 3.67 (1.03, 0.20, 1.03, 0.95, 0.46), IV 5.74 (1.48, 0.21, 1.78, 1.50, 0.77). Palp (Fig. 5A–D): femur four times longer than patella; patella not swollen; tibia 2/3 length of femur; cymbium with distal protrusion, half length of femur, length ratio of dorsal protrusion and cymbium 0.76; bulb light brown, slender pyriform-shaped with embolus and conductor arising distally; embolus hooked with pointed tip; conductor bifurcated, one narrower and with slightly hooked tip, adjacent to embolus.

Female (paratype). General features and colouration similar to those of the male (Fig. 6D, E). Measurements: total length 1.28; carapace 0.65 long, 0.56 wide; abdomen 0.59 long, 0.50 wide. Leg measurements: I 4.33 (1.08, 0.21, 1.31, 1.06, 0.67), II 3.36 (0.84, 0.20, 0.93, 0.82, 0.57), III 2.98 (0.78, 0.20, 0.80, 0.75, 0.45), IV 4.39 (1.11, 0.20, 1.31, 1.11, 0.66). Epigastric area (Fig. 6B): dark brown oval patch with light brown slit medially. Endogyne (Fig. 6A) with pair of elongated spermathecae slightly concave toward posterior.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera galle* Li, sp. nov.**

http://zoobank.org/17373A33-AC34-4331-A192-2F6C85188E39

Figures 7, 8, 52

Type material. ***Holotype*:** male (IZCAS), Rumassala Mountain (6°1.48'N, 80°14.55'E, elevation 51 m), Unawatuna Village, Galle District, **Southern Province**, **Sri Lanka**, 12–13 October 2014, S. Kosala leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males can be distinguished from congeners by the distinctly longer (longer than tegular) and bent embolus (Fig. 7B); from *M. ratnapura* sp. nov.

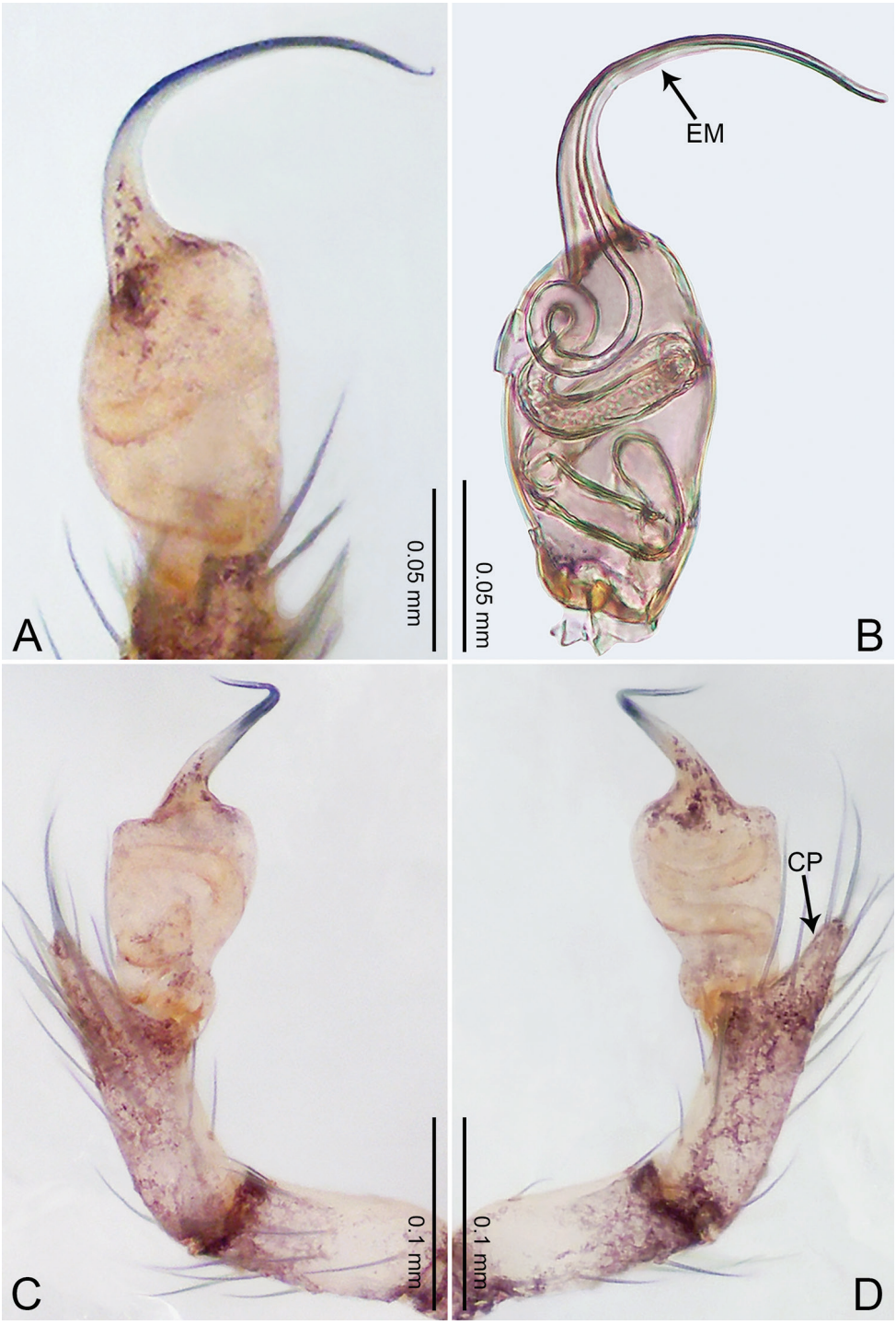

Figure 7. *Merizocera galle* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CP = cymbial protrusion, EM = embolus.

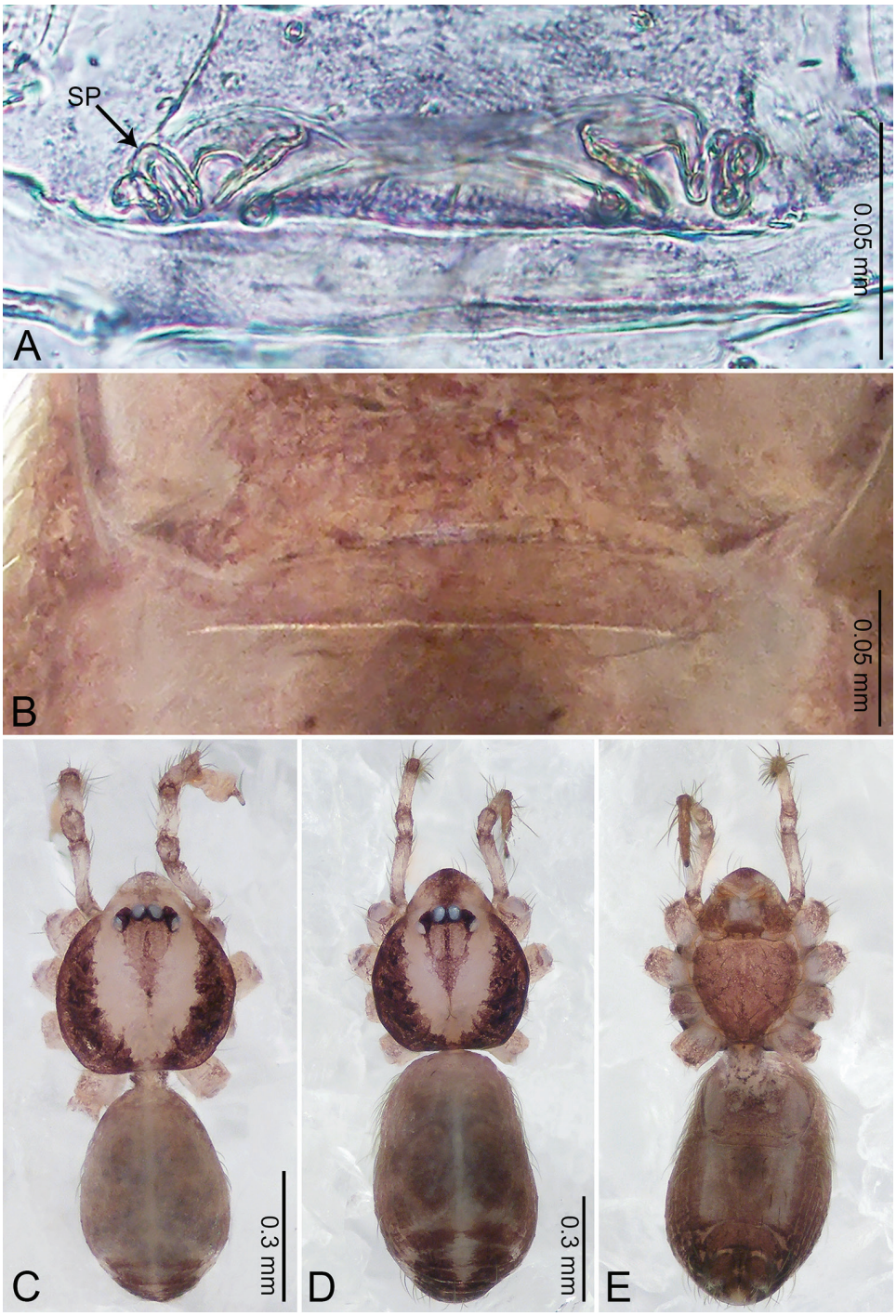

Figure 8. *Merizocera galle* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

(Fig. 33B), *M. phuket* sp. nov. (Fig. 27B), and *M. hponkanrazi* sp. nov. (Fig. 9B) by the absence of conductor (vs. presence of distinct conductor projected from the base of embolus). The females can be distinguished by a pair of horizontally twisted spermathecae (Fig. 8A).

Description. Male (holotype). Total length 1.00; carapace 0.48 long, 0.42 wide; abdomen 0.51 long, 0.36 wide. Carapace circular, brownish, with dark brown marks laterally and brown median stripe on anterior half (Fig. 8C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium and sternum dark brown. Abdomen slightly elongated, dark grey, with dark marks posteriorly and ventrally. Legs brown; measurements: I 3.73 (1.00, 0.17, 1.13, 0.90, 0.53), II 2.98 (0.79, 0.16, 0.85, 0.72, 0.46), III 2.49 (0.70, 0.13, 0.67, 0.63, 0.36), IV 3.74 (0.98, 0.16, 1.13, 0.96, 0.51). Palp (Fig. 7A–D): femur slender, thrice longer than patella; patella not swollen; tibia similar length as femur; cymbium with distal protrusion, half length of femur, length ratio of dorsal protrusion and cymbium 0.54; bulb pale yellow, pyriform with embolus arising distally, conductor absent; embolus distinctly elongated and bent, 1.5 times longer than the tegular.

Female (paratype). General features and colouration similar to those of male (Fig. 8D, E). Measurements: total length 1.24; carapace 0.53 long, 0.45 wide; abdomen 0.70 long, 0.48 wide. Leg measurements: I 3.62 (0.94, 0.17, 1.08, 0.89, 0.54), II 3.03 (0.78, 0.17, 0.87, 0.73, 0.48), III missing, IV 3.70 (0.95, 0.16, 1.13, 0.92, 0.54). Epigastric area (Fig. 8B): brown, lanceolate patch. Endogyne (Fig. 8A) with pair of horizontally twisted spermathecae, ratio of the width of twisted spermatheca and the interdistance of spermathecae 1:4.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera hponkanrazi* Li, sp. nov.**

http://zoobank.org/6059ACD5-748E-4F8B-B8A0-6EB09F36BFF0

Figures 9, 10, 53

Type material. ***Holotype*:** male (IZCAS), Roadside between Camp 2 and Camp 3 (27°37.15'N, 96°58.92'E, elevation 2806 m), Hponkanrazi Wildlife Sanctuary, Putao, **Kachin State**, **Myanmar**, 16 December 2016, J. Wu leg.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble *M. krabi* sp. nov. but can be distinguished by the embolus longer than the tegular (Fig. 9B) (vs. embolus length half the tegular (Fig. 17B)), presence of notch at tegular tip (Fig. 9A) (vs. absence of notch), bulb shortened pyriform (vs. elongated pyriform bulb).

Description. Male (holotype). Total length 1.56; carapace 0.71 long, 0.62 wide; abdomen 0.85 long, 0.71 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 10A). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium and sternum dark brown. Abdomen ovoid, dark brown (Fig. 10B). Legs brown; measurements: I 5.43 (1.44, 0.25, 1.66, 1.33, 0.75), II 4.65 (1.28, 0.24, 1.41, 1.11,

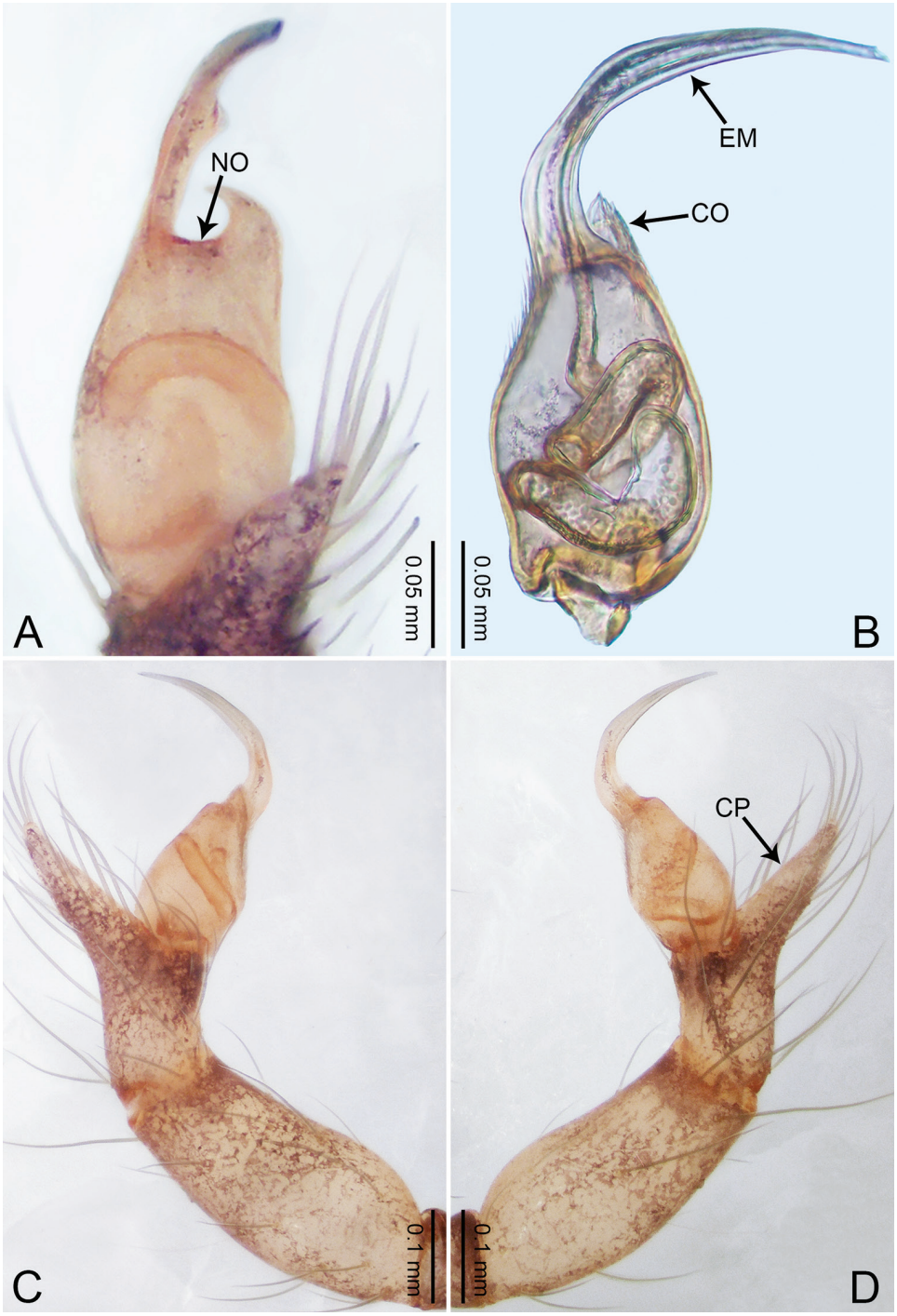

Figure 9. *Merizocera hponkanrazi* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolatero-dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus, NO = notch.

Figure 10. *Merizocera hponkanrazi* sp. nov., holotype male. **A** Habitus, dorsal view **B** habitus, ventral view.

0.61), III 3.46 (0.95, 0.20, 0.92, 0.85, 0.54), IV 4.83 (1.25, 0.22, 1.42, 1.21, 0.73). Palp (Fig. 9A–D): tibia swollen proximally; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 1.13; bulb brown, pyriform, with embolus and conductor arising distally; embolus distinctly bent and 1.2 times longer than tegular; conductor with pointed tip, 1/6 length of embolus, adjacent to a notch.

Female. Unknown.

Distribution. Known only from the type locality (Myanmar; Fig. 53).

***Merizocera kachin* Li, sp. nov.**

http://zoobank.org/17A235EF-2414-43F7-97AC-5AD66FC8314A

Figures 11, 12, 53

Type material. ***Holotype*:** male (IZCAS), Roadside between Nahteukhu and BaAve (27°18.00'N, 97°23.27'E, elevation 535 m), Putao, **Kachin State**, **Myanmar**, 8 December 2016, J. Wu leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble *M. putao* sp. nov. but can be distinguished by the absence of a pit on the bulb (vs. presence of a distinct pit resulting from the basal con-

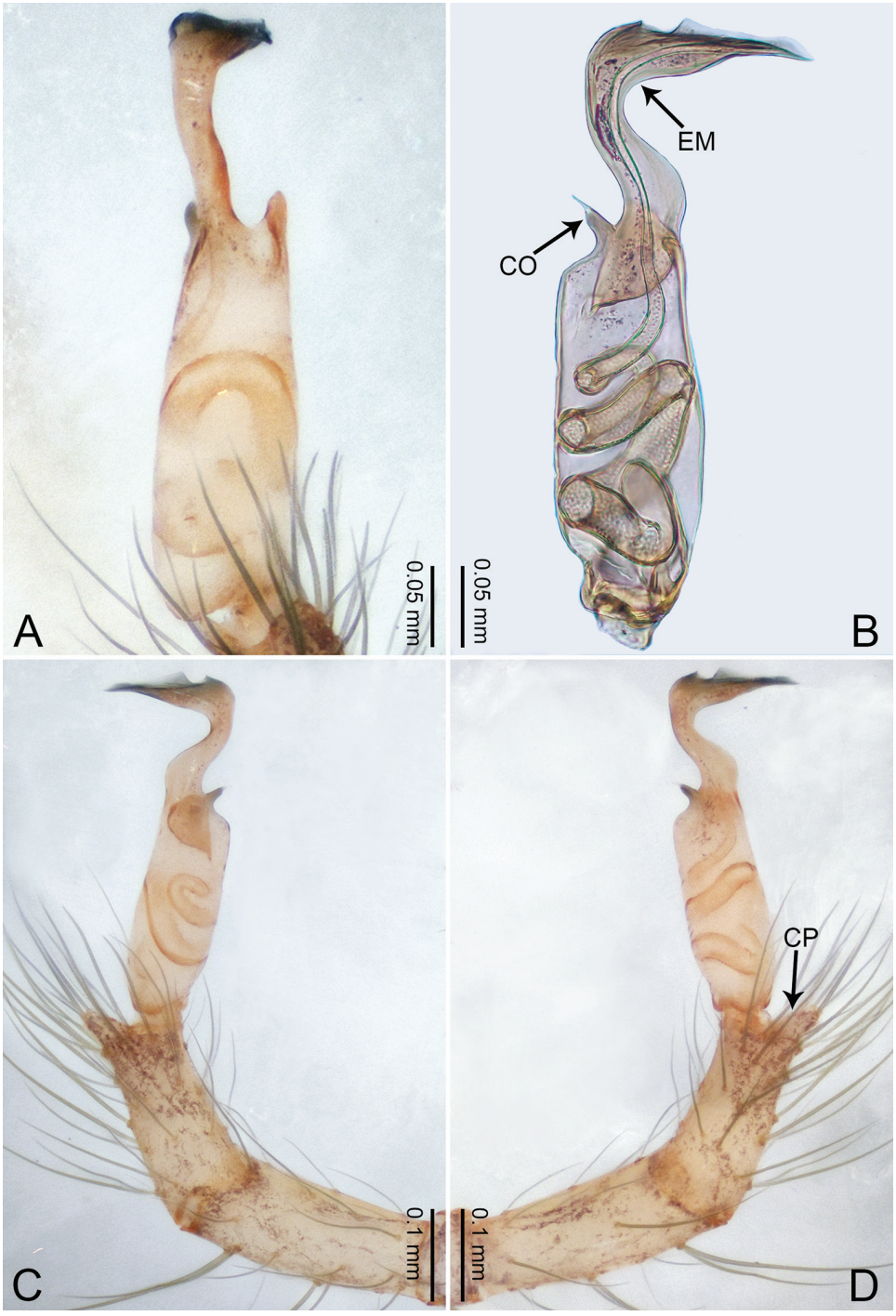

Figure 11. *Merizocera kachin* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

Figure 12. *Merizocera kachin* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviations: OB = ovoid body, PT = clypeal protrusion, SP = spermatheca.

nection of embolus and conductor (Fig. 29B)), presence of a relatively short clypeal protrusion (Fig. 12C) (vs. relatively long clypeal protrusion (Fig. 30C). The females can be distinguished by a pair of conically tipped spermathecae (Fig. 12A) (vs. spermathecae each with a rounded tip (Fig. 30A)).

Description. Male (holotype). Total length 1.44; carapace 0.67 long, 0.56 wide; abdomen 0.79 long, 0.74 wide. Carapace circular, brownish, with dark brown radiating marks (Fig. 12C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with small protrusion provided with long setae. Labium dark brown. Sternum dark brown, with distinct dark radiating lines. Abdomen ovoid, dark grey (Fig. 12C). Legs light brown; measurements: I 6.87 (1.86, 0.21, 2.10, 1.92, 0.78), II 5.25 (1.44, 0.20, 1.60, 1.38, 0.63), III 3.85 (1.05, 0.19, 1.10, 1.00, 0.51), IV 5.58 (1.45, 0.21, 1.72, 1.45, 0.75). Palp (Fig. 11A–D): femur slender, four times longer than patella; patella not swollen; tibia half length of femur; cymbium with distal protrusion, half length of femur, length ratio of dorsal elongation and cymbium 0.28; bulb pale yellow, elongated pyriform with embolus and conductor arising distally; embolus hooked, almost similar in length with tegular, with pointed tip, width of anterior horizontal hooked part half width of tegular; conductor short with pointed tip, basally connected with embolus.

Female (paratype). General features and colouration similar to those of male except for the absence of clypeus protrusion (Fig. 12D, E). Measurements: total length 1.25; carapace 0.58 long, 0.49 wide; abdomen 0.69 long, 0.57 wide. Leg measurements: I 3.52 (0.89, 0.19, 1.06, 0.85, 0.53), II 2.95 (0.75, 0.19, 0.85, 0.70, 0.46), III 2.41 (0.63, 0.16, 0.63, 0.59, 0.40), IV 3.49 (0.87, 0.18, 1.05, 0.83, 0.56). Epigastric area (Fig. 12B): brown semi-circular patch with pale slit medially. Endogyne (Fig. 12A) with a pair of spermathecae each with a conical tip, posteriorly with a pair of ovoid bodies, ratio of the width of conical tip spermathecae to the interdistance of spermathecae 1:7.

Distribution. Known only from the type locality (Myanmar; Fig. 53).

***Merizocera kandy* Li, sp. nov.**

http://zoobank.org/6D7BEBE2-66DE-4F46-BBF3-A0212C24E21D

Figures 13, 14, 52

Type material. ***Holotype*:** male (IZCAS), Koththol Lena (= cave) (6°54.22'N, 80°29.88'E, elevation 669 m), Abagamuwa Division, Maskeliya Oya Village, Maskeliya, Adam's Peak Area, Kandy District, **Central Province**, **Sri Lanka**, 6 October 2014, S. Kosala leg. ***Paratypes*:** 1 male and 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males can be distinguished from other congeners by the blunt bifurcate embolus tip, two similar components of conductor, and swollen bulb with a notch anteriorly (Fig. 13B). The females can be distinguished by a pair of angular shaped tubular spermathecae (Fig. 14A).

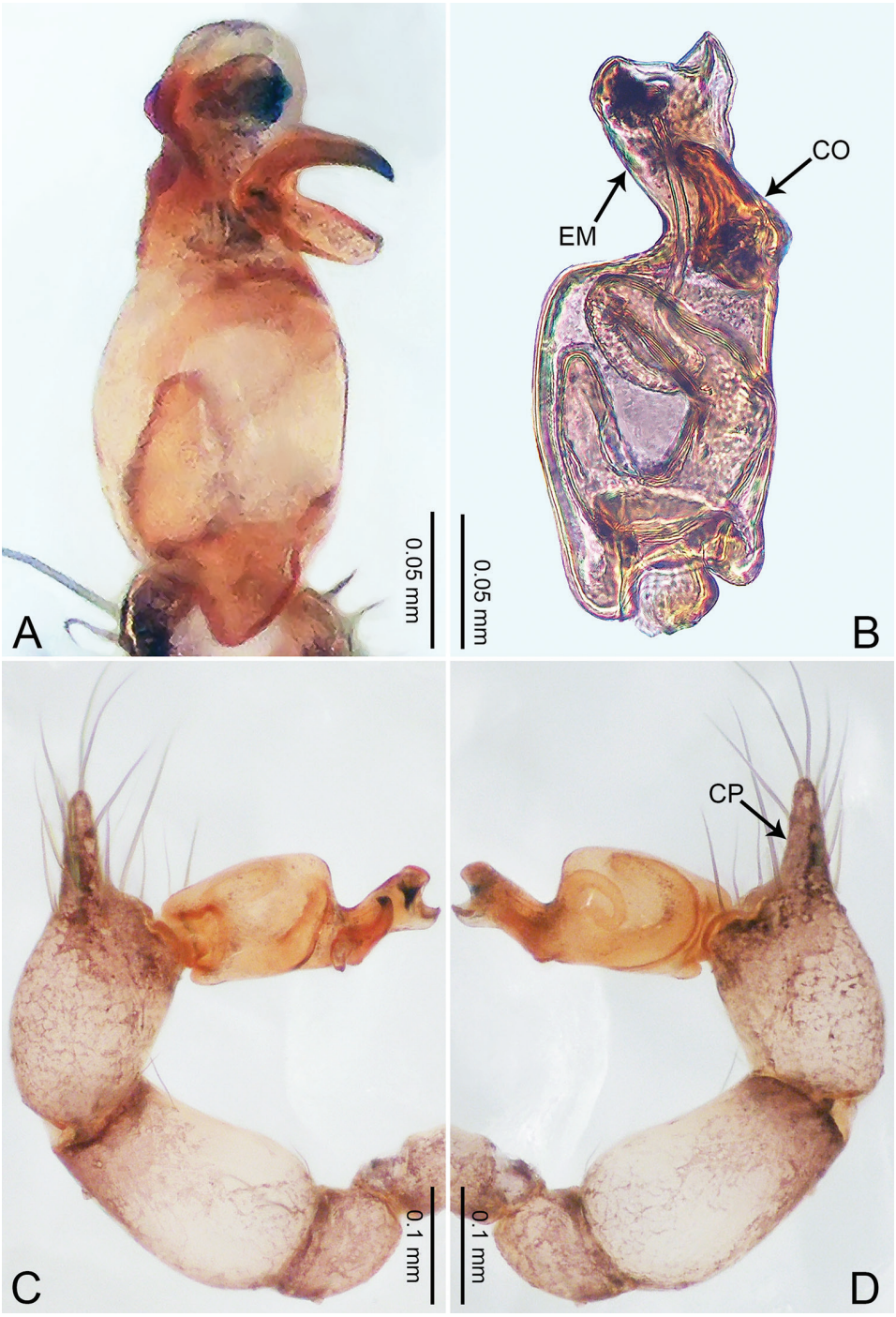

Figure 13. *Merizocera kandy* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, prolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

Figure 14. *Merizocera kandy* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

Description. Male (holotype). Total length 1.33; carapace 0.63 long, 0.54 wide; abdomen 0.63 long, 0.56 wide. Carapace rounded, brownish, with dark brown marks laterally and dark median stripe on anterior half (Fig. 14C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish with dark brown marks medially. Labium dark brown. Sternum dark brown with distinct dark radiating lines. Abdomen ovoid, brownish, with dark brown marks dorsally and ventrally. Legs brown; measurements: I 6.48 (1.70, 0.19, 1.96, 1.76, 0.87), II 4.51 (1.19, 0.20, 1.30, 1.18, 0.64), III 3.66 (0.98, 0.20, 1.05, 0.96, 0.47), IV missing. Palp (Fig. 13A–D): femur slender, thrice longer than patella, patella not swollen; tibia swollen, twice wider than and almost similar in length to femur; cymbium with distal protrusion, half as long as femur, length ratio of dorsal elongation and cymbium 0.59; bulb brown, with embolus and conductor arising distally, tegular with a notch anteriorly; embolus bifurcated with blunt tips, two similar components of conductor resemble a C-shape attached adjacent to embolus.

Female (paratype). General features and colouration similar to those of male (Fig. 14D, E). Measurements: total length 1.39; carapace 0.65 long, 0.56 wide; abdomen 0.72 long, 0.61 wide. Leg measurements: I missing, II 3.46 (0.90, 0.19, 0.99, 0.85, 0.53), III 2.96 (0.76, 0.19, 0.81, 0.75, 0.45), IV 4.40 (1.10, 0.20, 1.30, 1.14, 0.66). Epigastric area (Fig. 14B): elliptical dark brown patch. Endogyne (Fig. 14A) with a pair sloped tubular spermathecae, medially with vertical spiral ducts.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera mandai* Li, sp. nov.**

http://zoobank.org/F8BB7D25-0E42-443C-A087-F16B0C4CB036

Figures 15, 16, 54

Merizocera sp. 279: Li and Li 2018 (molecular data).

Type material. ***Holotype*:** male (IZCAS), near Mandai Agrotechnology Park (1°24.90'N, 103°47.94'E, elevation 46 m), Central Catchment Nature Reserve, **Singapore**, 1 September 2015, S. Li and Y. Tong leg. ***Paratypes*:** 2 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition. Mandai is an important biodiversity conservation area in Singapore.

Diagnosis. Males resemble *M. salawa* sp. nov. but can be distinguished by strongly swollen palpal tibia (Fig. 15D) (vs. palpal tibia not swollen (Fig. 35D)), presence of swollen embolus base (Fig. 15B) (vs. normal embolus base (Fig. 35B)), conductor tip not divided (Fig. 15B) (vs. bifurcate (Fig. 35B)), bulb with a notch (Fig. 15B) (vs. without notch (Fig. 35B)). The females can be distinguished by a pair of slight twisted, stalked spermathecae each bearing a globose distal part, directed downwards (Fig. 16A).

Description. Male (holotype). Total length 1.41; carapace 0.62 long, 0.59 wide; abdomen 0.76 long, 0.54 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe (Fig. 16C). Fovea shallow. Thoracic region dis-

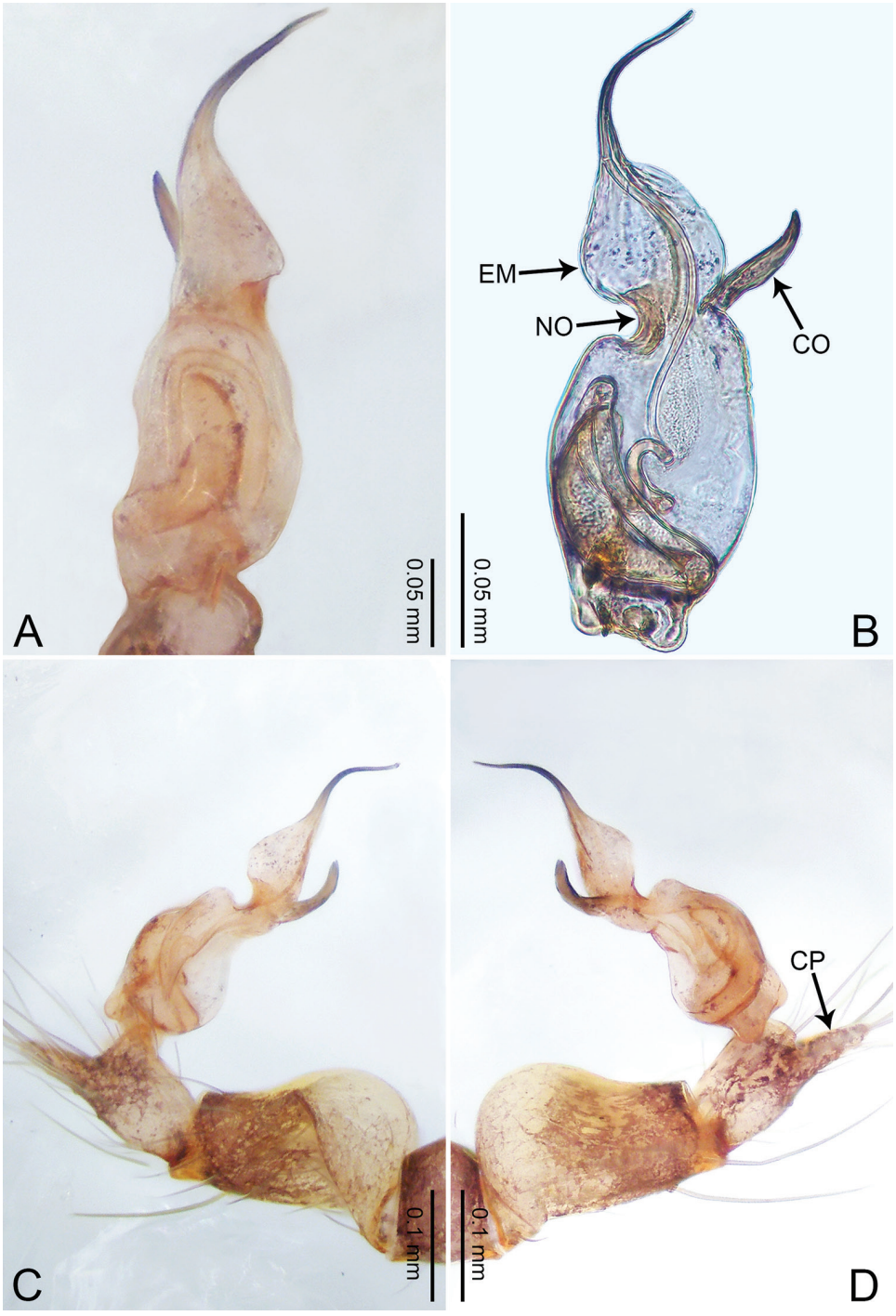

Figure 15. *Merizocera mandai* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, prolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus, NO = notch.

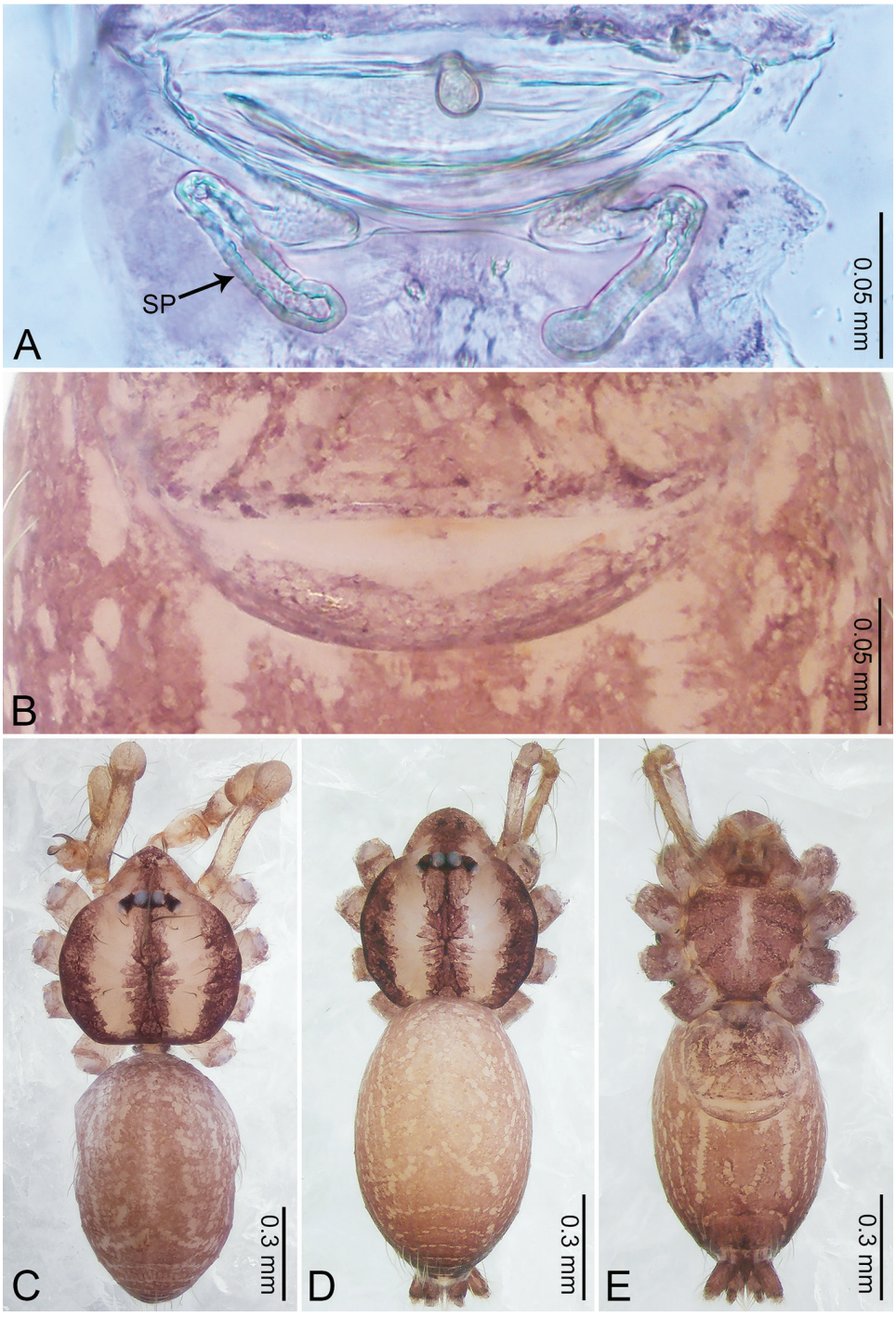

Figure 16. *Merizocera mandai* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

tinctly elevated medially. Clypeus and labium dark brown. Sternum dark brown but lighter medially, with dark radiating lines. Abdomen slightly elongated, dark brown. Legs brown; measurements: I and II missing, III 4.09 (1.11, 0.19, 1.24, 1.05, 0.50), IV 6.30 (1.64, 0.20, 1.94, 1.68, 0.84). Palp (Fig. 15A–D): femur slender, thrice longer than patella, patella not swollen; tibia swollen proximally, half as long as femur; cymbium with distal protrusion, 1/3 femur length, length ratio of dorsal elongation and cymbium 0.67; bulb pale yellow, embolus and conductor arising distally, tegular with a notch anteriorly; embolus basally swollen, swollen part occupies half length of embolus and almost half width of bulb; conductor basally connected with embolus, tentacle-like, 1/3 length of embolus.

