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Thirty-one new species of the spider genus *Leclercera* from Southeast Asia (Araneae, Psilodercidae)

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Abstract
Thirty-one new species of the genus *Leclercera* Deeleman-Reinhold, 1995 from China, Indonesia, Malaysia, Myanmar, Nepal, and Thailand are described: *L. mianqiu* **sp. nov.** (♂♀), *L. thamsangensis* **sp. nov.** (♂♀), *L. yandou* **sp. nov.** (♂♀), *L. thamkaewensis* **sp. nov.** (♂♀), *L. xiangbabang* **sp. nov.** (♂♀), *L. jianzuiyu* **sp. nov.** (♂♀), *L. yamaensis* **sp. nov.** (♂♀), *L. banensis* **sp. nov.** (♂♀), *L. dumuzhou* **sp. nov.** (♀), *L. suwanensis* **sp. nov.** (♂♀), *L. maochong* **sp. nov.** (♀), *L. shanzi* **sp. nov.** (♀), *L. duandai* **sp. nov.** (♂♀), *L. hponensis* **sp. nov.** (♂♀), *L. lizi* **sp. nov.** (♂), *L. xiaodai* **sp. nov.** (♀), *L. yanjing* **sp. nov.** (♀), *L. ekteenensis* **sp. nov.** (♂), *L. zhamensis* **sp. nov.** (♂), *L. sanjiao* **sp. nov.** (♀), *L. selasihensis* **sp. nov.** (♂♀), *L. paiensis* **sp. nov.** (♀), *L. yuanzhui* **sp. nov.** (♀), *L. zanggaensis* **sp. nov.** (♀), *L. aniensis* **sp. nov.** (♂♀), *L. renqinensis* **sp. nov.** (♂♀), *L. shergylaensis* **sp. nov.** (♂♀), *L. pulongensis* **sp. nov.** (♂), *L. tudao* **sp. nov.** (♂♀), *L. duibaensis* **sp. nov.** (♂), and *L. jiazhongensis* **sp. nov.** (♂♀). Types are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing.

Keywords
Chelicerae, copulatory organs, endemic, Ochyroceratidae, taxonomy, tropical Asia

Introduction

The spider family Psilodercidae Machado, 1951 was previously a subfamily of Ochyroceratidae Fage, 1912 until Wunderlich (2004) elevated it to the family level. To date, Psilodercidae includes a total of 165 species in 11 genera (WSC 2019), and the family has been shown to be monophyletic (Li and Li 2018). It is distributed in Southeast Asia, southern China, and parts of South Asia (WSC 2019, Li et al. 2020). The number of species has ballooned to almost three times its size in the 21st century, from only 53 species known by the end of 20th century (Platnick 2000). More than half of the psilodercid genera, including *Flexicrurum* Tong & Li, 2007, *Luzonacera* Li & Li, 2017, *Priscaleclercera* Wunderlich, 2017, *Qiongocera* Li & Li, 2017, *Relictocera* Li & Li, 2017, *Sinoderces* Li & Li, 2017, and *Thaiderces* Li & Li, 2017, have been described only recently.

The genus *Leclercera* Deeleman-Reinhold, 1995 was placed in the subfamily Psilodercinae in the family Ochyroceratidae Fage, 1912 before the subfamily was elevated to family rank. A total of 11 species of the genus have been described so far (WSC 2019). More than half of these are found in Nepal (*Leclercera machadoi* (Brignoli, 1973), *L. mulcata* (Brignoli, 1973), *L. nagarjunensis* Li & Li, 2018, *L. niuqu* Li & Li, 2018, *L. sidai* Li & Li, 2018, *L. zhaoi* Li & Li, 2018), and the rest are distributed in Borneo (*L. ocellata* Deeleman-Reinhold, 1995), China (*L. undulata* Wang & Li, 2013), the Philippines (*L. negros* Deeleman-Reinhold, 1995), and Thailand (*L. khaoyai* Deeleman-Reinhold, 1995, *L. longiventris* Deeleman-Reinhold, 1995).

While examining spider collections from tropical Asia, we found 31 new species of *Leclercera* from China, Indonesia, Malaysia, Myanmar, Nepal, and Thailand. The goal of this paper is to provide detailed descriptions of these new species with images of their copulatory organs and chelicerae.

Materials and methods

Types are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing. All specimens collected were studied and preserved in 95% 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 (except for *Leclercera xiangbabang* sp. nov. whose right palp was detached). 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).

Taxonomy

Family Psilodercidae Machado, 1951

Genus *Leclercera* Deeleman-Reinhold, 1995

Type species. *Leclercera khaoyai* Deeleman-Reinhold, 1995 from Thailand.

Emended diagnosis. *Leclercera* resembles *Luzonacera* Li & Li, 2017 by having a shallow fovea, a slanted clypeus and labium, cheliceral lamina with two triangular extensions, and one promarginal cheliceral tooth and two retromarginal cheliceral teeth. However, they can be differentiated by the following combination of characters: 1) absence of a cymbial protrusion (vs. presence of a cymbial protrusion); 2) presence or absence of a conductor (vs. absence of a conductor); 3) palp with a retrolateral apophysis on tibia or cymbium (vs. palp without a retrolateral apophysis); 4) a non-pyriform bulb (vs. a pyriform bulb); and 5) different forms of spermathecae, with only one pair of stalked spermathecae.

Composition. *Leclercera khaoyai* Deeleman-Reinhold, 1995 (♂♀) (the type species), *L. longiventris* Deeleman-Reinhold, 1995 (♂), *L. machadoi* (Brignoli, 1973) (♂♀), *L. mulcata* (Brignoli, 1973) (♀), *L. nagarjunensis* Li & Li, 2018 (♂♀), *L. negros* Deeleman-Reinhold, 1995 (♀), *L. niuqu* Li & Li, 2018 (♂), *L. ocellata* Deeleman-Reinhold, 1995 (♀), *L. sidai* Li & Li, 2018 (♂♀), *L. undulata* Wang & Li, 2013 (♂♀), *L. zhaoi* Li & Li, 2018 (♂♀), *L. mianqiu* sp. nov. (♂♀), *L. thamsangensis* sp. nov. (♂♀), *L. yandou* sp. nov. (♂♀), *L. thamkaewensis* sp. nov. (♂♀), *L. xiangbabang* sp. nov. (♂♀), *L. jianzuiyu* sp. nov. (♂♀), *L. yamaensis* sp. nov. (♂♀), *L. banensis* sp. nov. (♂♀), *L. dumuzhou* sp. nov. (♀), *L. suwanensis* sp. nov. (♂♀), *L. maochong* sp. nov. (♀), *L. shanzi* sp. nov. (♀), *L. duandai* sp. nov. (♂♀), *L. hponensis* sp. nov. (♂♀), *L. lizi* sp. nov. (♂), *L. xiaodai* sp. nov. (♀), *L. yanjing* sp. nov. (♀), *L. ekteenensis* sp. nov. (♂), *L. zhamensis* sp. nov. (♂), *L. sanjiao* sp. nov. (♀), *L. selasihensis* sp. nov. (♂♀), *L. paiensis* sp. nov. (♀), *L. yuanzhui* sp. nov. (♀), *L. zanggaensis* sp. nov. (♀), *L. aniensis* sp. nov. (♂♀), *L. renqinensis* sp. nov. (♂♀), *L. shergylaensis* sp. nov. (♂♀), *L. pulongensis* sp. nov. (♂), *L. tudao* sp. nov. (♂♀), *L. duibaensis* sp. nov. (♂), and *L. jiazhongensis* sp. nov. (♂♀)

Distribution. The genus is known from China to Philippines and south to Malaysia and Indonesia.

Leclercera mianqiu sp. nov.

http://zoobank.org/4A9A07DD-1443-4EC7-8C72-3A9796CFB242
Figs 1, 2, 56H, 58

Types. ***Holotype*:** ♂ (IZCAS), Indonesia, Sulawesi, mountain in Palopo, 2°57.7790'S, 120°8.5230'E, elevation ca 370 m, 13.IX.2017, H. Liu and Z. Chen leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "miánqiú" (cotton ball) and refers to the unique fluffy ball of bristles on the bulb resembling a cotton ball (Fig. 2B).

Figure 1. *Leclercera mianqiu* sp. nov., male holotype and female paratype. **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.

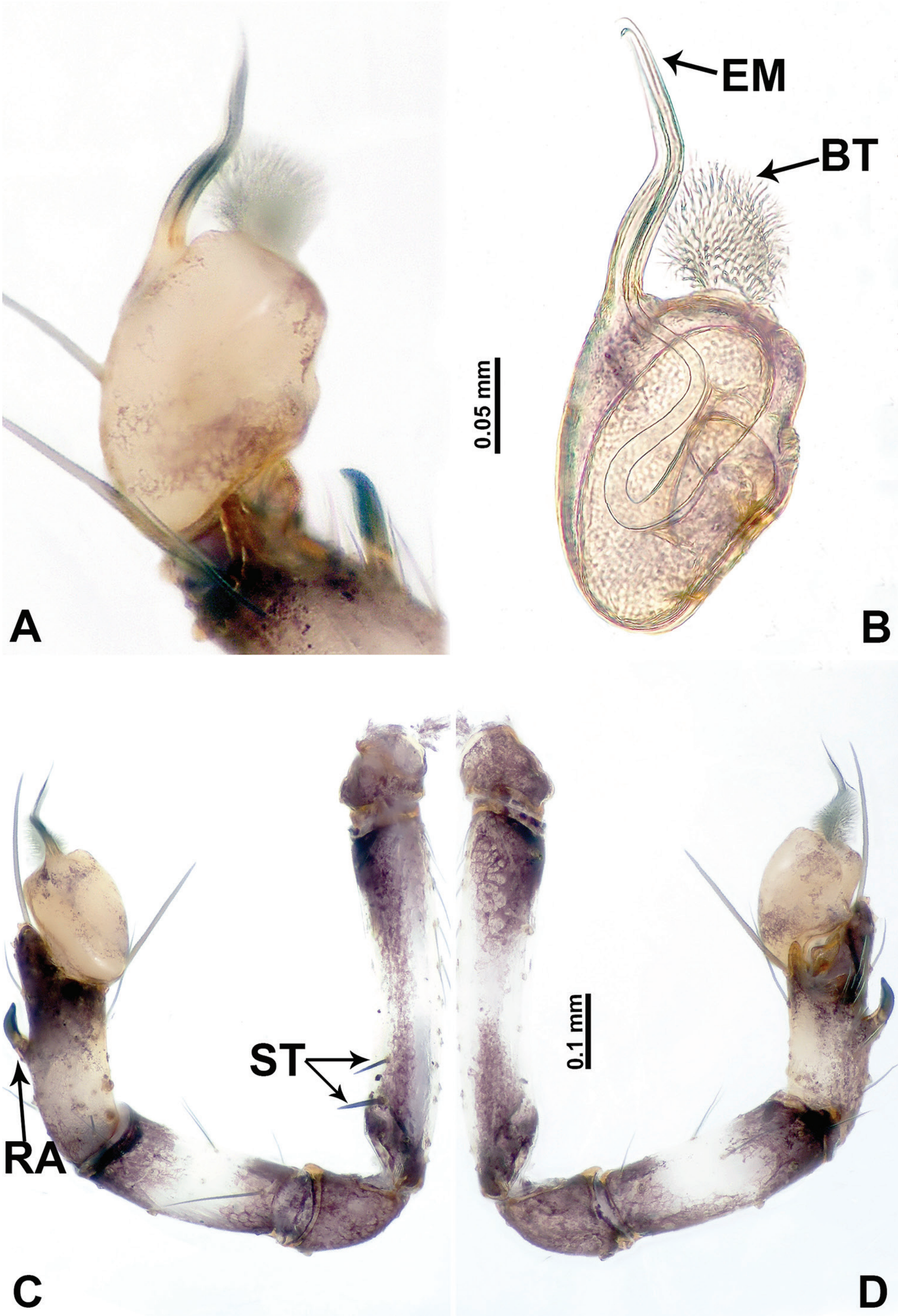

Figure 2. *Leclercera mianqiu* sp. nov., male holotype. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: BT = bristle, EM = embolus, RA = retrolateral apophysis, ST = strong setae.

Diagnosis. Males of *L. mianqiu* sp. nov. resemble *L. selasihensis* sp. nov. but can be distinguished by the presence of an attached fluffy ball of bristles adjacent to the embolus (vs. an absence of bristles but the presence of a conductor adjacent to embolus), presence of a medial-retrolateral apophysis on the cymbium (Fig. 2C) (vs. the presence of a postero-retrolateral apophysis on the cymbium (Fig. 37D)), the presence of two strong prolateral setae on the femur (Fig. 2C) (vs. the presence of one strong prolateral seta on the femur (Fig. 37D)); females can be distinguished by their rather pale coloration (vs. dark coloration), their stalked spermathecae that are globose distally (Fig. 1A) (vs. bean-shaped spermathecae that are strongly depressed anteriorly, and with median spiralled ducts (Fig. 36A)).

Description. Male (Holotype). Total length 2.60; carapace 1.00 long, 1.00 wide; abdomen 1.60 long, 0.80 wide. Carapace round and pale yellow, margin with black bands laterally (Fig. 1C). Chelicerae dark brown (Fig. 56H). Clypeus greyish brown. Endites pale yellow with dark edges. Labium light brown. Sternum pale yellow, with dark brown spots centrally. Abdomen elongated, dorsum with complex dark brown sports, antero-ventrally with rectangular brown patch, posterior half pale yellow with dark and light brown spots. Legs uniformly brown; measurements: I 31.16 (7.69, 0.40, 8.01, 12.82, 2.24), II 19.21 (5.45, 0.40, 5.13, 6.73, 1.50), III 14.90 (4.25, 0.40, 4.25, 4.75, 1.25), IV 20.97 (6.41, 0.40, 6.09, 6.47, 1.60). Palp (Fig. 2A–D): femur slender, four times longer than patella, anteriorly with two strong setae prolaterally, dark purplish proximally and distally; patella not swollen, dark purplish; tibia 1.5 times shorter than femur, dark purplish proximally and distally; cymbium two times shorter than femur, dark purplish distally, with broad and slightly curved medio-retrolateral apophysis; bulb light brown, obovoid, with embolus and a clump of bristles distally; embolus slightly curved, as long as tegulum, adjacent to bristles; bristles forming a rounded fluffy clump anteriorly, adjacent to embolus (Fig. 2B).

Female (Paratype). General features and coloration similar to those of male (Fig. 1D, E). Measurements: total length 2.76; carapace 0.88 long, 0.86 wide; abdomen 1.88 long, 1.00 wide. Leg measurements: I 20.59 (5.13, 0.40, 5.45, 7.69, 1.92), II 12.25 (3.25, 0.40, 3.40, 4.00, 1.20), III missing, IV 14.49 (4.00, 0.40, 4.00, 4.81, 1.28). Epigastric area (Fig. 1B): an elliptical patch with distinct dark brown lines anteriorly and posteriorly, posterior pale yellow. Endogyne (Fig. 1A): stalked spermathecae, globose distally and with a pair of deltoid-shaped receptacles, spermathecal heads almost five times wider than the stalks, stalks three times longer than heads.

Distribution. Known only from the type locality (Fig. 58).

Leclercera thamsangensis sp. nov.

http://zoobank.org/0A664B6A-03A5-4A15-BBEE-06D754270C97

Figs 3, 4, 56E, 58

Types. ***Holotype*****:** ♂ (IZCAS), Thailand, Loei Province, Phu Kradueng District, Phan Nok Kao Subdistrict, Tham Wat Phu Sang One, 16°49.0620'N, 101°56.4330'E, elevation ca 385 m, 29.XI.2016, H. Zhao leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

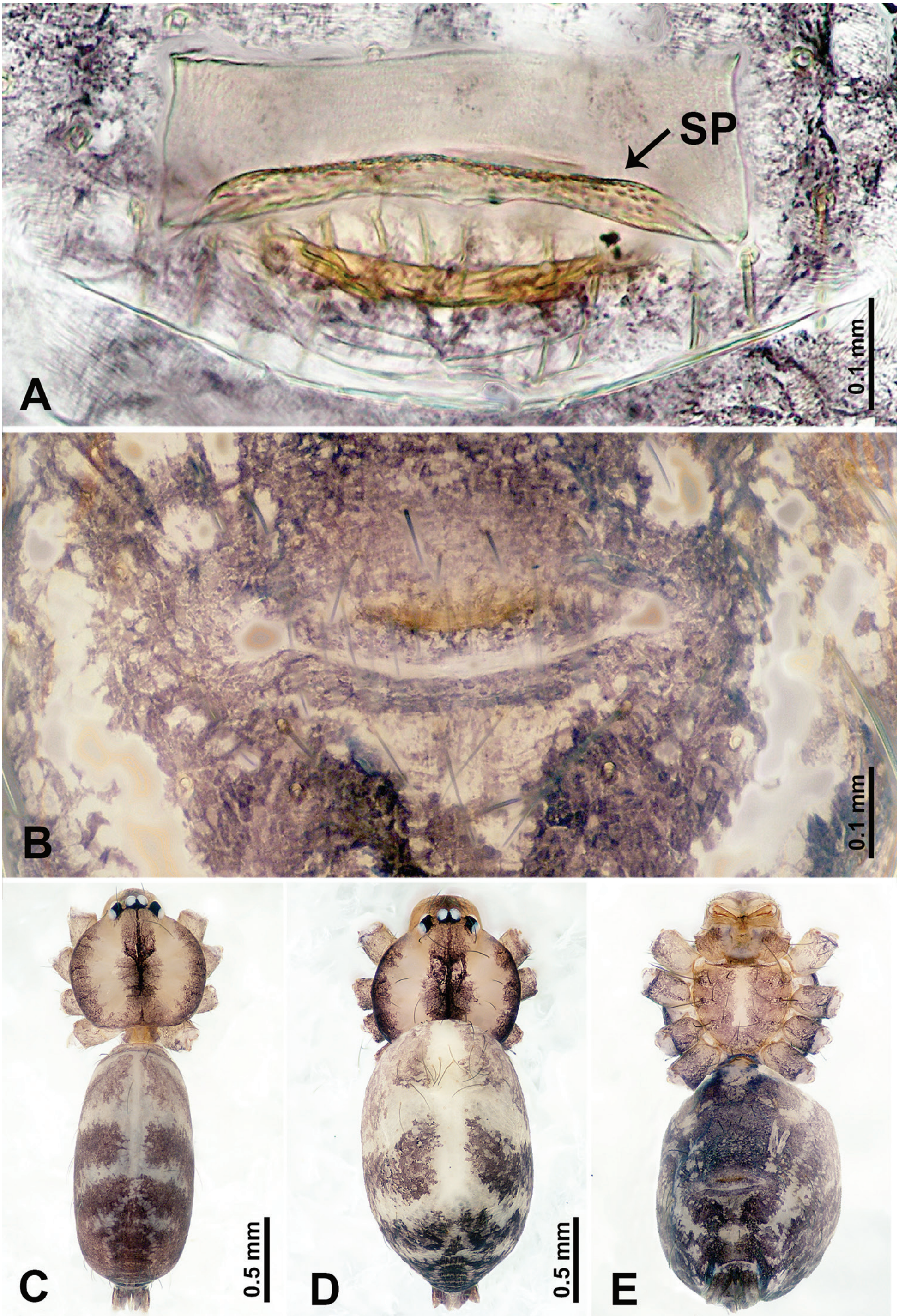

Figure 3. *Leclercera thamsangensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

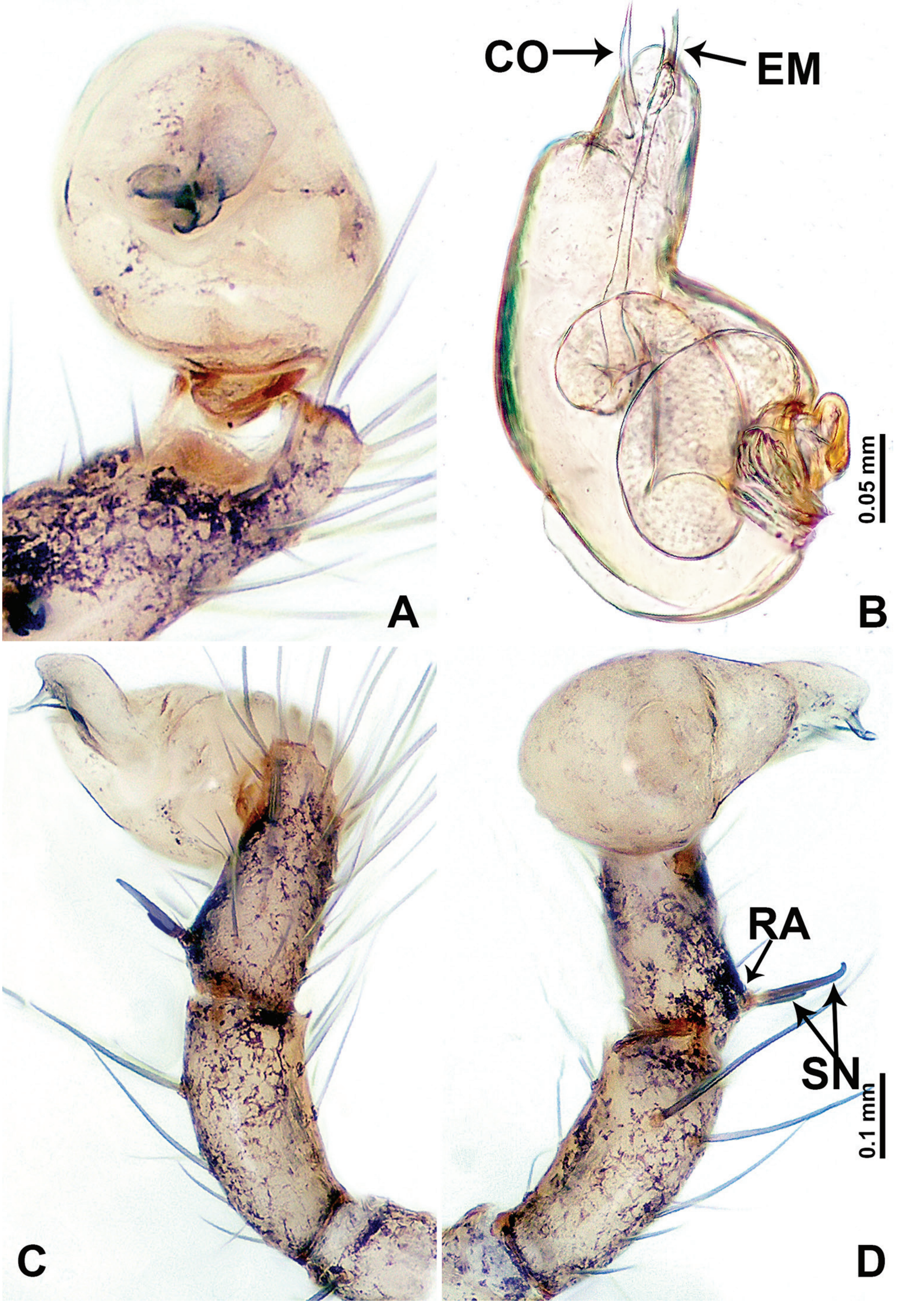

Figure 4. *Leclercera thamsangensis* sp. nov., male holotype. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, RA = retrolateral apophysis, SN = spines.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. thamsangensis* sp. nov. can be distinguished from congeners by the presence of two spines on a small retrolateral protrusion (retrolateral apophysis) of the cymbium (Fig. 4D) (vs. the absence of a retrolateral apophysis with two spines on the cymbium), the conductor and embolus are not widely separated, appearing to be similar in length and width (Fig. 4B) (vs. conductor and embolus different in congeners); females can be differentiated from congeners by rectangular, sheet-like spermathecae (Fig. 3A) (vs. absence of sheet-like spermathecae in congeners).

Description. Male (Holotype). Total length 2.44; carapace 0.82 long, 0.84 wide; abdomen 1.62 long, 0.74 wide. Carapace round and brown, with three longitudinal dark brown bands, median band two times as wide as lateral band (Fig. 3C). Chelicerae pale brown (Fig. 56E). Clypeus brown. Endites brown. Labium dark brown basally. Sternum purplish, delimiting a light brown band medially. Abdomen elongated, dorsum with dark brown stripes laterally, delimiting a light brown band medially, antero-ventrally dark brown with elliptical patch, posterior part with indistinct dark and light brown pattern. Legs uniformly brown; measurements: I 9.76 (2.69, 0.38, 3.13, 2.53, 1.03), II 7.48 (2.09, 0.30, 2.34. 1.94, 0.81), III 5.56 (1.56, 0.30, 1.63, 1.41, 0.66), IV 8.74 (2.50, 0.30, 2.69. 2.31, 0.94). Palp (Fig. 4A–D): femur slender, 3.5 times longer than patella; patella not swollen; tibia 1.5 times shorter than femur; cymbium 2.5 times shorter than femur, with a small retrolateral apophysis bearing two spines basally, one spine half the length of the other; bulb light brown, pyriform, with embolus and conductor arising distally; embolus straight and thin, basally connected to conductor; conductor almost as long and wide as embolus (Fig. 4B).

Female (Paratype). General features and coloration similar to that of male (Fig. 3D, E). Measurements: total length 1.97; carapace 0.81 long, 0.84 wide; abdomen 1.16 long, 1.00 wide. Leg measurements: I 8.97 (2.44, 0.31, 2.91, 2.34, 0.97), II 6.72 (1.94, 0.31, 1.91, 1.78, 0.78), III 5.19 (1.41, 0.31, 1.50, 1.31, 0.66), IV 7.87 (2.19, 0.31, 2.50, 2.03, 0.84). Epigastric area (Fig. 3B): purplish crescent-shaped patch with a few setae, with random purplish patterns. Endogyne (Fig. 3A): pair of spermathecae slightly concave toward the posterior, bearing a rectangular sheet anteriorly.

Distribution. Known only from the type locality (Fig. 58).

Leclercera yandou **sp. nov.**

http://zoobank.org/71776DDF-B11C-4F46-9650-9D56E92D76BC
Figs 5, 6, 55I, 58

Types. ***Holotype*:** ♂ (IZCAS), Malaysia, Malay Peninsula, Pahang States, Fraser's Hill, Telecom loop, Secondary Forest, 3°43.1050'N, 101°45.1643'E, elevation ca 1300 m, 17.II.2015, H. Zhao leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "yāndǒu" (smoking pipe) and refers to the palpal bulb which resembles a smoking pipe (Fig. 6B).

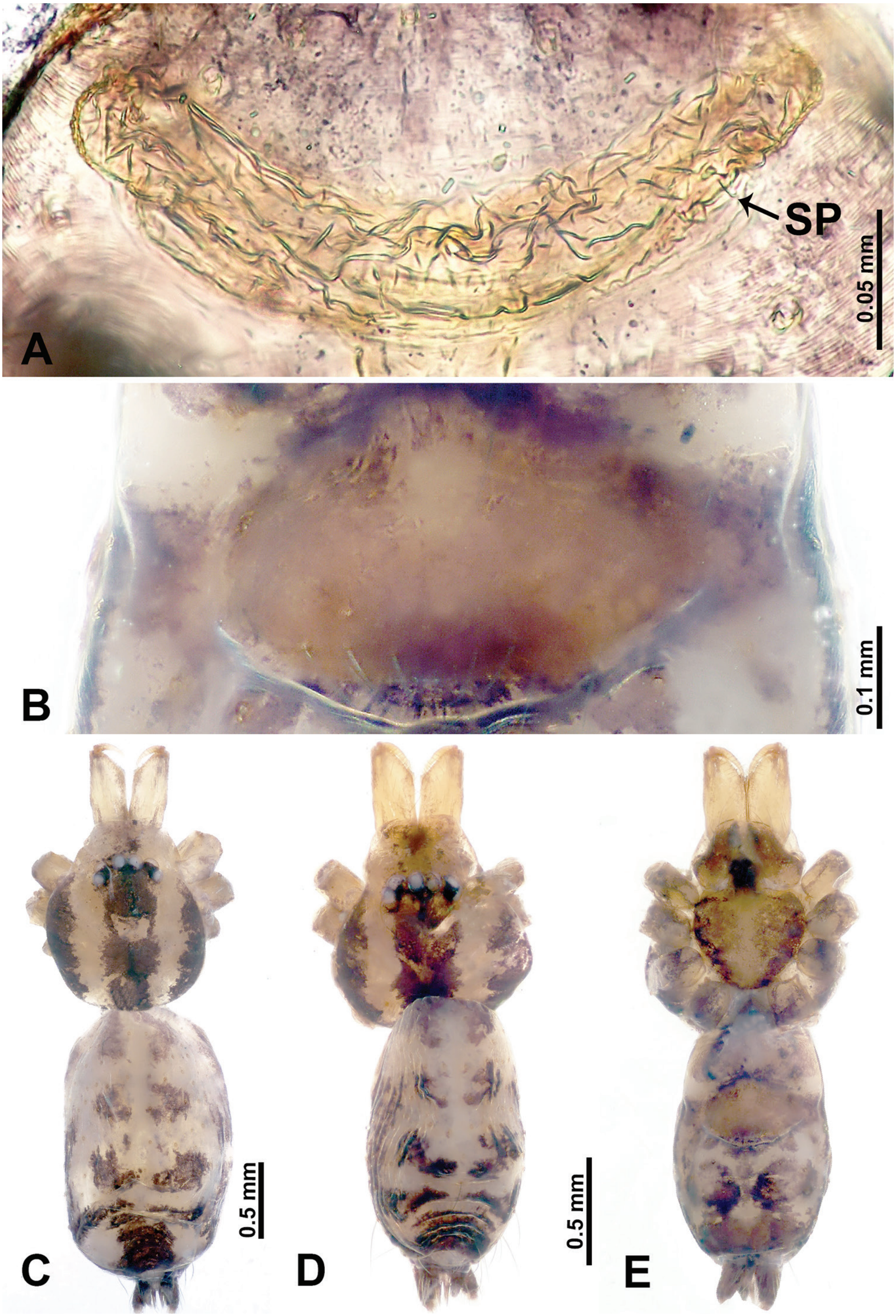

Figure 5. *Leclercera yandou* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

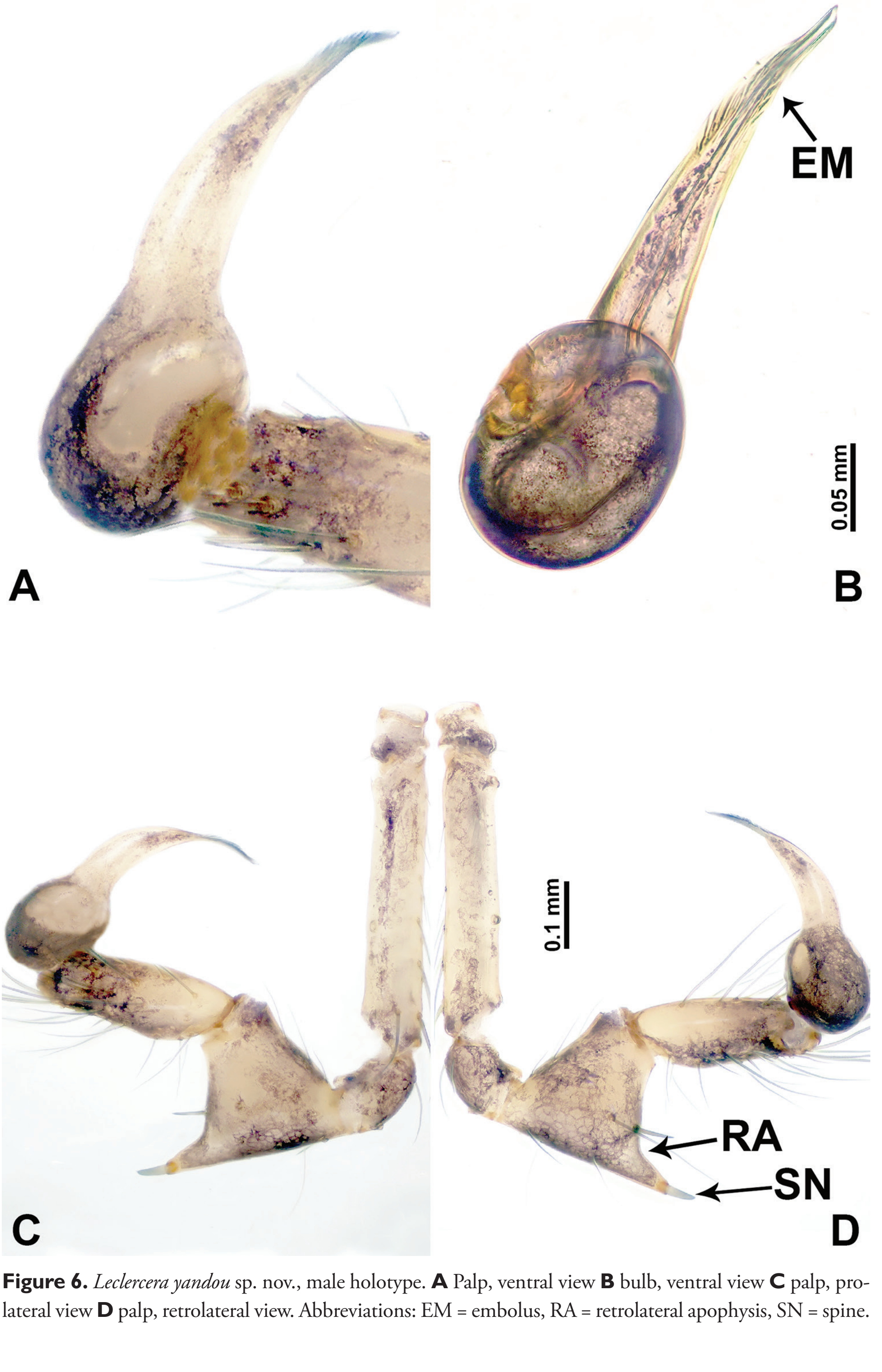

Figure 6. *Leclercera yandou* sp. nov., male holotype. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, RA = retrolateral apophysis, SN = spine.

Diagnosis. Males of *L. yandou* sp. nov. can be distinguished from congeners by the structure of the bulb, with a rounded base bearing a slightly curved and elongated embolus (Fig. 6B), the presence of a swollen triangular tibia with a retrolateral apophysis (Fig. 6D) (vs. absence of swollen triangular tibia in congeners); females can be differentiated from congeners by a pair of saucer-shaped, sinuous spermathecae (Fig. 5A)

Description. Male (Holotype). Total length 2.50; carapace 0.75 long, 0.94 wide; abdomen 1.75 long, 0.80 wide. Carapace round and brown, with three longitudinal dark brown bands, median band twice as wide as lateral band (Fig. 5C). Chelicerae brown (Fig. 55I). Clypeus brown. Endites dark brown, light brown basally. Labium dark brown. Sternum brown, with dark brown patched laterally. Abdomen elongated, dorsum with 3 pairs of dark brown spots medially, median dark brown bands concentrated posteriorly, antero-ventrally brown with elliptical patch, posterior part with indistinct dark and light brown pattern. Legs uniformly brown; measurements: I 8.54 (2.81, 0.25, 2.97, 1.88, 0.63), II missing, III missing, IV 8.09 (2.40, 0.25, 2.19, 2.25, 1.00). Palp (Fig. 6A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter than femur, forming a triangular shape with a retrolateral apophysis bearing a spine; cymbium two times shorter than femur, dark brown anteriorly; bulb spatulate with circular base, elongated embolus arises distally; embolus slightly bent, two times longer than the length of rounded tegulum and half the width of tegulum (Fig. 6B).

Female (Paratype). General features and coloration similar to those of male (Fig. 5D, E). Measurements: total length 2.10; carapace 0.80 long, 0.88 wide; abdomen 1.30 long, 0.70 wide. Leg measurements: I–III missing, IV 5.78 (1.63, 0.25, 1.60, 1.50, 0.80). Epigastric area (Fig. 5B): ovoid dark brown patch. Endogyne (Fig. 5A): a pair of sinuous spermathecae arching towards the anterior, ratio of width to length of entire spermathecae 1:7.

Distribution. Known only from the type locality (Fig. 58).

***Leclercera thamkaewensis* sp. nov.**

http://zoobank.org/5CB1D41A-D4C8-4056-B27C-3AD6A0284E4C
Figs 7, 8, 56C, 58

Types. ***Holotype*:** ♂ (IZCAS), Thailand, Sakaew Province, Klong Hat Subdistrict, Tham Phet Sai Kaew, 13°24.9620'N, 102°19.5890'E, elevation ca 243 m, 9.XI.2016, H. Zhao leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. thamkaewensis* sp. nov. can be distinguished from congeners by the presence of a laminar apophysis adjacent to the embolus (vs. absence of a laminar apophysis, or if present, with more than one laminar apophyses or apophysis adheres to embolus in congeners), cymbium with fine retrolateral apophysis anteriorly, tibia swollen with retrolateral apophyses bearing two spines anteriorly (Fig. 8D) (vs. absence of such a combination of retrolateral apophyses in congeners); females can be differentiated from congeners by a pair of transverse, ovoid spermathecae (Fig. 7A).

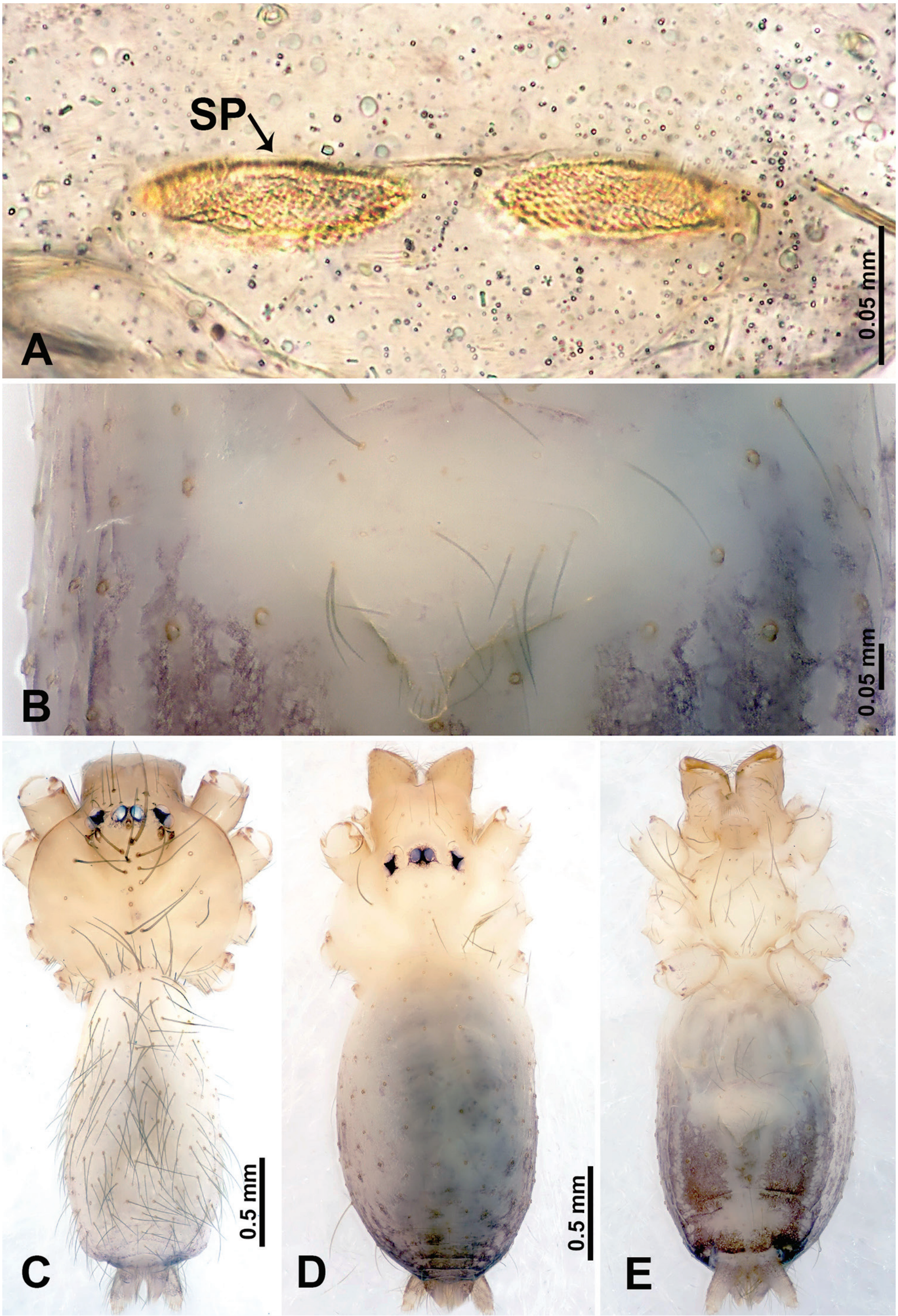

Figure 7. *Leclercera thamkaewensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

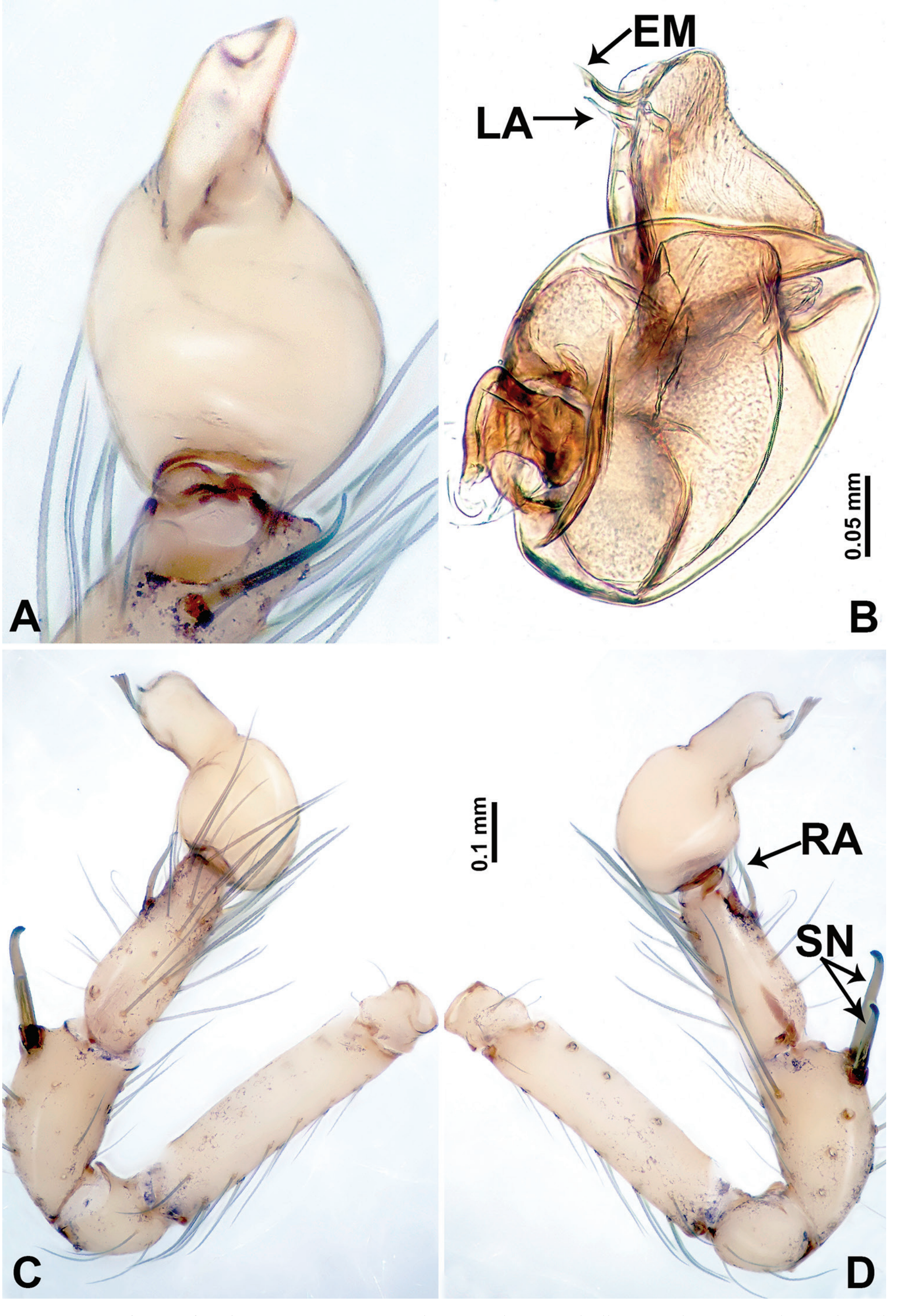

Figure 8. *Leclercera thamkaewensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, LA = laminar apophysis, RA = retrolateral apophysis, SN = spines.