Female (paratype). General features and colouration similar to those of male (Fig. 16D, E). Measurements: total length 1.41; carapace 0.58 long, 0.51 wide; abdomen 0.84 long, 0.51 wide. Leg measurements: I and IV missing, II 3.97 (1.05, 0.19, 1.14, 1.00, 0.59), III 3.10 (0.83, 0.18, 0.82, 0.79, 0.48). Epigastric area (Fig. 16B): brown crescent-shaped patch. Endogyne (Fig. 16A) with a pair of slightly twisted stalked spermathecae, bearing globose distal ends pointed posteriorly, anterior-medially with a spherical structure.

Distribution. Known only from the type locality (Singapore; Fig. 54).

***Merizocera krabi* Li, sp. nov.**

http://zoobank.org/6EDA6125-F3EF-4D4D-AF5C-F78E2301B303

Figures 17, 18, 54

Merizocera sp. 185: Li and Li 2018 (molecular data).

Type material. ***Holotype*:** male (IZCAS), Ban Chong Plee Village (8°5.12'N, 98°51.22'E, elevation 442 m), Muang District, **Krabi**, **Thailand**, 25 October 2014, P. Wongprom leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males are discussed under *M. hponkanrazi* sp. nov. Males can be distinguished by an elongated pyriform bulb with a triangular conductor adjacent to the base of the embolus (Fig. 17D), embolus approx. half as long as the tegulum. The females can be distinguished from congeners by two pairs of twisted stalked spermathecae bearing globose distal ends (Fig. 18A).

Description. Male (holotype). Total length 1.44; carapace 0.72 long, 0.63 wide; abdomen 0.72 long, 0.48 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 18C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus and labium dark brown. Sternum dark brown, with dark radiating lines. Abdomen slightly elongated, dark brown. Legs brown; measurements: I and IV missing, II 6.50 (1.84, 0.23, 2.00, 1.68, 0.75), III 4.83 (1.39, 0.23, 1.47, 1.19, 0.55). Palp (Fig. 17A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen; cymbium with

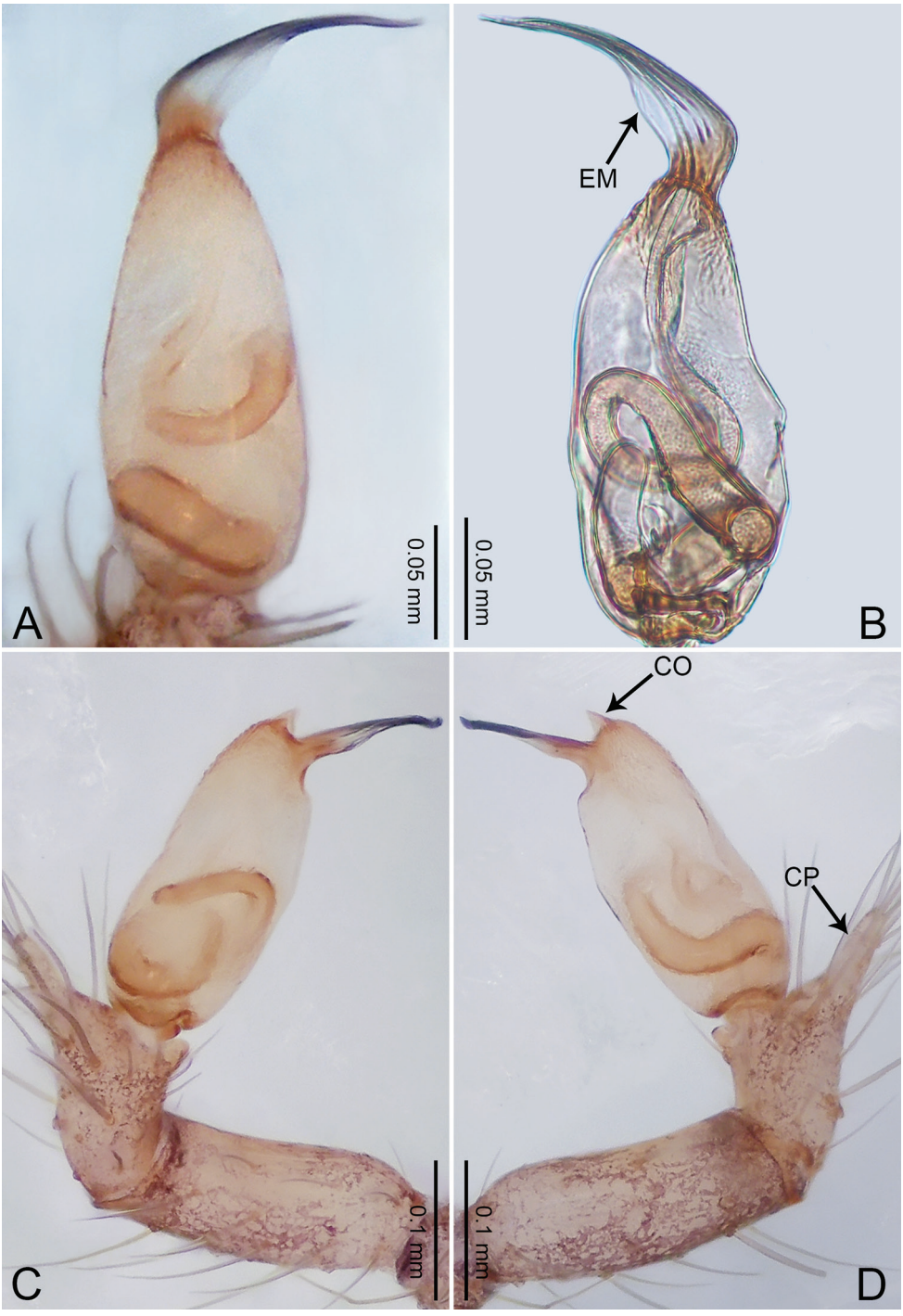

Figure 17. *Merizocera krabi* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

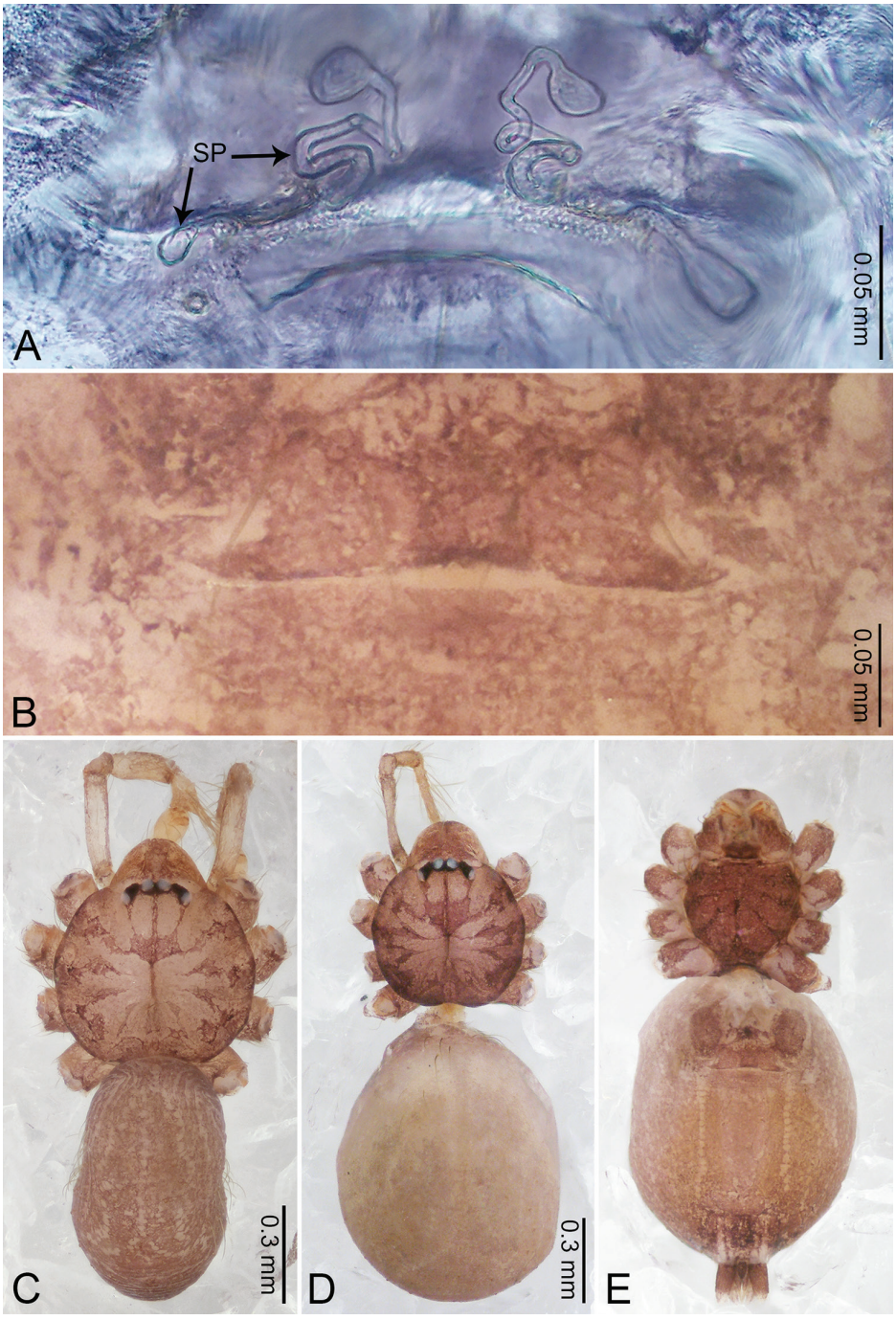

Figure 18. *Merizocera krabi* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

distal protrusion, 1/3 femur length, length ratio of dorsal elongation and cymbium 0.88; bulb pale yellow, elongated pyriform-shaped with embolus and conductor arising distally; embolus bent with laminar base, laminar part 1/2 length of embolus, entire embolus 1/2 length of tegular; conductor triangular, adjacent to embolus, 1/5 length of embolus.

Female (paratype). General features and colouration similar to those of male (Fig. 18D, E). Measurements: total length 1.70; carapace 0.67 long, 0.54 wide; abdomen 0.98 long, 0.82 wide. Leg measurements: I 5.44 (1.44, 0.19, 1.66, 1.38, 0.77), II missing, III 3.43 (0.90, 0.19, 1.00, 0.83, 0.51), IV 4.89 (1.28, 0.19, 1.48, 1.25, 0.69). Epigastric area (Fig. 18B): dark brown, semi-circular. Endogyne (Fig. 18A) with two pairs of twisted stalked spermathecae with globose distal ends, lateral pairs almost horizontal, median pairs upright.

Distribution. Known only from the type locality (Thailand; Fig. 54).

***Merizocera kurunegala* Li, sp. nov.**

http://zoobank.org/B7C22440-1A06-4347-9F4E-900002716789

Figures 19, 20, 52

Type material. ***Holotype*:** male (IZCAS), near Arankele Cave (7°38.42'N, 80°25.33'E, elevation 114 m), Kubukwewa Village, Hiripitiya, Kurunegala District, **Northwestern Province**, **Sri Lanka**, 11 October 2014, S. Kosala leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble *M. peraderiya* sp. nov. and *M. picturata* but can be distinguished by a relatively shorter bulb (Fig. 19B) (1/2 length of that in *M. peraderiya* sp. nov. (Fig. 25B) and *M. picturata*), an evenly bent embolus in *M. kurunegala* sp. nov. (Fig. 19B) and *M. picturata* (vs. an angularly bent embolus in *M. peraderiya* sp. nov. (Fig. 25B)), furcate conductor in *M. kurunegala* sp. nov. (Fig. 19B) and *M. peraderiya* sp. nov. (Fig. 25B) (vs. conductor not furcate in *M. picturata*), conductor arising medially in *M. picturata* (vs. conductor not arising medially in *M. kurunegala* sp. nov. (Fig. 19B) and *M. peraderiya* sp. nov. (Fig. 25B)). The females can be distinguished by having sessile wavy spermathecae in *M. kurunegala* sp. nov. (Fig. 20A) and *M. picturata* (vs. a pair of S-shaped spermathecae in *M. peraderiya* sp. nov. (Fig. 26A)).

Description. Male (holotype). Total length 1.33; carapace 0.67 long, 0.53 wide; abdomen 0.65 long, 0.49 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 20C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium and sternum dark brown. Abdomen ovoid, dark grey, with dark brown marks dorsally and ventrally. Legs brown; measurements: I 7.14 (1.94, 0.22, 2.20, 1.96, 0.82), II missing, III 3.66 (1.03, 0.19, 1.05, 0.95, 0.44), IV 5.87 (1.53, 0.19, 1.80, 1.62, 0.73). Palp (Fig. 19A–D): femur slender, thrice longer than patella,

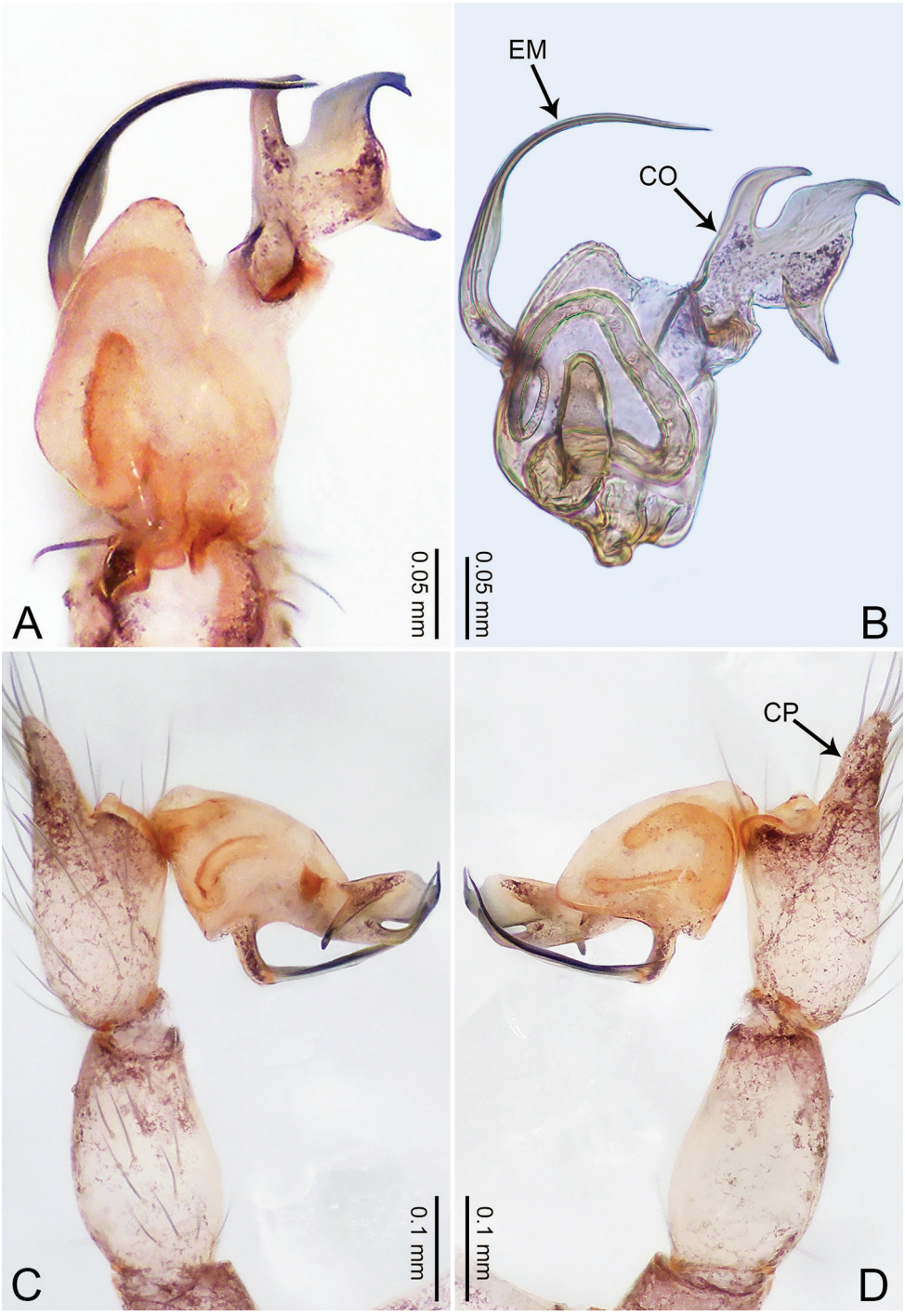

Figure 19. *Merizocera kurunegala* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

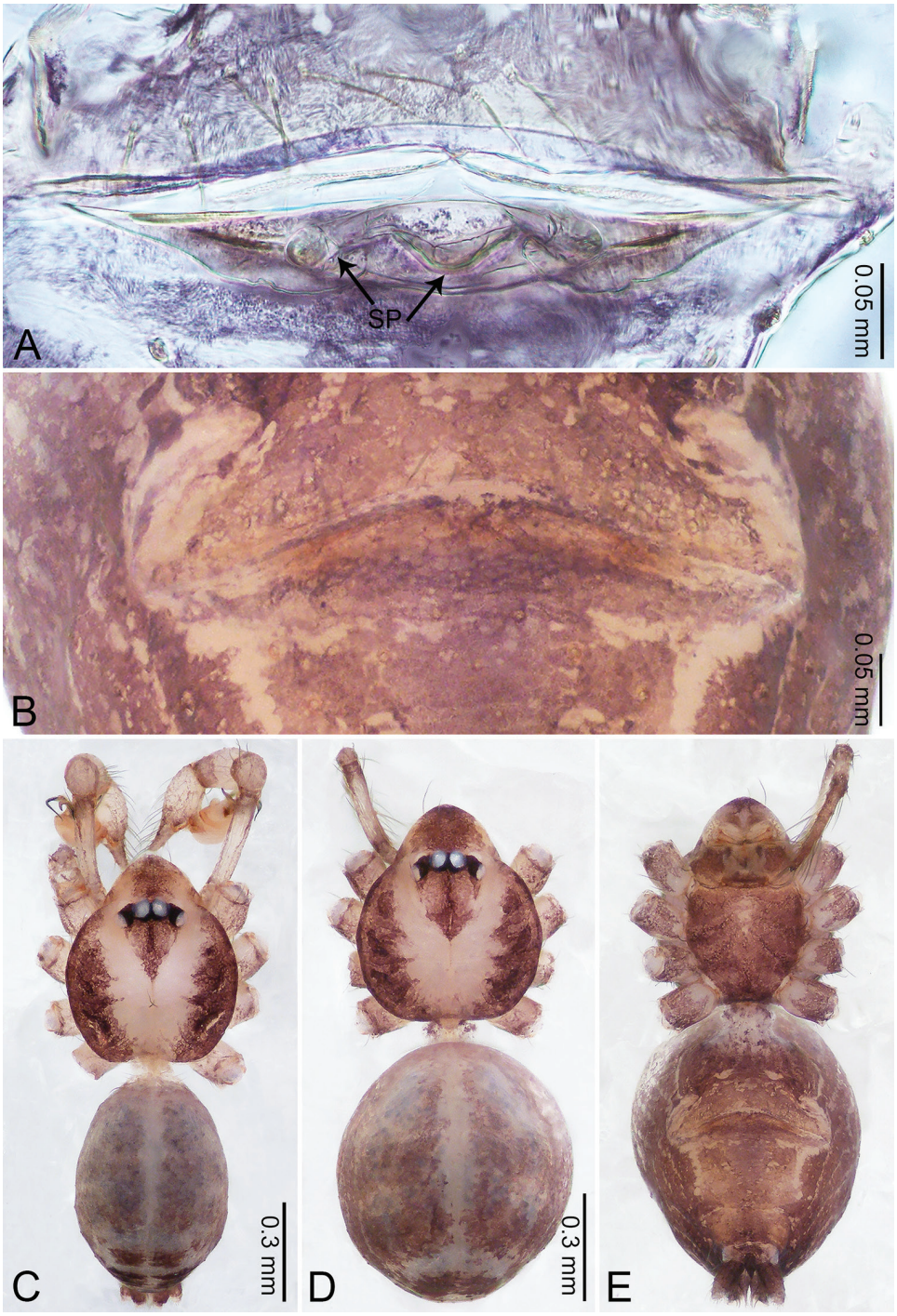

Figure 20. *Merizocera kurunegala* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

patella not swollen; tibia slightly swollen proximally, twice wider and half length of femur; cymbium with distal protrusion, half length of femur, length ratio of dorsal elongation and cymbium 0.64; bulb pale yellow; embolus dark, evenly bent, twice as long as bulb; conductor trifurcate with two pointed upwards, and third pointed downwards, stem of conductor thrice wider than that of embolus.

Female (paratype). General features and colouration similar to those of male (Fig. 20D, E). Measurements: total length 1.41; carapace 0.62 long, 0.53 wide; abdomen 0.76 long, 0.67 wide. Leg measurements: I 3.99 (1.00, 0.19, 1.20, 0.98, 0.62), II 3.11 (0.82, 0.19, 0.87, 0.75, 0.48), III missing, IV 3.84 (0.98, 0.18, 1.11, 0.99, 0.58). Epigastric area (Fig. 20B): dark brown nearly trapezoidal patch. Endogyne (Fig. 20A) with a pair of wavy spermathecae with globose distal ends.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera lincang* Li, sp. nov.**

http://zoobank.org/DA6E2AD1-B1E6-4144-9DFA-11718FD84CE6

Figures 21, 53

Type material. ***Holotype*:** female (IZCAS), Qingquan Cave (23°52.16'N, 99°12.42'E, elevation 295 m), Minglang Town, Yongde County, Lincang, **Yunnan**, **China**, 7 August 2015, Y. Li and Z. Chen leg. ***Paratypes*:** 2 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Females of *M. lincang* sp. nov. can be distinguished from all congeners by a pair of large bulbous spermathecae (Fig. 21A).

Description. Female (holotype). Total length 1.58; carapace 0.64 long, 0.53 wide; abdomen 0.92 long, 0.81 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 21C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium, and sternum dark brown. Abdomen ovoid, dark brown (Fig. 21B). Legs brown; measurements: I 3.50 (0.88, 0.20, 1.05, 0.81, 0.56), II 3.04 (0.79, 0.20, 0.87, 0.70, 0.48), III 2.58 (0.67, 0.17, 0.67, 0.63, 0.44), IV 3.71 (0.92, 0.19, 1.10, 0.88, 0.62). Epigastric area (Fig. 21B): dark brown, nearly trapezoidal patch. Endogyne (Fig. 21A): ratio of the width of spermathecae to the interdistance of spermathecae 1:3.

Male. Unknown.

Distribution. Known only from the type locality (China; Fig. 53).

***Merizocera mainling* Li, sp. nov.**

http://zoobank.org/598BF801-F7D7-42BB-9219-1A2838068922

Figures 22, 23, 53

Merizocera sp. 46: Li and Li 2018 (molecular data).

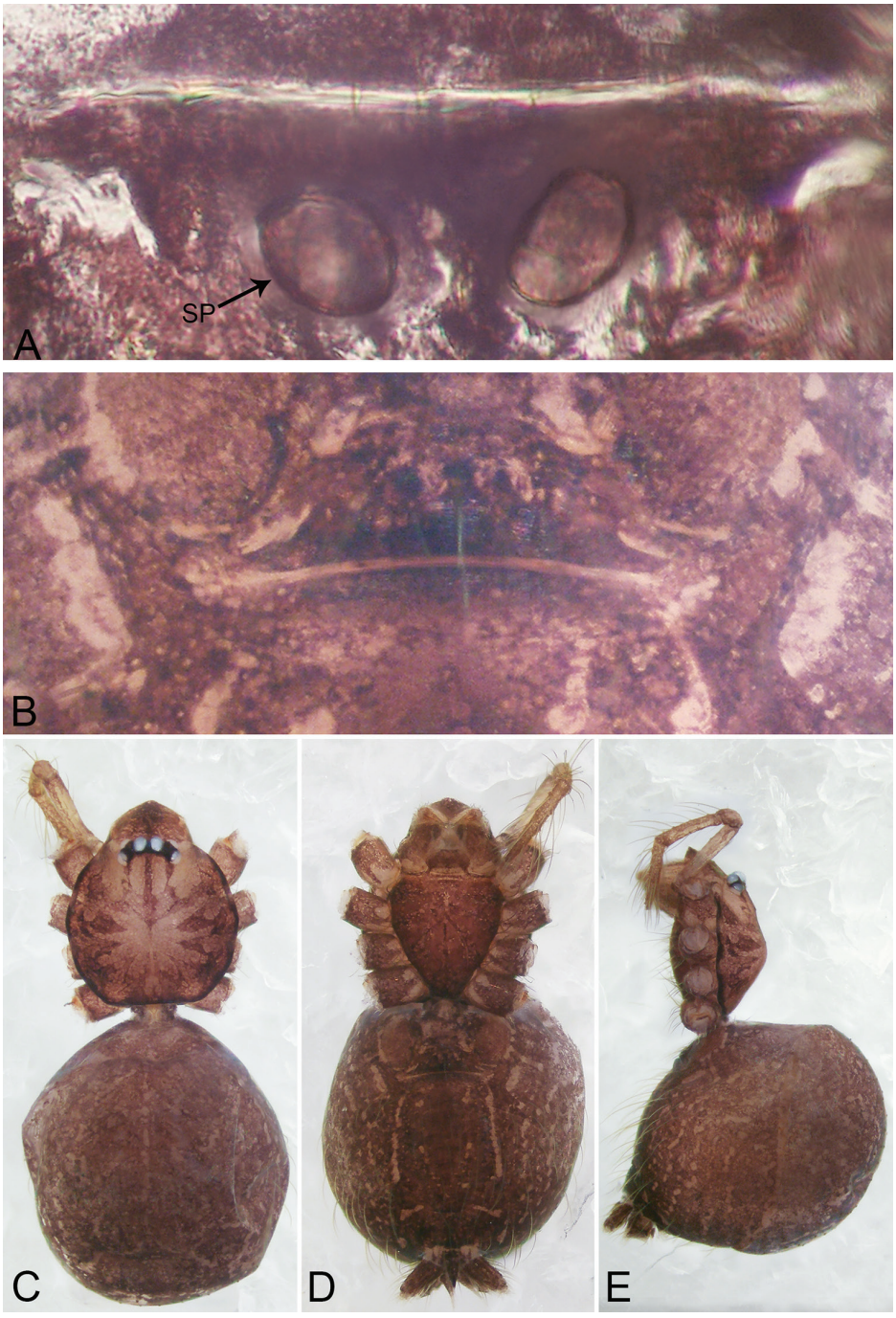

Figure 21. *Merizocera lincang* sp. nov., holotype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view **E** female habitus, lateral view. Abbreviation: SP = spermatheca.

Type material. ***Holotype*****:** male (IZCAS), northern Mainling County (29°13.31'N, 94°13.31'E, elevation 3050 m), Nyingchi, **Tibet**, **China**, 13 August 2013, L. Lin leg. ***Paratypes*****:** 1 male and 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble *M. tanintharyi* sp. nov. but can be distinguished by a thin darkened embolus (Fig. 22B) (vs. thick and dark only at tip (Fig. 38A)), conductor lamina-like and shorter than embolus (Fig. 22B) (vs. conductor appendage-like and similar length as embolus (Fig. 38B)), presence of clypeus protrusion (Fig. 23C) (vs. absence of clypeal protrusion), absence of cymbial protrusion (vs. presence of cymbial protrusion (Fig. 38D)). The females can be distinguished by two pairs of twisted spermathecae (Fig. 23A) (vs. three pairs of short tubular spermathecae (Fig. 39A)).

Description. Male (holotype). Total length 1.72; carapace 0.84 long, 0.65 wide; abdomen 0.82 long, 0.66 wide. Carapace circular, brownish, with dark brown radiating marks (Fig. 23C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with large protrusion provided with long setae (Fig. 23C). Labium and sternum dark brown. Abdomen ovoid, dark brown (Fig. 23E). Legs light brown; measurements: I 6.34 (1.70, 0.26, 1.92, 1.68, 0.78), II missing, III 3.74 (1.05, 0.22, 1.05, 0.93, 0.49), IV 5.10 (1.36, 0.24, 1.53, 1.27, 0.70). Palp (Fig. 22A–D): femur slender, thrice longer than patella; patella not swollen; tibia slightly swollen proximally; cymbium without dorsal protrusion, 1/3 femur length; bulb pale yellow, pyriform with embolus and conductor arising distally; embolus thin and dark, arising laterally, longer than the width of bulb; conductor lamina-like, half the width of bulb.

Female (paratype). General features and colouration similar to those of male (Fig. 23D, E). Measurements: total length 1.76; carapace 0.79 long, 0.65 wide; abdomen 0.94 long, 0.82 wide. Leg measurements: I 4.48 (1.18, 0.25, 1.38, 1.04, 0.63), II 3.70 (1.00, 0.24, 1.08, 0.85, 0.53), III 3.19 (0.89, 0.23, 0.87, 0.75, 0.45), IV 4.38 (1.15, 0.23, 1.33, 1.04, 0.63). Epigastric area (Fig. 23B): dark brown, nearly trapezoidal patch. Endogyne (Fig. 23A) with two pairs of long, twisted, stalked spermathecae with blunt ends.

Distribution. Known only from the type locality (China; Fig. 53).

Merizocera nyingchi **sp. nov.**

http://zoobank.org/B1A4B9F0-9C4F-4E0E-B5D8-9EAC98A73FA6

Figures 24, 53

Type material. ***Holotype*****:** female (IZCAS), mountain behind a farmhouse resort (29°19.09'N, 95°18.88'E, elevation 1280 m), Medog County, Nyingchi, **Tibet**, **China**, 4 August 2013, L. Lin leg. ***Paratype*****:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

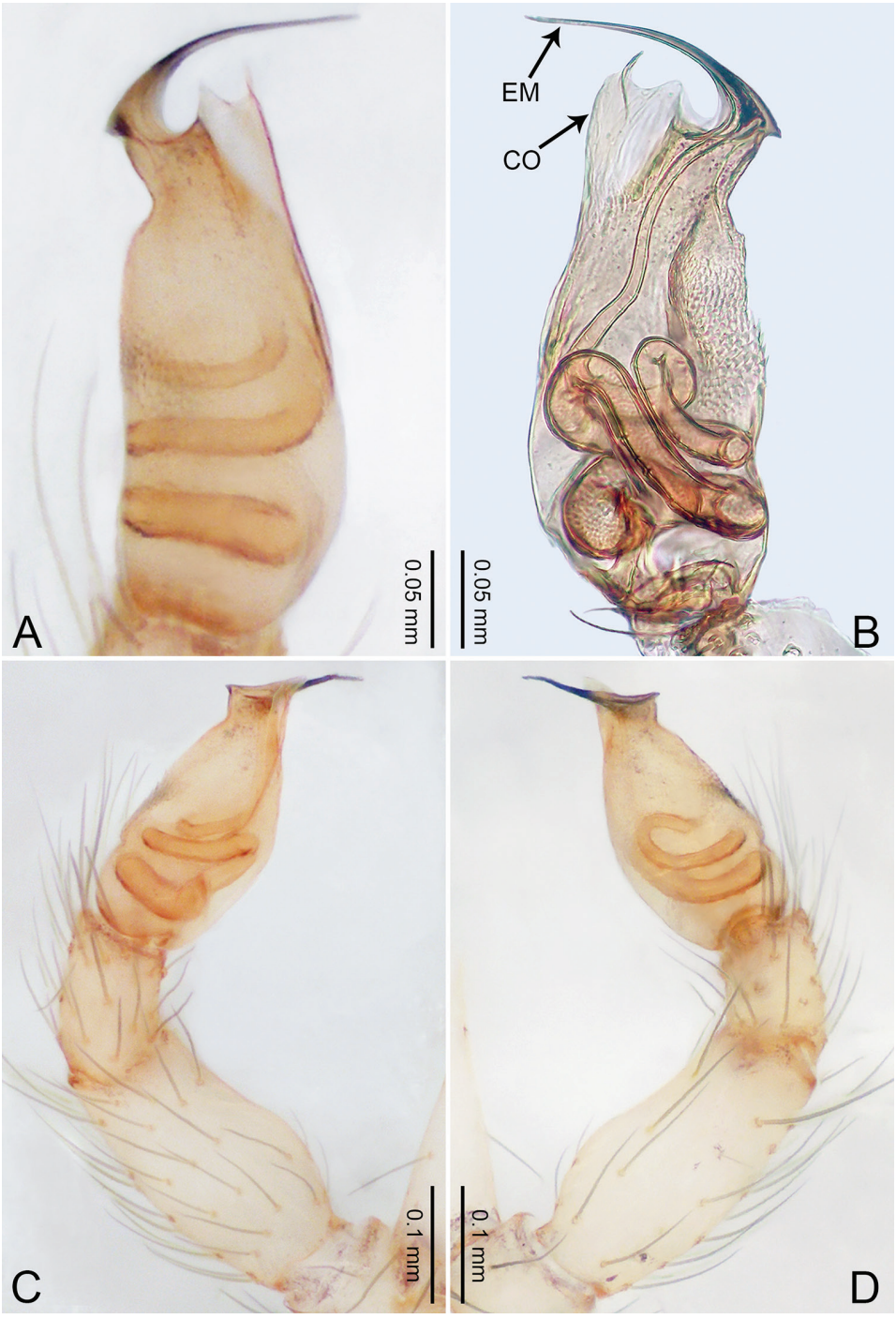

Figure 22. *Merizocera mainling* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus.

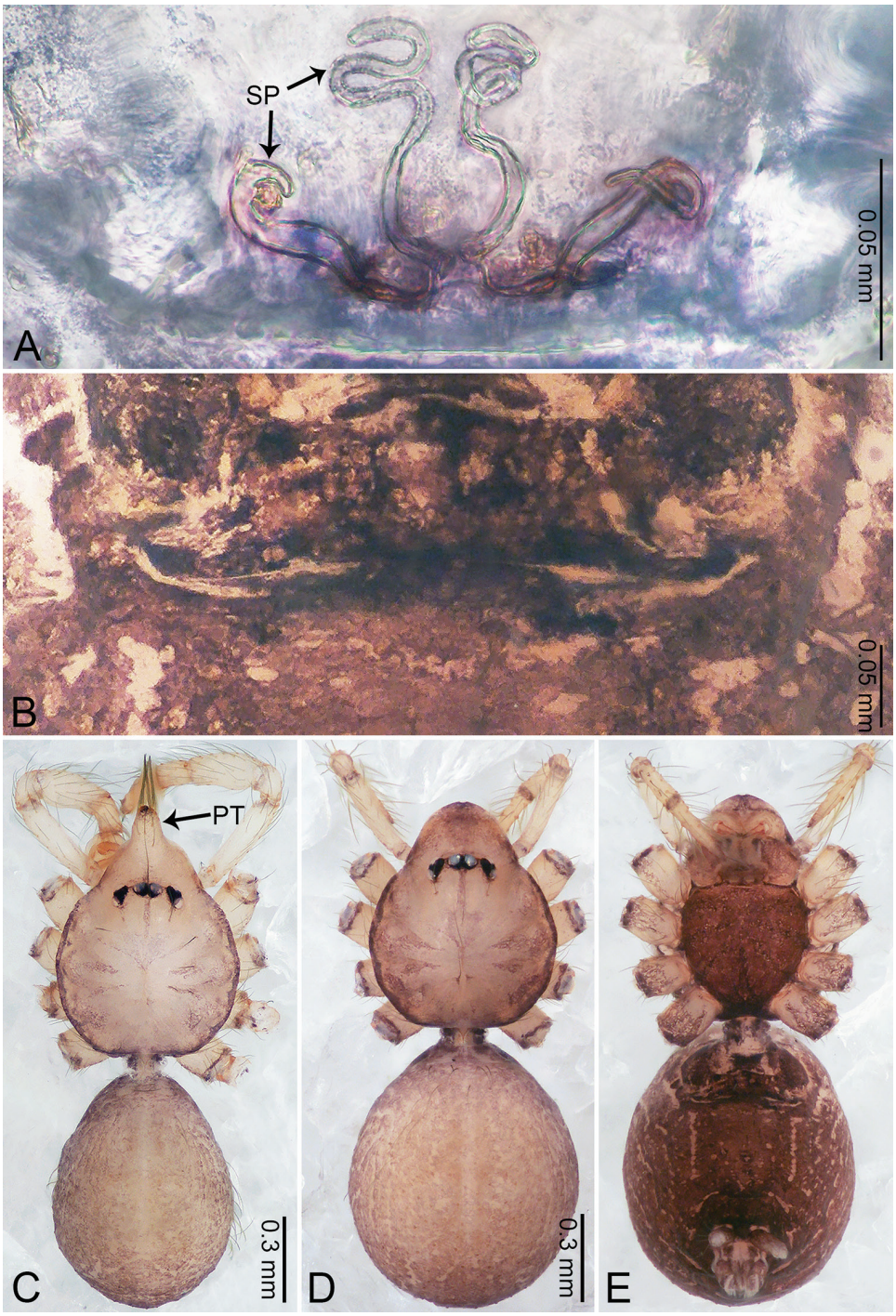

Figure 23. *Merizocera mainling* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviations: PT = clypeal protrusion, SP = spermatheca.

Diagnosis. Females can be distinguished from congeners by two pairs of twisted stalked spermathecae bearing globose distal ends, where lateral pairs are at least half as short as median pairs and have globose ends twice the size of the former (Fig. 24A).

Description. Female (holotype). Total length 1.42; carapace 0.65 long, 0.53 wide; abdomen 0.75 long, 0.53 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 24C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium, and sternum dark brown. Abdomen slightly elongated, dark brown (Fig. 24B). Legs light brown; measurements: I, II, and III missing, IV 4.06 (1.05, 0.19, 1.19, 1.00, 0.63). Epigastric area (Fig. 24B): dark brown patch, medially with pale yellow horizontal strip. Endogyne (Fig. 24A) with two pairs of twisted stalked spermathecae bearing globose distal ends, lateral pairs half as short as median pairs, globose ends of lateral pairs twice larger than median pairs.

Male. Unknown.

Distribution. Known only from the type locality (China; Fig. 53).

***Merizocera peraderiya* Li, sp. nov.**

http://zoobank.org/1773F0E5-4FF0-4028-AB88-4BF281731579

Figures 25, 26, 52

Type material. ***Holotype*:** male (IZCAS), Royal Botanic Gardens (7°16.52'N, 80°35.71'E, elevation 484 m), Peraderiya Town, Kandy District, **Central Province**, **Sri Lanka**, 7 October 2014, S. Kosala leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. kurunegala* sp. nov. Males with angularly bent embolus and furcate conductor (Fig. 25B). Females with a pair of twisted spermathecae (Fig. 26A).

Description. Male (holotype). Total length 1.33; carapace 0.66 long, 0.59 wide; abdomen 0.67 long, 0.46 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 26C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium dark brown. Sternum dark brown but lighter medially. Abdomen slightly elongated, dark grey, with dark brown marks dorsally and ventrally. Legs light brown; measurements: I 7.81 (2.05, 0.22, 2.38, 2.20, 0.96), II 5.35 (1.41, 0.22, 1.60, 1.41, 0.71), III 4.11 (1.13, 0.19, 1.19, 1.06, 0.54), IV 6.49 (1.66, 0.21, 2.00, 1.78, 0.84). Palp (Fig. 25A–D): femur slender, 2.5 times longer than patella; patella not swollen; tibia slightly swollen, half as long as femur; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.72; bulb pale yellow, pyriform with embolus and conductor arising distally; embolus thin and dark with pointed tip, emerging laterally, bent at right-angle; conductor basally attached with embolus, bifurcate, one slender and slightly bent, the other hooked and twice as wide, conductor stem half as long as the width of bulb.

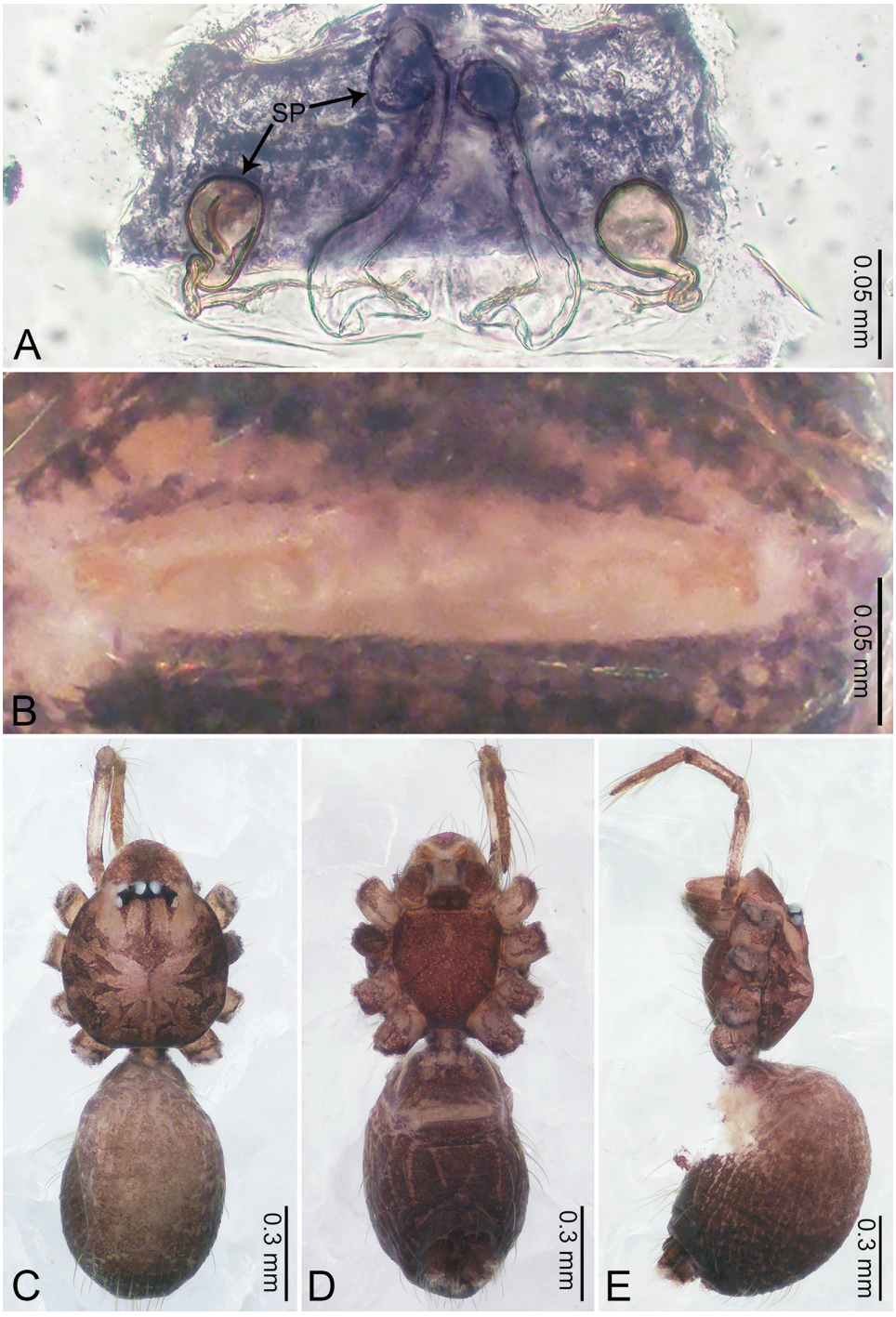

Figure 24. *Merizocera nyingchi* sp. nov., holotype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view **E** female habitus, lateral view. Abbreviation: SP = spermatheca.

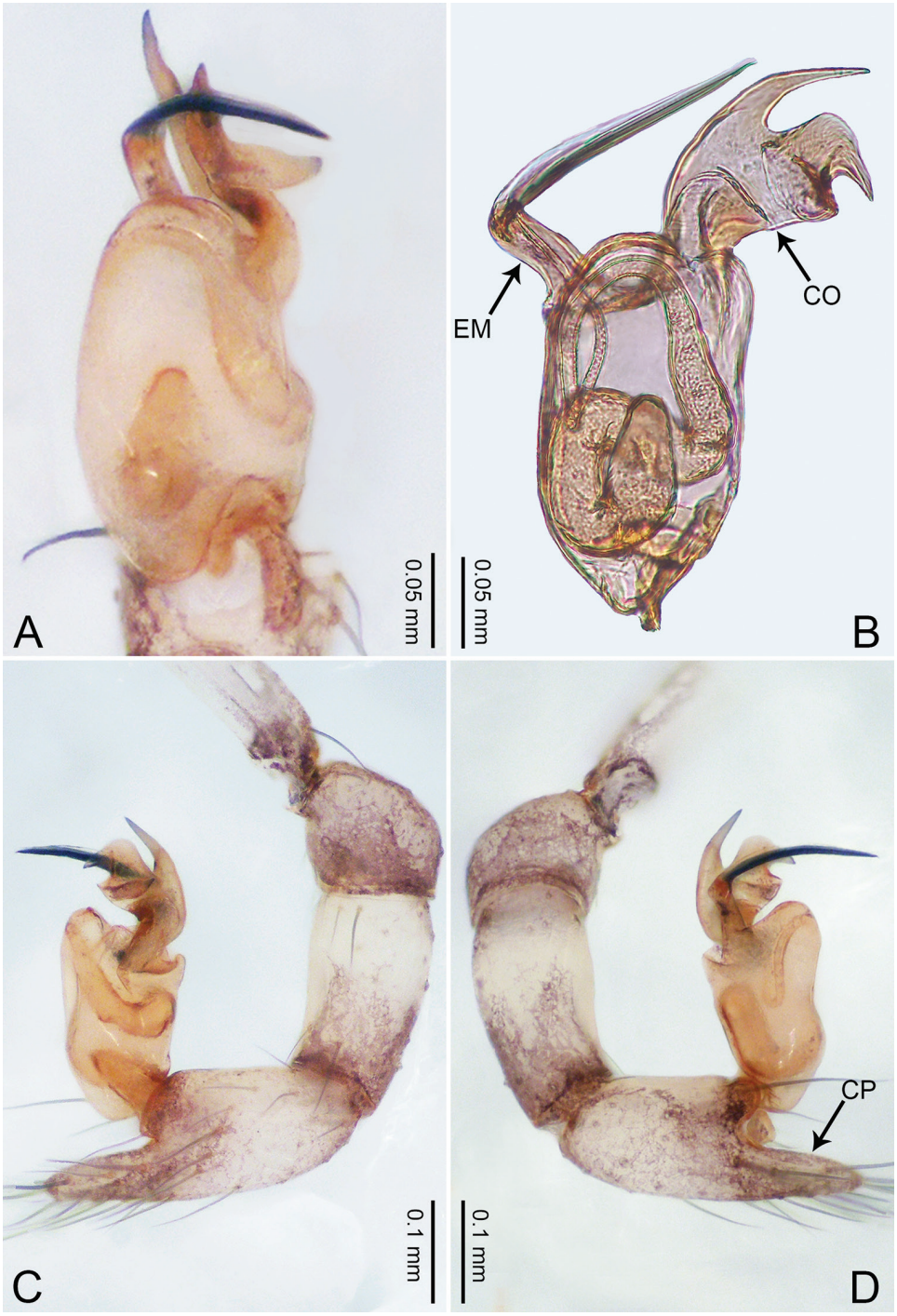

Figure 25. *Merizocera peraderiya* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view, embolus and conductor distorted **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

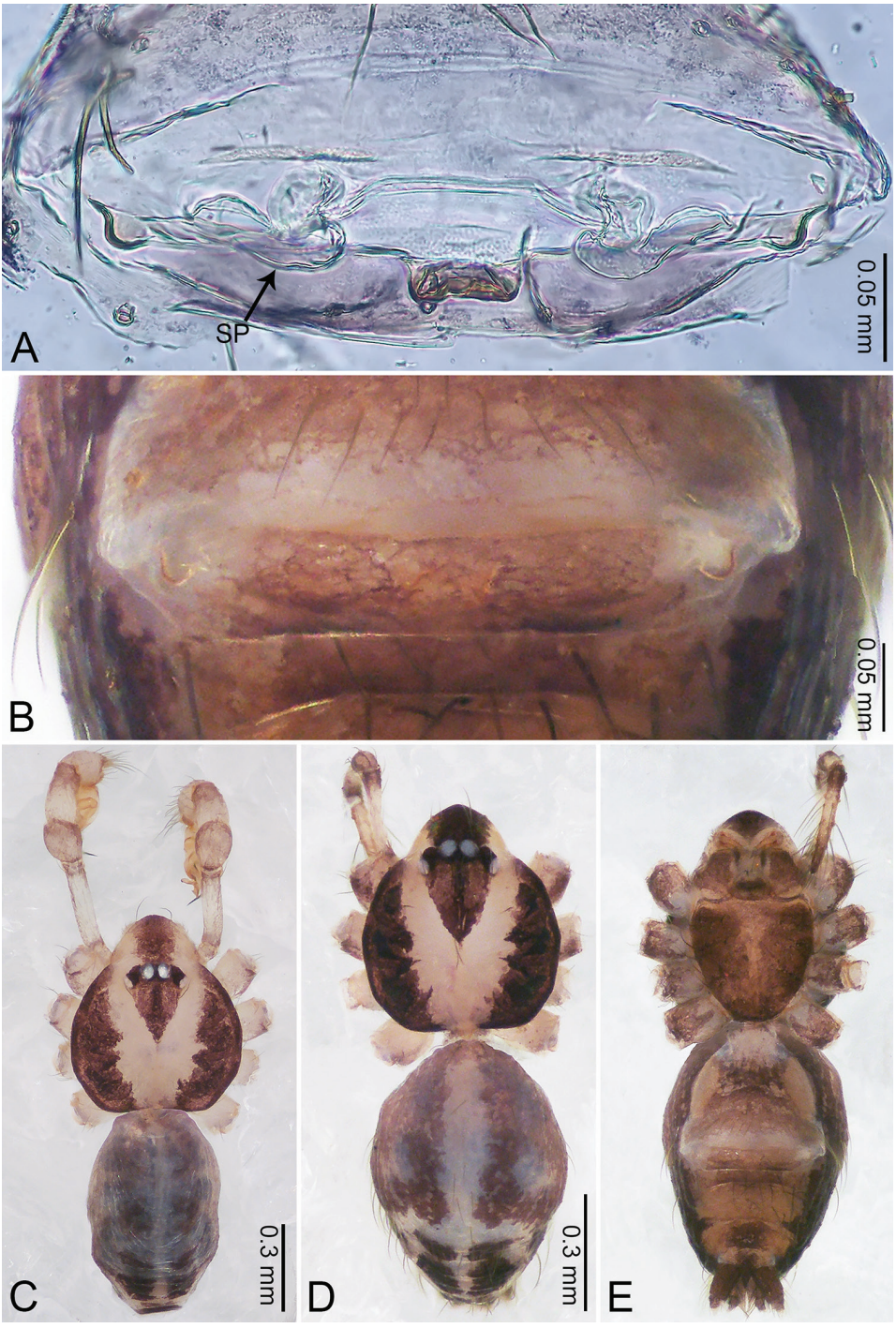

Figure 26. *Merizocera peraderiya* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

Female (paratype). General features and colouration similar to those of male (Fig. 26D, E). Measurements: total length 1.28; carapace 0.61 long, 0.51 wide; abdomen 0.69 long, 0.52 wide. Leg measurements: I 4.25 (1.06, 0.20, 1.28, 1.05, 0.66), II 3.25 (0.83, 0.19, 0.92, 0.80, 0.51), III 2.66 (0.67, 0.17, 0.71, 0.68, 0.43), IV missing. Epigastric area (Fig. 26B): dark brown, patch nearly elliptical. Endogyne (Fig. 26A) with a pair of twisted S-shaped spermathecae, ratio of the width of spermatheca to the interdistance of spermathecae 1:4.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera phuket* Li, sp. nov.**

http://zoobank.org/01F5775C-4E6A-40F7-853A-EE6974F7037A

Figures 27, 28, 54

Type material. ***Holotype*:** male (IZCAS), Toh Sae Mountain (7°53.96'N, 98°23.98'E, elevation 203 m), Mueang District, **Phuket**, **Thailand**, 29 October 2015, P. Wongprom leg. ***Paratypes*:** 2 males and 2 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble those of *M. ratnapura* sp. nov. but can be distinguished by the relatively thin and long conductor (Fig. 27B) (vs. relatively thick and short conductor (Fig. 33B)), embolus with consistent width (Fig. 27B) (vs. embolus gradually thinner towards tip (Fig. 33B)), embolus length similar to bulb length (Fig. 27B) (vs. embolus twice longer than bulb (Fig. 33B)). Females can be distinguished by their horizontally angled elongated spermathecae (Fig. 28A) (vs. wide tubular spermathecae with globose stalked spermatheca medially (Fig. 34A)).

Description. Male (holotype). Total length 1.39; carapace 0.64 long, 0.59 wide; abdomen 0.72 long, 0.49 wide. Carapace circular, brownish, with dark brown radiating marks and narrow dark brown stripe (Fig. 28C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium dark brown. Sternum dark brown, with dark radiating lines. Abdomen slightly elongated, dark brown. Legs light brown; measurements: I 7.37 (1.98, 0.22, 2.25, 2.08, 0.84), II 5.26 (1.44, 0.21, 1.60, 1.41, 0.60), III 3.96 (1.13, 0.20, 1.15, 0.99, 0.49), IV 6.05 (1.62, 0.21, 1.90, 1.60, 0.72). Palp (Fig. 27A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen, half length of femur; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 1.39; bulb pale yellow; pyriform with embolus and conductor arising distally; embolus slightly bent, 1/3 width of and similar length as bulb, conductor basally connected with embolus, thin, short, needle-like, 1/5 embolus length.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 28D, E). Measurements: total length 1.70; carapace 0.64 long, 0.56 wide; abdomen 0.99 long, 0.86 wide. Leg measurements: I 5.24 (1.34, 0.20, 1.56, 1.39, 0.75), II 4.04 (1.06, 0.20, 1.20, 0.99, 0.59), III 3.29 (0.86, 0.20, 0.92, 0.82, 0.49), IV 4.81 (1.21, 0.20, 1.47, 1.23, 0.70). Epigastric area (Fig. 28B): dark brown patch,

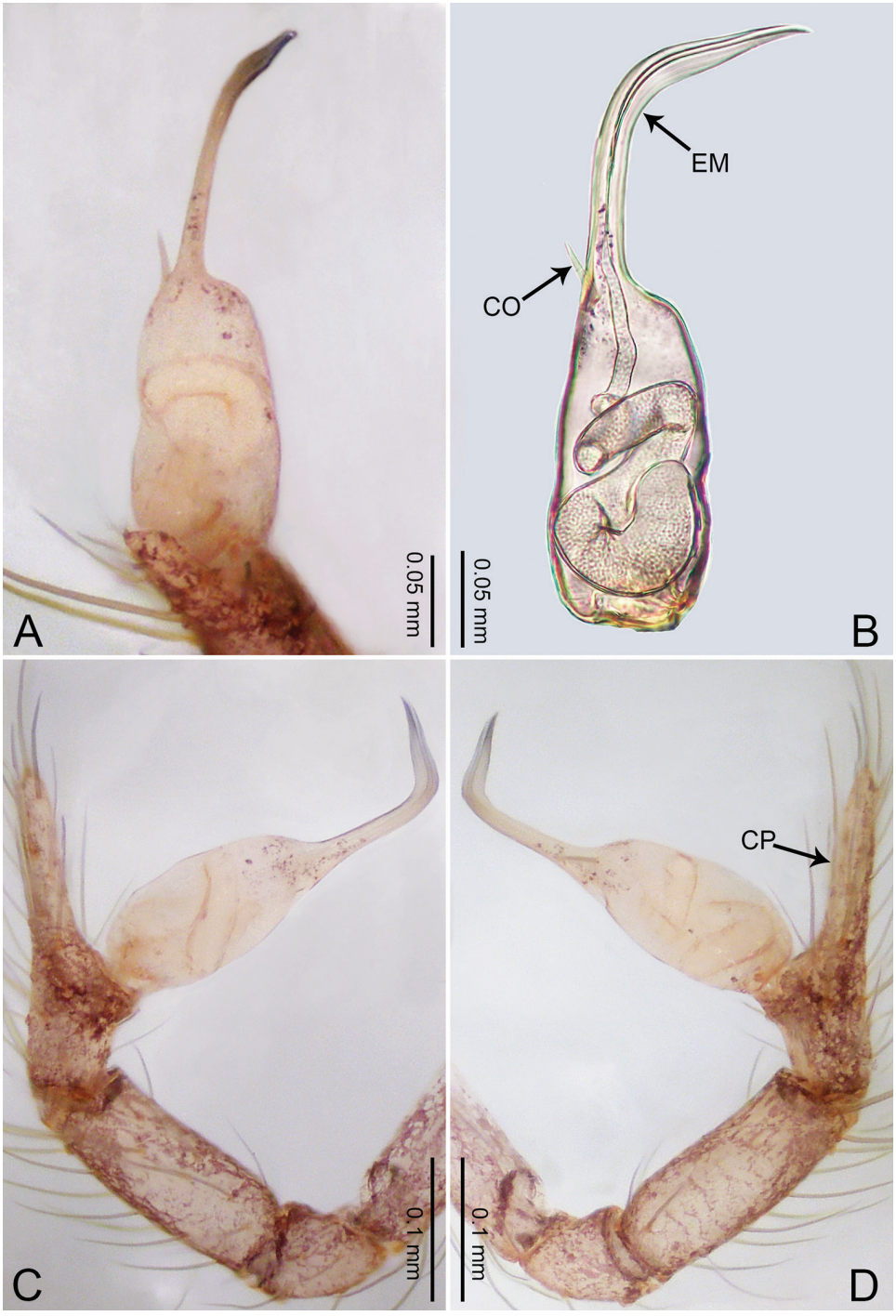

Figure 27. *Merizocera phuket* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolatero-dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

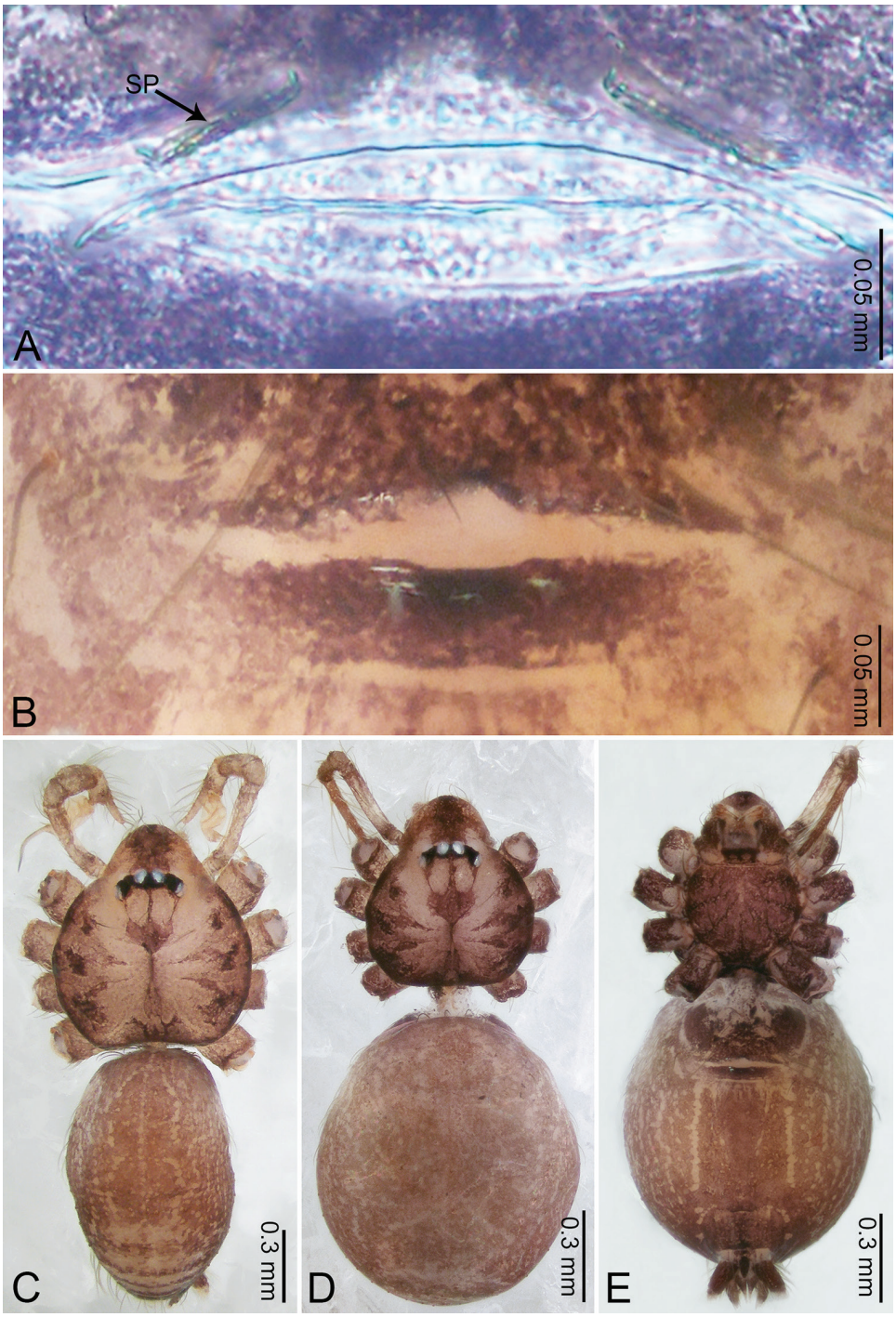

Figure 28. *Merizocera phuket* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

medially with horizontal pale brown slit. Endogyne (Fig. 28A) with a pair of slight horizontally angled elongated spermathecae, tip pointed upright, ratio of the width of spermatheca to the interdistance of spermathecae 1:4.

Distribution. Known only from the type locality (Thailand; Fig. 54).

***Merizocera putao* Li, sp. nov.**

http://zoobank.org/0438A332-A054-4D27-8830-EDED85A7B8DD

Figures 29, 30, 53

Type material. ***Holotype*:** male (IZCAS), Roadside between Upper Shankhaung Village and Wasadum (27°27.38'N, 97°13.65'E, elevation 1396 m), Putao, **Kachin State**, **Myanmar**, 11 December 2016, J. Wu leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. kachin* sp. nov. Bulb with a distinct pit and hooked embolus (Fig. 29B). Clypeal protrusion present in males (Fig. 30C). Females with elongated horizontal spermathecae with globose tips (Fig. 30A).

Description. Male (holotype). Total length 1.60; carapace 0.83 long, 0.58 wide; abdomen 0.75 long, 0.61 wide. Carapace circular, brownish, with dark brown radiating marks and dark brown median line (Fig. 30C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with large protrusion provided with long setae. Labium dark brown. Sternum dark brown, with dark radiating lines. Abdomen ovoid, brown. Legs light brown; measurements: I 7.61 (2.23, 0.24, 2.25, 2.00, 0.89), II 5.46 (1.48, 0.22, 1.64, 1.42, 0.70), III 4.17 (1.10, 0.21, 1.15, 1.15, 0.56), IV 5.84 (1.48, 0.22, 1.74, 1.52, 0.88). Palp (Fig. 29A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.39; bulb pale yellow, elongated pyriform with embolus and conductor arising distally, presence of distinct pit resulting from the basal connection of embolus and conductor; embolus hooked, similar in length with tegular, with pointed tip, width of anterior horizontal hooked part slightly longer than the width of bulb; conductor upright and needle-like, 1/3 length of embolus.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 30D, E). Measurements: total length 1.42; carapace 0.67 long, 0.56 wide; abdomen 0.75 long, 0.63 wide. Leg measurements: I 4.68 (1.19, 0.21, 1.42, 1.19, 0.67), II missing, III 3.17 (0.83, 0.20, 0.85, 0.79, 0.50), IV 4.50 (1.11, 0.20, 1.38, 1.09, 0.72). Epigastric area (Fig. 30B) dark brown semi-circular patch, medially with horizontal pale brown slit. Endogyne (Fig. 30A) with a pair of elongated horizontal spermathecae with blunt tips.

Distribution. Known only from the type locality (Myanmar; Fig. 53).

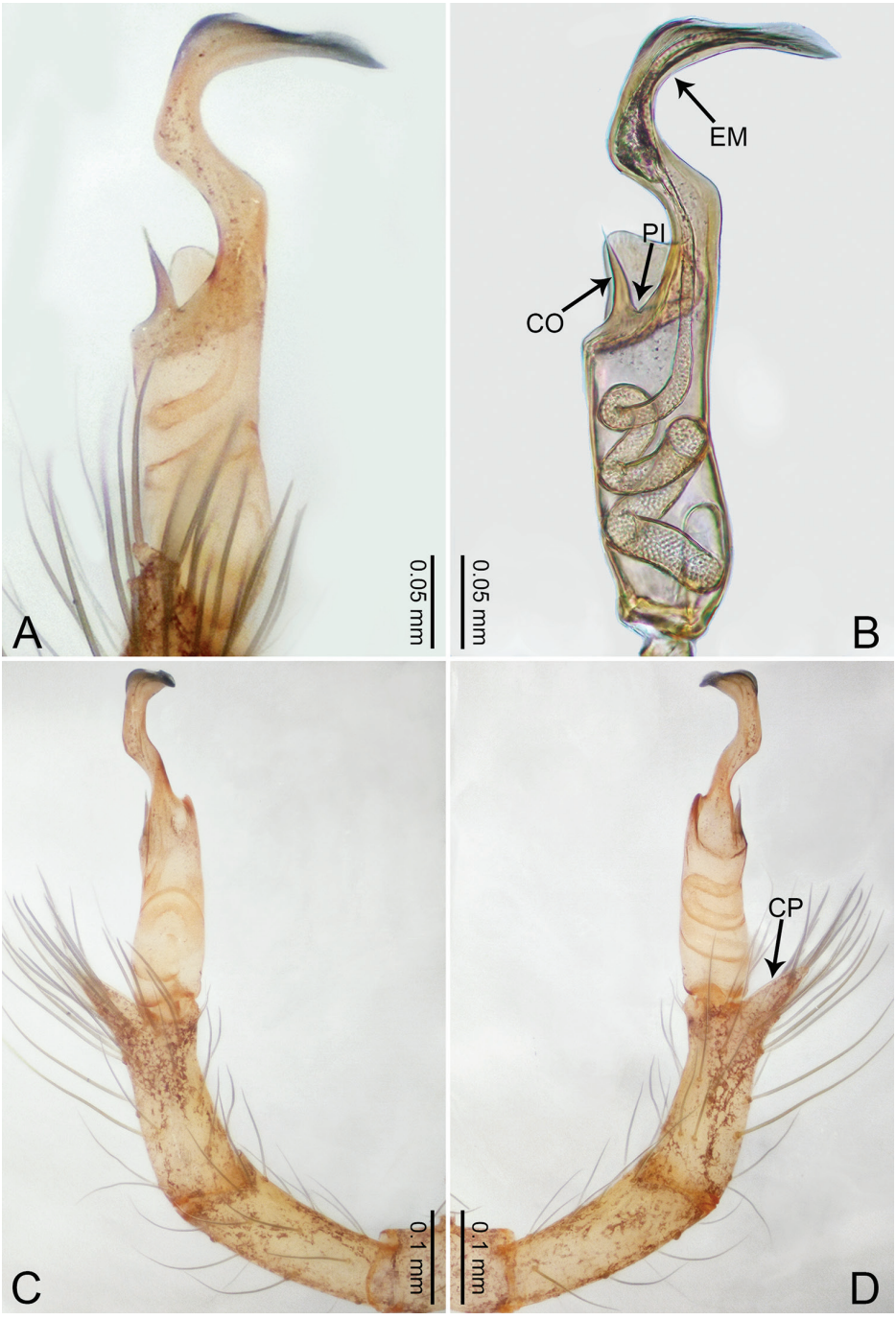

Figure 29. *Merizocera putao* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus, PI = pit.

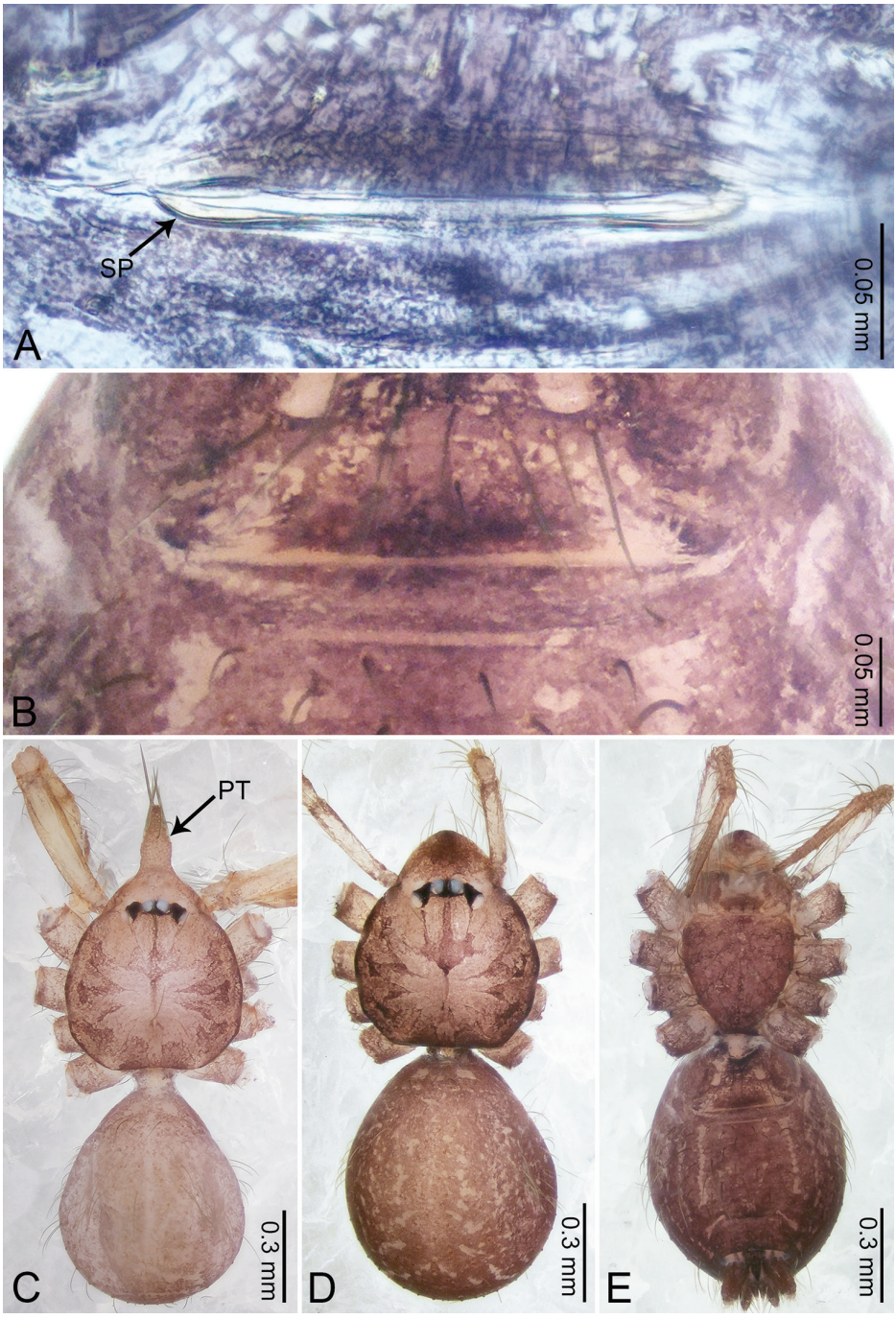

Figure 30. *Merizocera putao* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviations: PT = clypeal protrusion, SP = spermatheca.

***Merizocera ranong* Li, sp. nov.**
http://zoobank.org/A1FBCDBB-C979-4A5B-9156-61C7ABB01FC1
Figures 31, 32, 54

Type material. *Holotype*: male (IZCAS), forest of Suk Sum Ran Village (9°28.80'N, 98°30.56'E, elevation 46 m), Kapoe District, **Ranong**, **Thailand**, 28 October 2014, P. Wongprom leg. ***Paratype*:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. betong* sp. nov. Males with a crinkly embolus, lamina-like embolus tip, and swollen pyriform bulb (Fig. 31B). Females with a pair of posteriorly directed tubular spermathecae (Fig. 32A).

Description. Male (holotype). Total length 1.28; carapace 0.59 long, 0.52 wide; abdomen 0.64 long, 0.49 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 32C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium dark brown. Sternum dark brown but lighter medially. Abdomen ovoid, brownish, with darker brown marks dorsally and ventrally. Legs light brown; measurements: I 6.19 (1.70, 0.21, 1.90, 1.62, 0.76), II 4.46 (1.20, 0.20, 1.33, 1.13, 0.61), III 3.40 (0.92, 0.19, 1.00, 0.84, 0.45), IV 5.05 (1.34, 0.20, 1.55, 1.27, 0.69). Palp (Fig. 31A–D): femur slender, thrice longer than patella; patella not swollen; tibia not swollen; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.90; bulb pale yellow, swollen pyriform with embolus arising distally; embolus with crinkly stalk and lamina-like at the tip, stalk 1/3 length of bulb; conductor absent.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 32D, E). Measurements: total length 1.28; carapace 0.62 long, 0.54 wide; abdomen 0.66 long, 0.51 wide. Leg measurements: I 5.19 (1.36, 0.21, 1.56, 1.33, 0.73), II 4.02 (1.06, 0.20, 1.15, 1.01, 0.60), III 3.25 (0.85, 0.19, 0.89, 0.83, 0.49), IV 4.75 (1.19, 0.20, 1.45, 1.20, 0.71). Epigastric area (Fig. 32B): dark brown elliptical patch, medially with horizontal pale brown slit. Endogyne (Fig. 32A) with a pair of posteriorly directed tubular spermathecae, gradually enlarged posteriorly.

Distribution. Known only from the type locality (Thailand; Fig. 54).