Description. Male (Holotype). Total length 2.50; carapace 0.90 long, 1.17 wide; abdomen 1.60 long, 0.86 wide. Carapace round and pale brown, with setae concentrated at ocular region (Fig. 7C). Chelicerae brown (Fig. 56C). Clypeus brown. Endites and labium pale brown. Sternum pale yellow, with sparse setae. Abdomen elongated, pale yellow, dorsum with dense setae, antero-ventrally pale yellow with inverted triangular genitalic lobe, dark brown posteriorly, defining pale yellow longitudinal band and a transverse band. Legs uniformly brown; measurements: I 12.90 (3.60, 0.40, 4.00, 3.50, 1.40), II 10.49 (3.00, 0.40, 3.25, 2.75, 1.09), III 8.08 (2.34, 0.40, 2.40, 2.00, 0.94), IV 11.40 (3.20, 0.40, 3.60, 3.00, 1.20). Palp (Fig. 8A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen, 1.2 times shorter than femur, with retrolateral apophyses bearing two spines slightly bent at tip, one spine half the length of the other; cymbium 1.5 times shorter than femur, with a thin retrolateral apophysis anteriorly; bulb pyriform with embolus and laminar apophysis arising distally; embolus thin and sheet-like, widening toward tip; laminar apophysis shorter and thinner than embolus, adjacent to embolus (Fig. 8B).

Female (Paratype). General features and coloration similar to those of male (Fig. 7D, E). Measurements: total length 2.57; carapace 0.94 long, 0.94 wide; abdomen 1.63 long, 1.09 wide. Leg measurements: I 11.61 (3.21, 0.40, 3.60, 3.00, 1.40), II–III missing, IV 9.76 (2.80, 0.40, 2.97, 2.50, 1.09). Epigastric area (Fig. 7B): inverted triangle with rounded tip. Endogyne (Fig. 7A): pair of transverse ovoid spermathecae, width/length ratio of a spermatheca: 1:3.

Distribution. Known only from the type locality (Fig. 58).

Leclercera xiangbabang **sp. nov.**

http://zoobank.org/63ED67F9-CF8B-4BD9-8579-66B1A8145341
Figs 9, 10, 55F, 58

Types. ***Holotype*****:** ♂ (IZCAS), Thailand, Kanchanaburi Province, Sai Yok District, Wang Krachae Subdistrict, Cave without name, 14°12.1820'N, 99°01.4161'E, elevation ca 342 m, 01.XI.2014, H. Zhao, Y. Li, Z. Chen leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin “xiàngbábàng” (geoduck) and refers to the entire structure of the bulb which resembles the appearance of a Pacific geoduck bivalve.

Diagnosis. Males of *L. xiangbabang* sp. nov. resemble *L. jianzuiyu* sp. nov. by having a spatulate bulb and a retrolateral apophysis on the tibia but can be distinguished by a rather bulging bulb and a wider embolus (Fig. 10B) (vs. a rather slender bulb and thin embolus (Fig. 12B)), a retrolateral apophysis on tibia, half the length of the tegulum (Fig. 10D) (vs. retrolateral apophysis on tibia equal in length to tegulum (Fig. 12C)); females can be differentiated by the elongated tubular spermathecae (Fig. 9A) (vs. rounded spermathecae (Fig. 11A)).

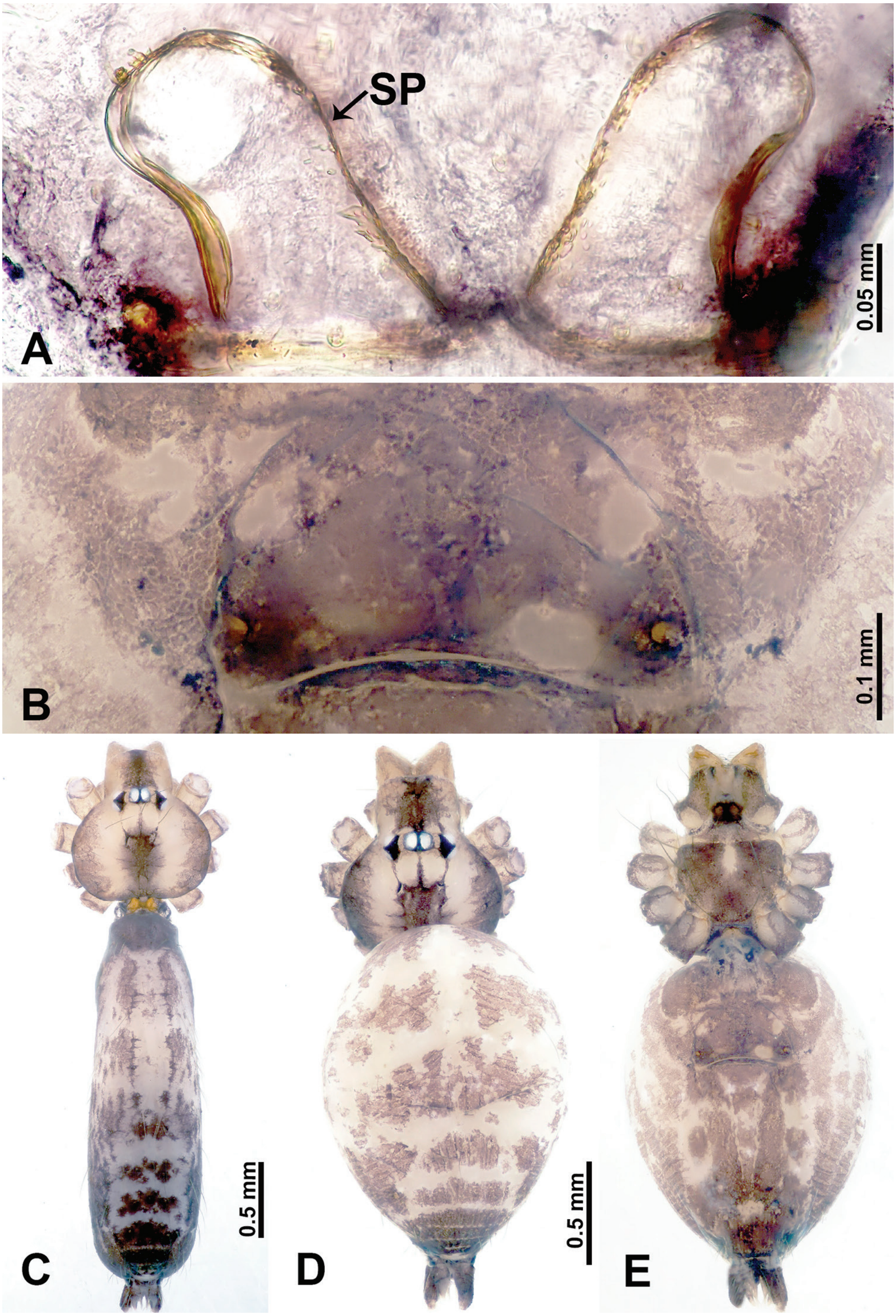

Figure 9. *Leclercera xiangbabang* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

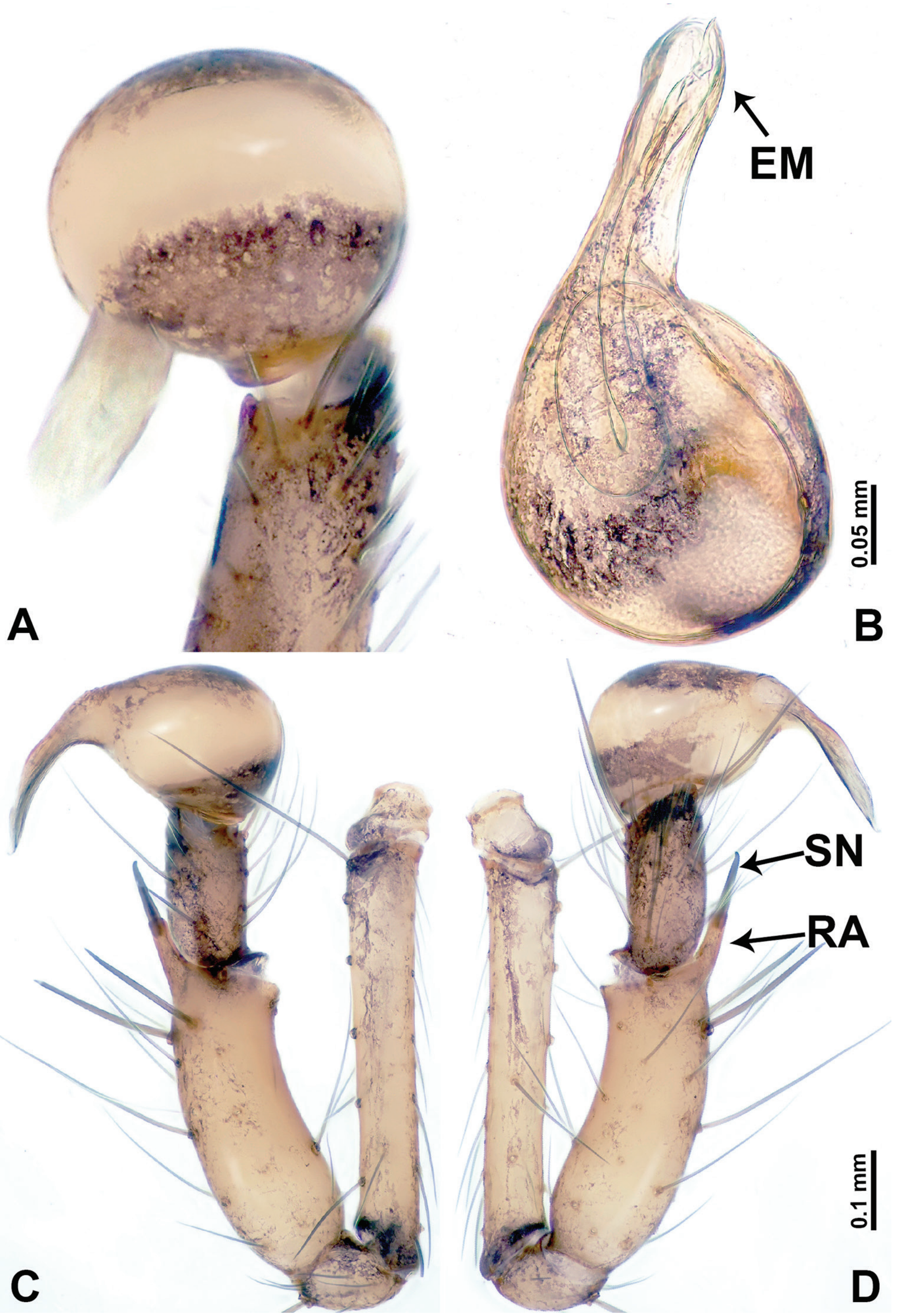

Figure 10. *Leclercera xiangbabang* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, RA = retrolateral apophysis, SN = spine.

Description. Male (Holotype). Total length 3.18; carapace 0.80 long, 0.88 wide; abdomen 2.38 long, 0.80 wide. Carapace round and brown, with three longitudinal dark brown bands, median band two times wider than lateral band (Fig. 9C). Chelicerae brown (Fig. 55F). Clypeus dark brown medially, light brown laterally. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown, delimiting a short, light brown band medially. Abdomen elongated, anterior and posterior edge dark brown, with scattered dark and light brown patterns, antero-ventrally with dark brown circular patches laterally, with complex dark and light brown patterns posteriorly. Legs uniformly brown; measurements: I 12.75 (4.00, 0.25, 3.75, 3.00, 1.75), II 9.06 (2.75, 0.31, 2.40, 2.60, 1.00), III 6.51 (1.88, 0.25, 1.88, 1.75, 0.75), IV 9.51 (3.20, 0.31, 2.40, 2.60, 1.00). Palp (Fig. 10A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and two times wider than femur, with retrolateral apophysis anteriorly bearing a spine, about half the length of tegulum, spine and apophysis almost equal in length; cymbium dark brown, three times shorter than femur; bulb bulging, spatulate, brown, with embolus arising distally; embolus elongated, with blunt tip, as long as tegulum, tegulum three times wider than embolus (Fig. 10B).

Female (Paratype). General features and coloration similar to those of male (Fig. 9D, E). Measurements: total length 2.26; carapace 0.63 long, 0.75 wide; abdomen 1.63 long, 1.13 wide. Leg measurements: I missing, II 7.51 (2.25, 0.25, 2.13, 2.00, 0.88), III 7.81 (2.25, 0.25, 2.34, 2.03, 0.94), IV 5.30 (1.60, 0.25, 1.50, 1.25, 0.70). Epigastric area (Fig. 9B): dark brown slit that slightly curves posteriorly. Endogyne (Fig. 9A): elongated tubular spermathecae, slightly slanting, length of a spermatheca is 2.5 times its width.

Distribution. Known only from the type locality (Fig. 58).

Leclercera jianzuiyu **sp. nov.**

http://zoobank.org/8294145B-88E3-41DC-9E2F-8B0AB36F6A53
Figs 11, 12, 55E, 58

Types. ***Holotype*:** ♂ (IZCAS), Thailand, Prachuap Kiri Khan Province, Hua Hin District, Nong Phlap Subdistrict, Laplae Cave and Kailone Cave, 12°36.2550'N, 99°43.3410'E, elevation ca 175 m, 30.X.2014, H. Zhao, Y. Li and Z. Chen leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "jiānzuǐyú" (bird wrasse – a type of fish) and refers to the entire structure of bulb which resembles the mouth of a bird wrasse.

Diagnosis. Diagnostic features of males and females are discussed in the diagnosis of *L. xiangbabang* sp. nov.

Description. Male (Holotype). Total length 2.88; carapace 0.63 long, 0.78 wide; abdomen 2.25 long, 0.63 wide. Carapace round and pale yellow, with three longitudinal dark brown bands, median band two times wider than lateral bands (Fig. 11C).

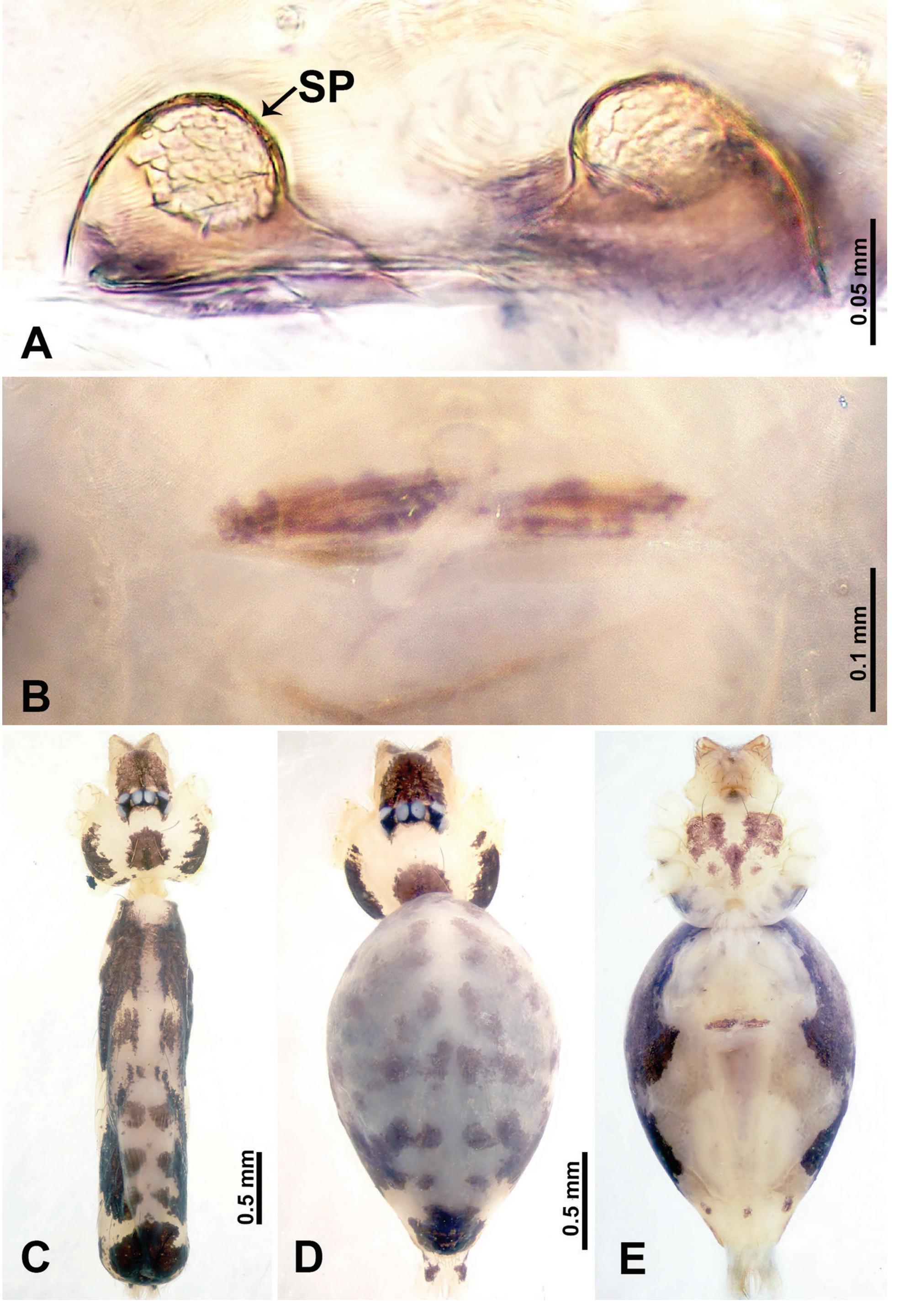

Figure 11. *Leclercera jianzuiyu* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

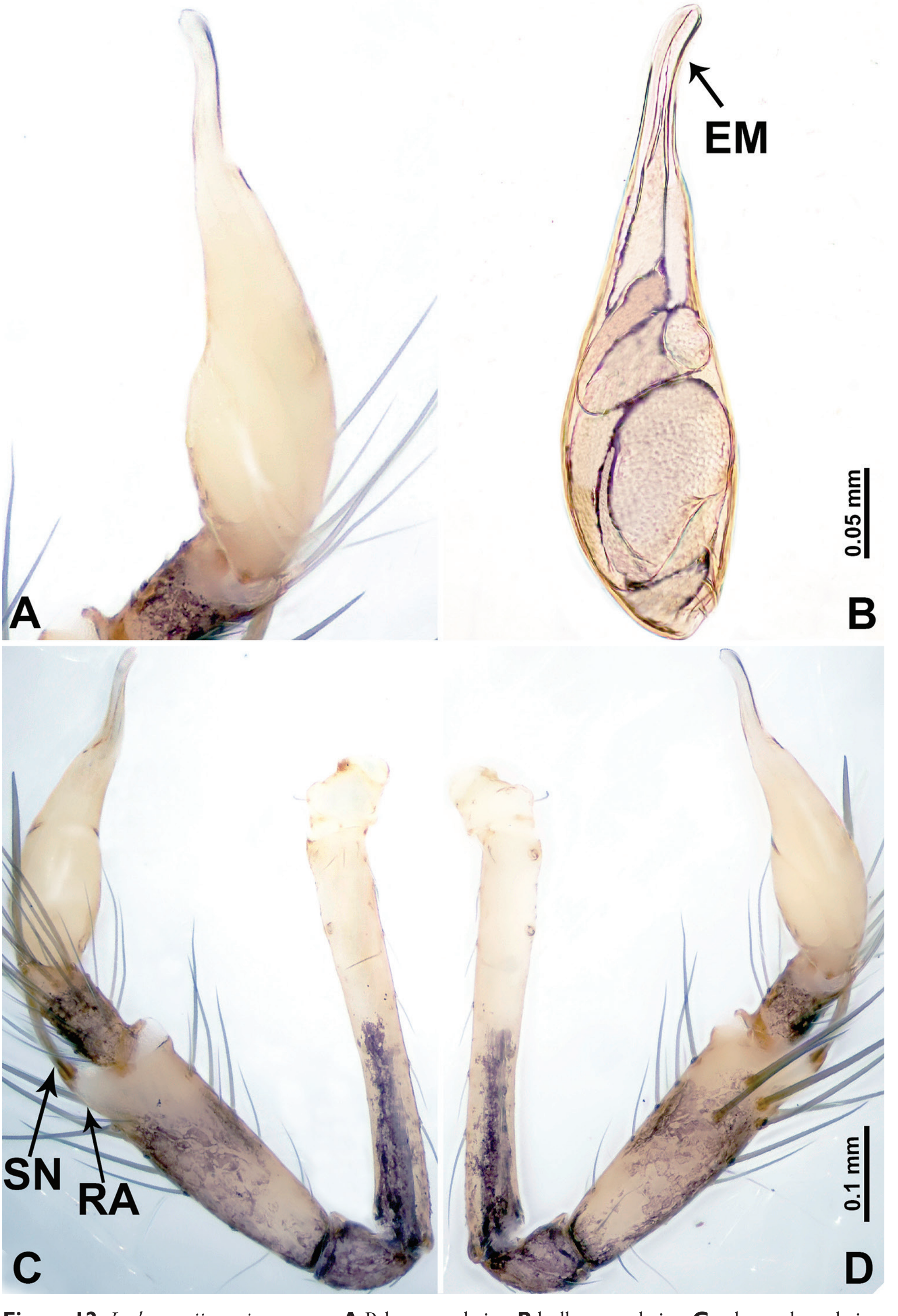

Figure 12. *Leclercera jianzuiyu* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, RA = retrolateral apophysis, SN = spine.