***Merizocera ratnapura* Li, sp. nov.**
http://zoobank.org/4F52770D-6E94-42C0-A1EE-CC0B32CEB28C
Figures 33, 34, 52

Type material. *Holotype*: male (IZCAS), Isthripura Cave (6°49.90'N, 80°22.46'E, elevation 268 m), Batatota Village, Adam's Peak Area, Ekneligoda Town, Kuruwita,

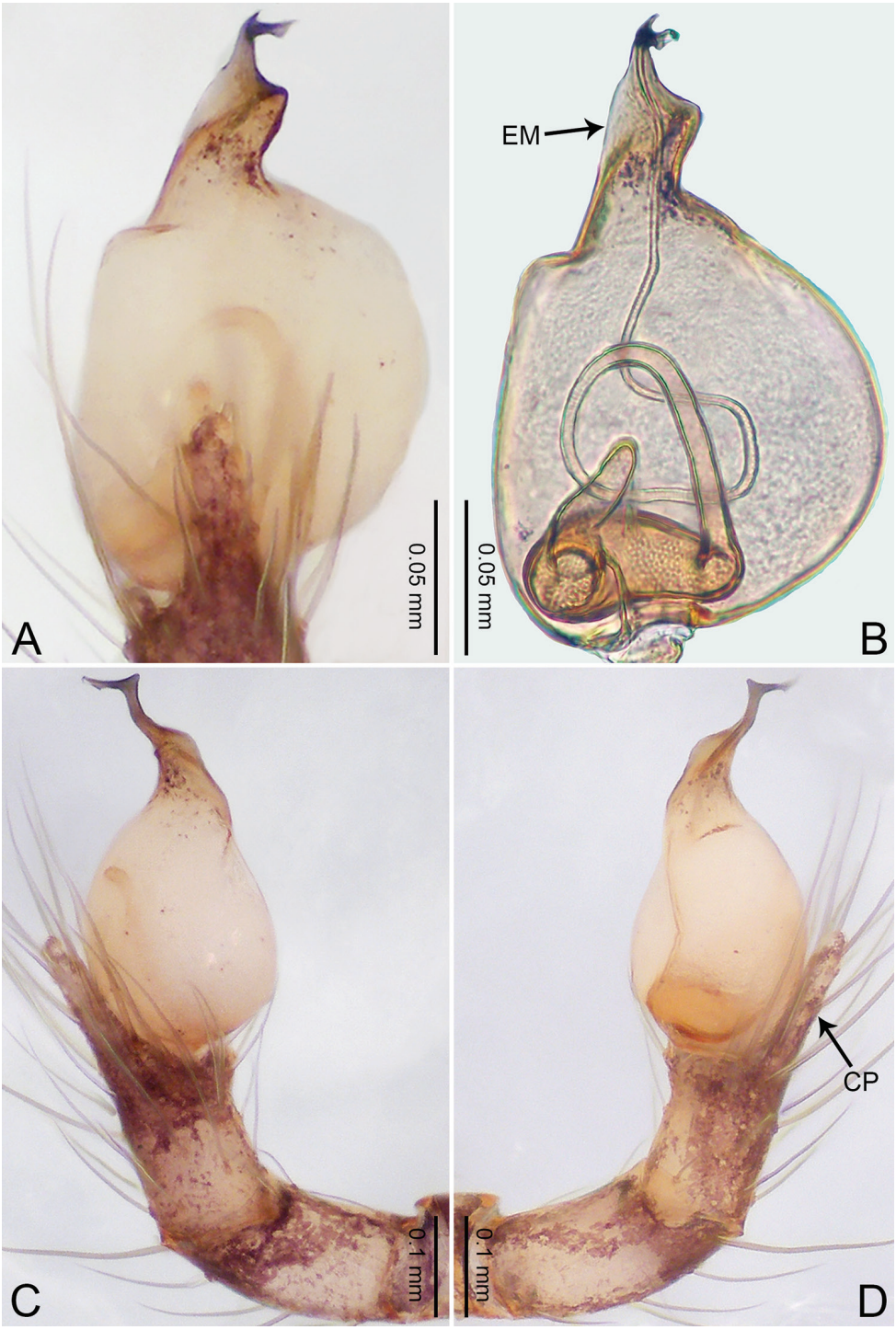

Figure 31. *Merizocera ranong* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CP = cymbial protrusion, EM = embolus.

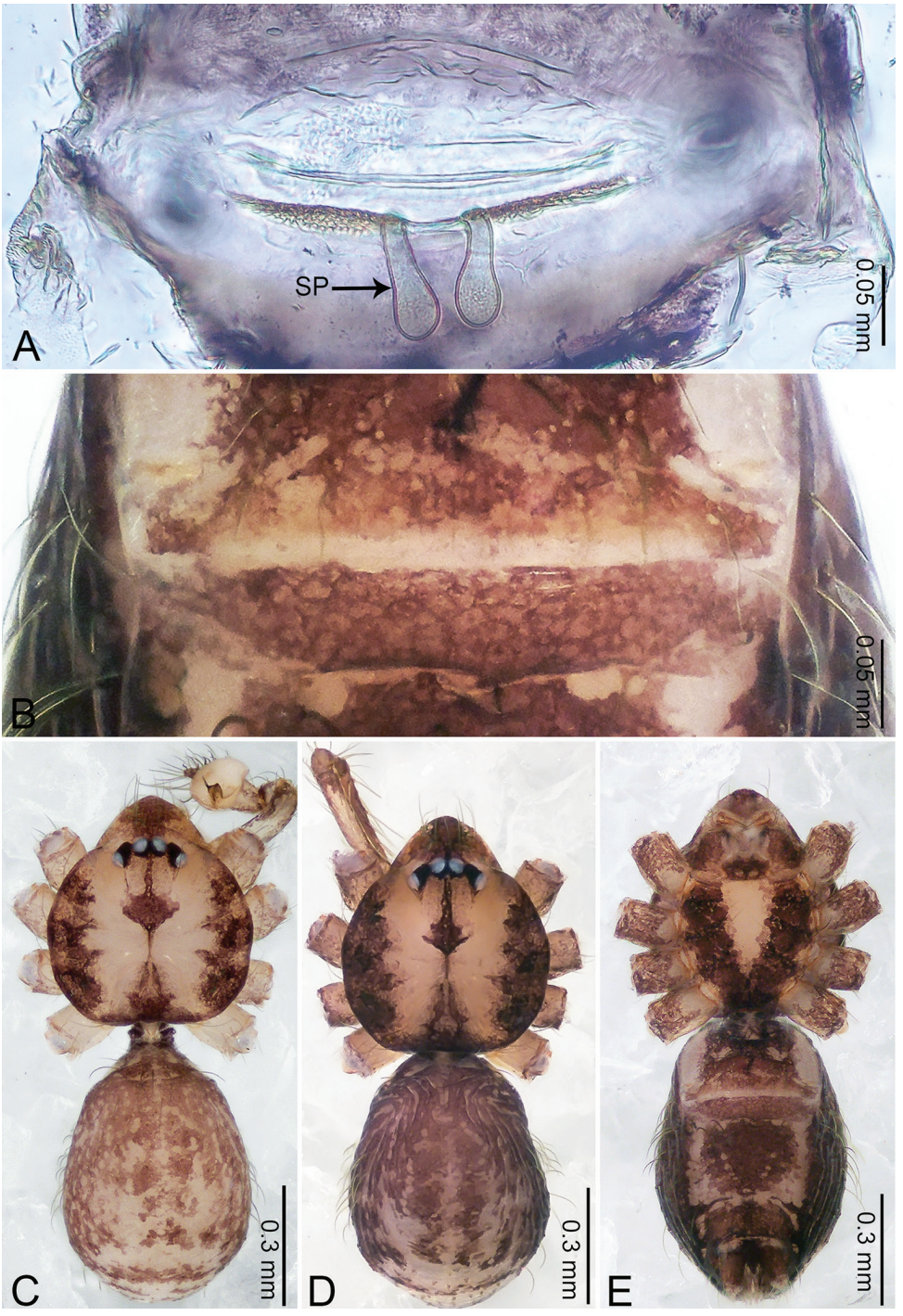

Figure 32. *Merizocera ranong* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

Ratnapura District, **Sabaragamuwa**, **Sri Lanka**, 28 September 2014, S. Kosala leg. ***Paratype*****:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. phuket* sp. nov. Males with a thick and short conductor and a gradually tapering embolus (Fig. 33B). Females with a pair of tubular spermathecae laterally and stalked spermathecae medially (Fig. 34A).

Description. Male (holotype). Total length 1.48; carapace 0.66 long, 0.59 wide; abdomen 0.80 long, 0.55 wide. Carapace circular, brownish, with dark brown marks laterally and brown median line on anterior half (Fig. 34C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus and labium brown. Sternum dark brown. Abdomen slightly elongated, dark brown. Legs light brown; measurements: I, III and IV missing, II 5.74 (1.66, 0.24, 1.76, 1.41, 0.67). Palp (Fig. 33A–D): femur slender, five times longer than patella; patella not swollen; tibia not swollen; tibia not swollen, 1/2 femur length; cymbium with distal protrusion, 1/3 femur length, length ratio of dorsal elongation and cymbium: 0.91; bulb pale yellow, pyriform with embolus and conductor arising distally; embolus elongated and bent, 2.5 times longer than bulb, gradually tapering and darkened at the tip; conductor basally connected with embolus.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 34D, E). Measurements: total length 1.48; carapace 0.70 long, 0.62 wide; abdomen 0.76 long, 0.51 wide. Leg measurements: I 9.38 (2.59, 0.24, 2.97, 2.45, 1.13), II 6.75 (1.92, 0.24, 2.10, 1.66, 0.83), III 5.10 (1.47, 0.23, 1.53, 1.24, 0.63), IV 7.36 (2.08, 0.23, 2.35, 1.82, 0.88). Epigastric area (Fig. 34B): dark brown elliptical patch. Endogyne (Fig. 34A) with a pair of widely tubular spermathecae, medially with stalked spermathecae bearing globose end.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

Merizocera salawa **Li, sp. nov.**

http://zoobank.org/C706A307-0868-44DA-AFAB-57E83D0924FC

Figures 35, 36, 52

Type material. ***Holotype*****:** male (IZCAS), Lenawara Lena (= cave) (6°56.77'N, 80°6.76'E, elevation 66 m), Salawa Village, Avissawella Town, Maniyangama, Colombo District, **Western Province**, **Sri Lanka**, 25 September 2014, S. Kosala leg.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males are discussed in *M. mandai* sp. nov. Bulb with a widely separated bifurcate conductor, and a curved embolus (Fig. 35B).

Description. Male (holotype). Total length 1.52; carapace 0.61 long, 0.54 wide; abdomen 0.88 long, 0.41 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 36C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks

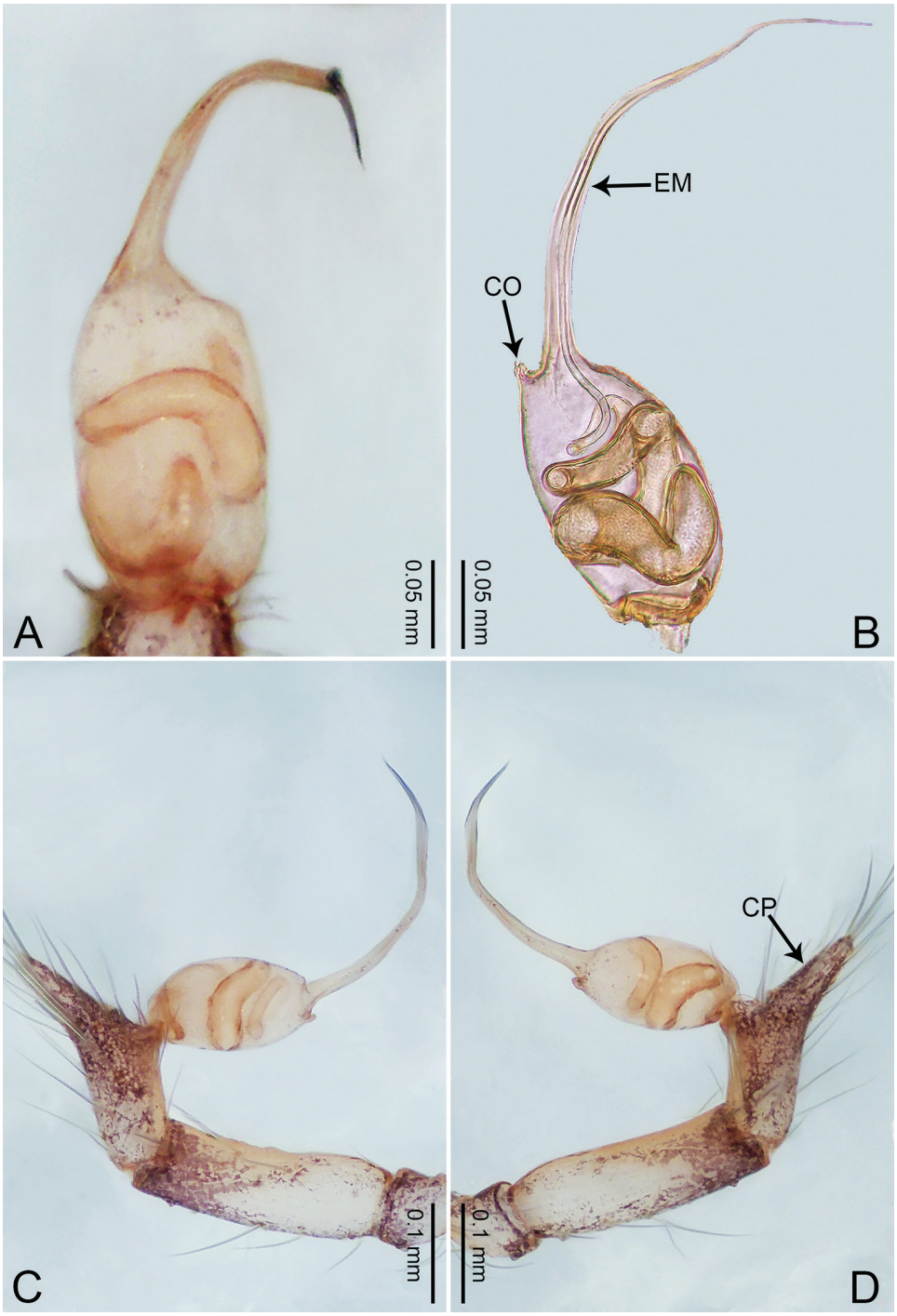

Figure 33. *Merizocera ratnapura* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

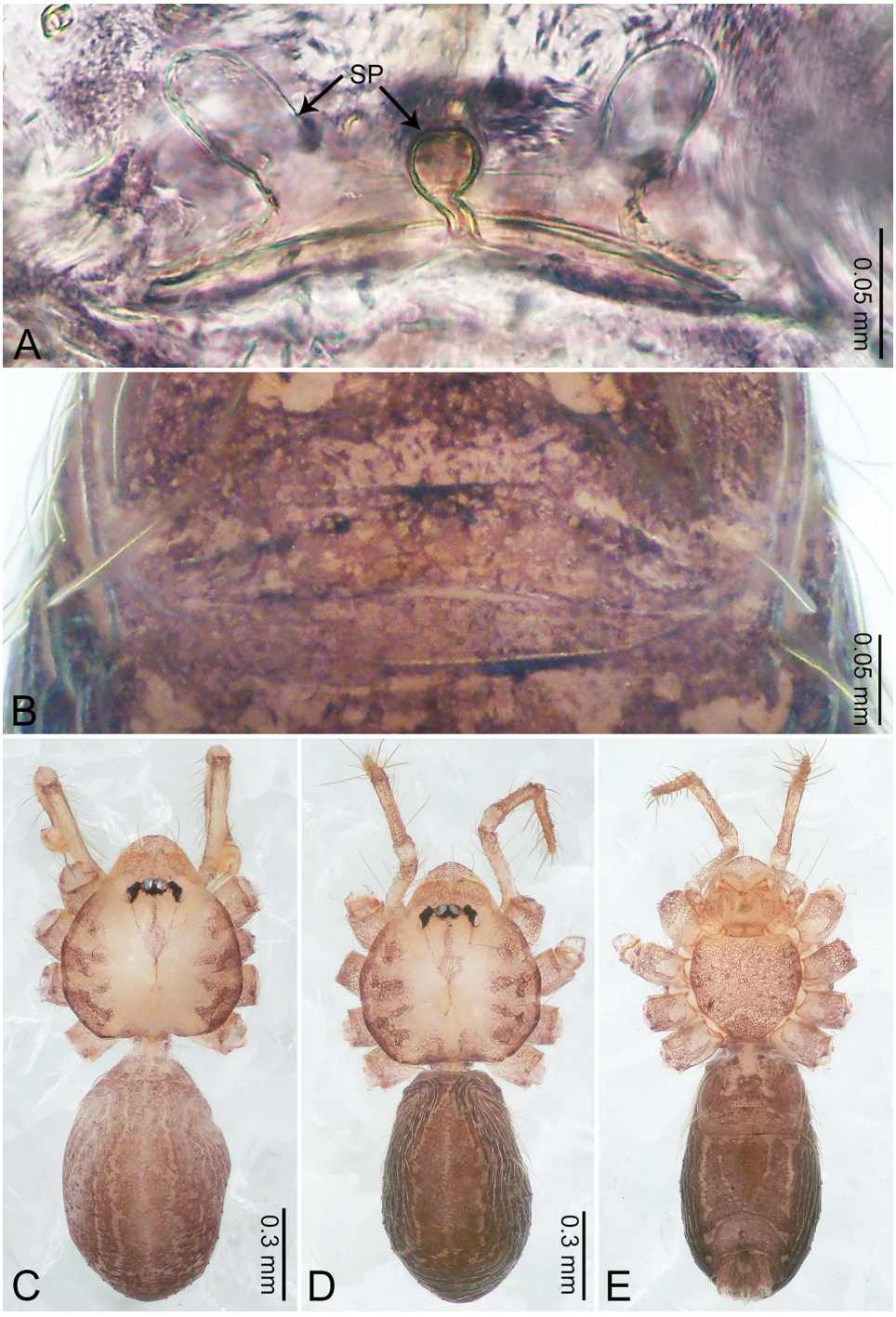

Figure 34. *Merizocera ratnapura* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

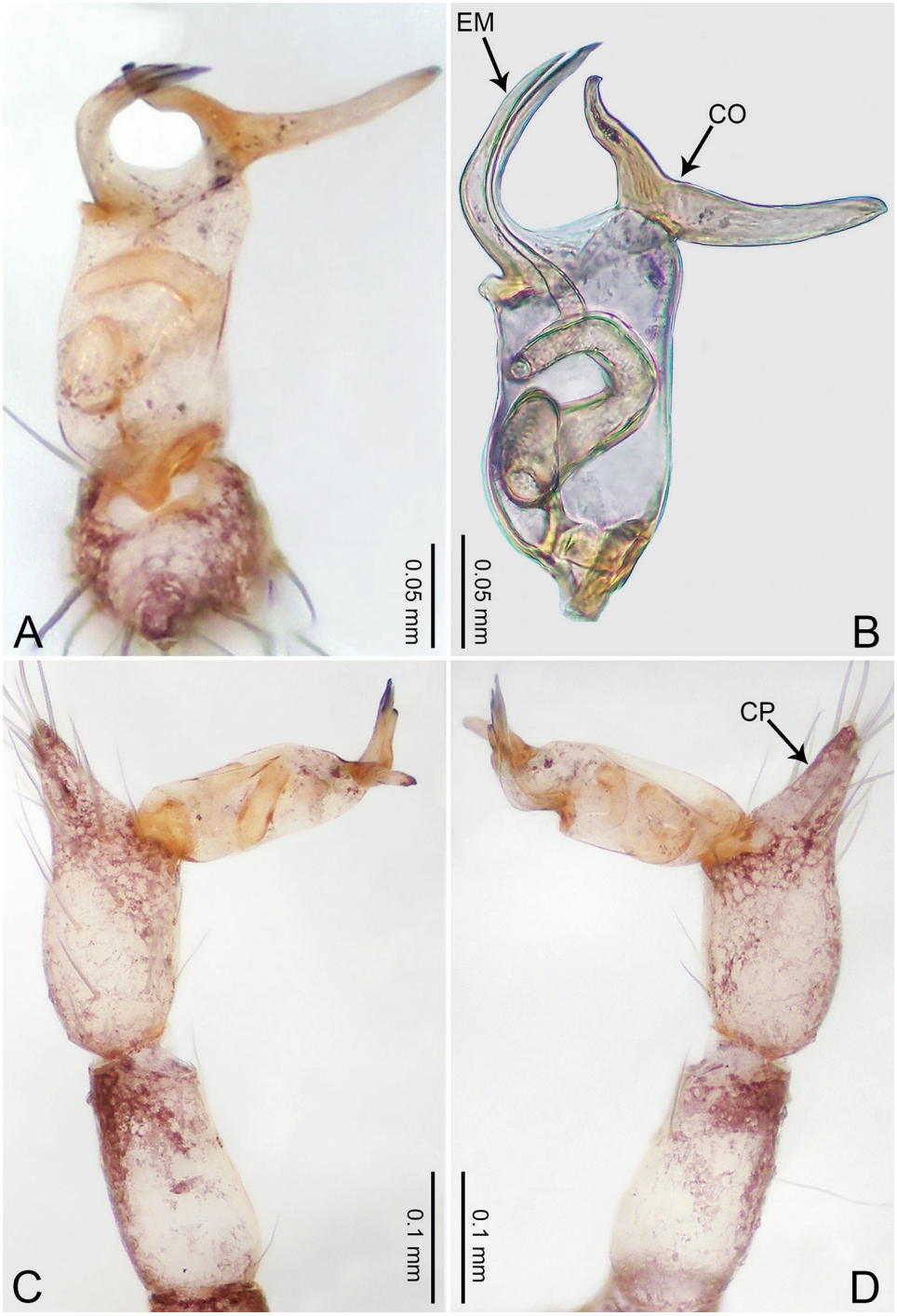

Figure 35. *Merizocera salawa* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view, embolus and conductor distorted **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

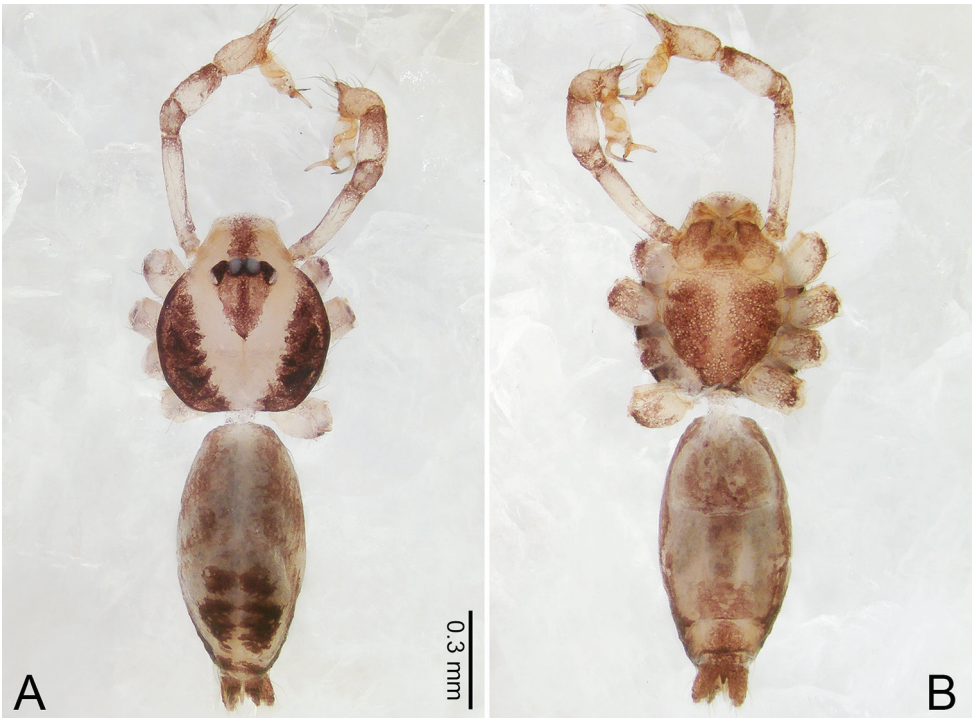

Figure 36. *Merizocera salawa* sp. nov., holotype male. **A** Habitus, dorsal view **B** habitus, ventral view.

medially. Labium dark brown. Sternum dark brown but brownish medially. Abdomen elongated, dark grey, with dark brown marks dorsally and ventrally. Legs missing. Palp (Fig. 35A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen, 1/2 femur length; cymbium with distal protrusion, 1/2 femur length, length ratio of dorsal elongation and cymbium: 0.63; bulb pale yellow, pyriform with embolus and conductor emerging distally; embolus arising laterally, bent, with consistent width; conductor bifurcate, arising laterally, similar width as embolus, resembles a widely open crescent-shape.

Female. Unknown.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera tak* Li, sp. nov.**

http://zoobank.org/8E300899-E573-4D65-8550-B531D5EB593C

Figures 37, 54

Type material. ***Holotype*:** female (IZCAS), Mae Klong Noi Subdistrict (16°14.64'N, 98°59.91'E, elevation 1228 m), Umphang District, **Tak**, **Thailand**, 17 November 2016, P. Wongprom leg.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Females can be distinguished from all congeners by the presence of two pairs of globose spermathecae, the median pair resembling the figure '8' (Fig. 37A).

Description. Female (holotype). Total length 1.21; carapace 0.58 long, 0.49 wide; abdomen 0.61 long, 0.47 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 37C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium, and sternum dark brown. Abdomen ovoid, dark brown (Fig. 37B). Legs light brown; measurements: I 3.47 (0.84, 0.19, 1.03, 0.85, 0.56), II 2.93 (0.73, 0.18, 0.84, 0.68, 0.50), III 2.41 (0.59, 0.16, 0.65, 0.58, 0.43), IV 3.48 (0.85, 0.19, 1.00, 0.85, 0.59). Epigastric area (Fig. 37B): dark brown semi-circular patch, medially with a slit. Endogyne (Fig. 37A) with two pairs of globose spermathecae, median pair made up of two overlying globose spermathecae resembling the figure '8', lateral pairs 1/4 size of median pair.

Male. Unknown.

Distribution. Known only from the type locality (Thailand; Fig. 54).

***Merizocera tanintharyi* Li, sp. nov.**

http://zoobank.org/7ECF3725-D050-4174-9B28-FB209AD7AB8B

Figures 38, 39, 54

Type material. ***Holotype*:** male (IZCAS), Tanintharyi Nature Reserve (14°44.12'N, 98°11.55'E, elevation 307 m), **Myanmar**, 24 October 2017, Z. Chen leg. ***Paratypes*:** 1 male and 3 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. mainling* sp. nov. Recognised by a wide and appendage-like conductor as long as the embolus (Fig. 38B). It can be distinguished from the *Psiloderces leucopygius* group by an inconspicuous cymbial protrusion and a distinct conductor (vs. distinct or short cymbial protrusion and an inconspicuous conductor in the *leucopygius* group).

Description. Male (holotype). Total length 1.76; carapace 0.85 long, 0.74 wide; abdomen 0.95 long, 0.59 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median line (Fig. 39C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium and sternum dark brown. Abdomen slightly elongated, dark brown. Legs light brown; measurements: I 9.11 (2.66, 0.31, 2.97, 2.25, 0.92), II 7.14 (1.90, 0.27, 2.10, 1.98, 0.89), III 5.50 (1.53, 0.26, 1.64, 1.44, 0.63), IV 8.18 (2.20, 0.29, 2.45, 2.28, 0.96). Palp (Fig. 38A–D): femur slender, 1/3 patella length; patella not swollen; tibia not swollen, 1/2 femur length; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.40; bulb pale yellow, pyriform with embolus and conductor emerging distally, attached but separated at the tip; embolus pointed and darken at the tip; conductor gradually thinner at the tip.

Female (paratype). Similar to the male in colouration and general features but slightly larger (Fig. 39D, E). Measurements: total length 1.66; carapace 0.75 long,

Figure 37. *Merizocera tak* sp. nov., holotype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view **E** female habitus, lateral view. Abbreviation: SP = spermatheca.

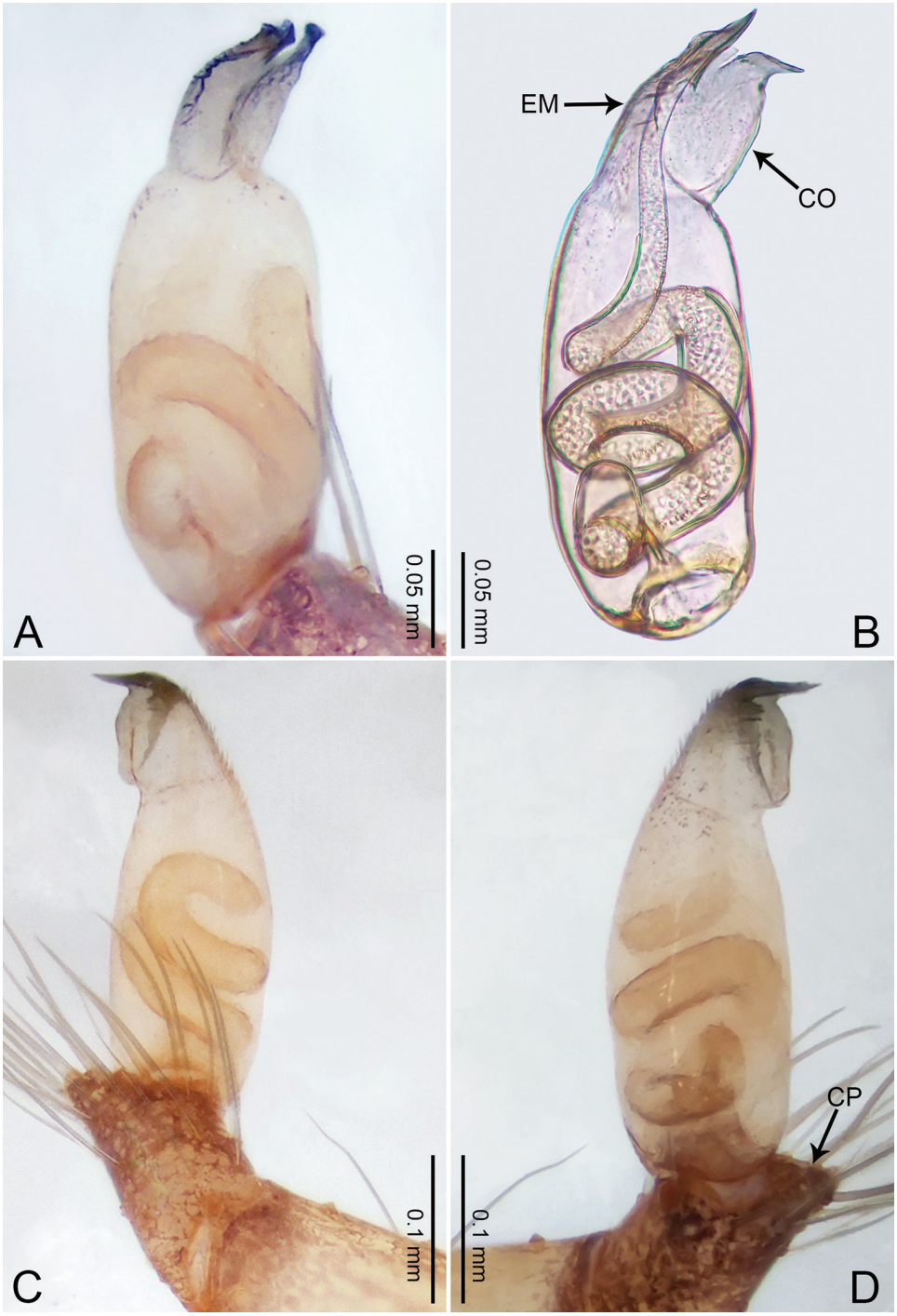

Figure 38. *Merizocera tanintharyi* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view, embolus and conductor distorted **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

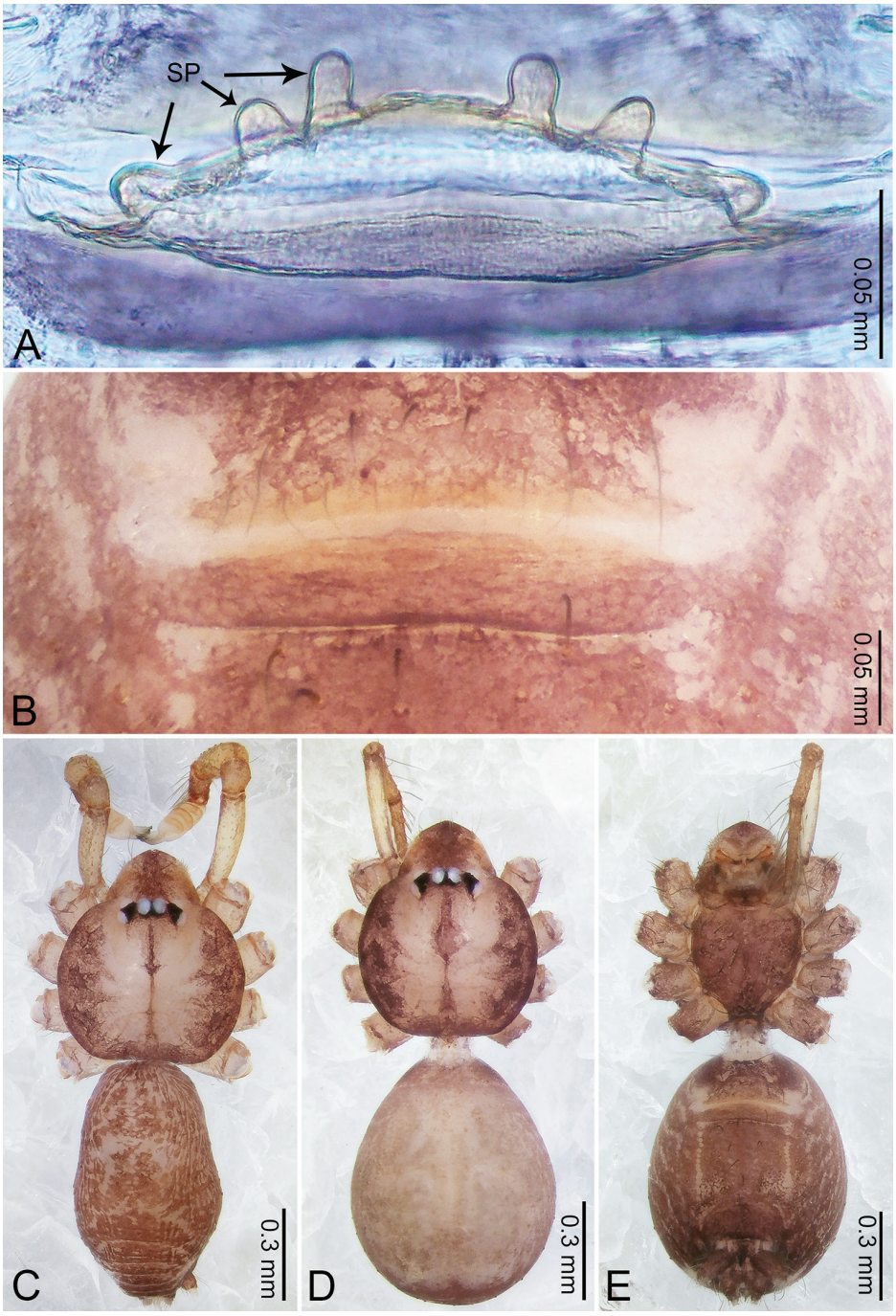

Figure 39. *Merizocera tanintharyi* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

0.62 wide; abdomen 0.91 long, 0.71 wide. Leg measurements: I 6.12 (1.55, 0.25, 1.82, 1.60, 0.90), II 4.80 (1.23, 0.23, 1.38, 1.24, 0.72), III 3.90 (1.03, 0.22, 1.09, 0.99, 0.57), IV missing. Epigastric area (Fig. 39B): dark brown elliptical patch, medially with pale yellow slit. Endogyne (Fig. 39A) with three pairs of short tubular spermathecae, lateral pairs relatively widely separated, median two pairs attached closely together.

Distribution. Known only from the type locality (Myanmar; Fig. 54).

***Merizocera tengchong* Li, sp. nov.**

http://zoobank.org/5BF76A00-C9E3-4B05-93BF-06E37778DD53

Figures 40, 41, 53

Type material. ***Holotype*:** male (IZCAS), Gaoligongshan National Nature Reserve (24°49.74'N, 98°46.06'E, elevation 2177 m), Tengchong County, Baoshan, **Yunnan**, **China**, 21–22 June 2013, Z. Zhao and J. Liu leg. ***Paratype*:** 1 male (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males can be recognised from congeners by the webbed feet-like embolus with a basally attached, stalked apophysis bearing a globose tip (Fig. 40B).

Description. Male (holotype). Total length 1.53; carapace 0.67 long, 0.59 wide; abdomen 0.81 long, 0.49 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 41C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium, and sternum dark brown. Abdomen slightly elongated, dark brown. Legs light brown; measurements: I 5.71 (1.50, 0.25, 1.76, 1.45, 0.75), II and III missing, IV 5.00 (1.31, 0.22, 1.53, 1.23, 0.71). Palp (Fig. 40A–D): femur slender, thrice longer than patella; patella not swollen; tibia swollen proximally; cymbium with distal protrusion, 1/3 length of femur, length ratio of dorsal elongation and cymbium 0.47; bulb light brown, elongated pyriform, with embolus and conductor arising distally; embolus webbed feet-like with darken tip, attached with thin stalked apophysis bearing globose end, embolus length similar to bulb length; conductor needle-like and slightly bent, 1/4 as long as embolus.

Female. Unknown.

Distribution. Known only from the type locality (China; Fig. 53).

***Merizocera thenna* Li, sp. nov.**

http://zoobank.org/17D2C8DC-6F36-43AC-A45D-0E464F936B96

Figures 42, 43, 52

Type material. ***Holotype*:** male (IZCAS), near the Suwargeya Cave of Archeaology place of Kuragala (6°37.45'N, 80°52.21'E, elevation 439 m), Thenna Village, Kaldoda

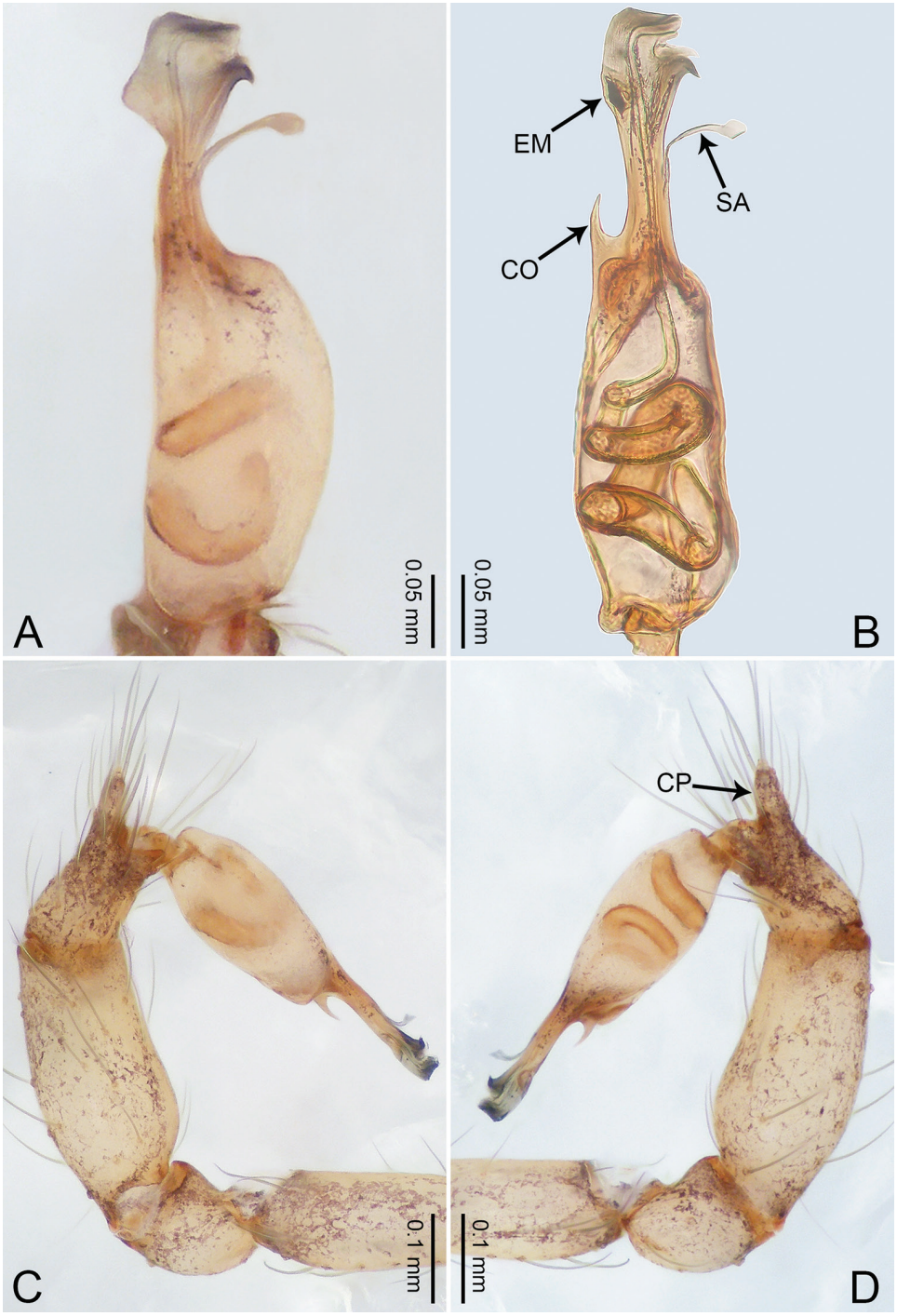

Figure 40. *Merizocera tengchong* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, retrolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus, SA = stalked apophysis.

Figure 41. *Merizocera tengchong* sp. nov., holotype male. **A** Habitus, dorsal view **B** habitus, ventral view.

Town, Balangoda, Ratnapura District, **Sabaragamuwa**, **Sri Lanka**, 1 October 2014, S. Kosala leg. ***Paratypes*:** 2 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males can be recognised from all other congeners by the twisted widened embolus and a trifurcate conductor (Fig. 42B). Females can be distinguished by a pair of horizontal, slender, stalked spermathecae, both ends bearing globose distal parts (Fig. 43A).

Description. Male (holotype). Total length 1.31; carapace 0.61 long, 0.50 wide; abdomen 0.65 long, 0.42 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 43C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium dark brown. Sternum dark brown but brownish medially, with distinct dark radiating lines. Abdomen slightly elongated, brownish, with dark brown marks dorsally and ventrally. Legs light brown; measurements: I 5.33 (1.36, 0.19, 1.64, 1.41, 0.73), II 3.85 (1.00, 0.20, 1.11, 0.97, 0.57), III 3.13 (0.84, 0.17, 0.88, 0.79, 0.45), IV missing. Palp (Fig. 42A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen proximally; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.46; bulb brown, pyriform with embolus and conductor arising dis-

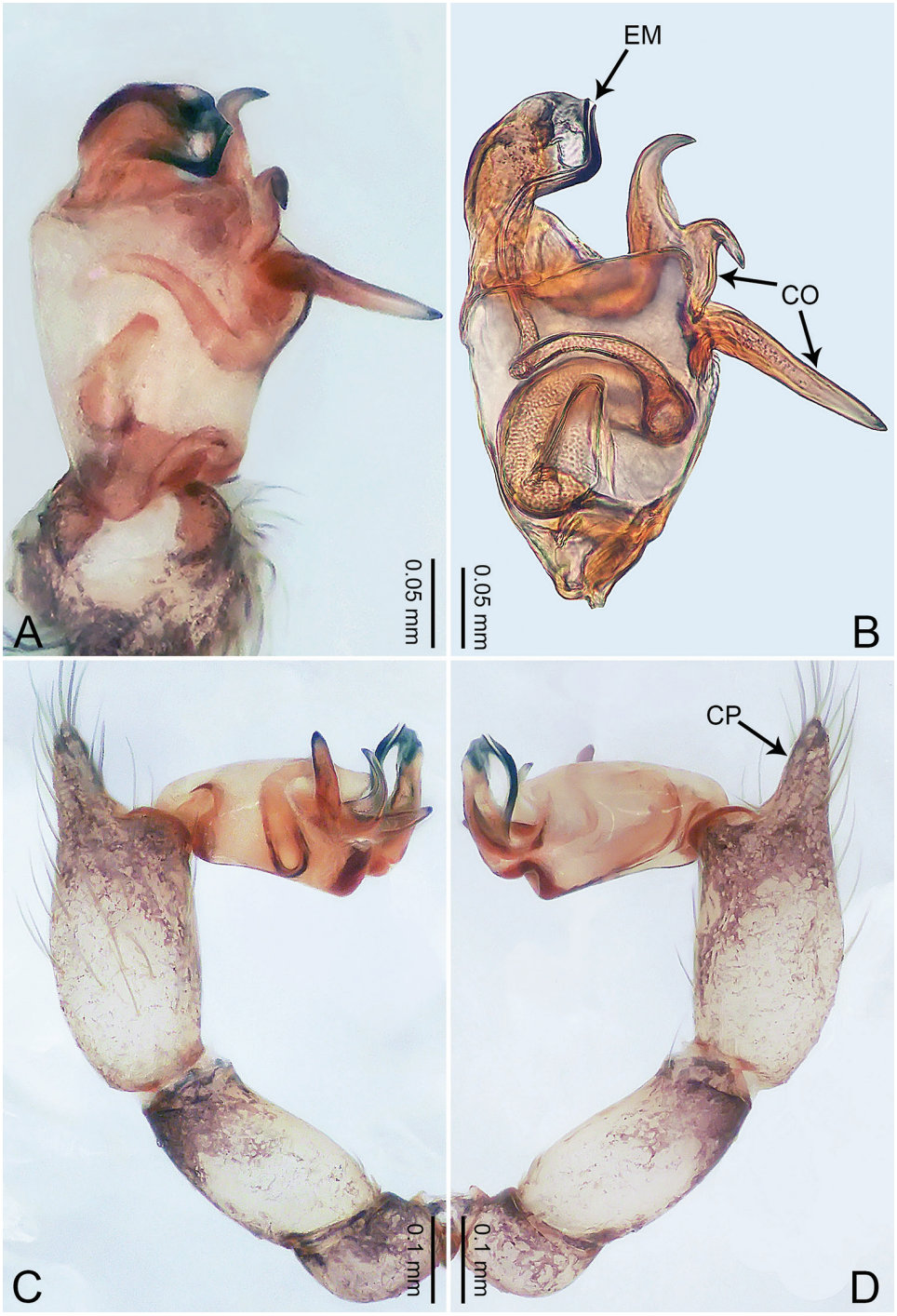

Figure 42. *Merizocera thenna* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view, embolus and conductor distorted **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

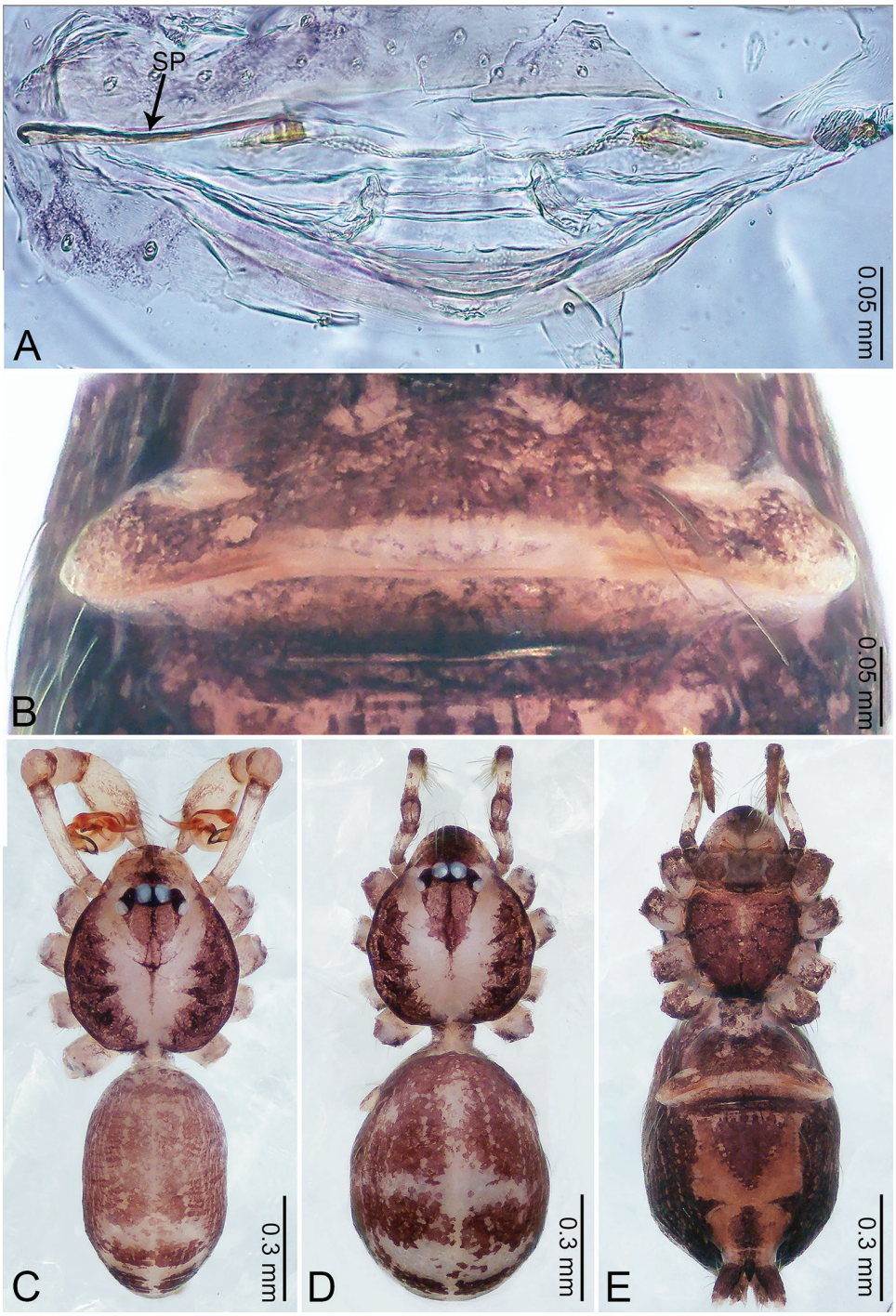

Figure 43. *Merizocera thenna* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

tally; embolus twisted and dark at the tip, approx. half the width and length of bulb; conductor arising laterally, trifurcate, two hooked, one twice as long as the other but with pointed tip.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 43D, E). Measurements: total length 1.31; carapace 0.56 long, 0.48 wide; abdomen 0.67 long, 0.57 wide. Leg measurements: I and II missing, III 2.26 (0.58, 0.16, 0.62, 0.54, 0.36), IV 3.35 (0.82, 0.18, 1.00, 0.84, 0.51). Epigastric area (Fig. 43B): light brown elongated patch. Endogyne (Fig. 43A) with a pair of horizontally stalked spermathecae, both ends bearing globose distal ends, ratio of the width of spermatheca to the interdistance of spermathecae 1:3.5.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera uva* Li, sp. nov.**

http://zoobank.org/E6D72E46-677F-4B14-AEBA-BC3FF497D2B1

Figures 44, 52

Merizocera sp. 158: Li and Li 2018 (molecular data).

Type material. ***Holotype*****:** female (IZCAS), Udakirinda Cave 1 (6°50.24'N, 81°3.85'E, elevation 855 m), Koradogolla Village, Ella, Badulla District, **Uva**, **Sri Lanka**, 3 October 2014, S. Kosala leg. ***Paratype*****:** 1 female (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Females resemble those of *M. yala* sp. nov. by having twisted stalked spermathecae but can be distinguished by having two pairs of twisted stalked spermathecae, with one end ellipsoid and the other end bifurcately globose (Fig. 44A) (vs. only globose distal ends (Fig. 49A)).

Description. Female (holotype). Total length 1.86; carapace 0.79 long, 0.66 wide; abdomen 1.01 long, 0.84 wide. Carapace circular, brownish, with dark brown marks laterally and dark brown median stripe on anterior half (Fig. 44C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus brownish, with dark brown marks medially. Labium dark brown. Sternum dark brown but brownish laterally. Abdomen ovoid, dark grey but dark brown posteriorly and ventrally (Fig. 44B). Epigastric area (Fig. 44B): dark brown ellipsoid patch, medially with a slit.

Male. Unknown.

Distribution. Known only from the type locality (Sri Lanka; Fig. 52).

***Merizocera wenshan* Li, sp. nov.**

http://zoobank.org/47807A72-FF91-4508-856C-F0B03DA0CB0C

Figures 45, 46, 53

Type material. ***Holotype*****:** male (IZCAS), near Daweishan National Nature Reserve (22°54.65'N, 103°41.78'E, elevation 2070 m), Pingbian County, Wenshan, **Yunnan**,

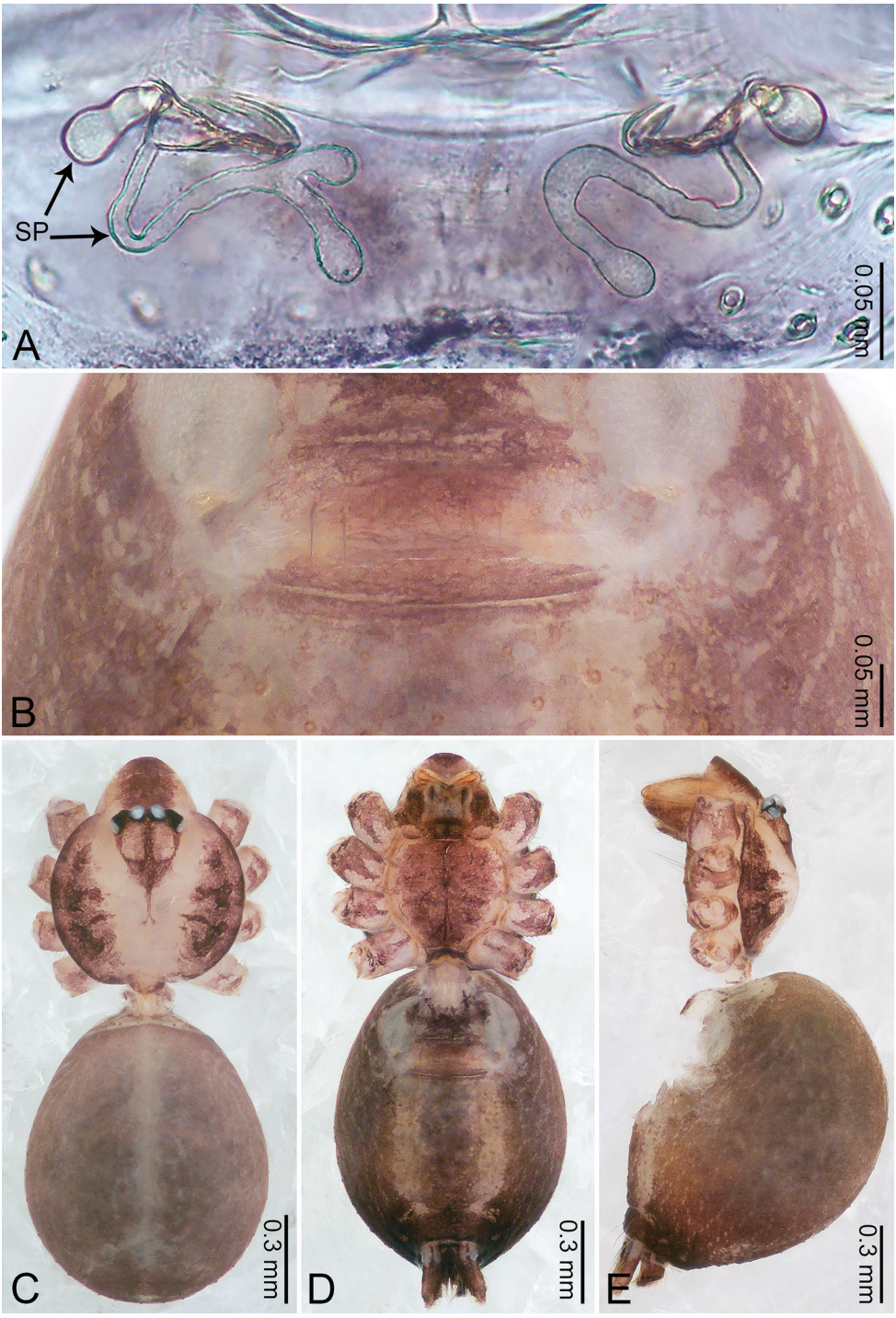

Figure 44. *Merizocera uva* sp. nov., holotype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view **E** female habitus, lateral view. Abbreviation: SP = spermatheca.

China, 21 May 2015, Z. Chen and Y. Li leg. ***Paratypes*:** 3 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Males resemble *M. wui* sp. nov. but can be distinguished by a broad embolus (Fig. 45B) (vs. narrow and thin embolus (Fig. 47B)), absence of a conductor (vs. presence of a short conductor (Fig. 47B)), a short and wide cymbium protrusion (Fig. 45D) (vs. long and thin cymbium protrusion (Fig. 47D)), and a pyriform bulb (Fig. 45B) (vs. spherical bulb (Fig. 47B)). Females can be distinguished by a pair of upright tubular spermathecae (Fig. 46A) (vs. a pair of angled clavate spermathecae (Fig. 48A)).

Description. Male (holotype). Total length 1.28; carapace 0.62 long, 0.51 wide; abdomen 0.67 long, 0.58 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 46C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus and labium dark brown. Sternum brown but dark brown laterally. Abdomen ovoid, dark brown. Legs light brown; measurements: I 3.45 (0.91, 0.22, 1.01, 0.80, 0.51), II missing, III 2.52 (0.67, 0.19, 0.65, 0.58, 0.43), IV 3.62 (0.94, 0.20, 1.05, 0.84, 0.59). Palp (Fig. 45A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen; cymbium with distal protrusion, half as long as femur; bulb pale yellow, pyriform with embolus merging distally; embolus clavate with blunt tip, similar in length to and approx. thrice narrower than tegular; conductor absent.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 46D, E). Measurements: total length 1.34; carapace 0.63 long, 0.55 wide; abdomen 0.71 long, 0.57 wide. Leg measurements: I 3.20 (0.81, 0.20, 0.95, 0.71, 0.53), II 2.78 (0.71, 0.22, 0.77, 0.60, 0.48), III 2.42 (0.63, 0.18, 0.63, 0.57, 0.41), IV 3.45 (0.87, 0.20, 1.04, 0.78, 0.56). Epigastric area (Fig. 46B): dark brown semi-circular patch. Endogyne (Fig. 46A) with a pair of anteriorly directed tubular spermathecae, ratio of the width of a spermatheca to the interdistance of spermathecae 1:5.

Distribution. Known only from the type locality (China; Fig. 53).

Merizocera wui Li, sp. nov.

http://zoobank.org/E17036ED-D627-4032-AA5A-A8959CCCC170
Figures 47, 48, 53

Type material. ***Holotype*:** male (IZCAS), Roadside between Wasadum and Ziradum (27°32.31'N, 97°7.54'E, elevation 978 m), Putao, **Kachin State**, **Myanmar**, 12 December 2016, J. Wu leg. ***Paratypes*:** 1 male and 2 females (IZCAS), same data as holotype.

Etymology. The specific name is a patronym in honour of the collector Jianglang Wu; noun (name) in genitive case.

Diagnosis. Diagnosis features of males and females are discussed in *M. wenshan* sp. nov. Males with a spherical bulb, thin narrow embolus (Fig. 47B), and a narrow cymbial protrusion (Fig. 47D). Females with angled clavate spermathecae (Fig. 48A).

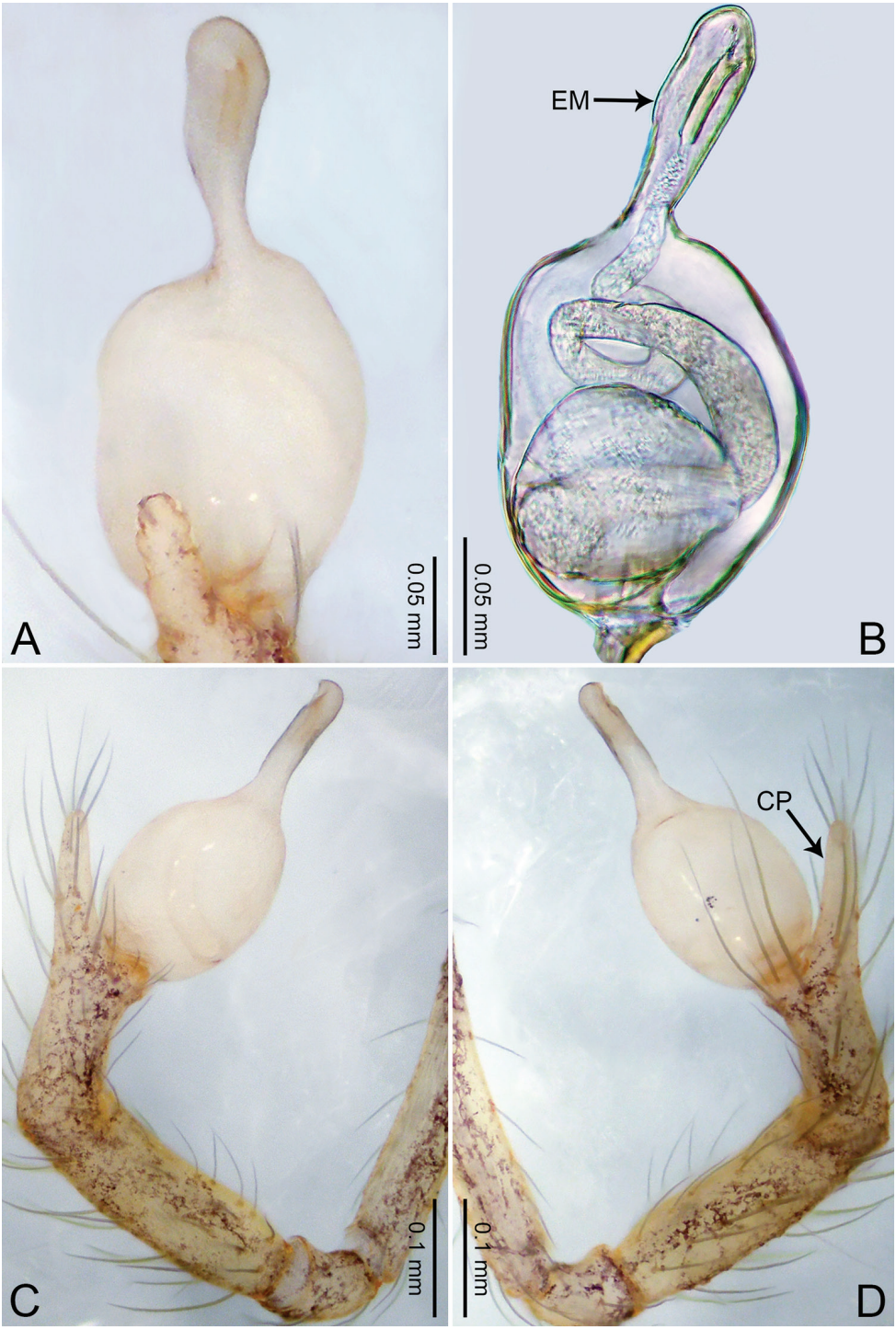

Figure 45. *Merizocera wenshan* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CP = cymbial protrusion, EM = embolus.

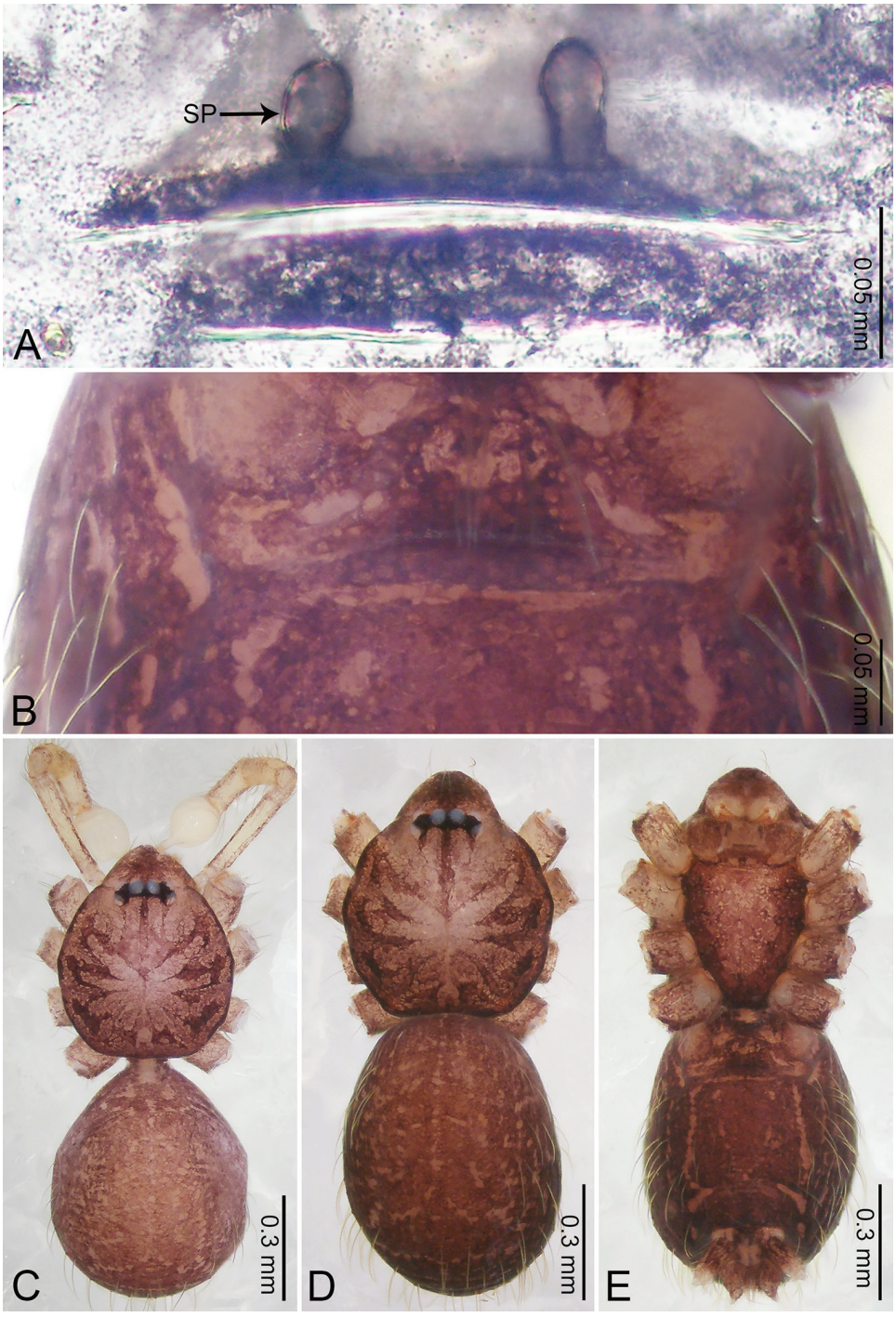

Figure 46. *Merizocera wenshan* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

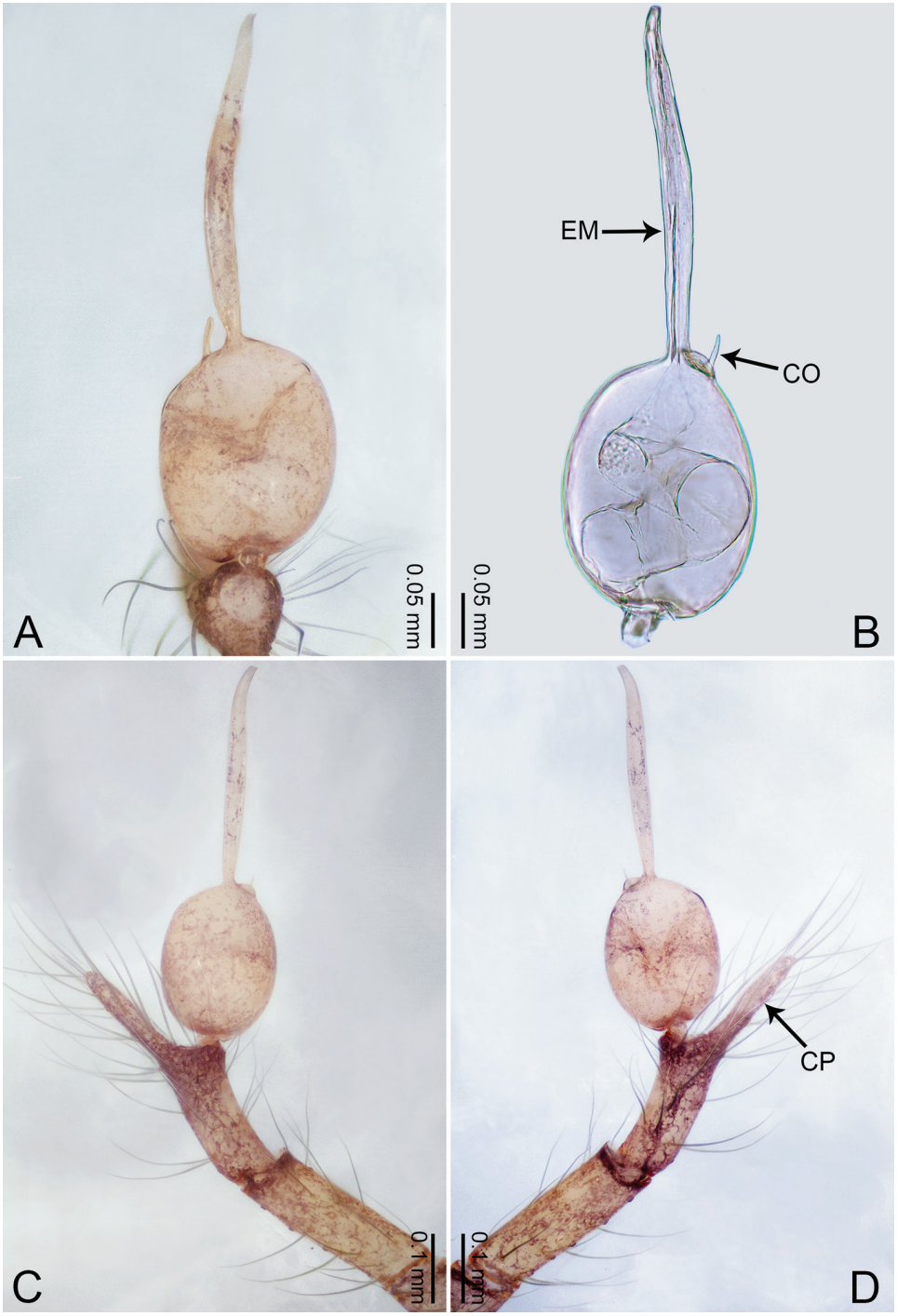

Figure 47. *Merizocera wui* sp. nov., holotype (**A, C, D**) and paratype (**B**) male. **A** Bulb, dorsal view **B** bulb, prolateral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, CP = cymbial protrusion, EM = embolus.

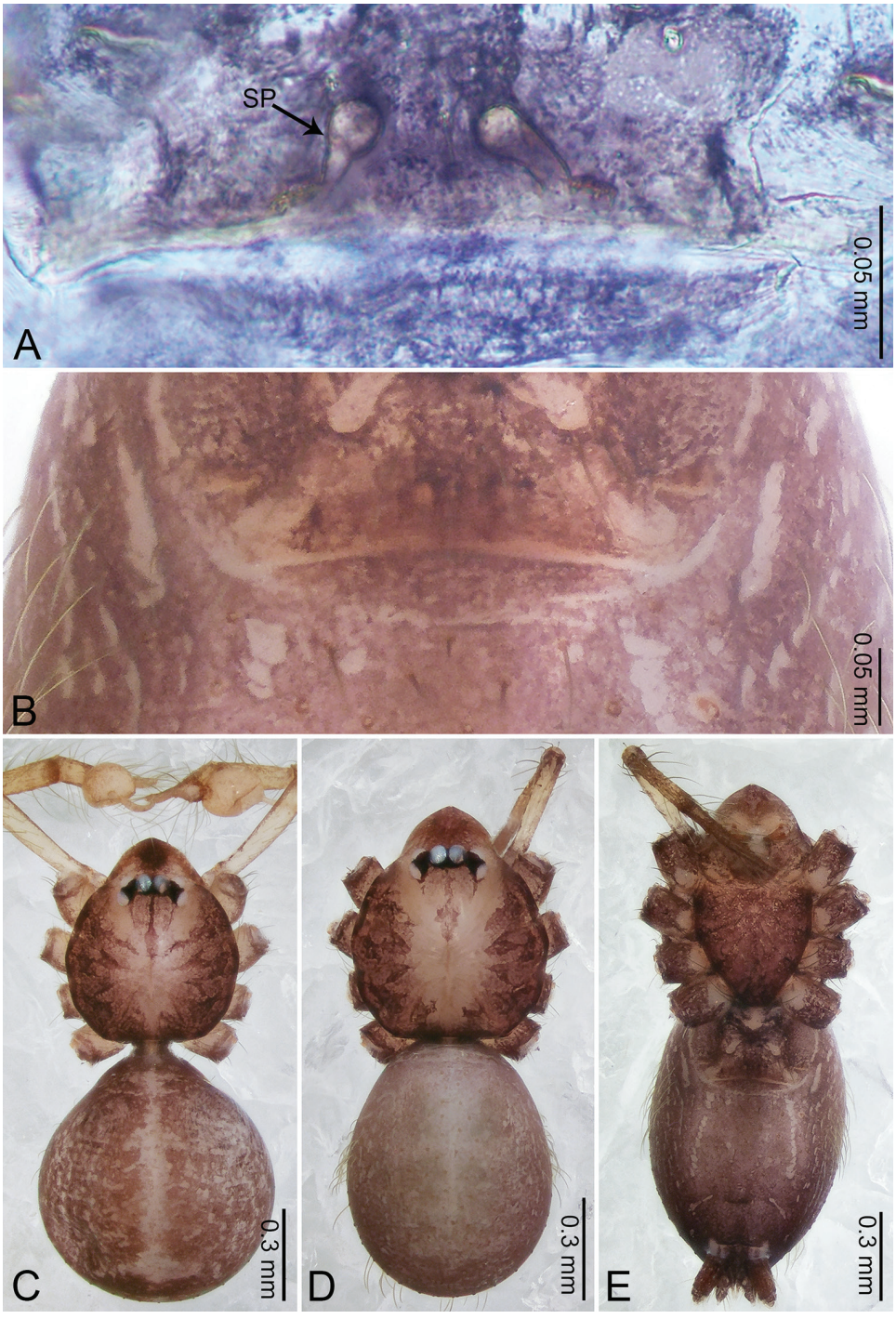

Figure 48. *Merizocera wui* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

Description. Male (holotype). Total length 1.53; carapace 0.67 long, 0.57 wide; abdomen 0.84 long, 0.79 wide. Carapace circular, brownish, with dark brown radiating marks (Fig. 48C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus, labium and Sternum dark brown. Abdomen ovoid, dark brown but dark grey dorso-medially. Legs light brown; measurements: I missing, II 4.34 (1.18, 0.22, 1.27, 1.10, 0.57), III 3.37 (0.88, 0.20, 0.95, 0.86, 0.48), IV 4.79 (1.19, 0.23, 1.45, 1.21, 0.71). Palp (Fig. 47A–D): femur slender, five times longer than patella; patella not swollen; tibia not swollen, half as long as femur; cymbium with distal protrusion, length ratio of dorsal elongation and cymbium 0.92; bulb spherical, with embolus and conductor arising distally; embolus slender and upright, twice longer than tegular; conductor needle-like, adjacent and basally connected to embolus.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 48D, E). Measurements: total length 1.42; carapace 0.70 long, 0.58 wide; abdomen 0.75 long, 0.60 wide. Leg measurements: I 4.11 (1.06, 0.21, 1.25, 0.99, 0.60), II missing, III 3.40 (0.89, 0.21, 0.97, 0.82, 0.51), IV 4.16 (1.06, 0.22, 1.24, 0.99, 0.65). Epigastric area (Fig. 48B): dark brown oval patch, medially with a pale brown slit. Endogyne (Fig. 48A) with a pair of clavate spermathecae, slightly angled toward each other, ratio of the width of a spermatheca to the interdistance of spermathecae 1:5.

Distribution. Known only from the type locality (Myanmar; Fig. 53).

***Merizocera yala* Li, sp. nov.**

http://zoobank.org/43BC8259-FDFE-471B-B90D-294820187195

Figures 49, 54

Type material. ***Holotype*:** female (IZCAS), near Suea Cave (6°31.36'N, 101°13.87'E, elevation 43 m), Mueang District, **Yala**, **Thailand**, 20 October 2015, P. Wongprom leg.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of females are discussed in *M. uva* sp. nov. Females with stalked spermathecae bearing globose ends (Fig. 49A).

Description. Female (holotype). Total length 1.33; carapace 0.59 long, 0.50 wide; abdomen 0.69 long, 0.54 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 49C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus and labium dark brown. Sternum dark brown, with distinct dark radiating lines. Abdomen ovoid, brownish but dark brown posteriorly and ventrally (Fig. 49B). Legs light brown; measurements: I, II, and IV missing, III 3.54 (0.97, 0.19, 1.01, 0.86, 0.51). Epigastric area (Fig. 49B): pale brown semi-circular patch, medially with dark brown horizontal slit. Endogyne (Fig. 49A) with a pair of twisted stalked spermathecae.

Male. Unknown.

Distribution. Known only from the type locality (Thailand; Fig. 54).