Chelicerae brown (Fig. 55E). Clypeus dark brown medially, pale yellow laterally. Endites pale yellow. Labium brown, circular dark brown spot basally. Sternum pale yellow, anterior with dark brown patches laterally, posterior with dark brown band medially. Abdomen elongated, edges of anterior and posterior dark brown, with complex scattered dark brown pattern, antero-ventrally pale yellow with transverse brown band medially, black patches from edges of anterior to posterior. Legs uniformly brown; measurements: I 13.06 (3.75, 0.31, 4.00, 3.60, 1.40), II 8.63 (2.50, 0.25, 2.60, 2.34, 0.94), III missing, IV 9.20 (2.80, 0.20, 2.66, 2.60, 0.94). Palp (Fig. 12A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and two times wider than femur, with retrolateral apophysis anteriorly bearing a spine almost as long as tegulum; cymbium dark brown, 3.5 times shorter than femur; bulb thinly spatulate, pale brown, with embolus arising distally; embolus elongated with slightly bent, blunt tip, half the width of tegulum (Fig. 12B).

Female (Paratype). General features and coloration similar to those of male (Fig. 11E, F). Measurements: total length 2.00; carapace 0.60 long, 0.70 wide; abdomen 1.40 long, 1.25 wide. Leg measurements: I–II missing, III 4.45 (1.25, 0.20, 1.30, 1.20, 0.50), IV 7.20 (2.19, 0.25, 2.13, 1.88, 0.75). Epigastric area (Fig. 11B): a pair of dark brown horizontal patches laterally. Endogyne (Fig. 11A): a pair of circular spermathecae with thin strips laterally, wavy patterns in spermathecae, lateral stripes two times longer than circular spermathecae.

Distribution. Known only from the type locality (Fig. 58).

Leclercera yamaensis sp. nov.

http://zoobank.org/BDB65387-B1D6-4D78-A322-767846BF4E06

Figs 13, 14, 56D, 58

Types. ***Holotype*:** ♂ (IZCAS), Thailand, Tak Province, Umphang District, Umphang Subdistrict, Ya Mae Cave, 16°02.3530'N, 98°50.8120'E, elevation ca 454 m, 15.XI.2016, H. Zhao leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. yamaensis* sp. nov. can be distinguished from congeners by an indentation on the anterior end of the palpal tibia formed by the presence of a retrolateral apophysis bearing a spine that is longer than the tegulum (Fig. 14D) (vs. the absence of such an indentation from a retrolateral apophysis in congeners), the presence of two strong setae on the retrolateral apophysis (Fig. 14D) (vs. the absence of setae on the retrolateral apophysis in congeners), the presence of a laminar apophysis adhering to the embolus (vs. absence of laminar apophysis, or if present, widely separated from the embolus in congeners); females can be differentiated from congeners by a pair of hook-like spermathecae (Fig. 13A).

Description. Male (Holotype). Total length 2.62; carapace 0.82 long, 0.92 wide; abdomen 1.80 long, 0.80 wide. Carapace round and pale brown, with dark brown traces medially (Fig. 13C). Chelicerae brown (Fig. 56D). Clypeus pale brown. Endites

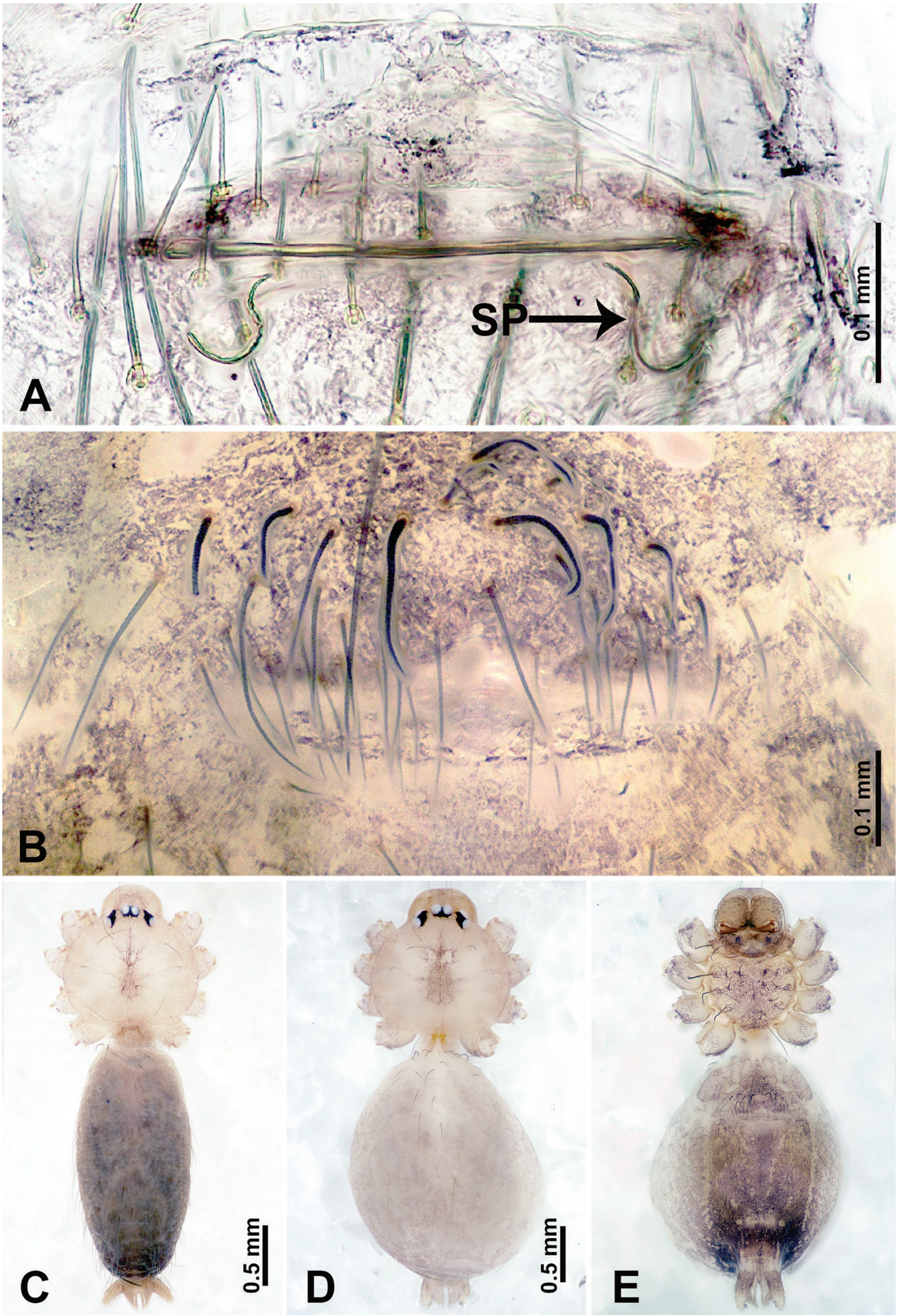

Figure 13. *Leclercera yamaensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

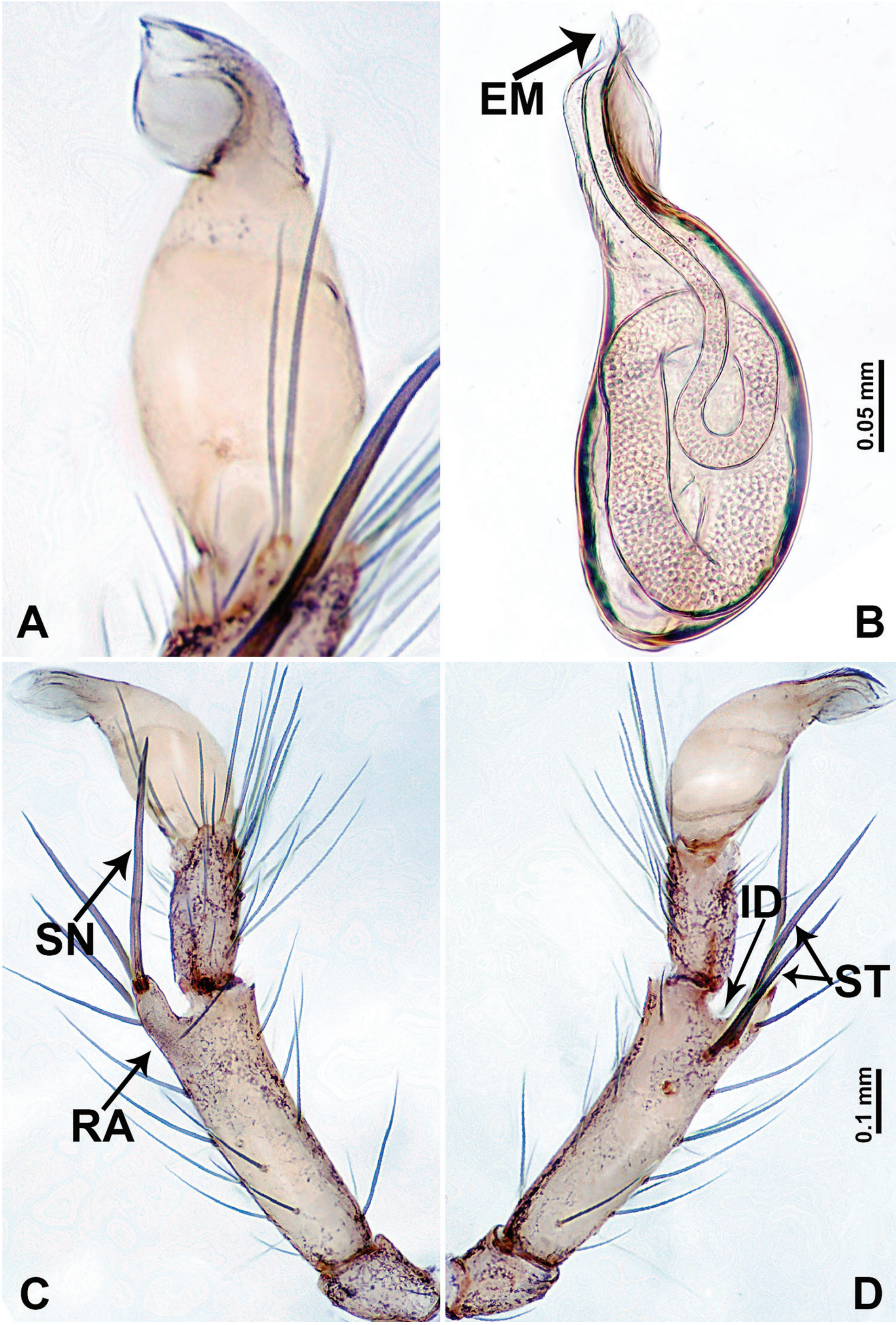

Figure 14. *Leclercera yamaensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, ID = indentation, RA = retrolateral apophysis, SN = spine, ST = strong setae.

and labium dark brown. Sternum with scattered purplish traces. Abdomen elongated, dorsum dark brown, antero-ventrally dark brown with triangular spot, posterior with dark brown, purplish pattern. Legs uniformly brown; measurements: I 13.91 (4.00, 0.31, 4.50, 3.75, 1.35), II 11.43 (3.32, 0.31, 3.60, 3.00, 1.20), III 8.22 (2.50, 0.31, 2.41, 2.03, 0.97), IV missing. Palp (Fig. 14A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and two times wider than femur, with retrolateral apophysis anteriorly bearing a spine longer than the length of the tegulum, apophysis forms an indentation on tibia anteriorly; cymbium 3.5 times shorter than femur; bulb pyriform, with embolus and laminar apophysis arising distally; embolus thin, with laminar apophysis attached; laminar apophysis five times shorter than the length of tegulum, adhering to embolus (Fig. 14B).

Female (Paratype). General features and coloration similar to those of male (Fig. 13E, F). Measurements: total length 2.50; carapace 0.80 long, 0.90 wide; abdomen 1.70 long, 1.20 wide. Leg measurements: I 12.45 (3.53, 0.31, 4.00, 3.33, 1.28), II 10.11 (2.84, 0.31, 3.20, 2.68, 1.08), III 6.99 (2.00, 0.31, 2.08, 1.76, 0.84), IV 10.15 (3.00, 0.31, 3.20, 2.60, 1.04). Epigastric area (Fig. 13B): brown slit surrounded with purplish spots. Endogyne (Fig. 13A): hook-like spermathecae, ratio of spermatheca width and spermatheca interdistance 1:4.5.

Distribution. Known only from the type locality (Fig. 58).

Leclercera banensis sp. nov.

http://zoobank.org/41B9DA08-475B-45BE-A8AC-6A23C903EAA5

Figs 15, 16, 55D, 58

Types. ***Holotype*:** ♂ (IZCAS), Thailand, Krabi Province, Muang District, Ban Chong Plee Village, 8°5.1218'N, 98°51.2228'E, elevation ca 442 m, 25.X.2014, H. Zhao, Y. Li and Z. Chen leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. banensis* sp. nov. resemble *L. suwanensis* sp. nov. but can be distinguished by an embolus that is longer and almost as wide as the conductor (Fig. 16B) (vs. an embolus that is equally as long as the conductor but almost four times wider basally (Fig. 19B)), bulb rather slender (vs. bulb rather expanded), patella swollen, cymbium not swollen (vs. patella not swollen, cymbium swollen), hexagonal swollen tibia (vs. pentagonal swollen tibia), tibia with three retrolateral apophyses, each bearing a spine (Fig. 16D) (vs. tibia with a single retrolateral apophysis bearing a spine and a strong seta (Fig. 19D)); females can be differentiated by a pair of flattened spermathecae with an anterior extension laterally (Fig. 15A) (vs. a pair of bulging, curled spermathecae with posterior extension laterally (Fig. 18A)).

Description. Male (Holotype). Total length 1.83; carapace 0.63 long, 0.75 wide; abdomen 1.20 long, 0.70 wide. Carapace round and pale brown, with three longitudinal dark brown bands, median band two times wider than the lateral bands (Fig. 15C). Chelicerae brown (Fig. 55D). Clypeus dark brown medially, light brown laterally. En-

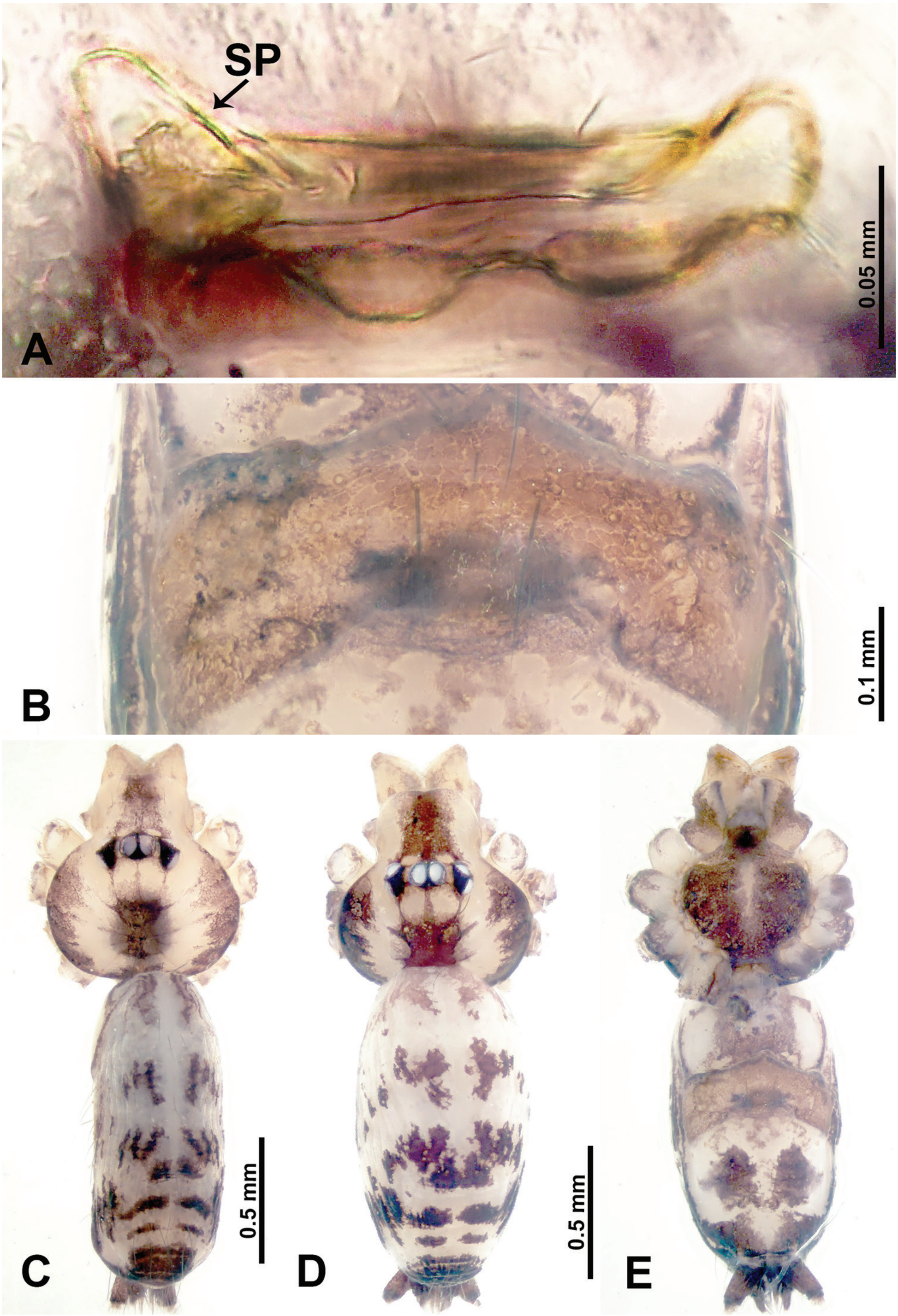

Figure 15. *Leclercera banensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

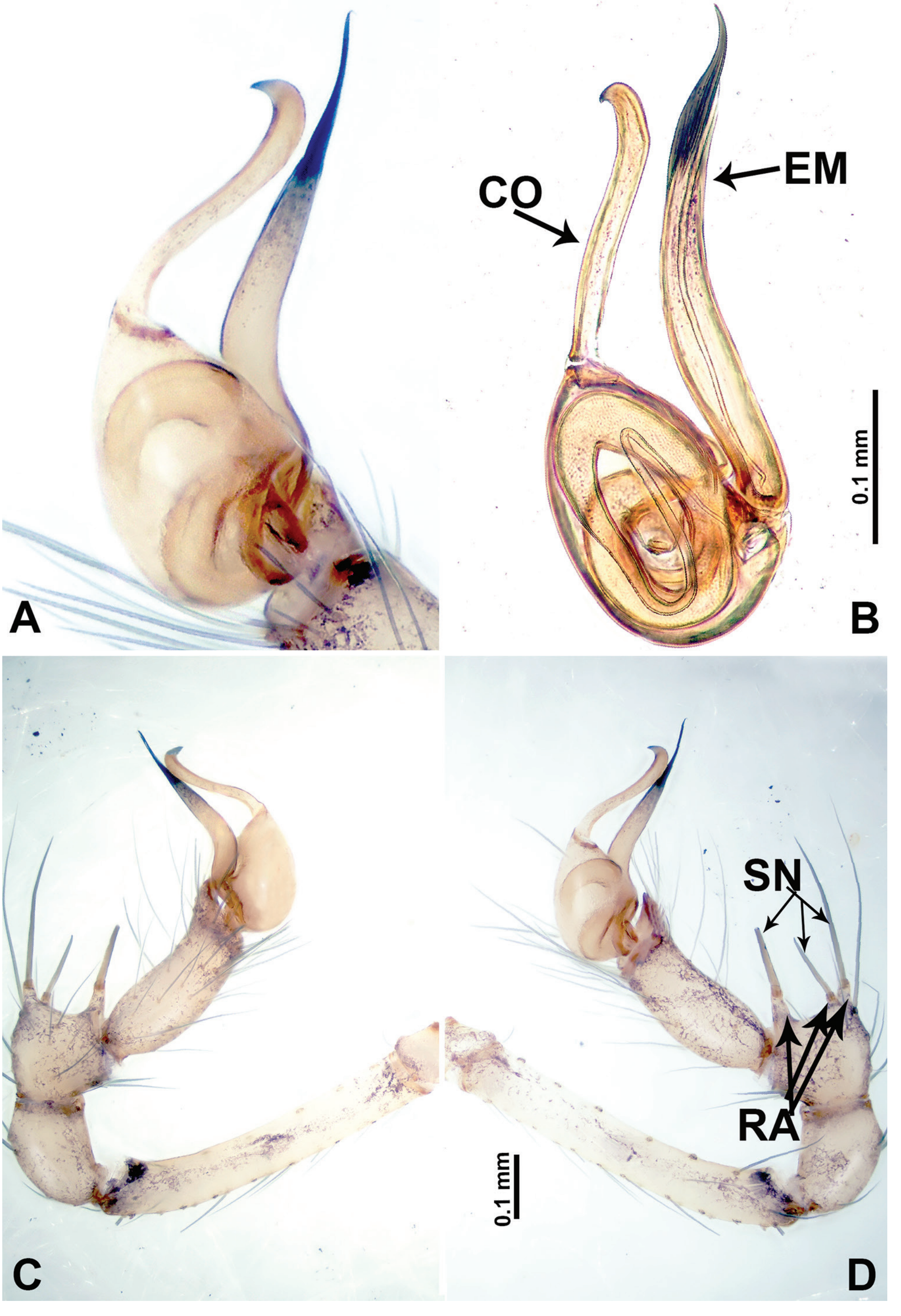

Figure 16. *Leclercera banensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, RA = retrolateral apophyses, SN = spines.

dites dark brown, light brown basally. Labium dark brown. Sternum dark brown with tiny light brown band medially. Abdomen elongated, dorsum with dark brown spots, antero-ventrally with brown horizontal band centrally, posterior with a pair of dark brown spots. Legs uniformly brown; measurements: I–II missing, III 5.21 (1.56, 0.25, 1.40, 1.40, 0.60), IV 7.85 (2.19, 0.25, 2.34, 2.19, 0.88). Palp (Fig. 16A–D): femur slender, 3 times longer than patella; patella swollen; tibia 3.5 times shorter than femur, hexagonally swollen, with three retrolateral apophyses anteriorly, each bearing a spine, with one spine longer than the other two; cymbium two times shorter than femur; bulb pale brown and ovoid, conductor and embolus separated, with conductor arising distally, embolus arising basally; conductor elongated and slightly hooked at tip, 2 times shorter than, but almost equally as wide as, embolus; embolus elongated, darkening distally (Fig. 16B).