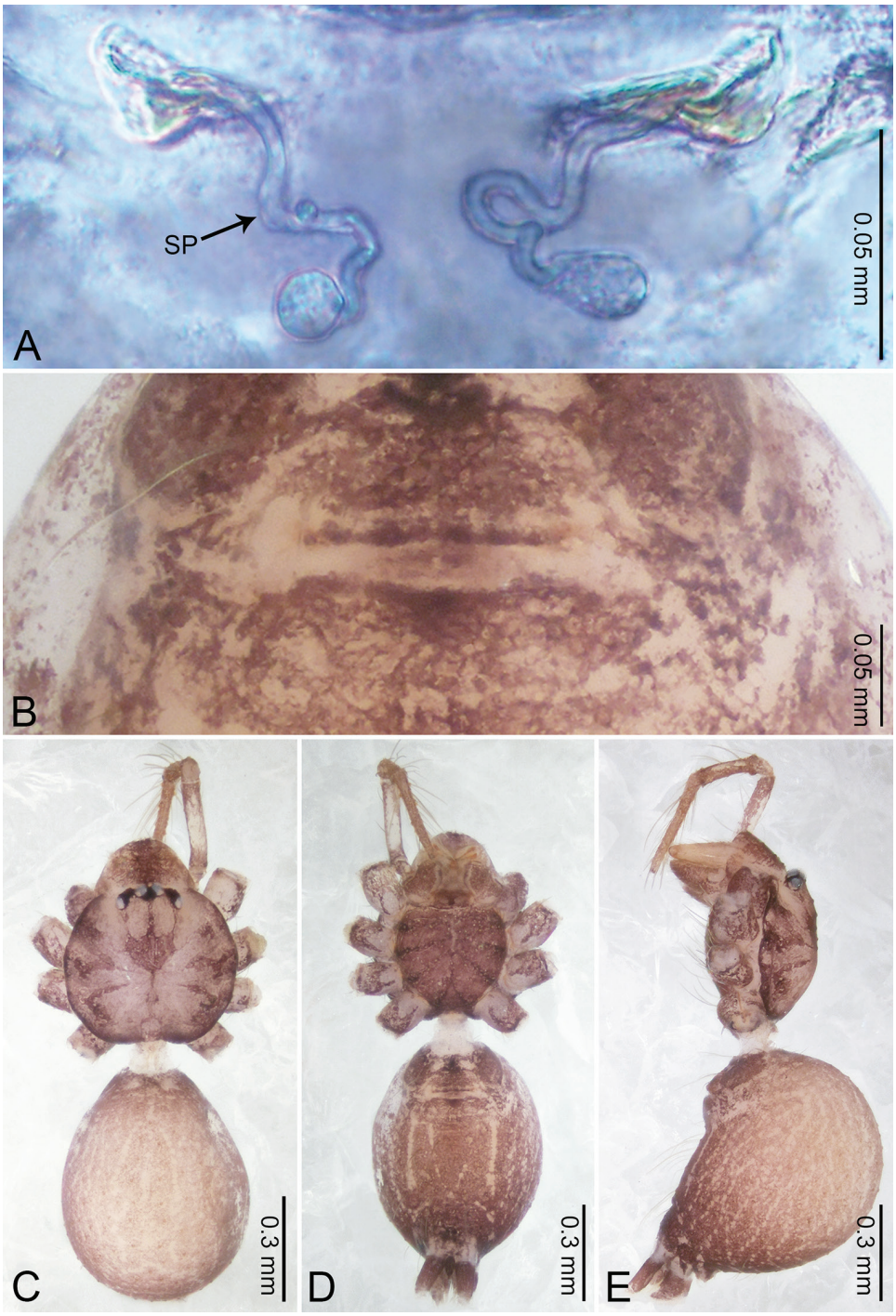

Figure 49. *Merizocera yala* sp. nov., holotype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view **E** female habitus, lateral view. Abbreviation: SP = spermatheca.

***Merizocera yuxi* Li, sp. nov.**
http://zoobank.org/31847E90-FA82-42CB-A238-B99637E64341
Figures 50, 51, 53

Merizocera sp. 249: Li and Li 2018 (molecular data).

Type material. ***Holotype*:** male (IZCAS), Guzhouyelin (24°6.63'N, 101°51.00'E, elevation 1987 m), Xinhua Town, Xinping County, Yuxi, **Yunnan**, **China**, 2 June 2015, Z. Chen and Y. Li leg. ***Paratypes*:** 1 male and 2 females (IZCAS), same data as holotype.

Etymology. The specific name refers to the type locality; noun in apposition.

Diagnosis. Diagnosis features of males and females are discussed in *M. betong* sp. nov. Males with swollen pyriform bulb, and embolus with a crinkly and flattened tip (Fig. 50B). Females with two pairs of tubular spermathecae (Fig. 51A).

Description. Male (holotype). Total length 1.25; carapace 0.61 long, 0.51 wide; abdomen 0.62 long, 0.48 wide. Carapace circular, brown, with dark brown radiating marks (Fig. 51C). Fovea shallow. Thoracic region distinctly elevated medially. Clypeus and labium dark brown. Sternum dark brown, with dark radiating lines. Abdomen ovoid, dark brown. Legs light brown; measurements: I, III, and IV missing, II 3.11 (0.83, 0.20, 0.89, 0.70, 0.49). Palp (Fig. 50A–D): femur slender, four times longer than patella; patella not swollen; tibia not swollen; cymbium with distal protrusion, 1/3 length of femur, length ratio of dorsal elongation and cymbium 1.13; bulb pyriform, with embolus arising distally; embolus crinkly with flattened tip, with distinct swollen section medially, similar length as the tegular; conductor absent.

Female (paratype). Similar to male in colouration and general features but slightly larger (Fig. 51D, E). Measurements: total length 1.45; carapace 0.66 long, 0.54 wide; abdomen 0.79 long, 0.63 wide. Leg measurements: I 3.46 (0.90, 0.22, 1.01, 0.79, 0.54), II 2.99 (0.79, 0.20, 0.84, 0.67, 0.49), III missing, IV 3.69 (0.91, 0.21, 1.10, 0.84, 0.63). Epigastric area (Fig. 51B): dark brown, nearly trapezoidal patch. Endogyne (Fig. 51A) with two pairs of spermathecae, lateral pairs globose, median pairs clavate, lateral pairs attached basally with the median pairs.

Distribution. Known only from the type locality (China; Fig. 53).

Discussion

Males of *Merizocera* can be distinguished from *Psiloderces* by the following characters: In *Merizocera* the cymbium and bulb are of similar lengths, or rarely the bulb is longer than the cymbium. In contrast, the cymbium is generally longer than the bulb in *Psiloderces*. *Merizocera* can be divided into six morphological groups of species based on male palps. *Merizocera betong* sp. nov., *M. ranong* sp. nov., *M. wenshan* sp. nov., *M. wui* sp. nov., and *M. yuxi* sp. nov. form a group of species with a rounded or almost pyriform bulb and a rather simple embolus (not overly elongated and curved); *M. thenna* sp. nov., *M. salawa* sp. nov., *M. kurunegala* sp. nov., *M. peraderiya* sp. nov., *M. colombo* sp. nov., *M. kandy* sp. nov.,

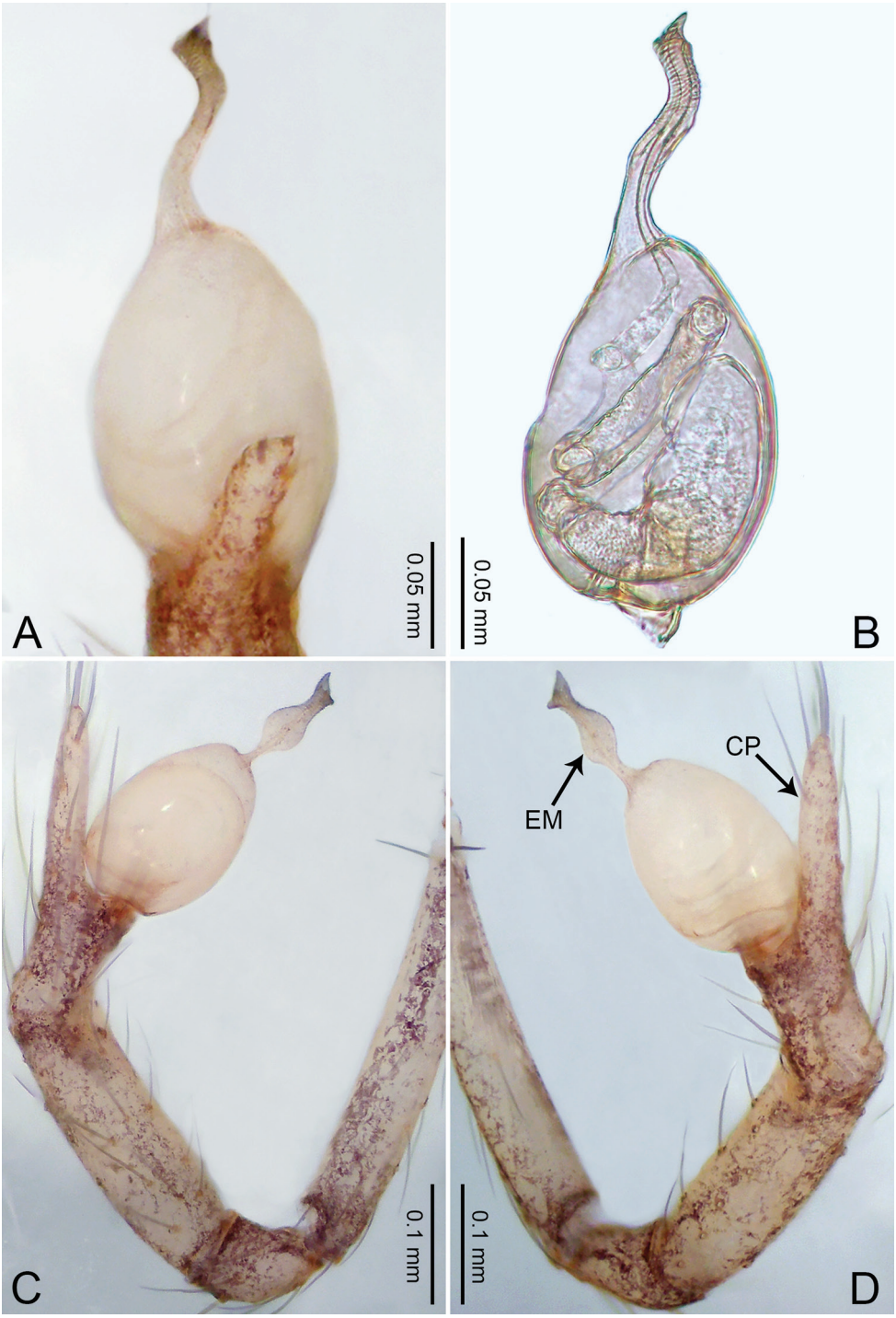

Figure 50. *Merizocera yuxi* sp. nov., holotype male. **A** Bulb, dorsal view **B** bulb, dorsal view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CP = cymbial protrusion, EM = embolus.

Figure 51. *Merizocera yuxi* sp. nov., holotype male and paratype female. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

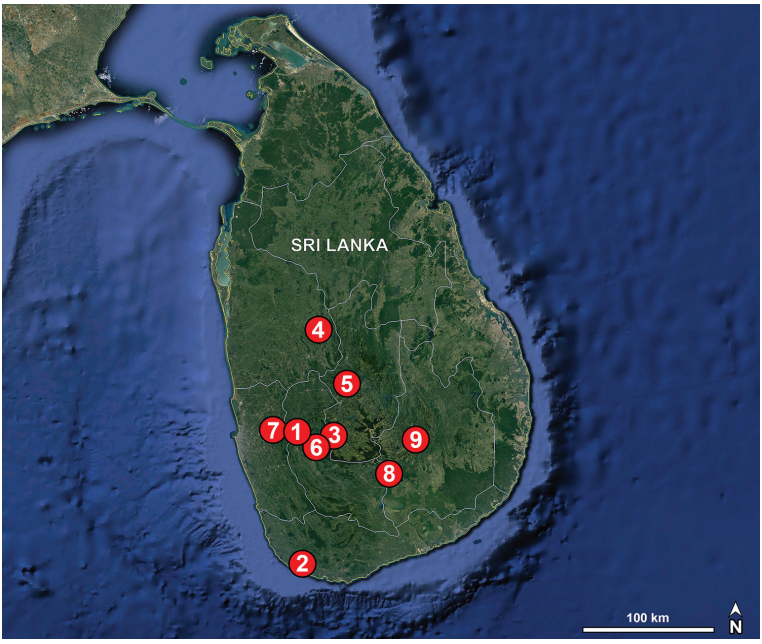

Figure 52. Distribution records of the new species of *Merizocera* from Sri Lanka. **1** *M. colombo* sp. nov. **2** *M. galle* sp. nov. **3** *M. kandy* sp. nov. **4** *M. kurunegala* sp. nov. **5** *M. peraderiya* sp. nov. **6** *M. ratnapura* sp. nov. **7** *M. salawa* sp. nov. **8** *M. thenna* sp. nov. **9** *M. uva* sp. nov.

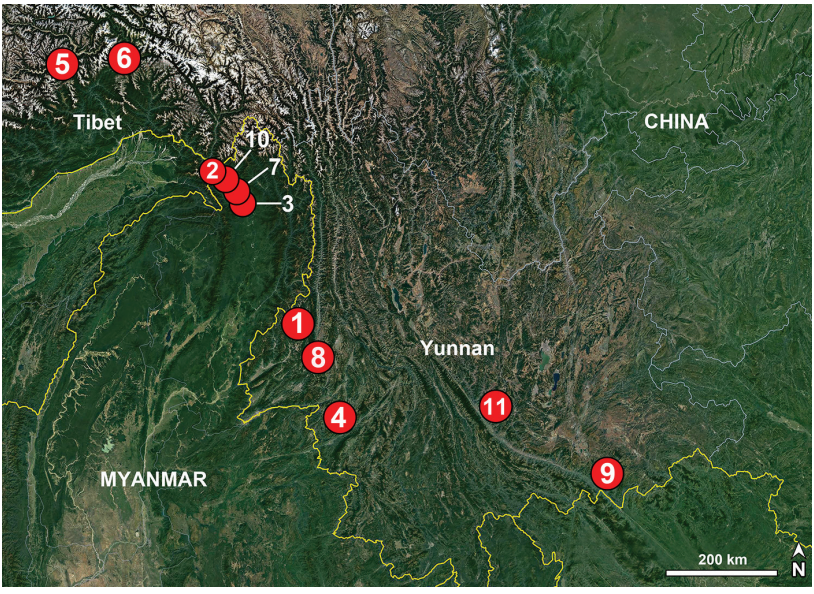

Figure 53. Distribution records of the new species of *Merizocera* from China and Myanmar. **1** *M. baoshan* sp. nov. **2** *M. hponkanrazi* sp. nov. **3** *M. kachin* sp. nov. **4** *M. lincang* sp. nov. **5** *M. mainling* sp. nov. **6** *M. nyingchi* sp. nov. **7** *M. putao* sp. nov. **8** *M. tengchong* sp. nov. **9** *M. wenshan* sp. nov. **10** *M. wui* sp. nov. **11** *M. yuxi* sp. nov.

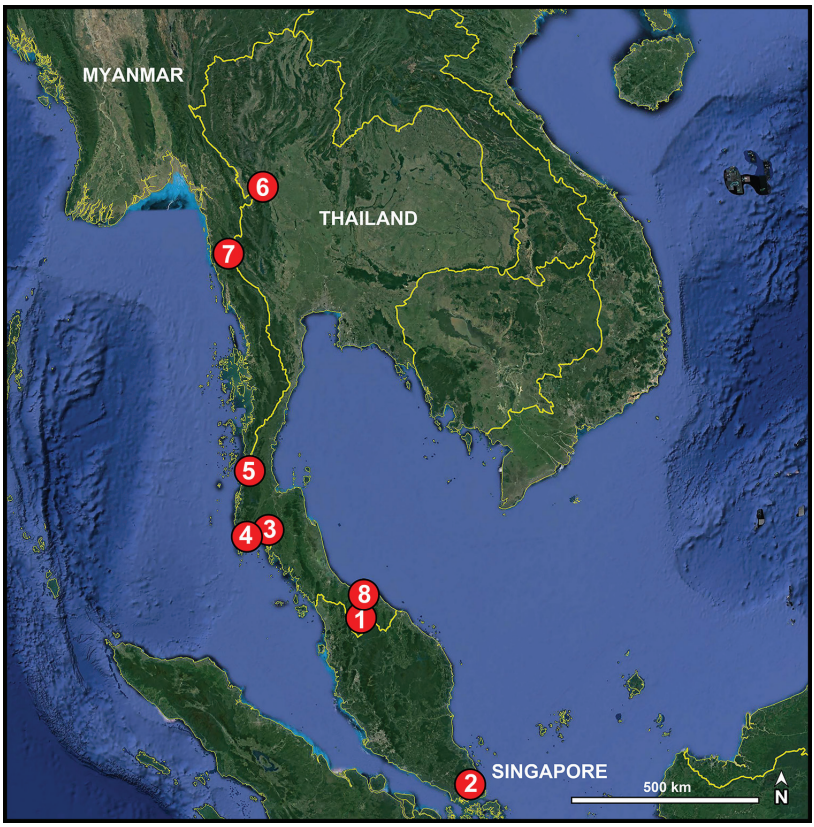

Figure 54. Distribution records of the new species of *Merizocera* from Thailand, Myanmar and Singapore. **1** *M. betong* sp. nov. **2** *M. mandai* sp. nov. **3** *M. krabi* sp. nov. **4** *M. phuket* sp. nov. **5** *M. ranong* sp. nov. **6** *M. tak* sp. nov. **7** *M. tanintharyi* sp. nov. **8** *M. yala* sp. nov.

M. oryzae, and *M. picturata* form a group of species with a furcate conductor and distally arising embolus; *M. tengchong* sp. nov., *M. putao* sp. nov., *M. kachin* sp. nov., and *M. baoshan* sp. nov. form a group of species with a distinctly elongated, slender bulb, distally with bent embolus or stalked apophysis; *M. mandai* sp. nov. and *M. crinita* form a group of species with similarly slender, distally arising embolus and conductor; *M. tanintharyi* sp. nov., *M. mainling* sp. nov., *M. cruciata*, and *M. brincki* form a group of species which have a short or inconspicuous cymbial protrusion, and distally arising embolus and conductor; and *M. krabi* sp. nov., *M. ratnapura* sp. nov., *M. phuket* sp. nov., *M. hponkanrazi* sp. nov., and *M. galle* sp. nov. form a group of species with a distinctly elongated and curved embolus. It is not feasible to co-relate the species groups based on female characters.

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RESEARCH ARTICLE

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Morphology of the immature stages of *Dasyhelea silvatica* Wang, Zhang & Yu with redescriptions of adults (Diptera, Ceratopogonidae)

Xue Lu[1], Chen Duan[1], Yuan Ning[1], Xiao Hong Jiang[1], Xiao Hui Hou[1]

1 *Zunyi Medical University, Zunyi 563000, Guizhou Province, China*

Corresponding author: Xiao Hui Hou (hxh19801122@163.com)

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Abstract

The immatures of the biting midge *Dasyhelea silvatica* are described and illustrated for the first time and a complete description of the adult male and female are provided using scanning electron and compound microscopes. The specimens were collected from flooded soil near a pond in Guizhou Province, China, and reared in the laboratory.

Keywords

Adult, aquatic, biting midge, fourth instar larva, pupa

Introduction

Biting midges of the genus *Dasyhelea* Kieffer, 1911 (Diptera, Ceratopogonidae) are a large and complex group of Ceratopogonidae with diverse morphology and biology, and are cosmopolitan in distribution except in Antarctica (Grogan and Wieners 2006). At present there are 192 extant species of *Dasyhelea* in China (Duan et al. 2019; Nie et al. 2019), but only eight of these species are known by their immature stages (Yu et al. 2005, 2013; Duan et al. 2019). This may be an indication that China has been under-

sampled historically compared to other countries. Therefore, efforts were made in order to study the immature stages of biting midges in China. During a recent entomological survey carried out in the vicinity of Xiaojiawan, a village in the Guizhou Province, immature specimens of *Dasyhelea silvatica* Wang, Zhang & Yu, 2014 were collected. The purpose of this paper is to provide a complete description, with illustrations, of the fourth instar larva and pupa of *D. silvatica* and a redescription of the adult male and female using a compound and a scanning electron microscope (LM and SEM).

Materials and methods

Larvae and pupae of *D. silvatica* were collected from flooded soil in Xiaojiawan, Guizhou Province in 2018, using a small shovel, and transferred to the laboratory. The larvae were individually placed in 24-well plates and fed with a sterile nutrient solution of *Chlorella*. Once they pupated, they were isolated in ampoule bottles on filter paper with sugar water. They were reared in an environmental chamber maintained at a temperature of 28 ± 2 °C, a relative humidity of 75 ± 2%, and a photoperiod of 12 h light and 12 h dark, and observed daily until adult emergence. The emergent adults, whole larvae, and pupae were preserved in ethanol at each stage. The specimens were mounted in Canada balsam following the technique described by Yu et al. (2005).

For the SEM study, one larva of *D. silvatica* was prepared following the technique of Ronderos et al. (2000, 2008). Ink illustrations were made using an attached camera lucida. Photographs were taken with a digital system adapted to an Olympus BX43 with a digital camera DP26. The studied material was deposited in the Insect Collection, Zunyi Medical University, Guizhou Province, China (**ICZU**). The morphological terms and identification methods of larvae, pupae and adults used follow Díaz et al. (2013), Borkent (2014) and Yu et al. (2005). The abbreviations used in this paper follow Duan et al. (2019).

Results

***Dasyhelea silvatica* Wang, Zhang & Yu, 2014**
Figures 1–3

Dasyhelea (*Dasyhelea*) *silvatica* Wang, Zhang & Yu, 2014: 312 (male and female, China).

Material examined. 3 males with pupal exuviae, 4 females with pupal exuviae, 3 fourth instar larvae, 2 larval exuviae. Xiaojiawan Village, Xinpu New District, Zunyi City, Guizhou Province, China, 27°43'22.83"N, 107°04'27.62"E, 7.VII.2018, alt. 866 m, Chen Duan leg. 2 larvae examined by SEM. Same data as above.

Descriptions. Fourth instar larva (Fig. 1A–J). Head capsule light brown, long, thin (Fig. 1A, B); chaetotaxy as in Fig. 1A. HL 0.25–0.27 (0.26, *N* = 2) mm; HW

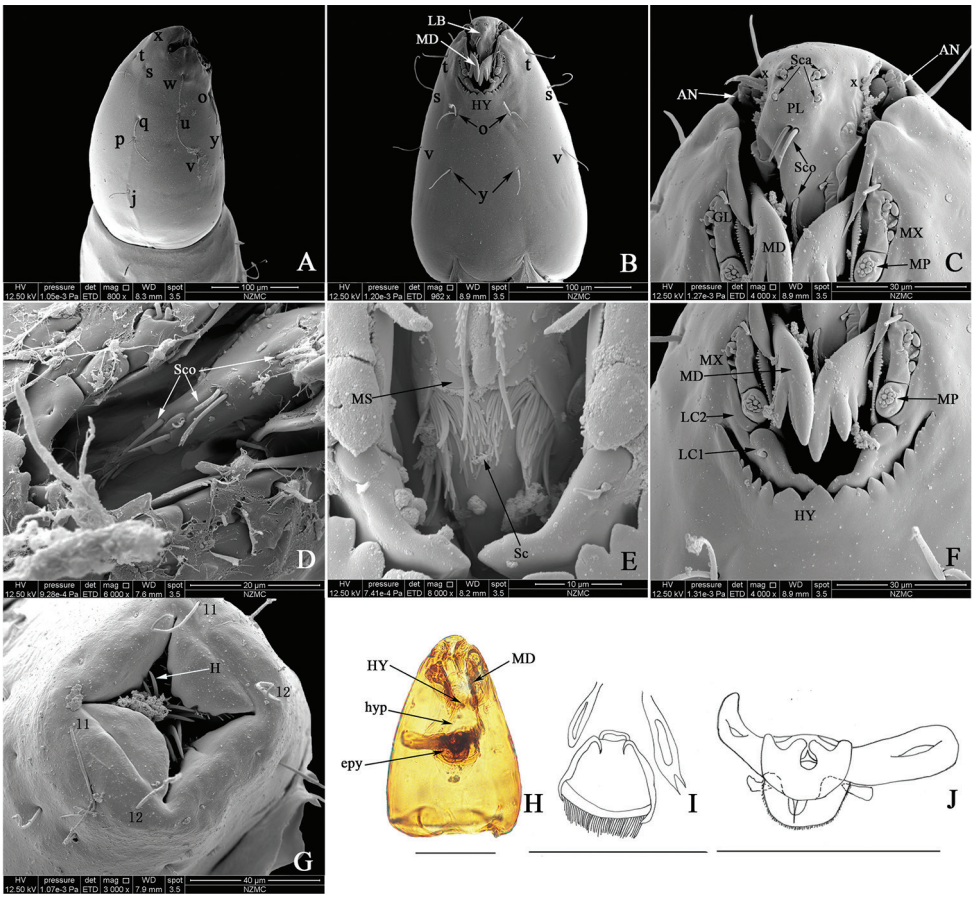

Figure 1. *Dasyhela silvatica* Wang, Zhang & Yu, fourth instar larva **A** chaetotaxy on the head capsule, lateral view (SEM) **B** chaetotaxy on the head capsule, ventral view **C** detail of labrum **D** sensilla coeloconica **E** detail of scopae **F** detail of mouthparts **G** caudal segment **H** head, ventral view **I** hypopharynx **J** epipharynx. Abbreviations: antenna (**AN**); epipharynx (**epy**); galeolacinia (**GL**); hypostoma (**HY**); hooks (**H**); hypopharynx (**hyp**); labrum (**LB**); lacinial sclerite 1 (**LC1**); lacinial sclerite 2 (**LC2**); mandible (**MD**); maxilla (**MX**); maxillary palpus (**MP**); messors (**MS**);palatum (**PL**); sensilla coeloconica (**Sco**); sensilla campaniformia (**Sca**); scopae (**Sc**); first lateral setae (**l1**); second lateral setae (**l2**). Scale bars: 0.1 mm (**G–I**).

0.16–0.17 (0.16, *N* = 2) mm; HR 1.56–1.58 (1.57, *N* = 2); SGW 0.07–0.08 (0.08, *N* = 2) mm; SGR 0.50–0.52 (0.49, *N* = 2). Antenna (Fig. 1C) short, cylindrical. Anterior portion of palatum (Fig. 1C) with four pairs of campaniformia sensilla; posterior portion with three pairs of coeloconica sensilla, two simple, one serrate (Fig. 1C, D); messors (Fig. 1E) well developed, stout, bisegment; scopae (Fig. 1E) well developed with elongate, strong pointed teeth. Mandible (Fig. 1B, C, F) stout, with four teeth, apical tooth more elongated, proximal tooth minute; MDL 0.07 (*N* = 2) mm, MDW 0.01 (*N* = 2) mm. Maxilla (Fig. 1C, F) well sclerotized; galeolacinia (Fig. 1C) with concentrated flap-like papillae, short seta; maxillary palpus (Fig. 1C, F)

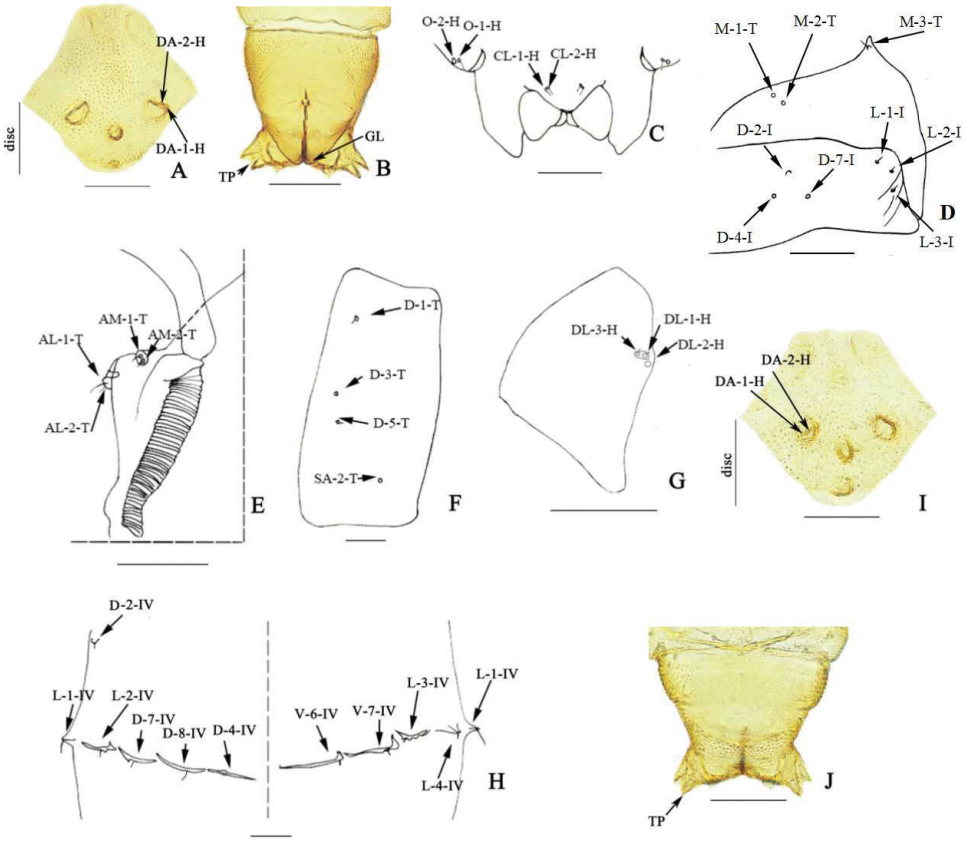

Figure 2. *Dasyhelea silvatica* Wang, Zhang & Yu. Male pupa (**A–H**), female pupa (**I, J**) **A, I** dorsal apotome **B** segment 9 **C** clypeal/labral sensilla and ocular sensilla **D** metathoracic sensilla, and first abdominal segment **E** anterolateral and anteromedial sensilla **F** dorsal and supra-alar sensilla **G** dorsolateral cephalic sclerite sensilla **H** segment 4 **J** segment 9. Abbreviations: Anterolateral sensilla (AL-1-T, AL-2-T, AL-3-T); clypeal/labral sensilla (CL-1-H, CL-2-H); dorsal apotome sensilla (DA-1-H, DA-2-H); dorsolateral cephalic sclerite sensilla (DL-1-H, DL-2-H, DL-3-H); dorsal setae (D-1-T, D-2-T, D-3-T); dorsal sensilla of segment 9 (D-5-IX); methatoracic sensilla (M-2-T, M-3-T); ocular sensilla (O-1-H, O-2-H) respiratory organ (RO); tergite 1 sensilla (D-2-I, D-4-I, D-7-I, L-1-I, L-2-I, L-3-I); genital lobe (**GL**); terminal process (**TP**). Scale bars: 0.1 mm.

cylindrical, with seven or eight apical papillae. Hypostoma (Fig. 1F) with three large mesal teeth, flanked with four strong, lanceolate lateral teeth each side. Lacinial sclerite 1 with one seta; lacinial sclerite 2 without seta (Fig. 1F). Epipharynx (Fig. 1H–J) strongly sclerotized, dorsal comb moderately wide, round, subequally elongate, the middle of trailing edge with a large number of spines on the semicircular transparent membranous structure; lateral arms stout, elongate, with two auxiliary sclerites; LAW 0.10–0.13 (0.12, *N* = 2) mm, DCW 0.03–0.04 (0.04, *N* = 3). Hypopharynx (Fig. 1H, I) stout, heavily sclerotized, posterior comb straight with fringe, labium

sclerotized. Thoracic pigmentation diffused, pale brown. Abdominal segments whitish, with diffused pale brown pigmentation. Caudal segment (Fig. 1G) with long stout hooks with pointed tips.

Pupa (Fig. 2A–J). ***Male.*** Total length 2.51–2.71 (2.63, *N* = 3) mm. General coloration of exuviae pale brown. Head: dorsal apotome (Fig. 2A) 2.15 × broader than long, apex rounded, surface covered with brown rounded tubercles, anterior margin straight, lateral margin smooth, with three anterior wrinkles; apotome sensilla (Fig. 2A): DA-1-H elongate, thin seta, insert on well-developed tubercle, DA-2-H sensillum campaniform at base; disc surface covered by stout, rounded spinules; DAL 0.12–0.13 (0.13, *N* = 2) mm, DAW 0.26–0.29 (0.28, *N* = 2) mm, DAW/DAL 2.15–2.25. Respiratory organ apex dark brown, 7.6 × longer than broad, with circular fold, 12 apical, five lateral pores; ROL 0.22–0.25 (0.23, *N* = 3) mm, ROW 0.03 (0.03, *N* = 3) mm; pedicel pale brown, short, length 0.01 mm, ROP/ROL 0.05–0.07 (0.05, *N* = 3). Mouthparts with mandible, lacinia absent; two clypeal/labrals (Fig. 2C), CL-1-H and CL-2-H medium-sized, thin setae; two ocular sensilla, O-1-H long, thin seta, O-2-H campaniform sensillum (Fig. 2C); metathoracic sensilla (Fig. 2D): M-1-T and M-2-T campaniform sensilla; M-3-T long, thin seta. Tergite 1 (Fig. 2D) setae as follows: D-2-I papilla; D-4-I, D-7-I campaniform sensilla; L-1-I, L-2-I, L-3-I medium-sized, thin setae; two anterolateral sensilla (Fig. 2E): AL-1-T long, thin seta, AL-2-T medium-sized, thin seta; two anteromedial sensilla (Fig. 2E): AM-1-T, AM-2-T medium-sized, thin setae. Cephalothorax surface with small rounded tubercles, cephalothorax length 0.78–0.83 (0.80, *N* = 3) mm, width 0.59–0.64 (0.62, *N* = 3) mm. Cephalothoracic sensilla as follows (Fig. 2F): three dorsal setae, D-1-T and D-5-T short, thin setae, D-3-T campaniform sensillum, SA-2-T supra-alar campaniform sensillum. Cephalothoracic sensilla as follows: three dorsolateral cephalic sclerite sensilla (Fig. 2G), DL-1-H and DL-3-H medium-sized, thin setae, DL-2-H campaniform sensillum. Abdomen covered with short, stout spinules on anterior, posterior margin. Segment 4 (Fig. 2H) with sensillar pattern as follows: D-2-IV short, stout seta; D-4-IV and D-7-IV campaniform sensilla, D-8-IV long, thin setae, all located on flattened tubercles; L-1-IV long, stout seta, L-2-IV short, thin seta, L-3-IV short, stout seta, L-4-IV short, thin seta, all located on triangular tubercles; V-6-IV and V-7-IV short, stout setae, also located on flattened tubercles. Segment 9 (Fig. 2B) 1.01 × longer than wide, length 0.20–0.22 (0.21, *N* = 3) mm, width 0.21–0.22 (0.22, *N* = 3) mm; ventral and dorsal surfaces with many spinules; TP triangular, elongated, acute, length 0.03 (0.03, *N* = 3) mm.

Female. Similar to male with usual sexual differences. General coloration of exuviae pale brown, except dorsolateral cephalic sclerite brown. Dorsal apotome (Fig. 2I), DAL 0.12–0.13 (0.13, *N* = 2) mm, DAW 0.26–0.29 (0.27, *N* = 2) mm, DAW/DAL 2.14–2.26 (2.20, *N* = 2). Cephalothorax length 0.83–1.07 (0.95, *N* = 2) mm, width 0.66–0.80 (0.72, *N* = 2) mm. ROL 0.23–0.27 (0.25, *N* = 2) mm, ROW 0.03 (0.03, *N* = 2) mm; pedicel length 0.01 (*N* = 2) mm, ROP/ROL 0.04 (0.04, *N* = 2). Segment 9 (Fig. 2J) length 0.18–0.23 (0.21, *N* = 2) mm, width 0.22–0.23 (0.23, *N* = 2) mm; ventral surface with many spicules, single funnel-like structure medially. TP triangular, elongated, pointed (Fig. 2J).

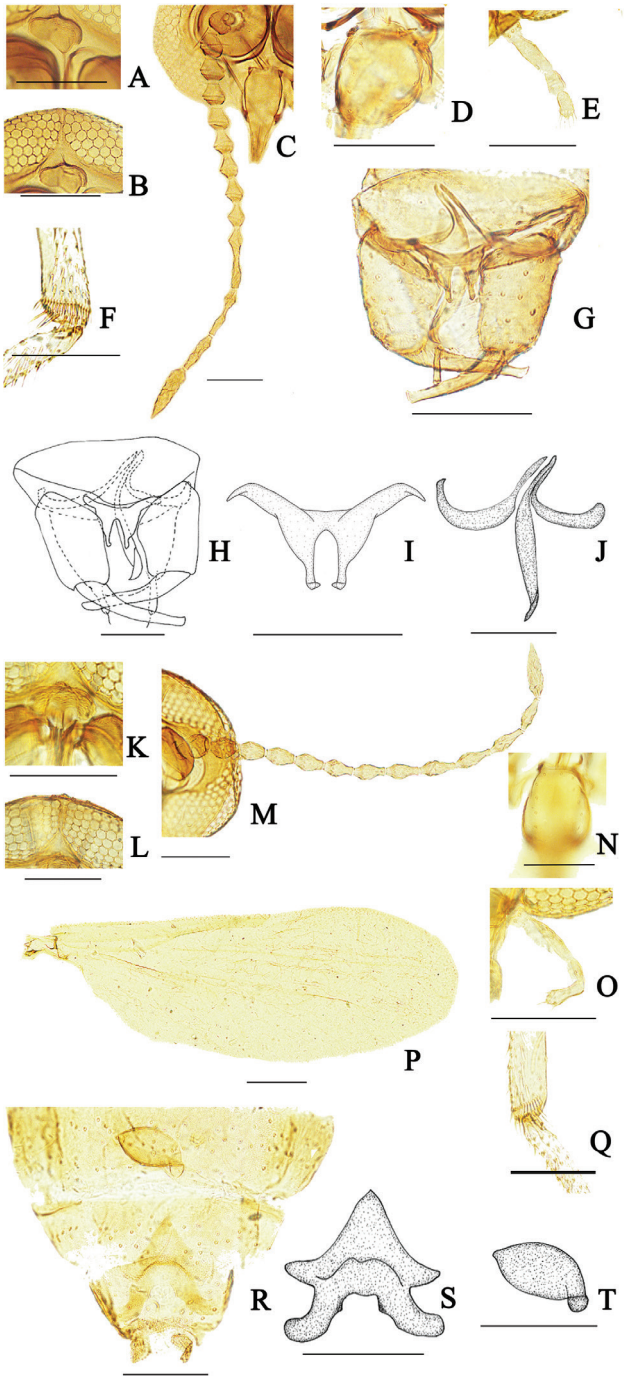

Figure 3. *Dasyhelea silvatica* Wang, Zhang & Yu. Male adult (**A–J**), female adult (**K–T**) **A, K** frontal sclerite, anterior view **B, L** eyes contiguous, anterior view **C, M** flagellomeres, anterior view **D, N** clypeus, anterior view **E, O** palpus, anterior view **F** metatibial distae comb **G** genitalia, ventral view **H** genitalia, ventral view **I** aedeagus **J** paramere **P** wing **Q** hind tibial comb **R** subgenital plate and spermatheca, ventral view **S** subgenital plate, ventral view **T** spermatheca, ventral view. Scale bars: 0.1 mm.

Redescription of adults (Fig. 3A–T). ***Male*** (Fig. 3A–J). ***Head.*** Brown. Frontal sclerite nearly round, with long, slender ventral projection (Fig. 3A). Eyes (Fig. 3B) contiguous, abutting medially for length of 1.0 ommatidia, with interfacetal hairs. Antennal flagellum (Fig. 3C) brown, flagellomere 13 with apical projection; AR 1.23. Clypeus (Fig. 3D) with five pairs of setae. Palpus (Fig. 3E) brown; third segment slender, PR 2.67, the length almost the sum of the fourth and fifth segments. Lengths of palpus segments in ratio of 10: 15: 30: 18: 17.

Thorax. Scutum shallow, scutellum yellow, with ten stout setae. Legs light brown, hind tibial comb with seven spines (Fig. 3F); foreleg TR 2.30, midleg TR 2.40, hind leg TR 2.46. Wing length 1.23 mm, width 0.40 mm, CR 0.50; wing membrane hyaline, densely covered with microtrichia, cubital fork at same level of distal portion of second radial cell. Halter light brown.

Abdomen. Brown. Genitalia: tergite 9 nearly trapezoidal with prominent, long with apical stout seta, apico-lateral processes. Posteromedial margin of sternite 9 with inconspicuous projection, Gonocoxite stout, 1.73 X longer than greatest width, gonostylus slender (Fig. 3G, H). Aedeagus (Fig. 3G, I) without median process, posterolateral arm symmetry, each arm tapers from the proximal portion to the distal portion, apex of arm curving inwards, arch high. Parameres (Fig. 3G, J) separate, with median lobe short, thin, lateral lobe curve, stout gradually.

Female (Fig. 3K–T). ***Head.*** Frontal sclerite oval, with long, slender ventral projection (Fig. 3K). Eyes (Fig. 3I) contiguous. Antennal flagellum (Fig. 3M) brown, with sculpture, flagellomere 13 with apical projection; AR 1.01. Clypeus (Fig. 3N) with five pairs of setae. Palpus (Fig. 3O) brown; third segment slender, PR 2.70, lengths of palpus segments in ratio of 3: 6: 14: 6: 8.

Thorax. Wing length 1.29–1.34 (1.22, $N = 2$) mm, width 0.51–0.54 (0.53, $N = 2$) mm, CR 0.48 (Fig. 3P). Hind tibial comb with ten spines (Fig. 3Q); foreleg TR 2.02, midleg TR 2.30, hind leg TR 2.38.

Abdomen. Similar to male. Subgenital plate (Fig. 3R, S) star-shaped, arch high, inner arch with a pair of processes. Spermatheca long ovoid (Fig. 3R, T), diameter 82 μm, neck long, curved, length 14.0 μm.

Distribution. China (Fujian Province, Guizhou Province).

Discussion

Dasyhelea silvatica belongs to the subgenus *D.* (*Dasyhelea*) (Wang et al. 2014). The fourth instar larva of *D. silvatica* is very similar to its congeners *D. azteca* Huerta & Grogan by virtue of the antenna being short, the lateral arms of the epipharynx stout and the anterior portion of palatum with four pairs of campaniformia sensilla, but it can be distinguished from the former by the posterior portion of palatum bearing two pairs of coeloconica sensilla, the MD with three teeth, and the MP with only three small papillae. In addition, the fourth instar larva of *D. silvatica* is also similar to that of *D. flavifrons* (Guérin-Méneville), recently described by Díaz et al. (2019) with the brown head capsule, the posterior portion of palatum with four pairs of campaniformia

sensilla and three pairs of coeloconica sensilla, the posterior comb of the hypopharynx has a fringe; however, *D. flavifrons* differs by the galeolacinia with 5–6 papillae and the MP with only three or four papillae.

The common characteristics of the pupae of *D. silvatica* and *D. azteca* are as follows: the small rounded tubercles on cephalothorax; the surface of dorsal apotome also has rounded tubercles; the abdominal segments covered with spinules, and the sensilla of the fourth abdominal segment are all located on flattened tubercles. But the pupa of *D. azteca* differs from *D. silvatica* by having a single ocular sensillum, the exuviae is brown in general coloration, and the RO has 22–24 apical and three or four lateral pores, and without a pedicel. The pupa of *D. silvatica* is similar to *D. flavifrons* by virtue of the three dorsolateral cephalic sclerite sensilla and the tergite of the first abdominal segment with the L-1-IV represented by a long and stout seta, but the one ocular sensilla, the RO bearing 14–16 apical and four or five lateral pores, anterolateral sensilla with AL-1-T, AL-2-T long, thin seta and AL-3-T short, stout seta distinguish from *D. silvatica*. Furthermore, the pupa of *D. silvatica* is similar to that of *Dasyhelea eloyi* Díaz & Ronderos, 2013 with small rounded tubercles on cephalothorax surface and the RO with scale-like spines, but the latter has 6–8 lateral pores compared to *D. silvatica* with 5 lateral pores.

Duan et al. (2019) described the larvae and pupae of *D. alula* collected in the same small wetland as *D. silvatica*. The fourth instar larva of *D. silvatica* shows similarities with that of *D. alula* in the rear comb of the hypopharynx with a fringe and two auxiliary sclerites on the lateral arms of the epipharynx. However, the fourth instar larva of *D. alula* is distinctly distinguished by its head capsule being yellowish, short, and wide; three teeth of the mandible are the same size; and hypostoma has the mesal portion smooth. The pupa of *D. alula* differs in the smaller total length (1.97 mm); RO having 7–8 apical and three lateral pores; anterolateral sensilla with AL-1-T medium-sized, thin seta and AL-3-T short, stout seta; the tergite I without L-2-I and L-3-I setae.

Finally, we found a semicircular, transparent membrane, strongly varying in shape, present at the trailing edge of the epipharynx of *D. silvatica*.

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RESEARCH ARTICLE

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A new Terrarana frog of genus *Pristimantis* from an unexplored cloud forest from the eastern Andes, Colombia

Andrés R. Acosta-Galvis[1], Ana M. Saldarriaga-Gómez[2], Beatriz Ramírez[4], Mario Vargas-Ramírez[2,3]

1 *Colecciones Biológicas, Subdirección de Investigaciones, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Carrera 8 No 15–08, Claustro de San Agustín, Villa de Leyva, Boyacá, Colombia* **2** *Grupo Biodiversidad y Conservación Genética, Instituto de Genética, Universidad Nacional de Colombia, Bogotá, Colombia. Calle 53 # 35–83, Edificio 426, Bogotá D.C., Colombia* **3** *Estación de Biología Tropical Roberto Franco (EBTRF), Carrera 33 #33–76, Villavicencio, Meta, Colombia* **4** *Asociación de Becarios de Casanare-ABC, Carrera 39#15–35, Yopal, Casanare, Colombia*

Corresponding author: Andrés R. Acosta-Galvis (aacosta@humboldt.org.co); Mario Vargas-Ramírez (maavargasra@unal.edu.co)

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Abstract

A new species of *Pristimantis* (Craugastoridae, subgenus *Pristimantis*) is described from a relict and unexplored cloud forest in the western slope from Cordillera Oriental of the Colombian Andes. The specific name was chosen by consensus expert scientists and local people. *Pristimantis chamezensis* **sp. nov.** is easily distinguished from congeneric species by having a gray iris with black reticulations in life, subconical tubercles on the upper eyelid, the chin edged with irregular, dark-brown blotches, and conical heel tubercles. The phylogenetic analyses suggest that the origin and radiation of its clade may have occurred in the highlands. With the description of *P. chamezensis* **sp. nov.**, we identify 14 species distributed throughout the eastern slope of the Andes that are associated with the Orinoco Basin.

Keywords

Casanare, Cis-Andean, Cordillera Oriental, diversity, phylogeny, South America, taxonomy

Introduction

The amphibian fauna from Colombia is among the richest and most diverse in the world (Lynch 1999; Grant et al. 2008) and includes 843 species (Acosta-Galvis 2020). A significant number of these species is grouped in the so-called Terrarana; an unranked taxonomic grouping of at least four closely related families characterized by direct development, egg embryos, and terrestrial reproduction (Hedges et al. 2008; Heinicke et al. 2009, 2018). Terrarana richness in Colombia includes 268 species in 13 genera (Acosta-Galvis 2020), among which the frogs of the *Pristimantis* genus represent the greatest diversity with 83% of the described species.

Morphologically, frogs of the genus *Pristimantis* are easily recognizable among other features by terminal discs on expanded digits and T-shaped terminal phalanges, a dentigerous process of the vomers usually present, and toe IV much longer than toe III (Hedges et al. 2008; Duellman and Lehr 2009). However, this genus still has latent phylogenetic challenges (Navarrete et al. 2016), and recent proposals, based on molecular phylogenies (Hedges et al. 2008; Padial et al. 2014; Páez and Ron 2019; Reyes-Puig et al. 2020), reassigned or excluded members of the species groups from evolutionary arrangements, which were previously based solely on morphological evidence (Lynch and Duellman 1980, 1997).

The genus *Pristimantis* in Colombia is represented by 223 formally described species (Acosta-Galvis 2020). The geographic and ecological complexity of the Andes harbors the greatest richness and rate of endemism in contrast to the lowlands of the Amazon and Pacific basins (Lynch et al. 1997). Current geological evidence of the north-Andean region indicates that the northern formations in Colombia (Occidental, Central, and Oriental mountains ranges) have promoted speciation processes in the genus *Pristimantis* and, therefore, have high diversity and endemism (Lynch and Duellman 1997; Lynch 1999; García-R et al. 2012; Mendoza et al. 2015; Meza-Joya and Torres 2016; Acevedo et al. 2020). Among these geographical units, the Cordillera Oriental contains 44 species, with 13 species inhabiting the Andean and sub-Andean forests on the eastern slopes (Table 1), as part of the Orinoco basin (Acosta-Galvis et al. 2010; Rivera-Correa et al. 2016; Ospina-Sarria and Angarita-Sierra 2020; Acevedo et al. 2020).

During field studies along an unexplored cloud forest (2140 m a.s.l.) in the Cordillera Oriental, we collected several specimens of *Pristimantis* that, due to their morphological characters, are not assignable to any described species in this region. Based on the analysis of its molecular data and morphology, we describe a new species recognized by its molecular and morphological distinctiveness.

Methods

Study area

We collected by actively searching from September 2 to November 29, 2010, using intensive visual encounter surveys (Crump and Scott 1994) during evenings in the cloud

Table 1. Species of the genus *Pristimantis* from the eastern slope of Cordillera Oriental (Orinoco Basin) in Colombia.

Genus (Subgenus) Species	Species group	Ecoregional distribution	Altitude(m a.s.l)	Reference
Pristimantis (*Pristimantis*) *vilarsi*	*conspicillatus* group	sub-Andean, Amazonian and Orinoco.	200–600	Lynch 1975; 1980, 1994; Padial et al. 2014; Heyer and Barrio-Amorós 2009.
Pristimantis (*Pristimantis*) *medemi*	*conspicillatus* group	Andean and sub-Andean.	450–2400	Lynch 1994, 2006; Malambo and Marin 2006; Acosta-Galvis et al. 2010; Acosta-Galvis and Alfaro-Bejarano 2011.
Pristimantis (*Pristimantis*) *carranguerorum*	*conspicillatus* group	Andean.	1350–2060	Lynch 1994; Renjifo-Rey 2005; Acosta-Galvis and Alfaro-Bejarano 2011; Anganoy-Criollo and Rámirez 2017.
Pristimantis (*Hypodictyon*) *w-nigrum*	*ridens* group	Andean and sub-Andean.	800–3000	Cochran and Goin 1970; Lynch and Duellman 1980; Bernal and Lynch 2008.
Pristimantis(*Pristimantis*) *savagei*	Unassigned	Andean and sub-Andean.	600–3000	Pyburn and Lynch 1981; Lynch 1994; Ruiz-Carranza et al. 1996; Acosta-Galvis 2000; Lynch 2006; Bernal and Lynch 2008; Acosta-Galvis et al. 2010; Acosta-Galvis and Alfaro-Bejarano 2011.
Pristimantis (*Pristimantis*) *frater*	Unassigned	Andean and sub-Andean.	600–3000	Pyburn and Lynch 1981; Lynch 1994; Ruiz-Carranza et al. 1996; Acosta-Galvis 2000; Lynch 2006; Bernal and Lynch 2008; Acosta-Galvis et al. 2010; Acosta-Galvis and Alfaro-Bejarano 2011.
Pristimantis (*Pristimantis*) *bogotensis*	Unassigned	Andean, sub-paramos and paramos.	2410–3520	Cochran and Goin 1970; Ruiz-Carranza et al. 1996; Acosta-Galvis 2000; Bernal and Lynch 2008.
Pristimantis (*Pristimantis*) *anolirex*	Unassigned	Andean, sub-paramos and paramos.	1800–3550	Lynch 1983; Ardila-Robayo and Acosta-Galvis 2000; Bernal and Lynch 2008.
Pristimantis (*Pristimantis*) *lynchi*	Unassigned	Andean, sub-paramos and paramos.	1600–3590	Duellman and Simmons 1977; Bernal and Lynch 2008; Acosta-Galvis 2015.
Pristimantis (*Pristimantis*) *dorado*	Unassigned	Andean.	2650	Rivera-Correa et al. 2016
Pristimantis (*Pristimantis*) *terrapacis*	Unassigned	sub-Andean	713	Ospina-Sarria and Angarita-Sierra 2020
Pristimantis (*Pristimantis*) *ardilae*	*conspicillatus* group	sub-Andean	400–700	Acevedo et al. 2020
Pristimantis (*Pristimantis*) *bowara*	Unassigned	sub-Andean	500–665	Acevedo et al. 2020

forests in the municipality of Chámeza (05°15'24.4"N, 072°53'51.6"W), Department of Casanare, Colombia (Fig. 1). This locality is part of an elevated area between 1700–2200 m a.s.l. in an unexplored northern portion of the Cordillera Oriental. This mountainous area consists mainly of pristine natural forests of the Andes orobiome (Fig. 2) within the ecoregion of the Eastern Cordillera montane forests of Colombia (Dinerstein et al. 1995; Olson and Dinerstein 2002). We recorded geographical coordinates and elevations at collecting sites using a Garmin GPSMAP 60CSx (map datum WGS 84).

Data collection and laboratory procedures

Molecular distinctiveness and phylogenetic relationships of the new species were assessed by analyzing DNA sequences of mitochondrial DNA (mtDNA) which included a fragment of the 16S ribosomal RNA (16S) and a fragment of the cytochrome oxidase subunit 1 (COI) genes. We assembled a data set that included only the 16S gene fragment by aligning sequences from all known *Pristimantis* species from the eastern slopes of the Cordillera Oriental of Colombia together with the most similar sequences already published in Genbank (Table 2). For this, we conducted a search for sequences similar to the 16S gene fragment of the new species using the BLAST algorithm in GenBank. The most similar 127 BLAST hits to the sequences from the new species

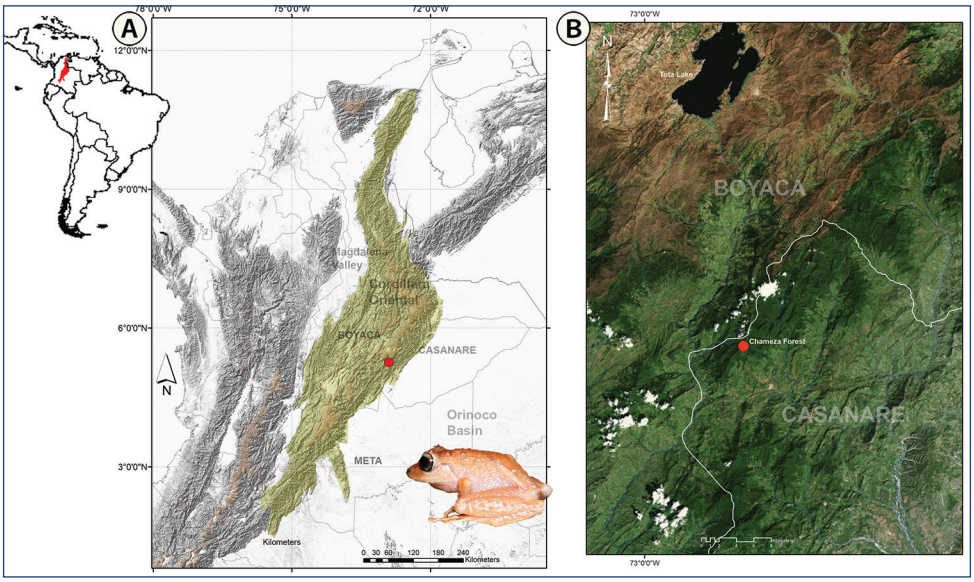

Figure 1. Geographic location in Colombia showing the type locality of *Pristimantis chamezensis* sp. nov. in the western slope of the Cordillera Oriental **A** red dot shows the type locality **B** the landscape of natural pristine forest on the eastern slopes of the Central Cordillera Oriental. Map produced using Arc Map, World Imagery.

were downloaded, aligned, and assessed using Bayesian (BA) and maximum likelihood (ML) analyses. After removing distant and redundant sequences, the final dataset contained 58 sequences of 827 base pairs (bp) of the 16S, including the new species and *Pristimantis medemi* (Lynch, 1994) obtained in this study (Table 1). We assembled a complete data set comprising sequences of the 16S, concatenated with sequences of the COI gene for a subset, including the new species and its following six most-related species, selected based on the results of the analyses: *Pristimantis carranguerorum* (Lynch, 1994), *P. bowara* Acevedo et al., 2020, *P. lutitus* (Lynch, 1984), *P. medemi* (Lynch, 1994), *P. nicefori* (Cochran & Goin, 1970), and *P. savagei* (Pyburn & Lynch, 1981).

From two tissue samples of the new species and a tissue sample of *Pristimantis medemi* we extracted total genomic DNA using a standard Phenol-Chloroform method (Sambrook et al. 1989). We amplified the gene fragments using the primers pairs 16Sbr-H/16SC-16L (Palumbi et al. 1991; Darst and Cannatella 2004, respectively) and LCO1490/HCO2198 (Folmer et al. 1994) for the 16S and COI, respectively. We carried out PCRs in a total volume of 30 µl containing one unit Taq polymerase (Bioline; Randolph, MA), 1× of a buffer (Bioline), a final concentration of 1.5 mM MgCl2 (Bioline), 0.5 µM of each primer, 0.2 mM of each dNTP (Bioline), 0.2 µg of bovine serum albumin (BSA), and approximately 50 ng of total DNA. We purified the PCR products using the ammonium acetate protocol (Bensch et al. 2000), and we sequenced them on an ABI 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) using the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied

Figure 2. A general landscape showing the mountains of the Vereda Centro Norte, Chámeza forest at Cerro Pan de Azúcar (black arrow); type locality of *Pristimantis chamezensis* sp. nov. **B** inside the cloud forests; microhabitat where individuals were found. Photographs by Andrés Acosta-Galvis.

Biosystems). We stored the remaining DNA extractions at –80 °C in the tissue collection of the Instituto de Genética, Universidad Nacional de Colombia (for voucher numbers see Table 2). We performed the thermocycling conditions as indicated by the authors, who reported the primers for the obtained fragments. The GenBank accession numbers of the obtained sequences are MK776946–MK776948 and MK789293–MK789295. We edited and aligned the sequences using Chromas 1.51 (http://www.technelysium.com.au/chromas.html) and BioEdit v. 7.0.5.2 (Hall 1999). To exclude divergent regions and poorly aligned bases from the 16S dataset, we used the software Gblocks v. 0.91b (Castresana 2000; Talavera and Castresana 2007; available as a web server at http://molevol.cmima.csic.es/castresana/Gblocks server.html), which resulted in a final alignment of 528 base pairs (bp). The COI alignment consisted of 652 bp.

Table 2. Species of *Eleutherodactylus*, *Pristimantis*, and GenBank accession numbers of the DNA sequences used in the phylogenetic analyses.

Species	Accession numbers		Voucher code	Source
	16S rRNA	COI		
E. johnstonei	EF493561	–	USNM336018	Heinicke et al. 2007
P. acatallelus	JN371032	–	UVC:15863	García-R et al. 2012
P. achatinus	EF493660	–	KU217809	Heinicke et al. 2007
P. achatinus	JN104676	–	UVC:15867	García-R et al. 2012
P. aniptopalmatus	EF493390	–	KU291627	Heinicke et al. 2007
P. bipunctatus	EF493702	–	KU291638	Heinicke et al. 2007
P. bogotensis	JN991432	JN991362	NRPS003	Pinto-Sanchez et al. 2012
P. bowara	MN215434	–	MCNUPH304	Acevedo, Armesto and Palma 2000
P. buccinator	KY652650	–	MUSM:33269	von May et al. 2017
P. buckleyi	EF493350	–	KU217836	Heinicke et al. 2007
P. caprifer	EF493391	–	KU177680	Heinicke et al. 2007
P. carranguerorum	KP149324	KP149128	LSB385	Guarnizo et al. 2015
P. chamezensis sp. nov.	MK776946	MK789293	ARA5848	This study
P. chamezensis sp. nov.	MK776947	MK789294	ARA5849	This study
P. citriogaster	EF493700	–	KU212278	Heinicke et al. 2007
P. condor	EF493701	–	KU217857	Heinicke et al. 2007
P. conspicillatus	EF493529	–	QCAZ28448	Heinicke et al. 2007
p. curtipes	EF493513	–	KU217871	Heinicke et al. 2007
P. devillei	EF493688	–	KU217991	Heinicke et al. 2007
P. dorado	KU496877	–	MRC636	Rivera-Correa et al. 2016
P. duellmani	AY326003	–	WED 53050	Darst and Cannatella 2004
P. fenestratus	EF493703	–	–	Heinicke et al. 2007
P. frater	KP149461	–	AJC 4015	Guarnizo et al. 2015
P. gentryi	EF493511	–	KU218109	Heinicke et al. 2007
P. koehleri	EU192279	–	MNKA 6627	Padial & De la Riva 2009
P. lasalleorum	KY494221	–	ICN55758	González-Durán et al. 2017
P. latro	MK174413	–	LZA 1340	Cornelio et al. unpublished
P. leptolophus	KY494226	–	JJS093	González-Durán et al. 2017
P. lutitus	KP149401	KP149196	AJC3490	Guarnizo et al. 2015
P. lymani	EF493392	–	KU218019	Heinicke et al. 2007
P. maculosus	KY494240	–	ICN55760	González-Durán et al. 2017
P. malkini	EU186663	–	QCAZ28296	Hedges et al. 2008
P. medemi	MK776948	MK789295	ARA2655	This study
P. nicefori	MN215436	MN218387	MCNUPH48	Acevedo, Armesto and Palma 2000
P. parectatus	KY627810	–	MHUAA9977	Rivera-Correa et al. 2017
P. peraticus	KY494224	–	WB1301	González-Durán et al. 2017
P. peruvianus	EF493707	–	–	Heinicke et al. 2007
P. quinquagesimus	EF493690	–	KU179374	Heinicke et al. 2007
P. rhabdolaemus	EF493706	–	KU173492	Heinicke et al. 2007
P. sagittulus	EF493705	–	KU291635	Heinicke et al. 2007
P. samaipatae	EU192290	–	MNCN 42988	Padial and De la Riva 2009
P. savagei	KP149382	KP149180	AJC3995	Guarnizo et al. 2015
P. scoloblepharus	KY494236	–	ICN55768	González-Durán et al. 2017
P. skydmainos	EF493393	–	–	Heinicke et al. 2007
P. simonbolivari	EF493671	–	KU218254	Heinicke et al. 2007
P. simonsii	EU186665	–	KU212350	Hedges et al. 2008
P. surdus	EF493687	–	KU177847	Heinicke et al. 2007
P. sp.1	KY494239	–	JJS122	González-Durán et al. 2017
P. sp.2	KY494238	–	ICN55759	González-Durán et al. 2017
P. sp.3	KY494230	–	ICN55756	González-Durán et al. 2017
P. sp.4	KY494234	–	ICN55774	González-Durán et al. 2017
P. sp.5	KY494223	–	ICN55775	González-Durán et al. 2017
P. stictogaster	EF493704	–	KU291659	Heinicke et al. 2007
P. thymalopsoides	EF493514	–	KU177861	Heinicke et al. 2007
P. toftae	EF493353	–	KU215493	Heinicke et al. 2007
P. unistrigatus	EF493387	–	KU218057	Heinicke et al. 2007
P. uranobates	KY494223	–	ICN55787	González-Durán et al. 2017
P. vertebralis	EF493689	–	KU177972	Heinicke et al. 2007
P. vilarsi	KP149391	KP149187	AJC2113	Guarnizo et al. 2015

Phylogenetic and genetic divergence analyses

We analyzed the complete evidence dataset using the following partition scheme: (i) unpartitioned; (ii) partitioned by gene (i.e., each gene fragment treated as a distinct partition); and (iii) maximum partitioning (i.e., we treated each codon of the protein-coding gene COI and the ribosomal gene fragment as distinct partitions). We assessed the optimal partitioning scheme and best-fit evolutionary models using PartitionFinder v. 1.1.1 and the Bayesian Information Criterion (Lanfear et al. 2012), resulting in the selection of the maximum partitioning scheme. For the 16S dataset, the obtained model (SYM + G) was applied in a Bayesian analysis (BA) with MrBayes v. 3.2.1 (Ronquist et al. 2012). For the complete evidence dataset, we applied the 16S fragment model plus the following complementary COI fragment resulting models in a Bayesian analysis with MrBayes: COI 1st codon – TrNef + G, COI 2nd codon – HKY, COI 3rd codon – HKY. We incorporated these models into a single tree search (mixed model partition approach; Nylander et al. 2004). For both analyses, we carried out two parallel runs using four Markov chains, each starting from a random tree. We ran the Markov chains for 10 million generations. The burn-in was set to sample only the plateau of the most likely trees that were used for generating a 50% majority rule consensus. We used the software TRACER v. 1.5.4 (Rambaut and Drummond 2007) to assess an acceptable level of the MCMC chain mixing and to estimate effective sample sizes for all parameters. Additionally, maximum likelihood (ML) analyses were run using RAxML 7.2.8 (Stamatakis 2006) and the GTR+G model. We performed five independent maximum likelihood searches with different starting conditions and the rapid bootstrap algorithm to explore the robustness of the branching patterns by comparing the best trees. Afterward, 1000 non-parametric thorough bootstrap values were computed and plotted against the best tree. The Genbank sequence of *Eleutherodactylus johnstonei* Barbour, 1914, EF493561, was used as outgroup. To assess the genetic divergence between the new and the other *Pristimantis* species, we calculated uncorrected *p* genetic distances for the 16S and the COI fragments using MEGA v. 7.0.21 (Kumar et al. 2016).

Morphology

We euthanized specimens using Clorethone, which were then fixed in 10% formalin, preserved in 70% ethanol, and deposited in the biological collections of the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia (IAvH-Am). Other specimens examined are listed in Suppl. material 1. The criteria for the definition of descriptions and diagnostic characters followed Duellman and Lehr (2009), Lynch and Duellman (1997), and Navarrete et al. (2016). To identify sex and sexual maturity, we made a small incision in the groin region for macroscopic observation of the gonads. Adult males have the granular testis, while females show enlarged, thickened, and convoluted oviducts. Morphometric measurements were made with digital calipers (nearest 0.01 mm) or a Nikon stereoscopic microscope SMZ-1B with high Intensity Illuminator NI-150 Nikon as follows: SVL

(snout-vent length), HW (head width), HL (head length from the tip of the snout to the posterior border of the skull, posterior edge of prootic, noted through the skin), IOD (interorbital distance), ED (eye diameter), EN (eyes-nares distance), UEW (upper eyelid width), ETS (distance between the anterior edges of the eye to the tip of the snout), TD (horizontal tympanum diameter), RW (rostral width), InD (internarial distance), TL (tibial Length), FL (femur length), FtL (foot length), and HnL (hand length). Means are reported ± one standard error. We photographed habitats and specimens using Canon EOS 30D and EOS 5D Mark II digital cameras inside a Photo Safe-box using 5.500 kelvins LED lights.

Results

Phylogenetic and genetic divergence analyses

The resulting phylogenetic tree including all 58 sequence of the 16S fragment is shown in the Suppl. material 2: Fig. S1. A reduced phylogenetic tree including the 16S fragment sequences of the new species and its closest 29 sequences is shown in Figure 3. The following description is referring to the reduced tree. Based on the phylogenetic relationships, the new species could be assigned to the genus *Pristimantis*, subgenus *Pristimantis*. Both tree-building methods revealed *Pristimantis chamezensis* sp. nov. with maximum support within a supported monophyletic group comprising *Pristimantis carranguerorum*, *P. bowara*, *P. lutitus*, *P. medemi*, *P. nicefori*, and *P. savagei* (Fig. 3). Both analyses concurred in placing the new species as a sister taxon of *P. nicefori* with low support (ML: 40%; BA: 0.80). The other 23 *Pristimantis* species were revealed by both analyses within three separated, weakly supported clades, exhibiting low supported evolutionary relationships (Fig. 3). For the complete evidence dataset, both tree building methods revealed *Pristimantis chamezensis* sp. nov., as part of a monophyletic clade also comprising *P. carranguerorum*, *P. bowara*, *P. lutitus*, *P. medemi*, *P. nicefori*, and *P. savagei* with maximum support (Suppl. material 3: Fig. S2). Both analyses revealed that the new species is the sister taxon of a clade showing the following weakly supported phylogenetic relationships: (((*P. lutitus* + *P. bowara*) *P. nicefori*) *P. carranguerorum*). Finally, *P. medemi* and *P. savagei* were revealed as successive sister taxa of the that clade plus the new species, with low support (Suppl. material 3: Fig. S2). Genetic distances for the 16S gene between *P. chamezensis* sp. nov. and *P. nicefori*, *P. carranguerorum*, and *P. savagei* were 4.8%, 5.2%, and 5.9%, respectively. Distances between *P. chamezensis* sp. nov. and *P. medemi*, *P. lutitus*, and *P. bowara* were 6.2%, 6.2%, and 6.7%, respectively (Table 3). The sequence divergence range of the monophyletic group compared to the other analyzed taxa was 5.9–4.1% (Table 3). The uncorrected *p* distances for the COI gene revealed that sequence differentiation values between *P. chamezensis* sp. nov. and *P. carranguerorum*, *P. nicefori*, *P. lutitus*, *P. savagei*, and *P. medemi* were 6.2%, 6.4%, 6.7%, 6.7%, and 6.7%, in that order. For the same gene fragment, the distance between *P. chamezensis* sp. nov. and *P. bowara* was 7.8%.

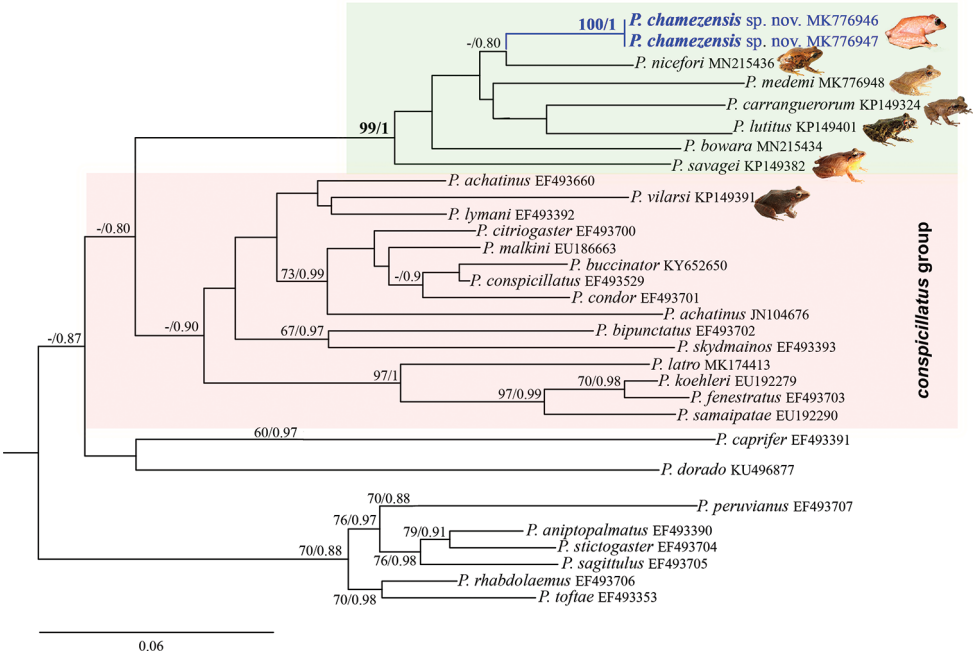

Figure 3. Maximum likelihood inference tree showing the evolutionary relationships of *Pristimantis chamezensis* sp. nov. (bold) and its 28 more closely related *Pristimantis* species based on 528 bp of the 16S rRNA gene. Numbers before nodes: thorough maximum likelihood (ML) bootstrap percentages left and Bayesian analysis (BA) posterior probability values right. Bootstrap values below 50% and posterior probabilities below 0.5 not shown. Outgroup taxon removed.

Description of new species

***Pristimantis chamezensis* sp. nov.**
http://zoobank.org/ff99cfe4-4fa7-402b-8d76-d921a93d1566
Figs 4, 5; Table 4

Holotype. IAvH-Am-10269 (field number ARA 5852. Figs 4, 5) an adult female collected on 3 September 2010 by Andrés R. Acosta-Galvis, Beatriz Ramirez, José Pérez, Luis Daniel Prada, and Natalia Novoa.

Type locality (Figs 1, 2). Colombia, Casanare Department, Chámeza Municipality, vereda Centro Norte, Chámeza forest, Cerro Pan de Azúcar, eastern flank of the Cordillera Oriental, Colombia. 05°15'24.4"N, 072°53'51.6"W, 2140 m a.s.l.

Paratypes (11) (Fig. 5; Table 4). IAvH-Am-10267, IAvH-Am-10270–10274, adult males; IAvH-Am-10275–10277, IAvH-Am-10282, adult females, collected on 13 November 2010 by Andrés R. Acosta-Galvis, Beatriz Ramirez, José Pérez, Luis Daniel Prada, and Natalia Novoa; same locality as the holotype.

Referred specimens. IAvH-Am-10268, IAvH-Am-10278–10281, IAvH-Am-10283–10287, juveniles, same locality and date as paratypes.