Female (Paratype). General features and coloration similar to those of the male (Fig. 15D, E). Measurements: total length 1.80; carapace 0.60 long, 0.70 wide; abdomen 1.20 long, 0.70 wide. Leg measurements: I 7.97 (2.40, 0.25, 2.66, 2.03, 0.63), II 6.64 (1.88, 0.25, 1.88, 1.88, 0.75), III 4.15 (1.30, 0.20, 1.00, 1.10, 0.55), IV 6.28 (1.88, 0.20, 1.70, 1.75, 0.75). Epigastric area (Fig. 15B): an elliptical dark brown patch surrounded with a brown horizontal band. Endogyne (Fig. 15A): a pair of flattened spermathecae with tubular extensions laterally, and a pair of ovoid ducts posteriorly.

Distribution. Known only from the type locality (Fig. 58).

***Leclercera dumuzhou* sp. nov.**

http://zoobank.org/30CC9F7A-D769-46DC-9EBE-6BFE69D9A1C3
Figs 17, 56A, 58

Types. ***Holotype*:** ♀ (IZCAS), Thailand, Krabi Province, Muang District, Ban Klom Nong Thale Subdistrict, 8°8.1550'N, 98°48.4300'E, elevation ca 89 m, 26.X.2014, H. Zhao, Y. Li, Z. Chen leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "dúmùzhōu" (canoe) and refers to the structure of the spermathecae which resembles a canoe.

Diagnosis. Female of *L. dumuzhou* sp. nov. resembles the female of *L. banensis* sp. nov. but can be differentiated by the antero-ventral dark brown band surrounding the external genitalia which does not extend across the entire width of the abdomen (Fig. 17B) (vs. the dark brown transverse band fully covering the entire width of the abdomen (Fig. 15B)), spermathecae slightly curved anteriorly with tip directed laterally (Fig. 17A) (vs. spermathecae flattened with tubular extensions laterally (Fig. 15A)).

Description. Female. Total length 1.76; carapace 0.63 long, 0.70 wide; abdomen 1.13 long, 0.70 wide. Carapace round and brown, with three longitudinal dark brown bands, median band 3 times wider than lateral bands, anterior with trident of dark brown stripes (Fig. 17C). Chelicerae brown (Fig. 56A). Clypeus dark brown medially, light brown laterally. Endites dark brown, delimiting circular light brown spots basally. Labium dark brown. Sternum dark brown with median light brown strip. Abdomen

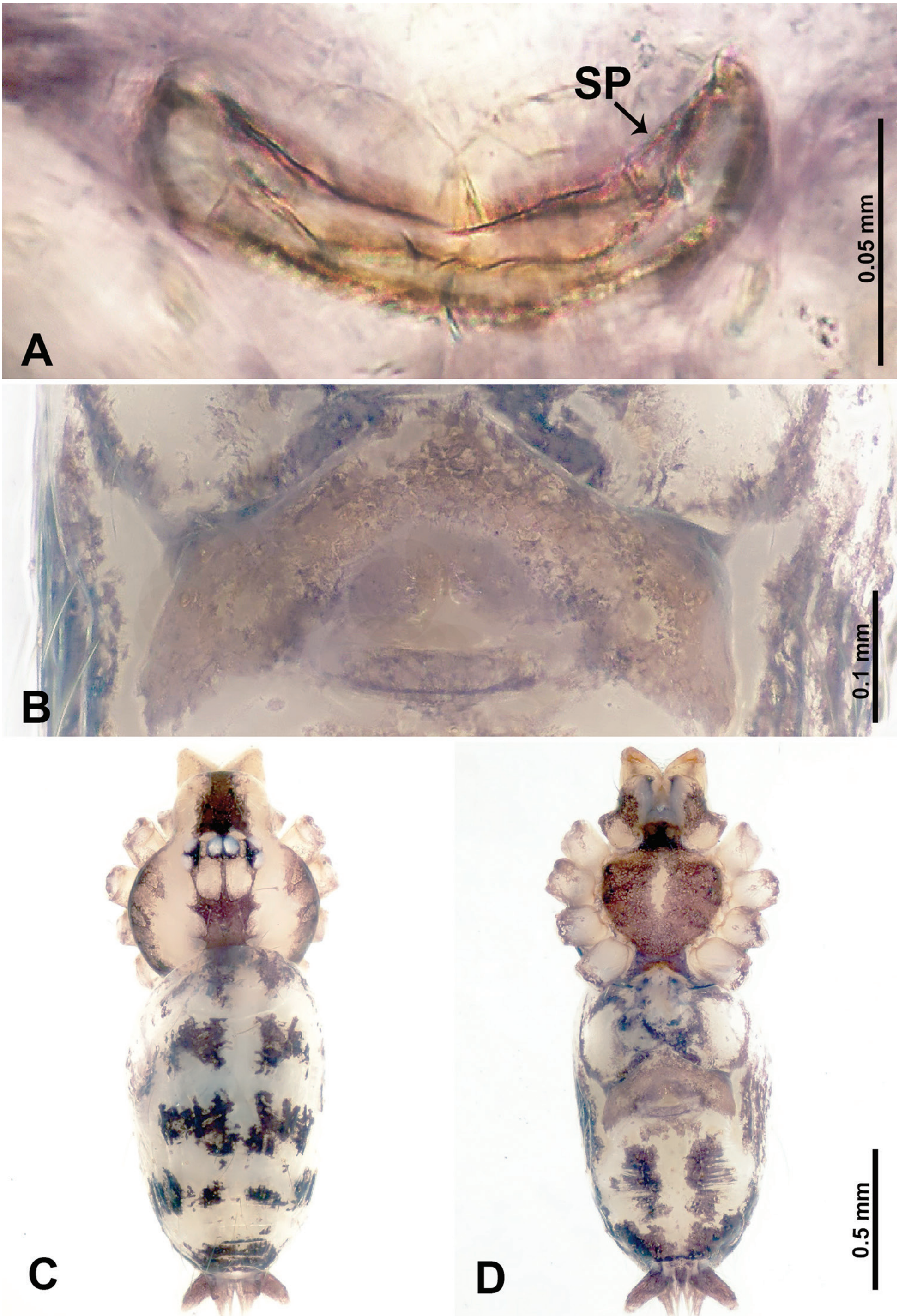

Figure 17. *Leclercera dumuzhou* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

elongated, dorsum with a few pairs of dark brown patches (Fig. 17C), antero-ventrally with a pair of dark brown circular lines laterally, external genitalia region dark brown with band, posterior with a pair of dark brown patches (Fig. 17D). Legs uniformly brown; measurements: I missing, II 5.73 (1.63, 0.20, 1.60, 1.60, 0.70), III 4.10 (1.20, 0.20, 1.00, 1.10, 0.60), IV 6.10 (1.72, 0.25, 1.75, 1.63, 0.75). Epigastric area (Fig. 17B): dark brown band delimiting a light brown triangle medially. Endogyne (Fig. 17A): spermathecae transverse, slightly curved upwards, with pointed tips.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera suwanensis sp. nov.

http://zoobank.org/1A2BC8D6-607F-4F10-BF56-97D0746BC611

Figs 18, 19, 55J, 58

Types. ***Holotype*:** ♂ (IZCAS), Thailand, Phangnga Province, Takuathung District, Suwankuha Cave, 8°25.7695'N, 98°28.2693'E, elevation ca 19 m, 9.X.2015, Q. Zhao, G. Zhou and Z. Chen leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Diagnostic features of males and females are discussed in the diagnosis of *L. banensis* sp. nov.

Description. Male (Holotype). Total length 2.45; carapace 0.70 long, 0.86 wide; abdomen 1.75 long, 0.78 wide. Carapace round and pale brown, with three longitudinal bands, median band 2 times wider than the lateral bands (Fig. 18C). Chelicerae pale brown (Fig. 55J). Clypeus slanting, dark brown medially, light brown laterally. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown, delimiting a light brown strip medially. Abdomen elongated, dorsum with pairs of dark brown spots, ventrum with pair of oval brown patches laterally followed by inverted 'U'-shaped brown band, posterior with a pair of dark brown patches. Legs uniformly brown; measurements: I 11.17 (3.21, 0.31, 3.40, 3.25, 1.00), II 8.27 (2.40, 0.25, 2.50, 2.34, 0.78), III 5.72 (1.72, 0.31, 1.50, 1.56, 0.63), IV 8.41 (2.50, 0.31, 2.40, 2.40, 0.80). Palp (Fig. 19A–D): femur slender, five times longer than patella; patella not swollen; tibia half the length of femur, swollen and pentagonal in lateral view, with a retrolateral apophysis bearing a distal spine which is as long as the apophysis itself and a strong seta near the base of the retrolateral apophysis (Fig. 19D); cymbium half the width and length of the femur; bulb pale brown, bulging, ovoid, conductor and embolus separated, with conductor and embolus arising distally; conductor elongated and slightly hooked at the tip, as long as embolus; embolus elongated, basally swollen and progressively darkening and thinning to a pointed tip (Fig. 19B).

Female (Paratype). General features and coloration similar to those of male (Fig. 18D, E). Measurements: total length 1.70; carapace 0.50 long, 0.60 wide; abdomen 1.20 long, 1.00 wide. Leg measurements: I missing, II 6.65 (1.92, 0.20, 2.03, 1.72, 0.78), III 4.70 (1.40, 0.25, 1.25, 1.20, 0.60), IV 6.63 (2.00, 0.25, 1.88, 1.75, 0.75). Epigastric area (Fig. 18B): brown patch resembles an inverted 'U' shape. Endogyne

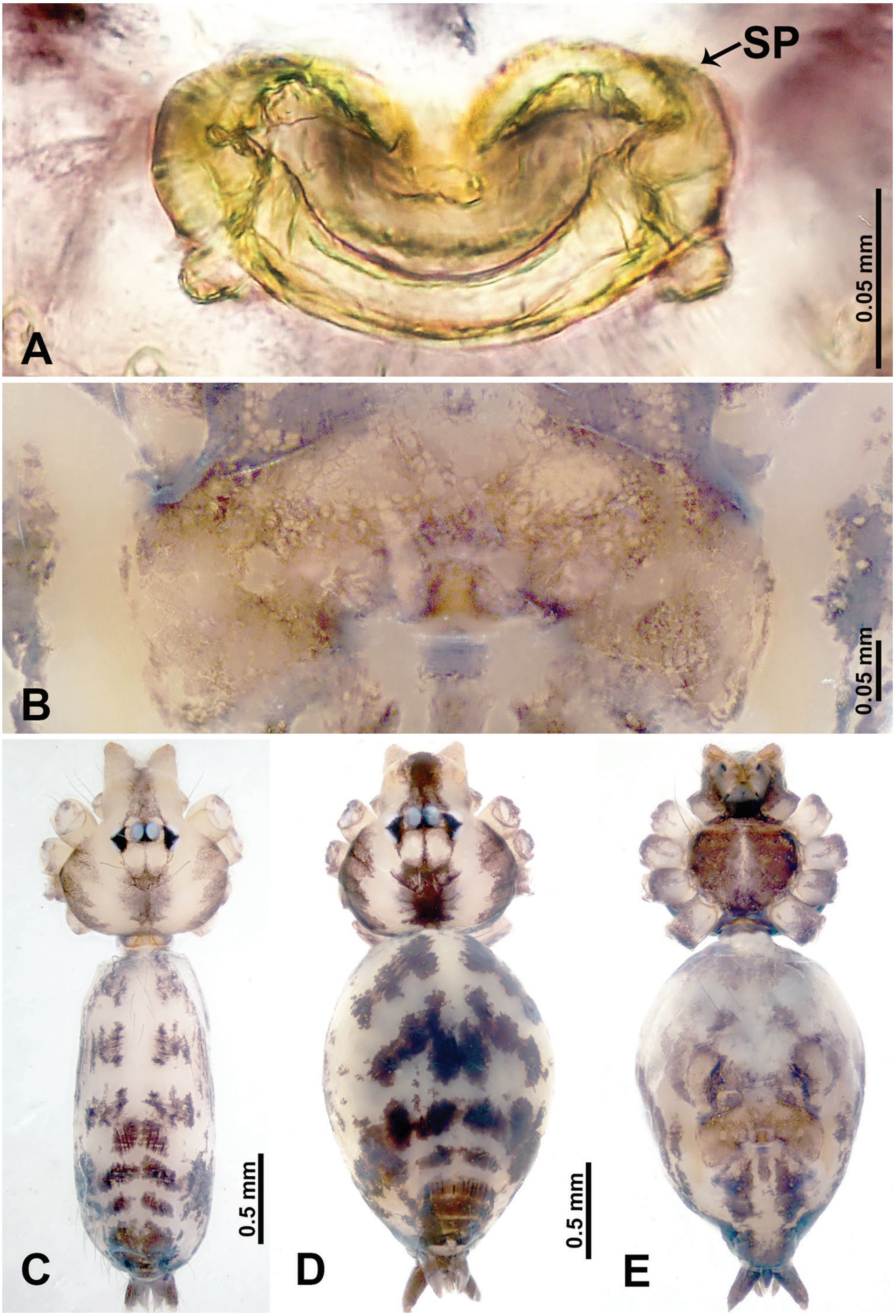

Figure 18. *Leclercera suwanensis* sp. nov. male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

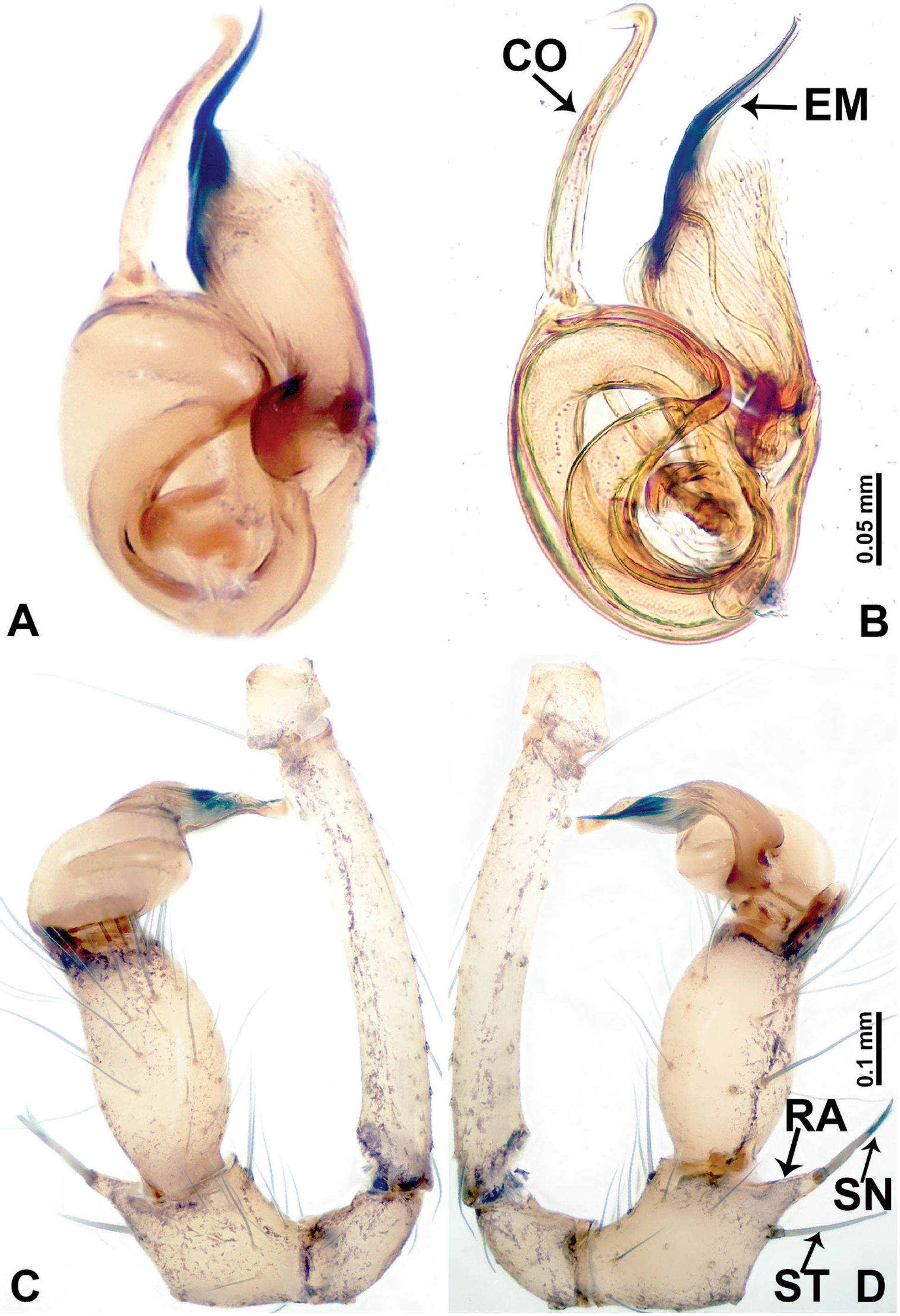

Figure 19. *Leclercera suwanensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, RA = retrolateral apophysis, SN = spine, ST = strong seta.

(Fig. 18A): a pair of spermathecae curling towards each other, with pointed tips and rounded posterior extensions laterally.

Distribution. Known only from the type locality (Fig. 58).

Leclercera maochong sp. nov.

http://zoobank.org/90E05F42-497A-4109-9E10-1CB16F79F6E5

Figs 20, 21, 55G, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Yunnan Province, Yuxi Town, Yuanjiang County, Yangchajiexiang Nature Reserves, Nanxi Region, 23°9.6320'N, 101°45.5640'E, elevation ca 2144 m, 4.VI.2015, Y. Li and Z. Chen leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "máochóng" (caterpillar) and refers to the structure of spermathecae which resemble a caterpillar in lateral view.

Diagnosis. Males of *L. maochong* sp. nov. resemble *L. shanzi* sp. nov. but can be distinguished by a pair of divided conductors (Fig. 21B) (i.e. – consisting of two components) (vs. a slightly twisted undivided conductor (Fig. 23B)), an absence of a laminar apophysis adjacent to embolus (vs. presence of a laminar apophysis adjacent to embolus), embolus two times longer than tegulum (vs. embolus of similar length to tegulum), presence of two dorsal apophyses anteriorly on tibia (Fig. 21D) (vs. the presence of two retrolateral tibial apophyses anteriorly (Fig. 23C)); females can be recognized by having more coils of the spermathecae and by having a pair of lateral, spherical structures connected via the duct system to the posterior ends of the spermathecae (Fig. 20A) (vs. an absence of posterior extensions of the spermathecae), external genitalia a dark purplish, rectangular patch (Fig. 20B) (vs. fan-shaped external genitalia (Fig. 22B)), dorsum with oblique lateral dark brown stripes (Fig. 20D) (vs. dark brown lateral bands with parallel lines on dorsum (Fig. 22D)).

Description. Male (Holotype). Total length 2.58; carapace 0.88 long, 1.20 wide; abdomen 1.70 long, 0.80 wide. Carapace round and brown, with three dark brown longitudinal bands, median band two times wider than lateral band (Fig. 20C). Chelicerae brown (Fig. 55G). Clypeus with dark brown band medially. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown with vertically thin median light brown band. Abdomen elongated, dorsum with pairs of dark brown spots, posterior with dark brown horizontal stripes, antero-ventrally with a pair of ovoid brown patches followed by rectangular dark brown patch, posterior with complicated dark brown pattern. Legs uniformly brown; measurements: I–IV missing. Palp (Fig. 21A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and 3 times wider than femur, with two dorsal apophyses anteriorly (apophyses almost as long as cymbium); cymbium three times shorter than femur, dark brown distally; bulb brown, pyriform, with conductor and embolus arising distally; conductor comprises two components, basally and distally merged with embolus; embolus elongated and sheet-like, slightly twisted, two times longer than tegulum (Fig. 21B).

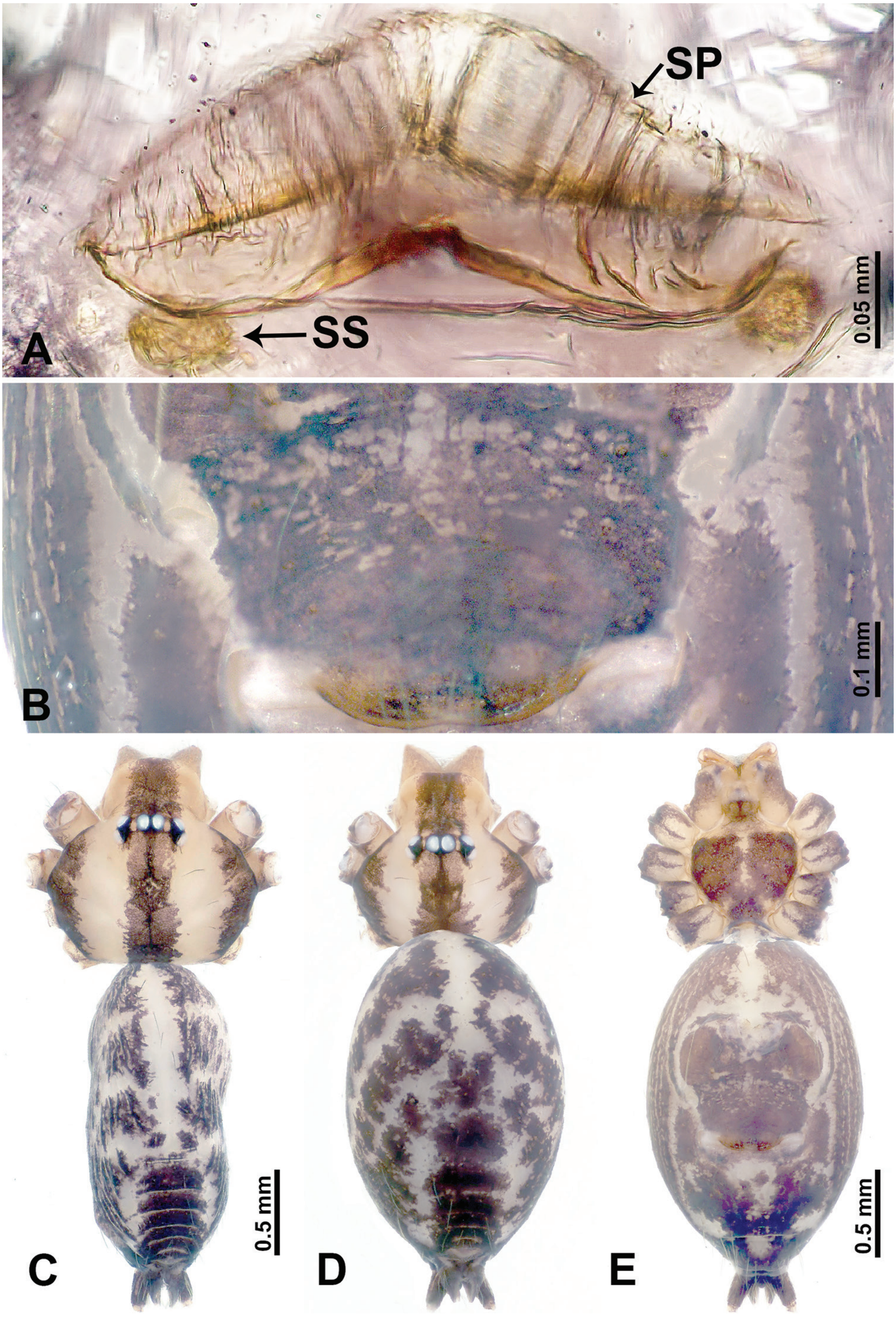

Figure 20. *Leclercera maochong* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviations: SP = spermatheca, SS = spherical structure.

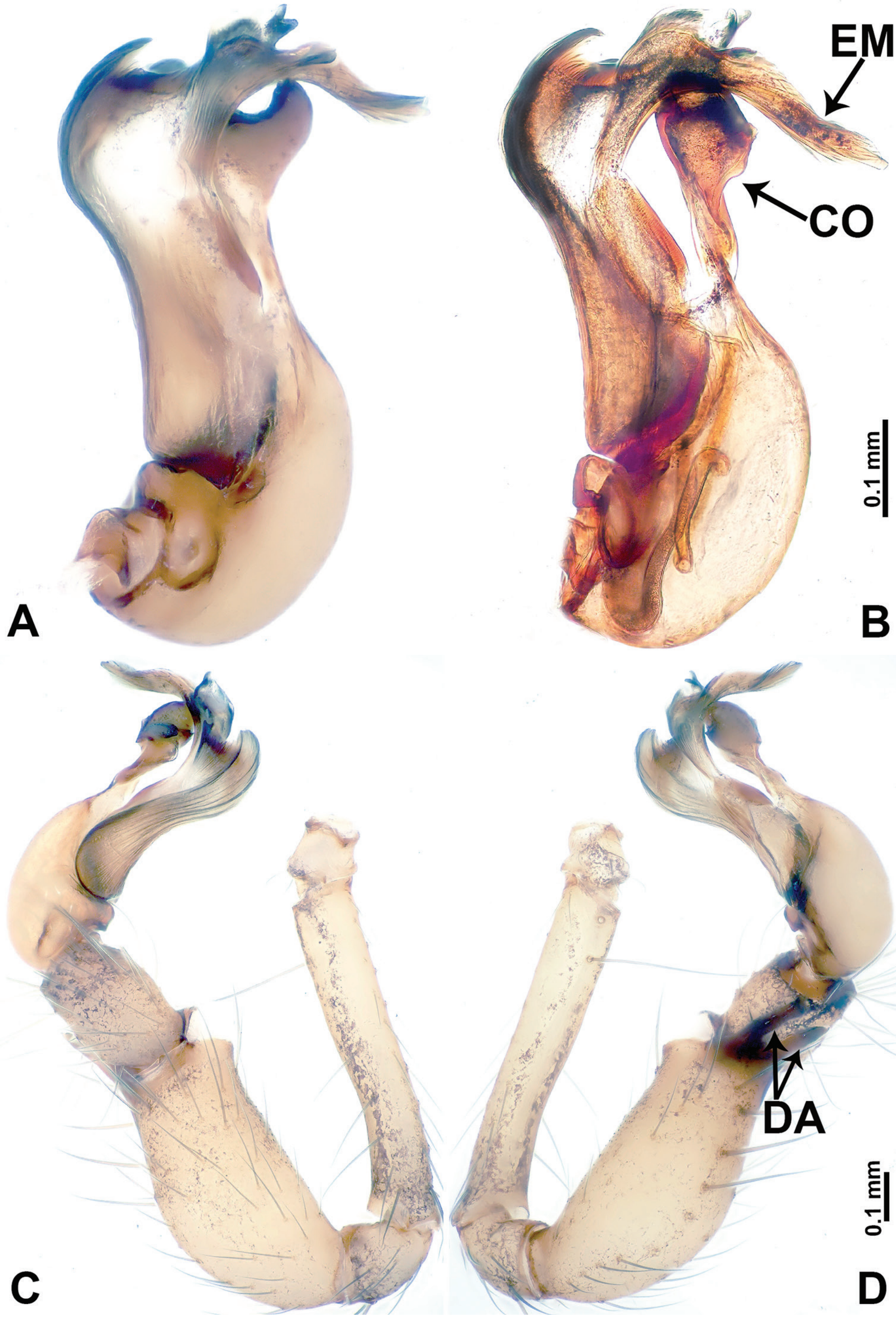

Figure 21. *Leclercera maochong* sp. nov. **A** Bulb, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, DA = dorsal apophysis, EM = embolus.

Female (Paratype). General features and coloration similar to those of male (Fig. 20D, E). Measurements: total length 2.66; carapace 0.78 long, 0.94 wide; abdomen 1.88 long, 1.25 wide. Leg measurements: I 8.84 (2.40, 0.31, 2.88, 2.00, 1.25), II 7.06 (2.00, 0.31, 2.03, 1.72, 1.00), III missing, IV 8.17 (2.40, 0.31, 2.34, 2.03, 1.09). Epigastric area (Fig. 20B): rectangular dark brown patch anteriorly, followed by brown crescent-shaped slit posteriorly. Endogyne (Fig. 20A): spermathecae resembles a crawling caterpillar in lateral view, with pointed ends, connected posteriorly to a pair of lateral spherical bodies by a duct system double-looped like a shallow "W".

Distribution. Known only from the type locality (Fig. 58).

Leclercera shanzi **sp. nov.**

http://zoobank.org/DFBA723A-2878-4E9E-A4A7-2AC218788D09
Figs 22, 23, 55H, 58

Types. ***Holotype*****:** ♂ (IZCAS), China, Yunnan Province, Wenshan State, Pingbian County, outside of Dawei Mountain Provincial Nature Reserves, 22°54.6450'N, 103°41.7810'E, elevation ca 2070 m, 21.V.2015, Y. Li and Z. Chen leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "shànzĭ" (fan) and refers to the resemblance of the external genitalia to a hand fan.

Diagnosis. Diagnostic features of males and females are discussed in the diagnosis of *L. maochong* sp. nov.

Description. Male (Holotype). Total length 2.63; carapace 1.00 long, 1.13 wide; abdomen 1.63 long, 0.80 wide. Carapace round and brown, with three dark brown longitudinal bands, median band five times wider than lateral band (Fig. 22C). Chelicerae brown (Fig. 55H). Clypeus with dark brown band medially. Endites dark brown delimiting light brown circular area basally. Labium dark brown. Sternum dark brown. Abdomen elongated, dorsum medially with dark brown lateral patches with parallel lines delimiting an inverted "Y"-shape (Fig. 22C), antero-ventrally with a pair of dark brown kidney-shaped lateral spots, followed by a fan-shaped dark brown region, with an indistinct dark brown pattern posteriorly. Legs uniformly brown; measurements: I 14.78 (4.25, 0.40, 4.50, 4.00. 1.63), II 13.17 (3.85, 0.40, 4.17, 3.25, 1.50), III 8.94 (2.75, 0.31, 2.60, 2.03, 1.25), IV missing. Palp (Fig. 23A–D): femur slender, three times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and wider than femur, with two retrolateral apophyses anteriorly, apophyses darken distally (Fig. 23C); cymbium three times shorter than femur; bulb brown, pyriform, with conductor, embolus, and laminar apophysis arising distally; conductor twisted distally, with blunt tip, slightly shorter than, and basally merged with, embolus; embolus stalk almost as long as tegulum, embolus finely pointed; laminar apophysis black, adjacent to embolus, basally merged with and slightly wider than embolus (Fig. 23B).

Female (Paratype). General features and coloration similar to those of male (Fig. 22D, E). Measurements: total length 2.60; carapace 0.80 long, 1.00 wide; abdomen

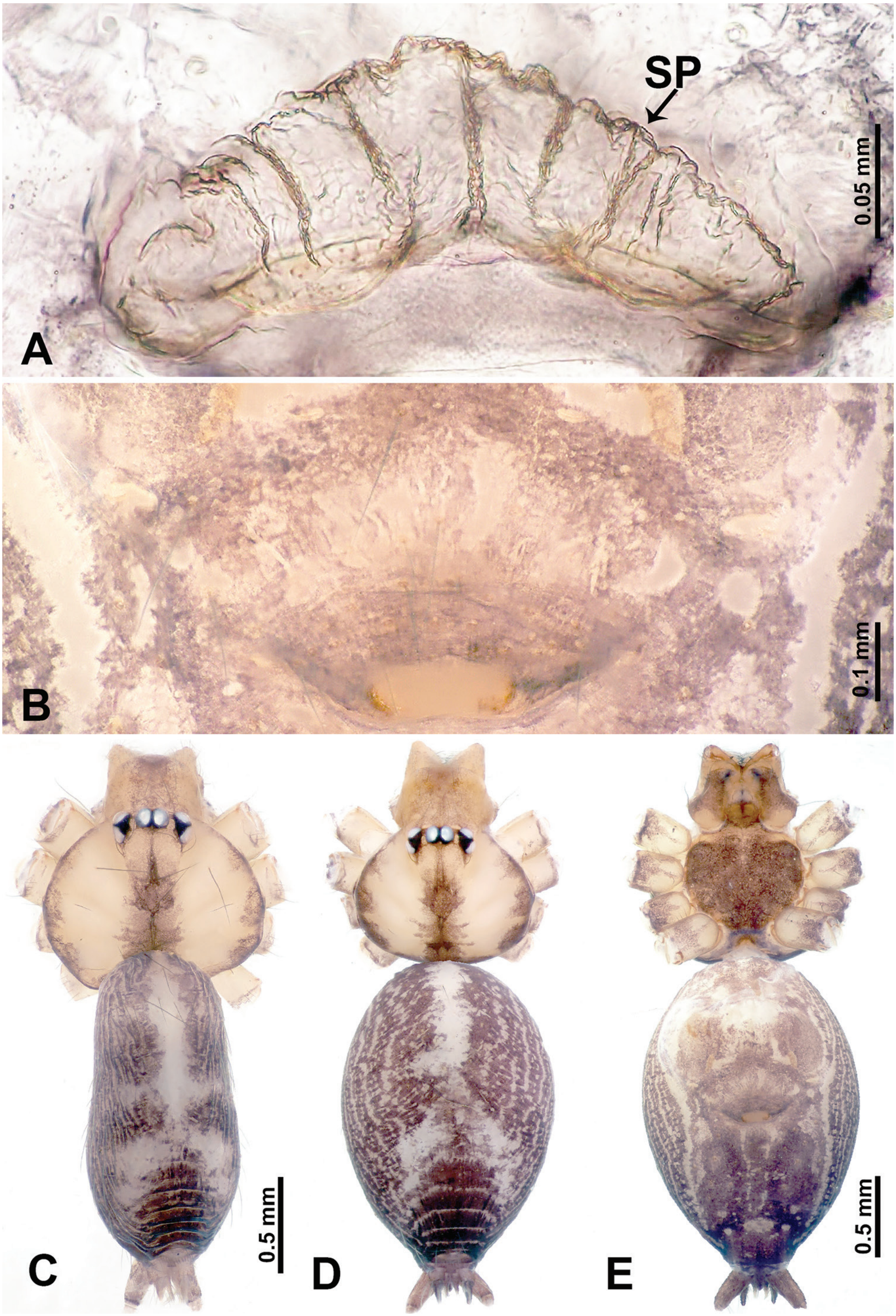

Figure 22. *Leclercera shanzi* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

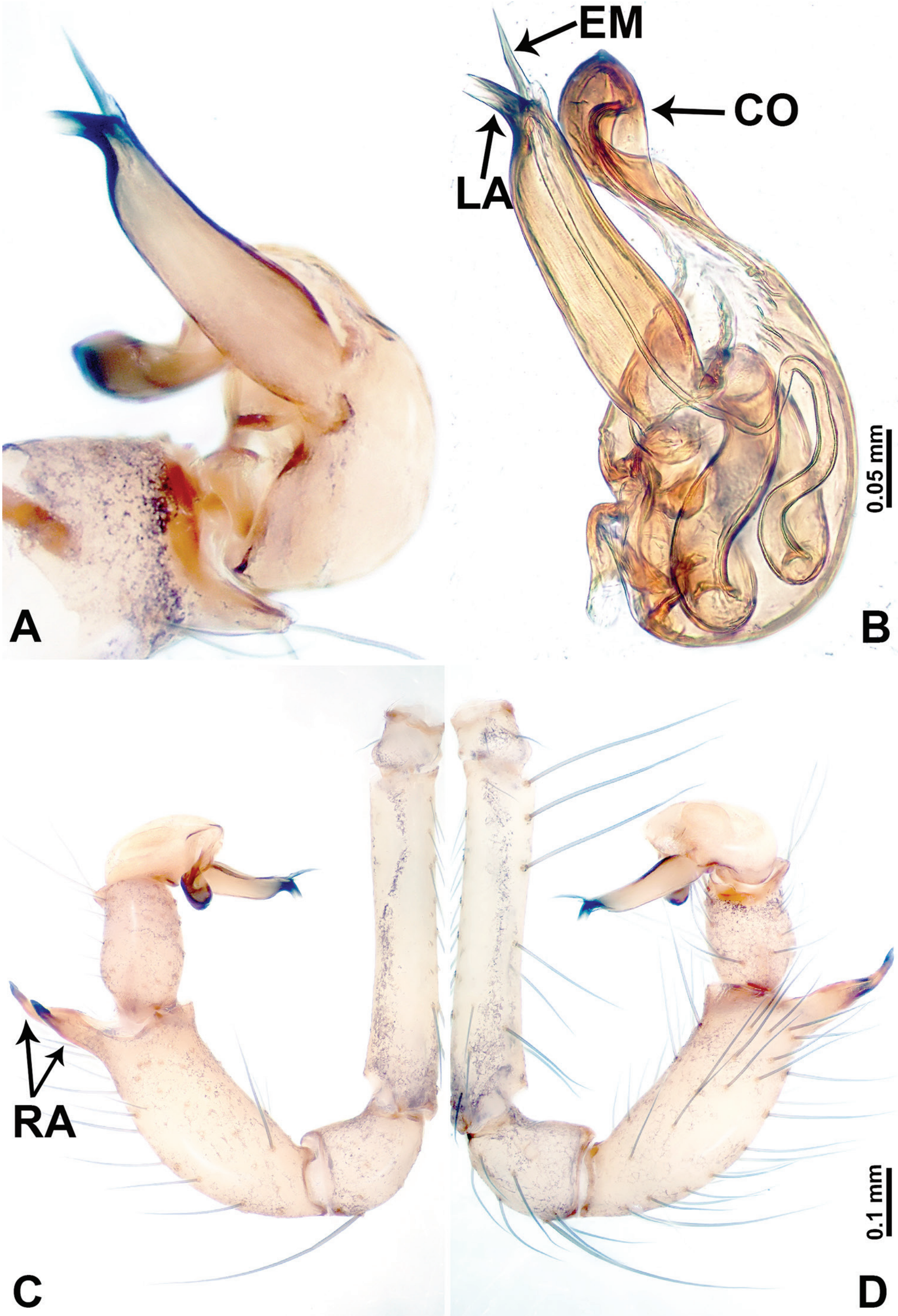

Figure 23. *Leclercera shanzi* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophysis, RA = retrolateral apophyses.

1.80 long, 1.25 wide. Leg measurements: I 13.15 (3.50, 0.40, 4.00, 3.50, 1.75), II 11.06 (3.21, 0.40, 3.25, 2.80, 1.40), III 7.85 (2.34, 0.31, 2.20, 1.80, 1.20), IV 10.91 (3.20, 0.31, 3.20, 2.80, 1.40). Epigastric area (Fig. 22B): purplish and brownish pattern resembling the shape of a hand fan. Endogyne (Fig. 22A): pair of spermathecae resembling an isosceles triangle but without flattened base, base convex, both ends rounded.

Distribution. Known only from the type locality (Fig. 58).

Leclercera duandai **sp. nov.**

http://zoobank.org/0106710C-BC7E-4174-8DBB-ADE9FF54715B

Figs 24, 55K, 58

Types. ***Holotype*****:** ♀ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Medog County, Beibung Village, around Jiagagou Bridge, 29°15.0670'N, 95°11.7170'E, elevation ca 805 m, 18.VI.2016, J. Wu leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "duàndài" (ribbon) and refers to the structure of the spermathecae resembling a ribbon knot (Fig. 24A).

Diagnosis. Females of *L. duandai* sp. nov. can be distinguished from other congeners by the unique orange coloration of the external genitalia and the spermathecae (Fig. 24A, B) which resemble a pair of orange-coloured ribbon knots (vs. absence of orange coloration on the external genitalia or spermathecae in congeners).