Table 3. Uncorrected *p*-distances for the fragment of 16S gene (528 bp) of the *Pristimantis* species, expressed as percentages (means).

	n	*cha*	*nic*	*car*	*sav*	*med*	*lut*	*bow*	*cit*	*mal*	*con*	*buc*	*lym*	*ach*	*con*	*sti*	*rha*	*cap*	*ach*	*tof*	*plu*	*ani*	*bip*	*lat*	*koe*	*fen*	*sam*	*sag*	*vil*	*dor*	*sky*
chamezensis sp. nov.	**2**	0.0																													
nicefori MN215436	1	4.8	–																												
carranguerorum KP149324	1	5.2	4.8	–																											
savagei KP149382	1	5.9	5.2	5.5	–																										
medemi MK776948	1	6.2	5.9	6.2	5.0	–																									
lutitus KP149401	1	6.2	6.2	6.9	5.9	7.6	–																								
bowara MN215434	1	6.7	6.2	6.4	4.0	5.7	6.9	–																							
citriogaster EF493700	1	7.8	6.7	6.2	5.9	6.4	7.1	6.4	–																						
malkini EU186663	1	8.3	7.8	8.6	9.0	8.8	10.2	9.2	10.0	–																					
conspicillatus EF493529	1	8.3	8.3	9.3	9.5	8.8	10.0	10.0	10.2	3.1	–																				
buccinator KY652650	1	8.3	8.3	9.7	8.8	9.3	9.7	10.4	10.0	2.8	2.4	–																			
lymani EF493392	1	8.3	8.3	10.5	8.3	8.8	9.7	10.0	10.9	4.0	3.8	2.1	–																		
achatinus EF493660	1	8.8	8.3	9.0	7.8	8.8	9.5	9.0	9.7	3.8	4.7	3.8	5.0	–																	
condor EF493701	1	8.8	8.8	9.8	9.3	10.0	10.2	10.5	11.7	5.2	5.0	4.8	5.9	4.3	–																
stictogaster EF493704	1	9.0	8.8	9.7	9.2	9.7	9.5	10.0	10.7	4.0	3.3	2.8	4.5	4.7	5.5	–															
rhabdolaemus EF493706	1	9.0	9.0	9.8	9.7	8.8	10.9	10.5	9.8	9.7	9.5	9.3	10.2	9.5	9.8	9.7	–														
caprifer EF493391	1	9.1	9.0	9.5	9.0	8.1	9.7	9.7	9.7	9.7	9.7	9.2	10.2	9.7	9.3	9.2	3.1	–													
achatinus JN104676	1	9.2	9.1	9.1	9.3	9.1	10.3	9.8	9.1	9.3	8.6	8.4	9.5	8.4	7.9	9.5	9.3	8.6	–												
tofiae EF493353	1	9.2	9.2	10.2	10.9	11.9	11.1	11.1	13.1	7.1	7.3	6.9	7.6	7.8	7.6	5.9	10.9	10.7	11.2	–											
aniptopalmatus EF493390	1	9.2	9.2	10.5	10.7	10.0	10.7	10.9	9.7	10.9	10.4	10.7	11.6	10.9	11.6	10.7	3.3	4.3	10.3	11.8	4.3	–									
bipunctatus EF493702	1	9.5	9.2	9.5	9.5	9.0	11.1	10.2	9.5	9.7	10.0	9.2	10.2	9.2	10.5	10.2	2.4	3.1	9.5	11.1	3.6	2.8	–								
latro MK174413	1	10.0	9.5	9.8	9.0	10.2	10.2	9.5	11.0	6.9	6.4	6.2	6.9	6.4	7.1	5.7	10.0	10.7	9.3	7.8	10.5	10.5	10.2	–							
koehleri EU192279	1	10.0	10.0	11.5	10.5	9.4	12.2	10.8	11.3	7.9	7.7	8.6	9.8	9.1	8.6	8.4	9.6	9.3	9.4	11.2	9.8	11.0	10.0	9.4	–						
fenestratus EF493703	1	10.0	10.0	11.4	11.4	10.2	11.1	11.6	11.6	7.8	8.1	8.8	9.2	7.6	8.6	7.6	10.9	10.4	10.0	8.5	10.4	11.8	11.1	8.6	6.9	–					
samaipatae EU192290	1	10.4	10.0	11.9	11.4	10.0	10.7	11.6	11.6	8.3	7.6	8.8	9.2	7.8	8.8	7.6	11.2	10.2	10.0	8.8	10.2	12.1	10.9	9.3	6.7	1.2	–				
sagittulus EF493705	1	11.1	10.4	10.5	10.2	9.7	10.2	10.9	10.2	8.1	7.6	7.6	8.8	7.6	8.6	7.8	10.5	10.2	10.0	10.2	10.9	11.1	9.7	9.3	7.2	3.3	3.6	–			
vilarsi KP149391	1	11.4	11.1	11.4	10.2	10.2	12.1	11.1	10.5	11.6	11.4	11.1	11.6	11.1	11.4	11.6	3.6	4.0	10.7	13.0	4.3	4.5	3.1	11.6	11.0	12.1	11.8	11.1	–		
dorado KU496877	1	11.4	11.4	10.0	9.5	10.0	12.1	11.2	11.4	8.1	7.6	7.8	8.6	7.6	7.6	7.8	11.2	10.9	10.8	10.9	12.8	13.1	11.4	9.0	9.1	10.2	10.5	9.3	12.6	–	
skydmainos EF493393	1	11.6	11.4	13.1	11.4	14.1	13.6	12.8	14.1	9.6	9.6	8.9	9.4	11.4	11.9	9.6	12.1	13.3	12.7	12.6	13.8	13.8	12.6	10.4	11.2	11.9	11.9	11.6	14.1	12.8	–

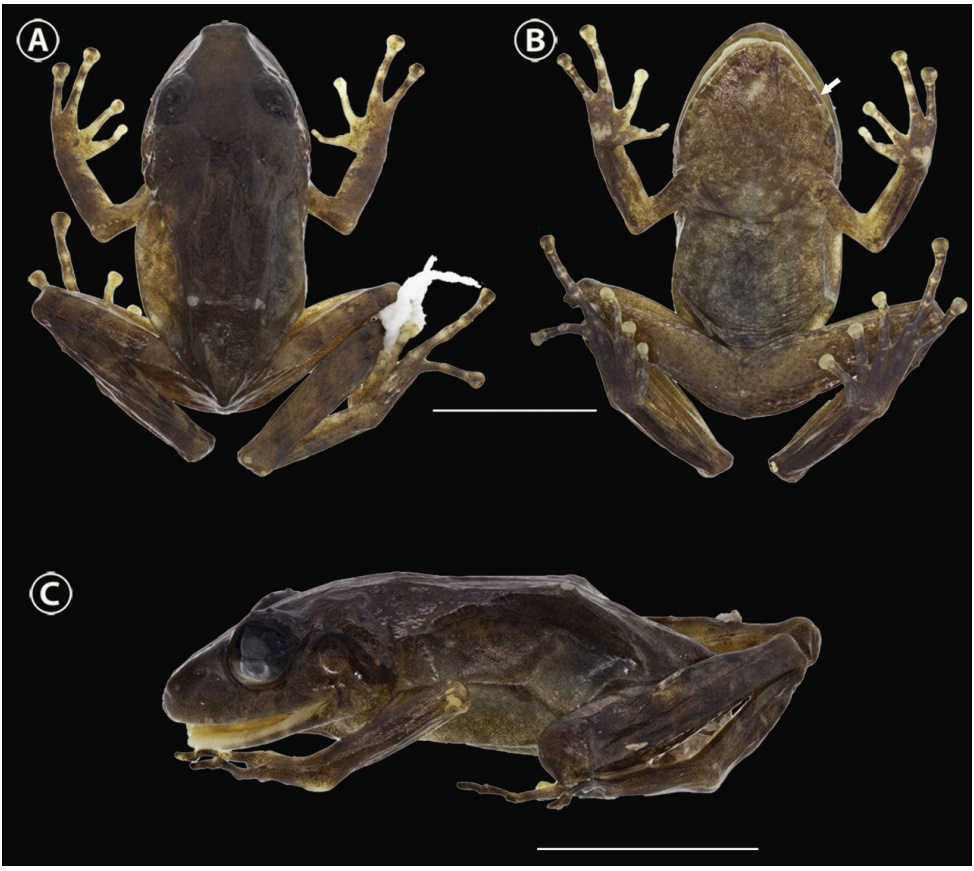

Figure 4. *Pristimantis chamezensis* sp. nov. preserved holotype, adult female, IAvH-Am-10269 (SVL = 23.8 mm) **A** dorsal view **B** ventral view **C** lateral view. White arrow = chin with irregular blotches of dark brown. Scale bar: 10 mm. Photographs by Andrés Acosta-Galvis.

Diagnosis (Figs 4–7). A species of *Pristimantis* characterized by the following combination of morphological characters: (1) dorsal skin shagreen with scattered larger tubercles; dorsolateral folds absent; discoidal fold visible; skin on venter areolate. (2) Tympanic membrane and tympanic annulus present, its dorsoposterior border converges with supratympanic fold; its diameters are 35.6–56.0% of the eye diameter; small, barely visible, subconical postrictal tubercles. (3) Snout short, broadly rounded in dorsal view and rounded in lateral view; *canthus rostralis* sharp and concave. (4) Upper eyelid bearing one to three subconical tubercles, narrower than IOD. (5) Choanae small, subovoid; dentigerous processes of vomers prominent, oblique, and widely separated from each other, bearing 8 or 9 teeth. (6) Males with vocal slits; subgular vocal sac observable; nuptial pads not evident. (7) Finger I shorter than II, with discs expanded and rounded; bifid palmar tubercle. (8) Fingers bearing narrow lateral fringes. (9) Ulnar tubercles absent. (10) Tarsal tubercles present, subconical; heel tubercles

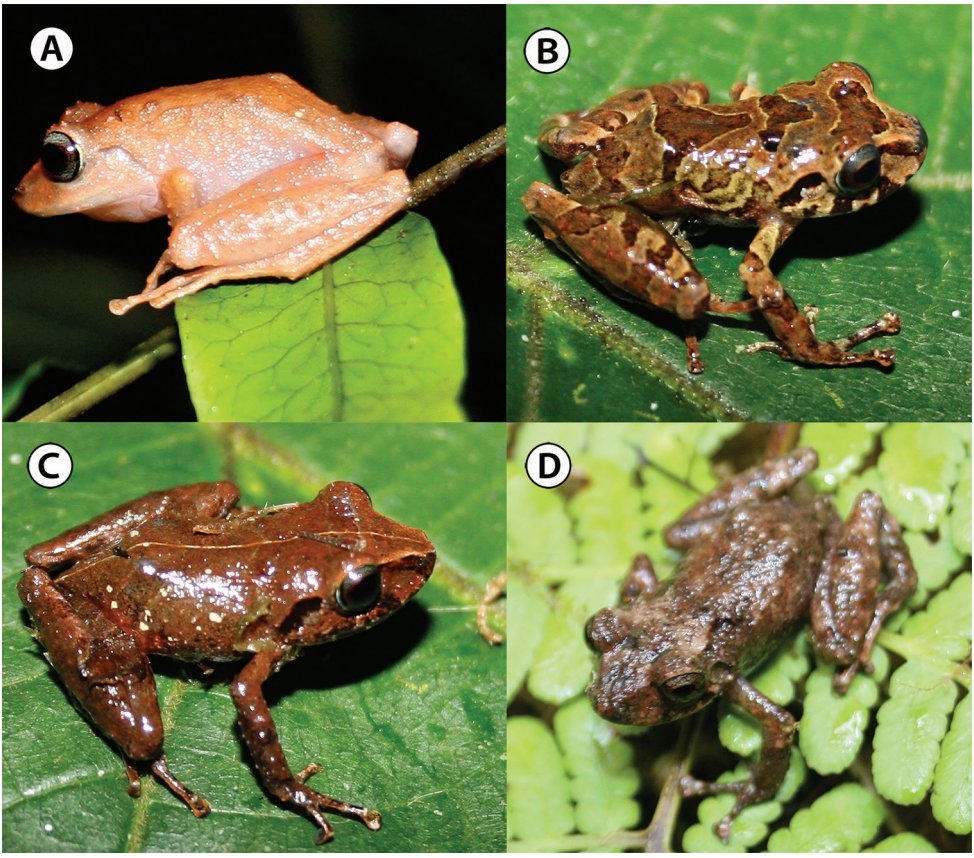

Figure 5. *Pristimantis chamezensis* sp. nov., live specimens. **A** Holotype, adult female, IAvH-Am-10269 (SVL= 23.8 mm) **B** juvenile, IAvH-Am-10283 (SVL = 17.5 mm) **C** paratype, adult female, IAvH-Am-10277 (SVL = 19.7 mm) **D** paratype, adult male, IAvH-Am-10267 (SVL = 22.6 mm). Photographs by Andrés Acosta-Galvis.

Table 4. Morphometric (in mm) of the type series of *Pristimantis chamezensis* sp. nov. Abbreviations are given in Methods.

IAvH–Am	Sex	SVL	HW	HL	IOD	ED	EN	UEW	ETS	TD	FL	FtL	InD	RW	TL	HnL
10267	M	22.6	7.9	10.1	3.1	3.1	3.0	1.8	4.1	1.7	10.6	10.9	2.5	3.2	12.5	6.4
10271	M	23.7	9.2	9.1	3.6	2.8	3.0	2.0	4.6	1.6	12.6	10.8	2.5	3.8	12.6	6.5
10273	M	20.9	7.5	7.6	2.8	2.8	2.4	2.1	3.7	1.1	10.9	9.6	2.5	3.6	11.6	5.9
10270	M	19.6	7.9	8.9	2.6	2.6	2.8	1.7	3.5	1.1	10.6	9.9	2.3	2.7	11.7	6.1
10274	M	21.2	8.3	9.4	2.8	2.9	3.1	1.8	4.0	1.2	10.5	9.9	2.4	3.3	11.8	5.9
10272	M	20.3	8.0	9.3	3.0	2.7	2.4	1.8	3.7	1.0	10.0	10.1	2.5	2.8	12.2	6.3
Means		21.4	8.1	9.1	3.0	2.8	2.8	1.9	3.9	1.3	10.9	10.2	2.5	3.2	12.1	6.2
Standard error		1.4	0.5	0.8	0.3	0.2	0.3	0.1	0.4	0.3	0.8	0.5	0.1	0.4	0.4	0.2
10276	F	24.9	11.0	11.3	3.4	3.5	3.1	2.6	4.7	1.2	14.3	12.9	3.1	3.8	14.4	8.4
10277	F	19.7	8.1	9.0	2.9	2.8	2.4	1.6	4.1	1.0	11.0	8.8	2.5	2.7	12.1	6.0
10269	F	23.8	9.8	10.4	3.8	3.3	3.2	2.1	4.5	1.1	13.6	12.1	2.9	3.9	14.5	7.4
10275	F	19.0	7.8	9.0	2.9	2.4	2.8	1.7	4.1	1.0	9.7	9.4	2.1	3.1	11.5	5.6
Means		21.9	7.9	8.5	2.9	2.6	2.6	1.8	3.8	1.1	10.6	9.6	2.3	3.1	11.5	6.8
Standard error		2.9	1.4	1.1	0.4	0.4	0.3	0.4	0.2	0.1	2.1	1.9	0.4	0.5	1.5	1.3

present but nearly inconspicuous and conical. (11) Two metatarsal tubercles, with inner tubercle elongate, three times the length of the rounded and prominent outer tubercle; supernumerary plantar tubercles numerous, enlarged, and rounded. (12) Toes with lateral fringes and broad discs; toe V much longer than toe III (disc on toe III extends to the proximal edge of the medial subarticular tubercle on toe IV, disc on toe V extends beyond the distal edge of the penultimate subarticular tubercle on toe IV); webbing absent. (13) Dorsal surface pattern variable, with homogeneous color brown (with or without paravertebral line) or inverted V-shaped markings with dark brown blotches edged with pale cream; iris gray, medially reddish, with black reticulations; ventral surfaces cream-colored to light brown, finely peppered with irregular, diffuse, dark-brown reticulations or blotches; posterior surface of thighs brown; dark-brown labial bars present or absent; edge of the chin with irregular blotches of dark brown (Fig. 5). (14) apparently sexually dimorphic in size (Table 4), with an SVL in adult males 19.6–23.7 mm and 19.0–24.9 mm in adult females.

Species comparisons (Figs 5–7, Suppl. material 1). The new species is compared to other species of *Pristimantis* in the eastern slope of the Cordillera Oriental in the Orinoco basin of Colombia. The character states of the compared species are enclosed in parentheses. *Pristimantis chamezensis* is distinguished from *P. carranguerorum* by the absence of short dorsolateral folds in the scapular region (present); snout rounded in dorsal view (subacuminate; Fig. 6); the dorsum brown, with some lighter and diffuse reticulations (pale dorsolateral lines; Fig. 6); and subconical tubercles on the upper eyelid (absent). The new species differs from *P. vilarsi* (Melin, 1941) in having the posterior surfaces of the thighs brown in life (reddish); adult females smaller, SVL 19.0–24.9 mm (SVL 25.4–43.2 mm); and the snout broadly rounded in dorsal view (subacuminate). *Pristimantis chamezensis* can be easily confused with *P. savagei* by the presence of one to three subconical tubercles on the upper eyelid; however, it differs by the absence of ulnar tubercles (present); snout broadly rounded in dorsal view (subacuminate); and posterior surface of thighs brown in life (pale orange). *Pristimantis chamezensis* is distinguished from *P. medemi* by having subconical tubercles on the upper eyelids (absent); dorsal and ventral iris gray in life (Fig. 5), medially reddish, with black reticules (orange to yellow); and smaller size, SVL 19.6–26.4 mm (SVL 29.4–43.1 mm). *Pristimantis chamezensis* differs from *P. anolirex* (Lynch, 1983) (Fig. 6) in lacking dorsolateral folds (present on half of the body); ulnar tubercles absent (present and small; Fig. 7); and snout broadly rounded in dorsal view (subacuminate). *Pristimantis chamezensis* is distinguished from *P. lynchi* (Duellman & Simmons, 1977) in having the edge of the chin with irregular blotches (Fig. 4) of dark brown (uniformly brown); palmar tubercle bifid (elliptical); and snout broadly rounded in dorsal view (subacuminate). Compared to *P. bogotensis* (Peters, 1863) (Fig. 6), *P. chamezensis* has a prominent dentigerous process on the vomers, oblique and widely separated from each other (concealed in the palatine tissue); and broadly rounded snout in dorsal view (rounded). *Pristimantis chamezensis* differs from *P. frater* (Werner, 1899) (Fig. 6) in having a broadly rounded snout in dorsal view (acuminate); and toes IV and V with narrow discs (broader). *Pristimantis chamezensis* is distinguished from *P. terrapacis*

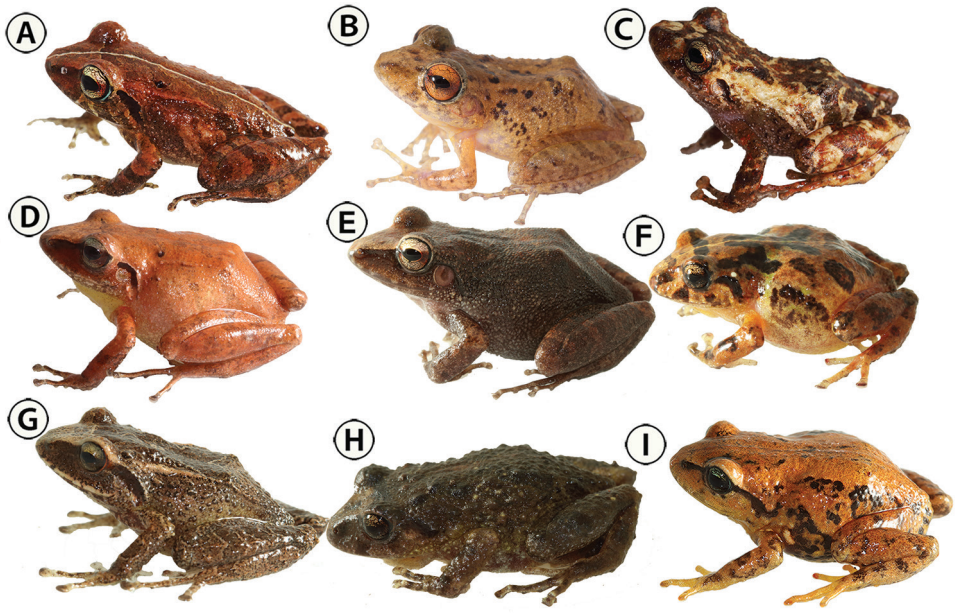

Figure 6. Live specimens (lateral view) of *Pristimantis* currently known from the eastern Andean Cordillera associated with the Orinoco basin in Colombia. **A** *Pristimantis carranguerorum*, Medina Municipality, Cundinamarca Department, IAvH-Am-14954 (adult female, SVL = 22.6 mm) **B** *Pristimantis medemi*, Medina Municipality, Cundinamarca Department, IAvH-Am-15025 (adult male, SVL = 32.5 mm) **C** *Pristimantis frater*, Medina Municipality, Cundinamarca Department, IAvH-Am-14923 (adult female, SVL = 27.8 mm) **D** *Pristimantis savagei*, Medina Municipality, Cundinamarca Department, IAvH-Am-14933 (adult male, SVL = 23.2 mm) **E** *Pristimantis vilarsi*, La Macarena Municipality, Meta Department, IAvH-Am-15095(Adult female, SVL = 44.8 mm) **F** *Pristimantis bogotensis*, Cabrera Municipality, Cundinamarca Department, IAvH-Am-15345 (adult male, SVL = 21.9 mm) **G** *Pristimantis anolirex*, Santa Barbara Municipality, Santander Department, IAvH-Am-15654 (juvenile female, SVL = 22.3 mm) **H** *Pristimantis lynchi*, Tasco Municipality, Boyacá Department, IAvH-Am-15871 (adult male, SVL = 22.1 mm) **I** *Pristimantis nicefori*, Santa Barbara Municipality, Santander Department, IAvH-Am-15730 (SVL = 24.5 mm). Photographs by Andrés Acosta-Galvis.

Ospina-Sarria & Angarita-Sierra, 2020 by having subconical tubercles on upper eyelid and heel (absent) and webbing absent between the toes (basal webbing). *Pristimantis chamezensis* differ from *P. ardilae* Acevedo et al. 2020 by the absence of short dorsolateral folds in the scapular region (present); broadly rounded snout in dorsal view (subacuminate); and upper eyelid with subconical tubercles (without tubercles). *Pristimantis chamezensis* is distinguished from *P. bowara* in having the broadly rounded snout in dorsal view (subacuminate) and dorsal skin shagreen with scattered larger tubercles (smooth). Lastly, *P. chamezensis* that can be distinguished from *P. nicefori* (Fig. 6) in having the discs of the digits expanded (slightly expanded), snout broadly rounded in dorsal view (acuminate), and snout broadly rounded in lateral view (pointed).

Description of the holotype. An adult female (Figs 4, 5) with a snout-vent length (SVL) of 23.8 mm; the skin of cephalic region, dorsum, eyelids, lateral surfaces, and

dorsal thighs shagreen with scattered larger tubercles; dorsolateral folds absent and discoidal folds visible; skin on venter areolate. Head length (HL), diagonally from the corner of mouth to tip of snout 10.4 mm; head width (HW) 9.8 mm, approximately equal to width of the body and 41.1% of the SVL. Snout broadly rounded in dorsal view (type F, *sensu* Duellman and Lehr 2009; Fig. 4) and rounded in lateral view (type A, *sensu* Duellman and Lehr 2009; Fig. 4); internarial distance (between center of naris) 2.9 mm; nostril moderately protuberant, directed dorsolaterally; *canthus rostralis* well defined; loreal region slightly concave; lips not prominent. Eye diameter (ED) from its posterior to anterior corner 3.3 mm; its length 73.3% of the ETS (distance between the anterior edge of the eye to the tip of snout); interorbital region wider than upper eyelid; the upper eyelid width (UEW) 55.2% of interorbital distance (IOD); upper eyelid bearing three smaller subconical tubercles (Figs 4, 5); no cranial crests. Supratympanic fold low and short. Tympanic membrane and tympanic annulus present, small, and rounded (Figs 4, 5), its dorsoposterior border converges with supratympanic fold; its diameter 1.1 mm and equivalent to 33% of eye diameter (ED). Choanae subovoid, not concealed by the palatal shelf of the maxillary arch; dentigerous processes of vomers prominent, nine teeth positioned posterior to level of choanae and widely separated from each other. Tongue rounded, its posterior border notched for half of its extension is adherent to the floor of mouth; teeth present on the maxillary arch.

Forelimbs of moderate size, forearm length 6.4 mm; ulnar tubercles absent. Hand length (HnL) 7.4 mm its length 31.0% of SVL. Palmar tubercle bifid, about two-thirds the length of oval thenar tubercle (Fig. 7). Supernumerary palmar tubercles present, rounded to elongated, and slightly elevated; subarticular tubercles large, round, and conical; fingers without lateral fringes; disks on all fingers rounded apically and extensively expanded (Fig. 7); disk of finger III equal in diameter to the tympanic annulus; disks bearing ventral pads; finger I shorter than II when appressed (Fig. 7). Relative lengths of appressed fingers III>IV>II>I. Subarticular tubercles 1–1–2–2.

Hindlimbs slender; foot length (FtL) 12.1 mm, 50.8% of SVL. Toe webbing and toe fringes absent. Relative lengths of appressed toes IV>V>III>II>I. Discs of the toes expanded; width of adjacent phalange 53.7% of disc of toe IV; disc of toe III does not reach penultimate subarticular tubercle of toe IV; toe V beyond that of the level of penultimate subarticular tubercle of toe IV. Femur length (FL) 13.6 mm, tibia length (TL) 14.5 mm, its length is equivalent to 60.9% of SVL. Subarticular tubercles 1–1–2–3–2; supernumerary plantar tubercles numerous, suboval, and low; inner metatarsal tubercle oval; outer metatarsal tubercle rounded, prominent, and smaller than inner metatarsal tubercle. Diameter outer metatarsal tubercle 52.8% of inner metatarsal tubercle; outer tarsal fold absent; inner tarsal fold short. Numerous supernumerary plantar tubercles rounded and barely visible; subarticular tubercles large, round, and conical; toes without lateral fringes; no webbing. Cloacal sheath absent; subcloacal tubercles absent.

Color of holotype in preservative (Fig. 4). Dorsum and flanks dark brown; hands in dorsal view, with fingers I and II cream-colored, while fingers III and IV brown with cream-colored bars; dorsal surfaces of the thigh with diffuse dark-brown transversal bars; hidden surfaces of thighs pale brown; venter light brown with a dark-brown suffu-

Figure 7. Hand and toes of adult male paratype, IAvH-Am-10271 of *Pristimantis chamezensis* sp. nov. in ethanol 70%. **A** Ventral view of foot **B** ventral view of hand. Scale bar: 2 mm. Photographs by Andrés Acosta-Galvis.

sion and mottled brown; ventral surfaces of hindlimbs and forelimbs dark brown with a cream-colored suffusion; edge of chin with irregular blotches of dark brown; hands, in ventral view, with palmar tubercle cream-colored and palmar region dark brown.

Color of holotype in life (Fig. 5). Dorsal surfaces of body and limbs pink-orange; flanks salmon and sides of the head pink-orange; venter reddish cream-colored on chest and belly, cream-colored on throat; axillary region, groin, and anterior thigh pale orange; ventral surfaces of thighs light brown; iris gray, medially reddish, with black reticulations.

Variation of type series (Fig. 5, Table 4). In this section, coloration refers to specimens in life and is based on field notes and digital photographs, unless otherwise noted. Dorsal coloration reddish brown with mottled, dark-brown chevrons, usually surrounded by a thin band of lighter color; canthal stripe black; dorsal surfaces of thigh with dark-brown transversal bars; axillary region, groin, and anterior thigh bright orange (e.g., IAvH-Am-10283, IAvH-Am-10276; Fig. 5) or uniformly dark brown (e.g., IAvH-Am-10267–68, IAvH-Am-10272; Fig. 5). An adult female (IAvH-Am-10277) has a gold paravertebral line (Fig. 5). Labial bars dark brown, and postorbital and supratympanic stripe dark (e.g., IAvH-Am-10268, IAvH-Am-10270, IAvH-Am-10272,

IAvH-Am-10276–7; Fig. 5). In IAvH-Am-10270 and IAvH-Am-10276, flanks with oblique, irregular, dark-brown bars (Fig. 5); IAvH-Am-10267 with a W-shaped, light-brown marking on scapula; some specimens with a dark-brown interorbital bar (e.g., IAvH-Am-10268, IAvH-Am-10273–4, IAvH-Am-10279–10280). *Pristimantis chamezensis* is metachromatic, being lighter in color at night. Teeth positioned posterior to level of choanae and widely separated from each other, which vary between eight to nine. The variation in the skin texture is noteworthy (Fig. 5), varying from smooth (e.g., IAvH-Am-10283) to shagreen with scattered tubercles (e.g., IAvH-Am-10267, IAvH-Am-10277). The SVL of adult males ranges from 19.6 to 23.7 mm (Table 4), and the SVL of adult females ranges from 19.0 to 24.9 mm (Table 4). The HW 35.9–40.3% of SVL in adult males and 41.2–44.1% in adult females. ED 61.6–75.0% of ETS in adult males and 59.1–74.9% in adult females. UEW 58.0–77.6% of interorbital distance (IOD) in adult males and 54.6–78.2% in adult females. TD 39.1–56.0% of ED in adult males and 33–41.8% in adult females. HnL in adult males 29.3% of SVL and 31.2% in adult females. FtL in adult males 45.6–50.4% of SVL and 44.9–51.8% in adult females.

Distribution and natural history. This species is only known from the type locality at an altitude between 2125–2160 m a.s.l. in an Andean and relictual cloud forest in the Casanare region on the eastern flank of the Cordillera Oriental of Colombia (Fig. 1). The locality is within the Cordillera Oriental montane forest ecoregion (*sensu* Dinerstein et al. 1995) in the Andean region (Middle Orobiome). The forest (Fig. 2) is unaffected by human activities and is typified by a canopt of medium-height (up to 20 m). The annual precipitation is between 4600 and 5600 mm with bimodal seasonality. Specimens were found active during the second annual rainy season (August to November) at a temperature of 14 °C resting on mosses and lower leaves of shrubs and ferns in the undergrowth. *Pristimantis chamezensis* is syntopic with an undescribed species of genus *Pristimantis*.

Etymology. The specific epithet is derived from the Municipality of Chámeza, a geopolitical area where the type locality is located. We decided on this name using a citizen science approach, where expert scientists and local people met and discussed a list of possible names and their corresponding meanings. There was consensus on *P. chamezensis* as the preferred name.

Conservation status. The direct evaluation of the landscape units (e.g., broad-leaved forest) at the type locality, as well as the map of land cover of Colombia (CORINE Land Cover, IDEAM 2010), allowed us to identify a rapid reduction and low connectivity of its habitat. Based on land cover maps of Chameza's forest, the potential extent of occurrence is 301,624 km^2. Consequently, we propose to categorize *P. chamezensis* as Vulnerable using the criteria B2a (IUCN Red List Categories and Criteria 2019).

Discussion

Colombian diversity of the genus *Pristimantis* in a biogeographical context

The genus *Pristimantis*, with 556 described species, comprises of a substantial number of identified taxa (Frost 2020). Colombia harbors 40% of this diversity. The Andean

Cordilleras harbor 183 species (Acosta-Galvis 2020), evidencing the high rate of speciation and endemism of the genus in this ecoregion (Lynch 1999), while in the lowlands (Pacific, Middle Magdalena, and Amazon basins) there are just 52 species. The diversity of *Pristimantis* of the Andean-Cordillera and Sierra Nevada of Santa Marta reflects the geological history of these mountains (Lynch and Ruiz-Carranza 1985; Lynch et al. 1997). Consequently, the geological formations of the Cordillera occidental (25 Ma old, with the greater species richness), Cordillera Central, and the Central Massif exhibit a 30% similarity of species. While, the Cordillera Oriental (10 Ma old; Gregory-Wodzicki 2000) and Sierra Nevada de Santa Marta (2.6 Ma old; Idárraga et al. 2011) have allowed the evolution of an unparalleled diversity with a high degree of endemism (Lynch et al. 1997) (Fig. 8).

Despite this rough correspondence between the geological history of the Colombian Andes and *Pristimantis* diversity, the inventory of species in each region is far from being completed. Socio-political factors affecting the various regions of Colombia have limited scientific access, leaving several crucial regions with pronounced gaps in our knowledge of amphibians. Among these regions, we highlight the northern lowland regions of the upper Amazon, including Putumayo, Caquetá, Guaviare, Guainía, and Vaupés departments, as well as neighboring areas such as the Darien region. Additionally, some other unsampled areas are the tropical rainforests in the Pacific basin and the Andean region, such as the Serranias of Perijá and San Lucas, southern Cordillera Oriental (including the Andean-Amazonian foothills) and mountainous areas associated with the Orinoco drainage (Fig. 8).

Over the past six years of scientific studies in unexplored mountainous areas within the Orinoco drainage, including cloud forests and foothills of the Cordillera Oriental, several species of *Pristimantis* have been described (e.g., Acosta-Galvis et al. 2010; Acosta-Galvis and Alfaro-Bejarano 2011; Pedroza-Banda et al. 2014; Rivera-Correa et al. 2016; Acevedo et al. 2020; Ospina-Sarria and Angarita-Sierra 2020). However, there is still a long way to go to characterize the amphibian fauna of this region.

Phylogenetic relationships of *Pristimantis chamezensis*

In our research, the integration of morphological and genetic data allowed us to establish that *P. chamezensis* is distinct from the other 13 *Pristimantis* species from Andean and sub-Andean forests on the eastern flank of the Cordillera Oriental. Taking into account the agreement between all phylogenetic analyses revealing a supported monophyletic group comprised of *P. chamezensis*, *P. carranguerorum*, *P. bowara*, *P. lutitus*, *P. medemi*, *P. nicefori*, and *P. savagei*, as well as the altitudinal (450–4170 m a.s.l.) and longitudinal distribution of those species along the Andean and sub-Andean forest on the eastern flank of the Cordillera Oriental (almost all are syntopic except by *P. lutitus* and *P. nicefori* from the western flank), it is probable that the origin of the new species and the radiation of the monophyletic group may have occurred at higher altitudes within this region. It might be possible that these *Pristimantis* lineages show the same

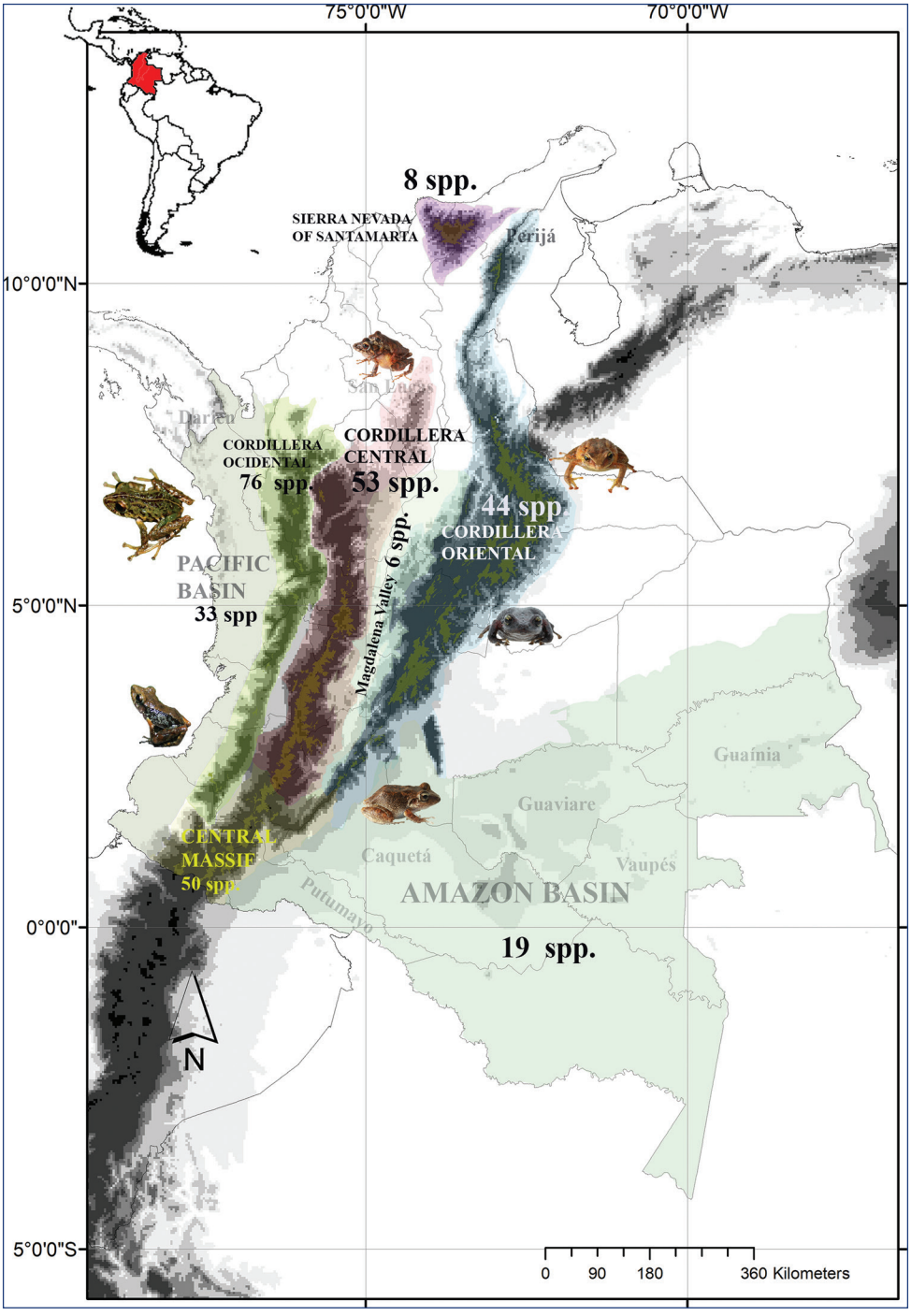

Figure 8. Geographic diversity of frogs of the genus *Pristimantis* in Colombia; the numerical values correspond to the number of species reported in each region.

pattern of recent diversification due to climatic changes, as seen in both, a high altitude dendrobatid frog (*Hyloxalus felixcoperari* Acosta-Galvis & Vargas-Ramírez, 2018) and a group of Andean anoles (*Anolis heterodermus* species group; Vargas-Ramírez and Moreno-Arias 2014) from the middle part of the eastern Cordillera.

Nevertheless, the generalized low support of the phylogenies emphasizes the need to increase the molecular dataset to reveal with confidence the evolutionary relationships within *Pristimantis*. This is clear from the recent changes in the phylogenetic position of several species (e.g., Hedges et al. 2008; Padial et al. 2014; Reyes-Puig et al. 2020). In addition, it is still required to incorporate a large number of unassigned Colombian taxa into evolutionary based species groups. There are about 117 species not yet analyzed using phylogenetic methods.

Our phylogenetic analyses unequivocally revealed that *P. chamezensis* is part of the subgenus *Pristimantis*. However, we do not force its allocation into one of the several species group (Hedges et al. 2008; Padial et al. 2014; Acevedo et al. 2020). Although our results validate some arrangements (e.g., *conspicillatus* or *danae* species groups; Fig. 3), some other individual assignments are weakly supported, and do not correspond to arrangements within the already proposed groups. Among the examples that we can identify, is the nesting of *P. chamezensis* with *P. nicefori*, which was formerly assigned within the *unistrigatus* group by Hedges et al. (2008) and later transferred to unassigned species group by Padial et al. (2014). Likewise, the close relationship of the *chamezensis*+ *P. nicefori* clade with the *P. lutitus* + *P. medemi* + *P. carranguerorum* clade (Fig. 3) is inconsistent with previous species groups assignments; *P. medemi* and *P. carranguerorum* were assigned to the *conspicillatus* species group by Hedges et al. (2008) and, later, validated by Padial et al. (2014). Additionally *P. lutitus* (Fig. 3), which was formerly assigned to the *unistrigatus* species group but subsequently transferred to an unassigned species group by Padial et al. (2014) and later inferred as sister to *P. anolirex* by Rivera et al. (2016).

Conclusion

Pristimantis chamezensis is described as an endemic species from Chámeza forest. This new species is closely related to *P. carranguerorum*, *P. bowara*, *P. lutitus*, *P. medemi*, *P. nicefori*, and *P. savagei*.

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Supplementary material 1

Additional specimens examined. IAvH-Am: Alexander von Humboldt Biological Resources Research Institute, Villa de Leyva, Colombia; MPUJ: Lorenzo Uribe Museum of Natural History, Pontificia Universidad Javeriana, Bogotá D.C., Colombia

Authors: Andrés R. Acosta-Galvis, Ana M. Saldarriaga-Gomez, Beatriz Ramirez, Mario Vargas-Ramirez

Data type: Additional Specimens of genus *Pristimantis* of Cordillera Orienta of Colombial

Link: https://doi.org/10.3897/zookeys.961.51971.suppl1

Supplementary material 2

Figure S1

Authors: Andrés R. Acosta-Galvis, Ana M. Saldarriaga-Gómez, Beatriz Ramírez, Mario Vargas-Ramírez

Data type: image

Explanation note: Maximum likelihood inference tree showing the evolutionary relationships of Pristimantis chamezensis sp. nov. (bold) and its 58 most closely related Pristimantis species based on 528 bp of the 16S rRNA gene. Numbers before nodes: thorough maximum likelihood (ML) bootstrap percentages left and Bayesian analysis (BA) posterior probability values right. Bootstrap values below 50% and posterior probabilities below 0.5 not shown. Outgroup taxon removed.

Link: https://doi.org/10.3897/zookeys.961.51971.suppl2

Supplementary material 3

Figure S2

Authors: Andrés R. Acosta-Galvis, Ana M. Saldarriaga-Gómez, Beatriz Ramírez, Mario Vargas-Ramírez

Data type: image

Explanation note: Bayesian (BA) and maximum likelihood (ML) topologies (right and left respectively) obtained based on 1185 bp of the 16S rRNA + COI genes. Numbers before nodes: BA posterior probability values and ML bootstrap percentages. Bootstrap values below 50% and posterior probabilities below 0.5 not shown.

Link: https://doi.org/10.3897/zookeys.961.51971.suppl3