Description. Female. Total length 2.88; carapace 0.96 long, 1.00 wide; abdomen 1.92 long, 0.80 wide. Carapace round and brown, with three longitudinal dark brown bands, median band 8 times wider than the lateral bands (Fig. 24C). Chelicerae brown (Fig. 55K). Clypeus light brown. Endites light brown, dark brown marginally. Labium dark brown. Sternum light brown, with longitudinal dark brown spots laterally. Abdomen elongated, dorsum with dark brown spots, with posterior dark brown stripes medially (Fig. 24C), antero-ventrally with ovoid, orangish external genitalia, with scattered dark brown spots posteriorly (Fig. 24D). Leg measurements: I–IV missing. Epigastric area (Fig. 24B): an elliptical, orangish patch. Endogyne (Fig. 24A): a pair of spermathecae resembling a ribbon knot, posterior receptacles with a pair of ovoid bodies with two-branched, upturned ends.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera hponensis **sp. nov.**

http://zoobank.org/8B33B61D-7B2C-4632-A1D8-9A6F335B04F3

Figs 25, 26, 56F, 58

Types. ***Holotype*****:** ♂ (IZCAS), Myanmar, Kachin State, Putao Town, Hponkanrazi Wildlife Sanctuary Roadside between Camp 2 to Camp 3, 27°37.1500'N, 96°58.9170'E, elevation ca 2806 m, 16.XII.2016, J. Wu leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

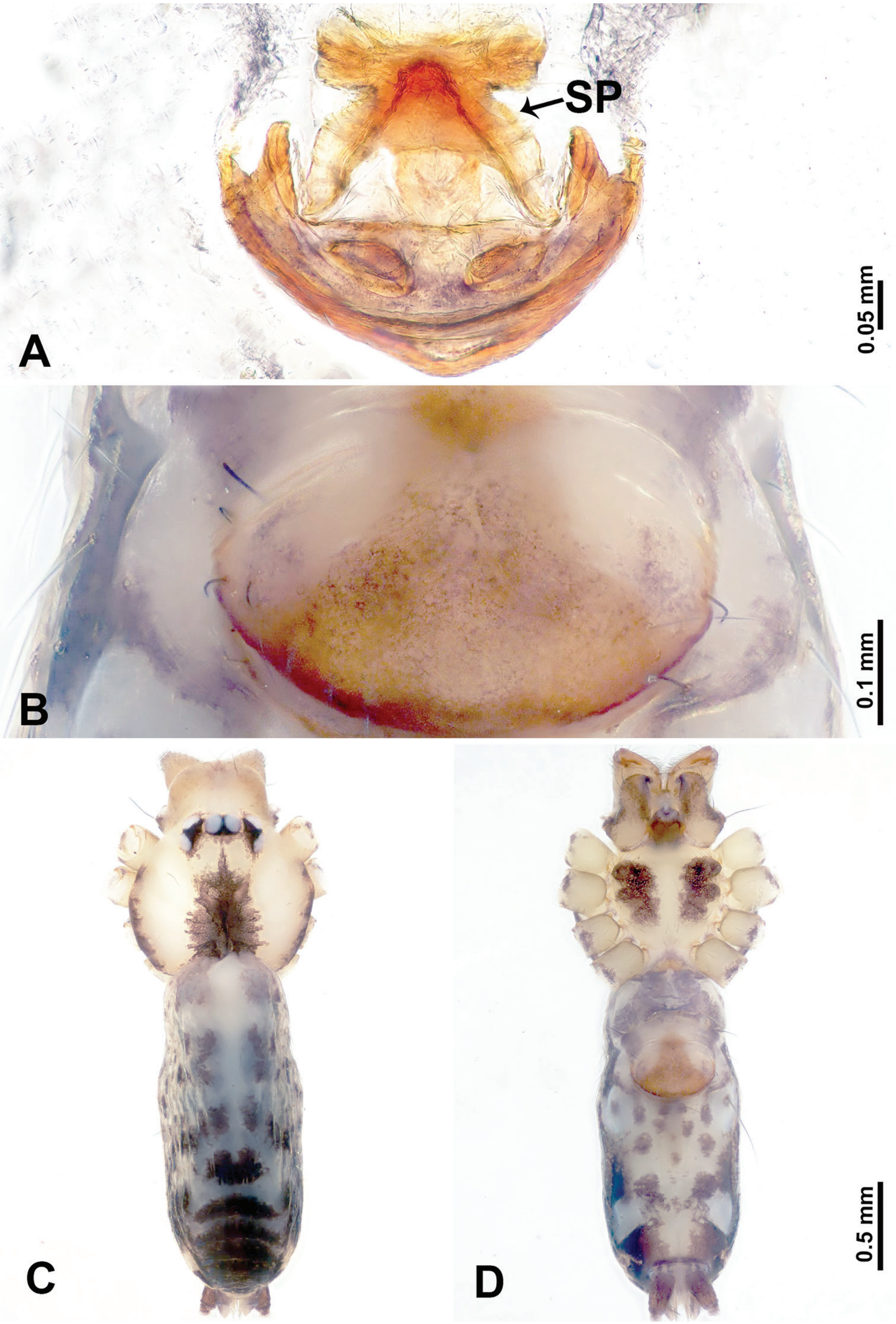

Figure 24. *Leclercera duandai* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

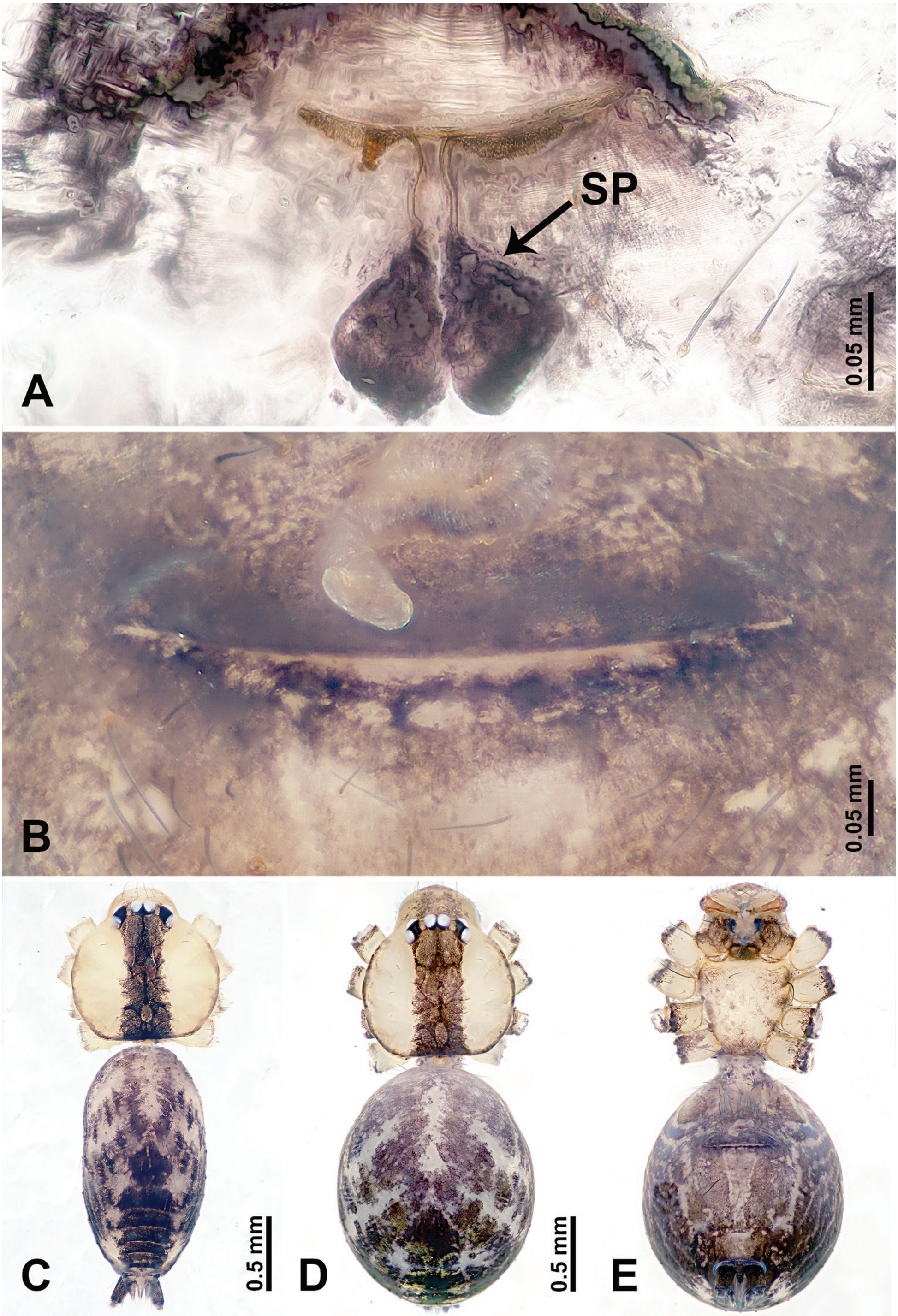

Figure 25. *Leclercera hponensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

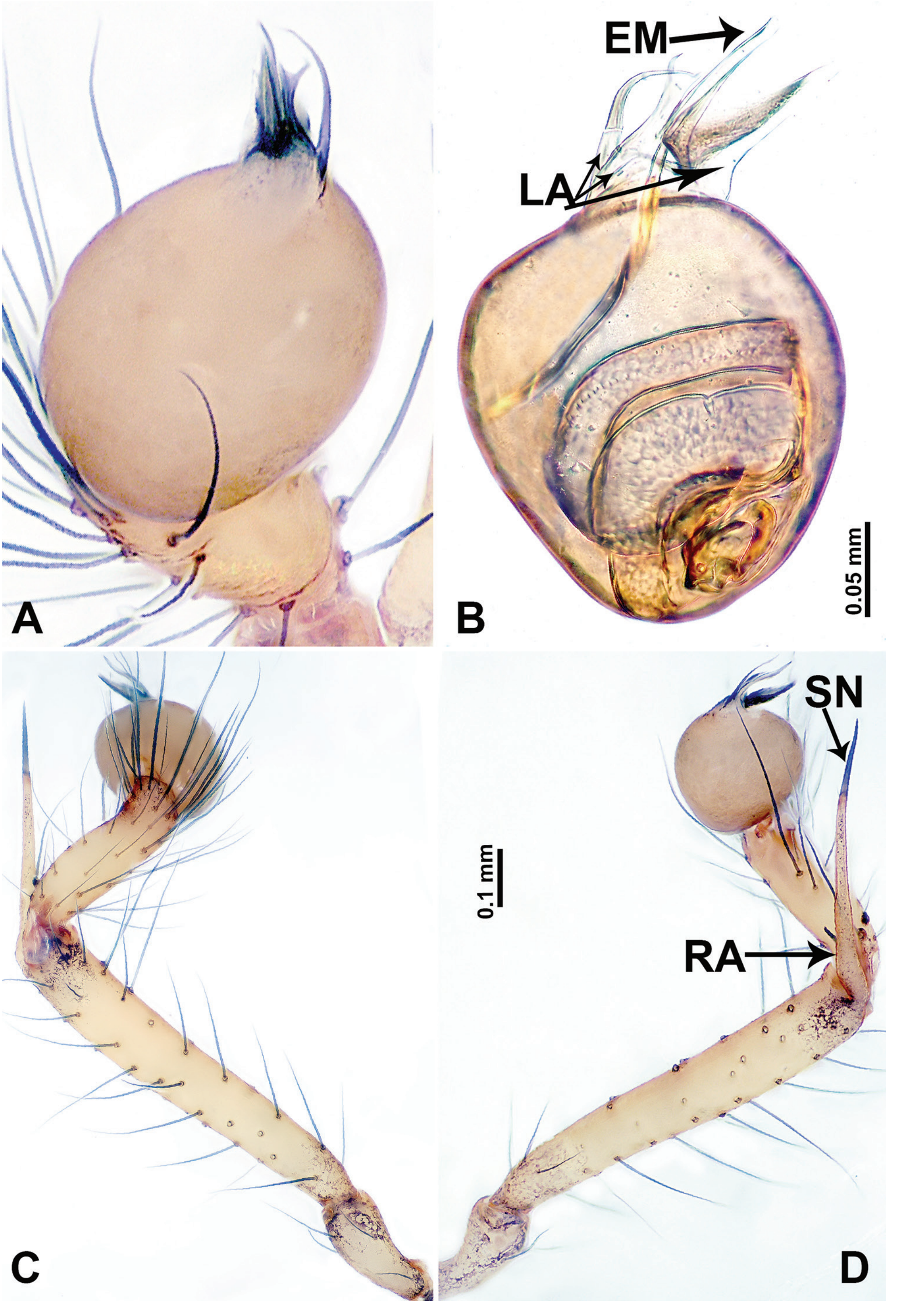

Figure 26. *Leclercera hponensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, LA = laminar apophysis, RA = retrolateral apophysis, SN = spine.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. hponensis* sp. nov. can be distinguished from congeners by the presence of a three-branched, laminar apophysis on the distal end of the bulb (Fig. 26B) (vs. the absence of a three-branched laminar apophysis in congeners), a spheroid bulb (vs. the bulb of congeners have other shapes), tibia with a retrolateral apophysis bearing a spine that is three times shorter than the apophysis, the entire apophysis, including the spine, is two times longer than the tegulum (Fig. 26D) (vs. the absence of such a combination of a tibia apophysis and spine in congeners); the female can be differentiated from congeners by the pair of stalked spermathecae with a triangular distal part (Fig. 25A).

Description. Male (Holotype). Total length 2.30; carapace 0.80 long, 0.88 wide; abdomen 1.50 long, 0.75 wide. Carapace round and brown, with dark brown longitudinal median band (Fig. 25C). Chelicerae brown (Fig. 56F). Clypeus light brown. Endites dark brown, light brown basally. Labium dark brown. Sternum light brown. Abdomen elongated, antero-dorsally with dark brown spots, posterior with dark brown stripes medially, antero-ventrally with dark brown elliptical patch, posterior with indistinct dark brown pattern. Legs uniformly brown; measurements: I 8.97 (2.53, 0.31, 2.81, 2.19, 1.13), II 7.10 (1.94, 0.31, 2.19, 1.72, 0.94), III 5.25 (1.44, 0.31, 1.47, 1.25, 0.78), IV 7.97 (2.06, 0.31, 2.13, 2.38, 1.09). Palp (Fig. 26A–D): femur slender, four times longer than patella; patella not swollen; tibia 1.5 times shorter than femur, with retrolateral apophysis anteriorly bearing a spine, two times longer than tegulum, spine three times shorter than apophysis (Fig. 26D); cymbium three times shorter than femur; bulb brown, spheroid, with embolus and laminar apophysis arising distally; three-branched, laminar apophyses almost equal in length but shorter than embolus; embolus laminar, longer than all other laminar apophyses of its own (Fig. 26B).

Female (Paratype). General features and coloration similar to those of male (Fig. 25D, E). Measurements: total length 2.40; carapace 0.84 long, 0.94 wide; abdomen 1.56 long, 1.19 wide. Leg measurements: I 7.75 (2.06, 0.31, 2.44, 1.88, 1.06), II 6.47 (1.72, 0.31, 1.94, 1.56, 0.94), III 4.53 (1.25, 0.31, 1.13, 1.09, 0.75), IV 6.44 (1.72, 0.31, 1.88, 1.56, 0.97). Epigastric area (Fig. 25B): dark brown patch delimiting a horizontal light brown slit. Endogyne (Fig. 25A): a pair of stalked spermathecae with anterior stalks and posteriorly a triangular distal part.

Distribution. Known only from the type locality (Fig. 58).

Leclercera lizi sp. nov.

http://zoobank.org/5CA634EB-DCB3-4CEA-803A-167BFBBFFC20
Figs 27, 28, 56G, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Tibet Autonomous Region, Xigaze, Dinggye County, Changga Village, 27°51.6290'N, 87°25.4802'E, elevation ca 2239 m, 7.VIII.2017, X. Zhang, Z. Bai leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "lízĭ" (pear) and refers to the structure of the bulb resembling a pear (Fig. 28B).

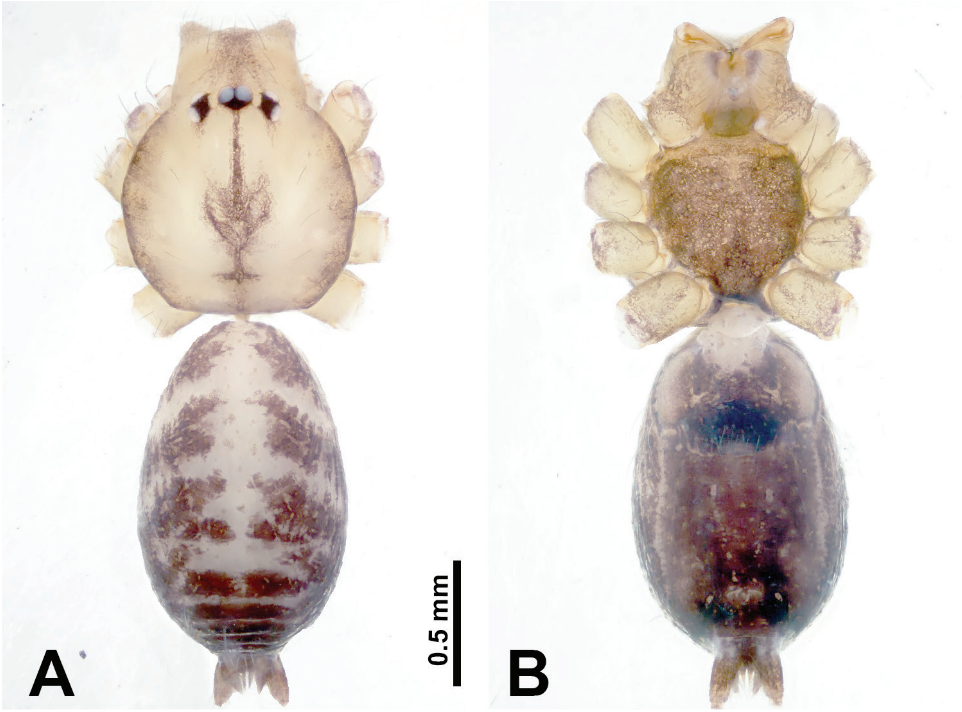

Figure 27. *Leclercera lizi* sp. nov., male holotype. **A** Habitus, dorsal view **B** habitus ventral view.

Diagnosis. Males of *L. lizi* sp. nov. can be distinguished from congeners by the abundance of apophyses and spines on the palp (Fig. 28C, D): cymbium with two retrolateral apophyses posteriorly, seven retrolateral apophyses on the swollen tibia with an anterior dorsal apophysis bearing two spines; embolus almost as long as the tegulum (Fig. 28B) (vs. the absence of congeners with such a profusion of apophyses and spines).

Description. Male (Holotype). Total length 2.13; carapace 0.88 long, 0.90 wide; abdomen 1.25 long, 0.90 wide. Carapace round and brown, with three dark brown longitudinal bands, median band three times wider than lateral bands (Fig. 27A). Chelicerae brown (Fig. 56G). Clypeus light brown, with a trace of dark brown medially. Endites dark brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, antero-dorsally with three pairs of dark brown spots laterally, posterior with dark brown stripes medially, antero-ventrally with black, elliptical patch delimiting kidney-shaped, light brown patch laterally, posterior with indistinct dark brown pattern. Legs uniformly brown; measurements: I–II missing, III 4.19 (1.25, 0.31, 0.94, 0.94, 0.75), IV 6.00 (1.60, 0.40, 1.60, 1.40, 1.00). Palp (Fig. 28A–D): femur slender, three times longer than patella; patella not swollen; tibia swollen, 1.2 times shorter and twice wider than femur, with seven anterior retrolateral apophyses bearing spines, anteriormost with longest apophysis and widest spine, antero-dorsally with dark brown apophysis bearing two spines resembling a fork; cymbium dark brown anteriorly, with two

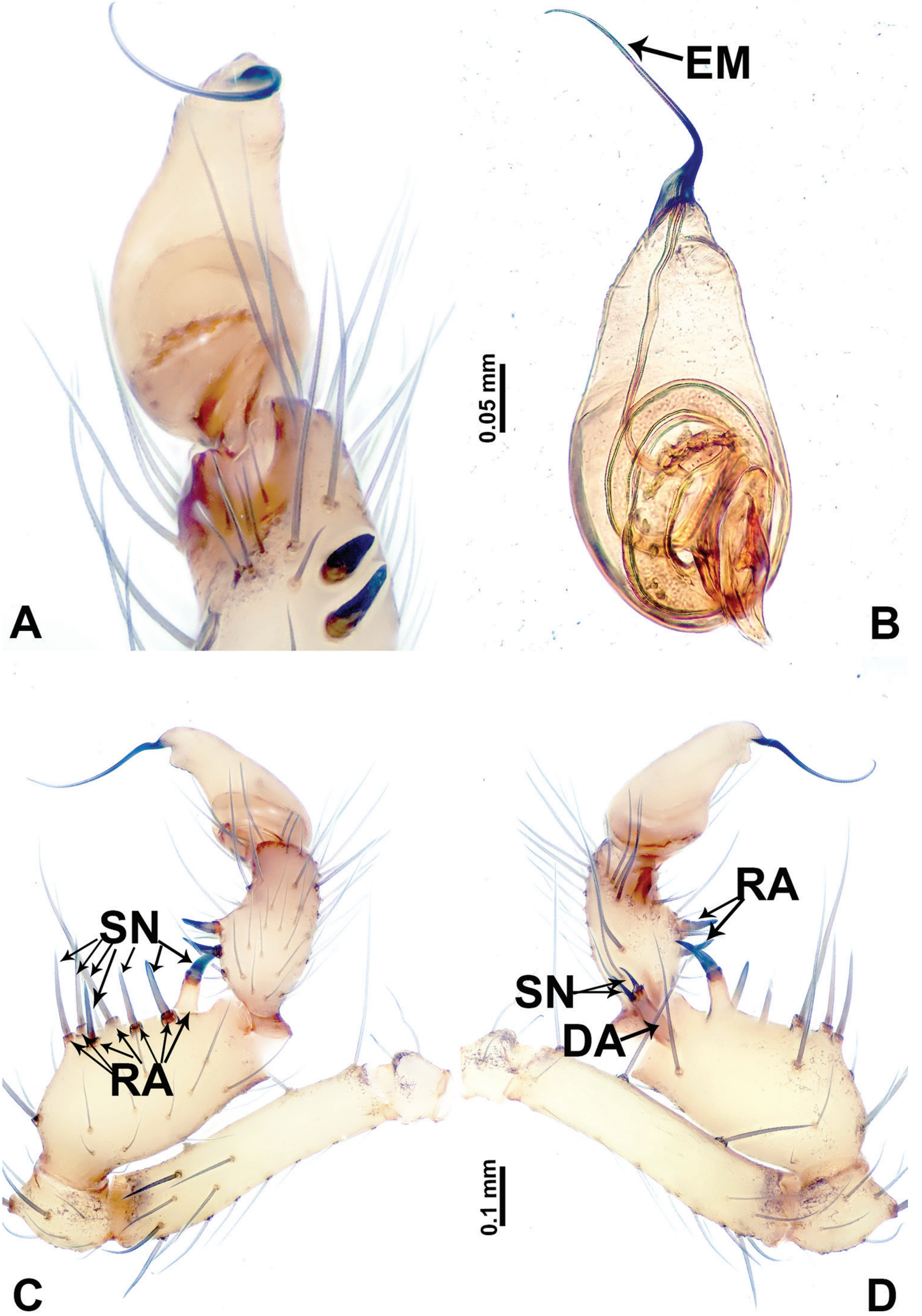

Figure 28. *Leclercera lizi* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, DA = dorsal apophysis, RA = retrolateral apophyses, SN = spines.

retrolateral apophyses posteriorly; bulb brown, pyriform with embolus arising distally, embolus thin and black, rather spiralled, almost equal in length to tegulum (Fig. 28B).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera xiaodai **sp. nov.**

http://zoobank.org/C8700959-8BAE-49AD-9FA0-3300650DB5FC

Figs 29, 55A, 58

Types. ***Holotype*****:** ♀ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Bomê County, around Zhamo Town, 29°50.8590'N, 95°45.8610'E, elevation ca 2800 m, 17.VII.2013, Y. Lin leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "xiǎodài" (small pouch) and refers to the distinct, pouch-like structure of the external genitalia (Fig. 29B).

Diagnosis. Females of *L. duandai* sp. nov. can be distinguished from other congeners by the unique, pouch-like external genitalia (Fig. 29B) and a pair of fusiform spermathecae with two pairs of apophyses extending both anteriorly and posteriorly (Fig. 29A) (vs. an absence of pouch-like external genitalia in congeners).

Description. Female. Total length 2.44; carapace 0.88 long, 0.90 wide; abdomen 1.56 long, 1.25 wide. Carapace round and brown, with three longitudinal dark brown bands, median band three times wider than lateral bands (Fig. 29C). Chelicerae brown (Fig. 55A). Clypeus light brown. Endites, labium, and sternum dark brown. Abdomen elongated, dorsum with indistinct dark brown spots (Fig. 29C), antero-ventrally with a pair of rounded dark brown patches laterally, followed by cone-shaped external genitalia resembling a small pouch, posterior dark brown (Fig. 29D). Legs uniformly brown; measurements: I 7.09 (2.03, 0.31, 2.19, 1.56, 1.00), II missing, III 4.53 (1.25, 0.31, 1.25, 1.09, 0.63), IV 6.64 (1.80, 0.31, 2.03, 1.56, 0.94). Epigastric area (Fig. 29B): inverted triangular pouch. Endogyne (Fig. 29A): pair of connected, fusiform spermathecae with anterior and posterior extensions.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera yanjing **sp. nov.**

http://zoobank.org/A4C77193-1588-4F4C-9646-3A82B6F532BC

Figs 30, 55L, 58

Types. ***Holotype*****:** ♀ (IZCAS), China, Tibet Autonomous Region, Shannan, Cona County, Lemenba Ethnic Village, along the road between Lewang Bridge to Zhisimuzha scenic area, 27°49.5710'N, 91°43.7560'E, elevation ca 2793 m, 1.VI.2016, J. Wu leg.

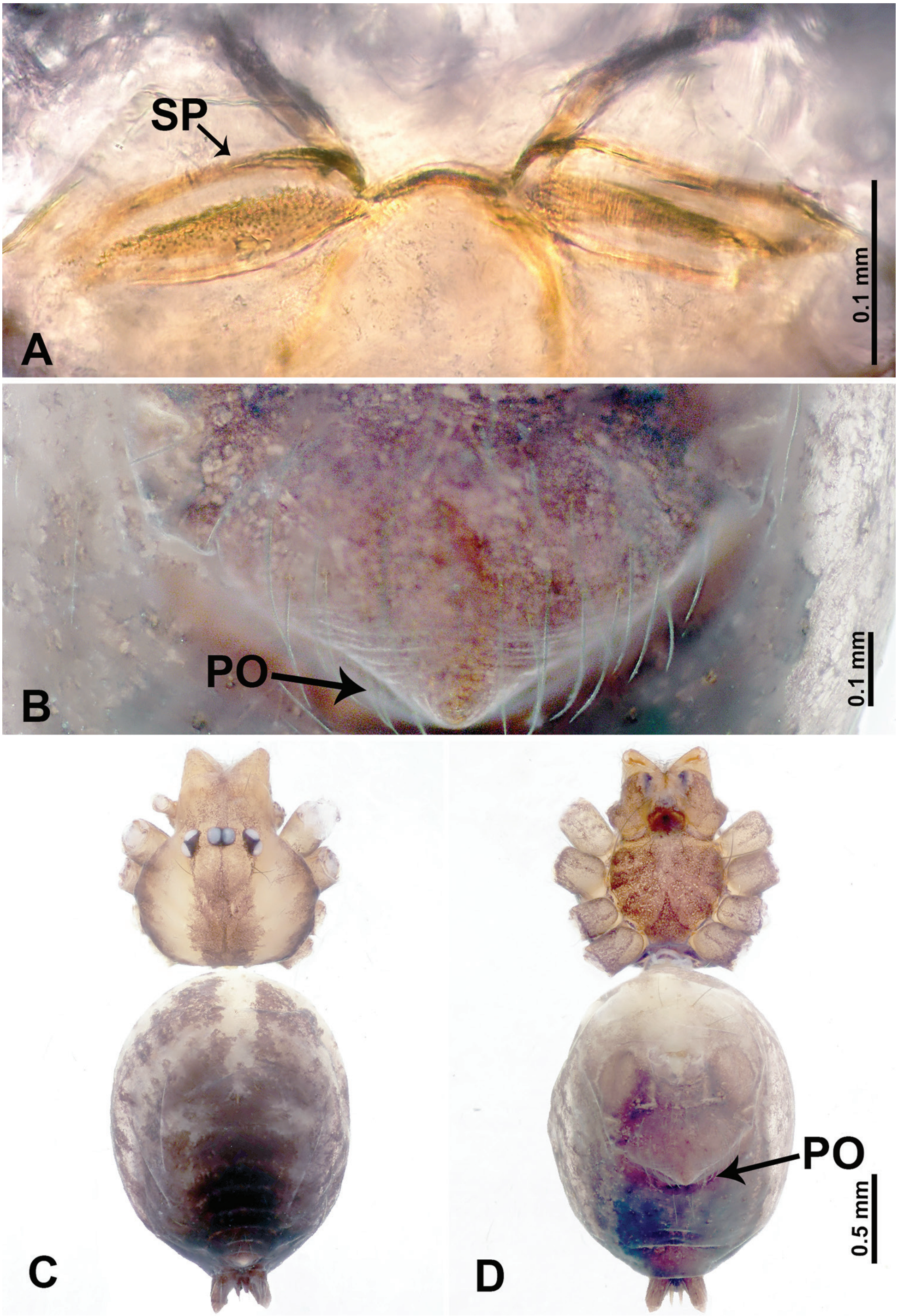

Figure 29. *Leclercera xiaodai* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviations: PO = pouch, SP = spermatheca.

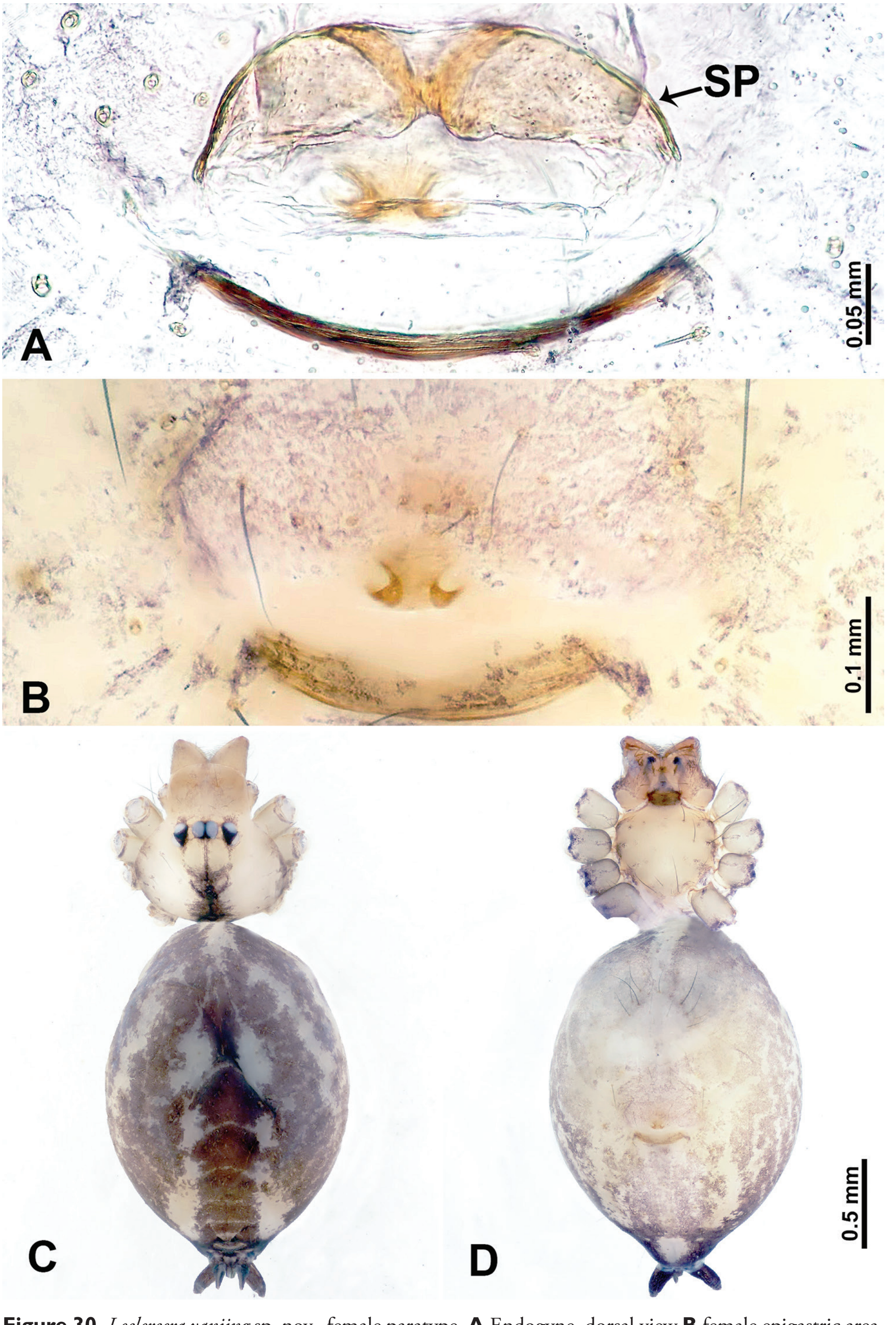

Figure 30. *Leclercera yanjing* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "yǎnjìng" (spectacles) and refers to the structure of the spermathecae resembling a pair of spectacles (Fig. 30A).

Diagnosis. Females of *L. yanjing* sp. nov. can be distinguished from other congeners by a unique curved 'x' spot on the external genitalia (Fig. 30B) and the spermathecae which resemble a pair of aviator glasses (Fig. 30A) (vs. absence of such characteristics in congeners).

Description. Female. Total length 2.88; carapace 0.88 long, 0.88 wide; abdomen 2.00 long, 1.50 wide. Carapace round and brown, with dark brown band medially (Fig. 30C). Chelicerae brown (Fig. 55L). Clypeus light brown. Endites dark brown, light brown basally. Labium dark brown. Sternum light brown. Abdomen elongated, dorsum with dark brown band laterally, medially with dark brown stripes (Fig. 30C), antero-ventrally pale brown with a distinct curved 'x' spot on external genitalia, with indistinct brown spots posteriorly (Fig. 30D). Legs uniformly brown; measurements: I 7.34 (2.03, 0.31, 2.19, 1.72, 1.09), II 6.57 (1.88, 0.31, 1.88, 1.56, 0.94), III 4.98 (1.41, 0.31, 1.28, 1.20, 0.78), IV 6.91 (1.88, 0.31, 2.00, 1.72, 1.00). Epigastric area (Fig. 30B): ovoid pinkish patch followed by a curvy 'x' mark and a brown slit posteriorly. Endogyne (Fig. 30A): a pair of connected, cuneate spermathecae resembling a pair of aviator glasses, with a curved 'x' spot posteriorly.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera ekteenensis sp. nov.

http://zoobank.org/8091EA7F-694F-489F-9384-633264AC554B

Figs 31, 32, 56B, 58

Types. ***Holotype*:** ♂ (IZCAS), Nepal, Mechi District, Ekteen Village, 27°13.1333'N, 87°50.7833'E, elevation ca 2088 m, 27.XI.2016, Q. Zhao leg.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. ekteenensis* sp. nov. can be distinguished from congeners by the presence of a conductor with two distinct branches (Fig. 32B) (vs. the absence of a two-branched conductor in congeners), the embolus arising from medial tegulum (vs. embolus arising distally in congeners), the presence of a distinct darkened apophysis anteriorly on the tibia (Fig. 32D) (vs. the absence of a darkened tibial apophysis in congeners).

Description. Male (Holotype). Total length 3.09; carapace 0.90 long, 1.00 wide; abdomen 2.19 long, 0.94 wide. Carapace round and brown, with three dark brown longitudinal bands, median band five times wider than the lateral bands (Fig. 31A). Chelicerae brown (Fig. 56B). Clypeus light brown, with dark brown band medially. Endites dark brown, light brown basally. Labium dark brown. Sternum with dark brown stripes laterally, delimiting light brown anterior and median region. Abdomen elongated, antero-dorsally with three pairs of dark brown spots laterally, light brown medially, posterior with dark brown stripes medially, antero-ventrally with dark brown elliptical patch, posterior with indistinct dark and light brown spots, posterior edge

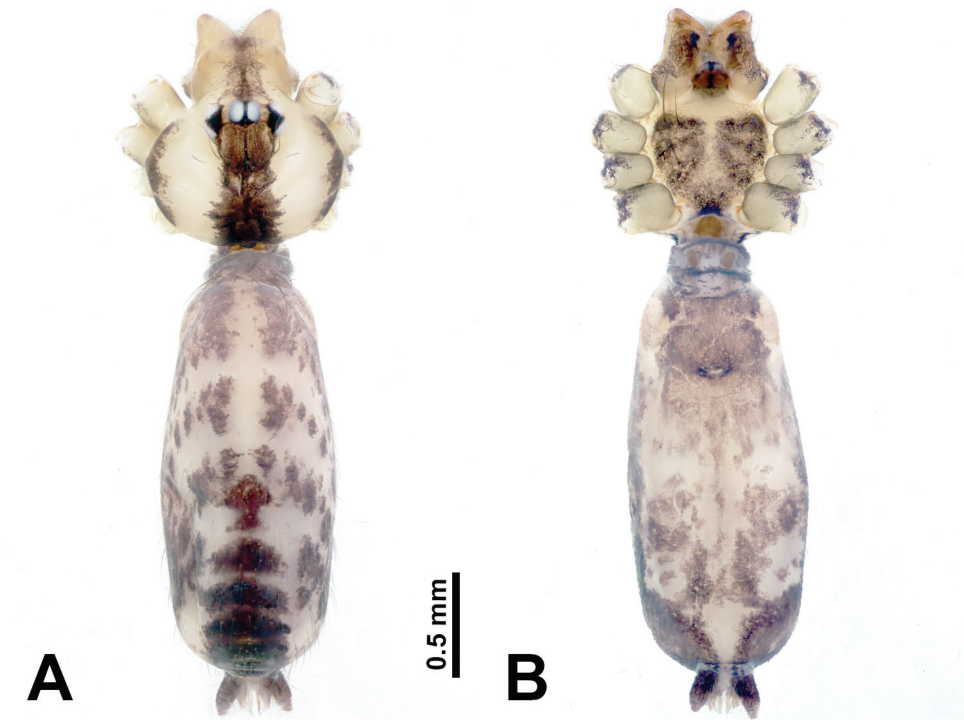

Figure 31. *Leclercera ekteenensis* sp. nov., male holotype. **A** Habitus, dorsal view **B** habitus, ventral view.

with a pair of dark brown fusiform patches laterally. Legs uniformly brown; measurements: I 12.76 (3.40, 0.31, 3.60, 3.53, 1.92), II 8.71 (2.40, 0.31, 2.40, 2.40, 1.20), III 6.39 (1.88, 0.25, 1.75, 1.63, 0.88), IV 9.82 (2.80, 0.31, 2.80, 2.66, 1.25). Palp (Fig. 32A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and wider than femur, antero-dorsally with a black apophysis, almost as long as tegulum; cymbium with dark brown spots, two times shorter than femur; bulb light brown, pyriform, with conductor arising distally, embolus arising medially; conductor dark and thin with two branches, one shorter than the other, short branch bends towards long branch; embolus arising from median tegulum, attached to short branch of conductor, almost as long as long branch of the conductor (Fig. 32B).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 58).

***Leclercera zhamensis* sp. nov.**
http://zoobank.org/9B9A0613-F125-4FD6-870D-A84219EA8955
Figs 33, 34, 55B, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Tibet Autonomous Region, Xigaze, Nyalam County, Zham Town, 27°59.0250'N, 85°58.9720'E, elevation ca 2450 m, 29.VIII.2014, Y. Li leg.

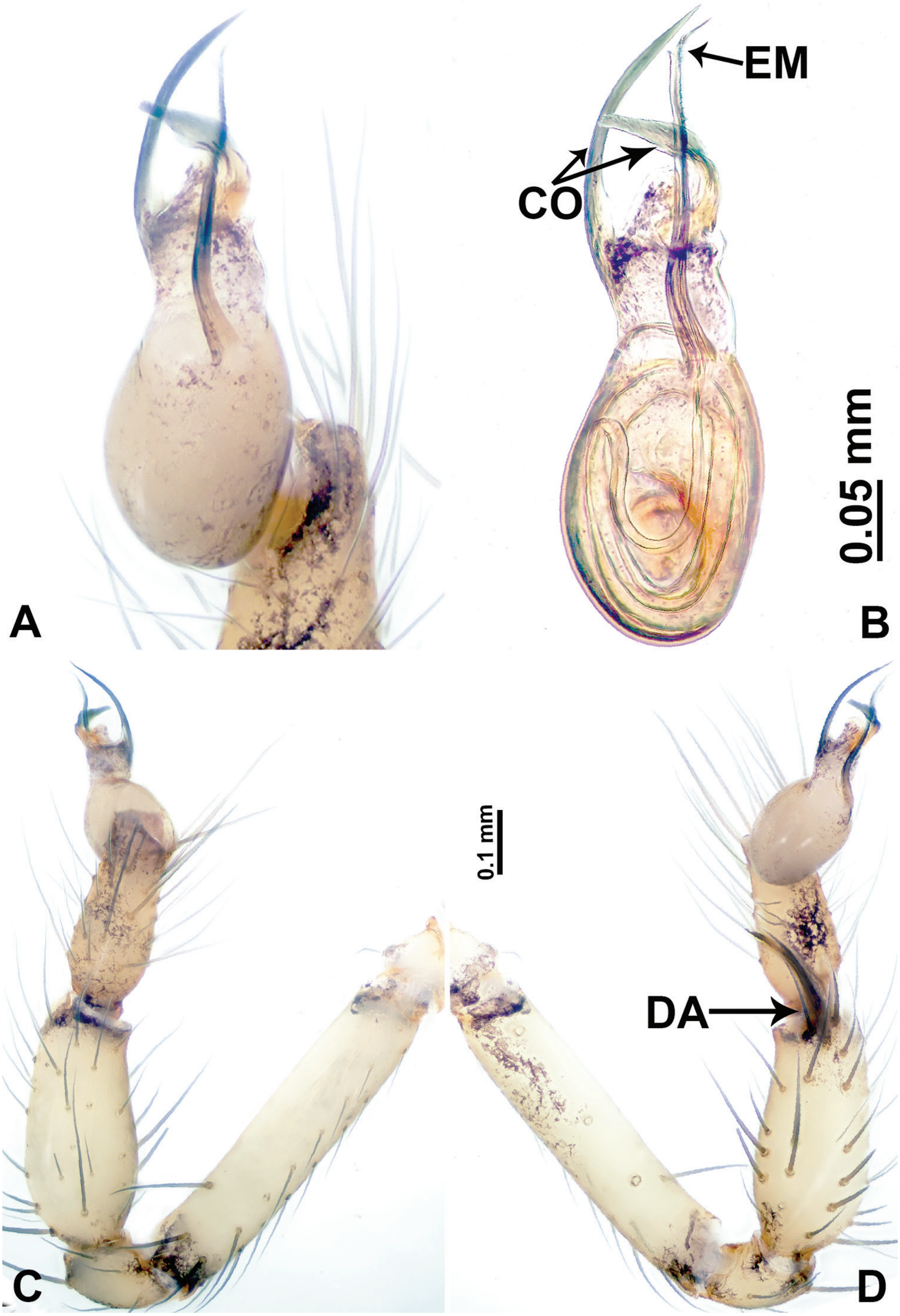

Figure 32. *Leclercera ekteenensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, DA = dorsal apophysis, EM = embolus.

Figure 33. *Leclercera zhamensis* sp. nov., male holotype. **A** Habitus, dorsal view **B** habitus ventral view.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. zhamensis* sp. nov. can be distinguished from congeners by the laminar-shaped embolus that is basally fused with the conductor (Fig. 34B) (vs. the absence of a basally fused conductor and embolus in congeners); the presence of a retrolateral apophysis on the tibia with a spine four times shorter than the apophysis (Fig. 34D) (vs. the absence of a spine with such characteristics in congeners).

Description. Male (Holotype). Total length 3.84; carapace 1.28 long, 1.25 wide; abdomen 2.56 long, 0.88 wide. Carapace round and brown, with three dark brown longitudinal bands, median band 3 times wider than lateral bands (Fig. 33A). Chelicerae brown (Fig. 55B). Clypeus brown, with dark brown band medially. Endites dark brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, antero-dorsally with three pairs of dark brown spots laterally, pale brown medially, posterior with dark brown stripes medially, antero-ventrally with dark brown patch, and a pair of longitudinal dark brown bands laterally, with dark brown posterior patches laterally. Legs uniformly brown; measurements: I 24.21 (7.05, 0.50, 7.37, 7.05, 2.24), II 17.81 (5.13, 0.50, 5.13, 5.13, 1.92), III 11.53 (3.53, 0.40, 3.00, 3.00, 1.60), IV 17.32 (4.81, 0.50, 5.13, 5.13, 1.75). Palp (Fig. 34A–D): femur slender, six times longer than patella; patella not swollen; tibia slightly swollen anteriorly, 1.5 times shorter than femur, with an anterior retrolateral apophysis bearing a spine four times shorter than the apophysis (Fig. 34D); cymbium dark brown anteriorly, 2.5 times shorter than femur;

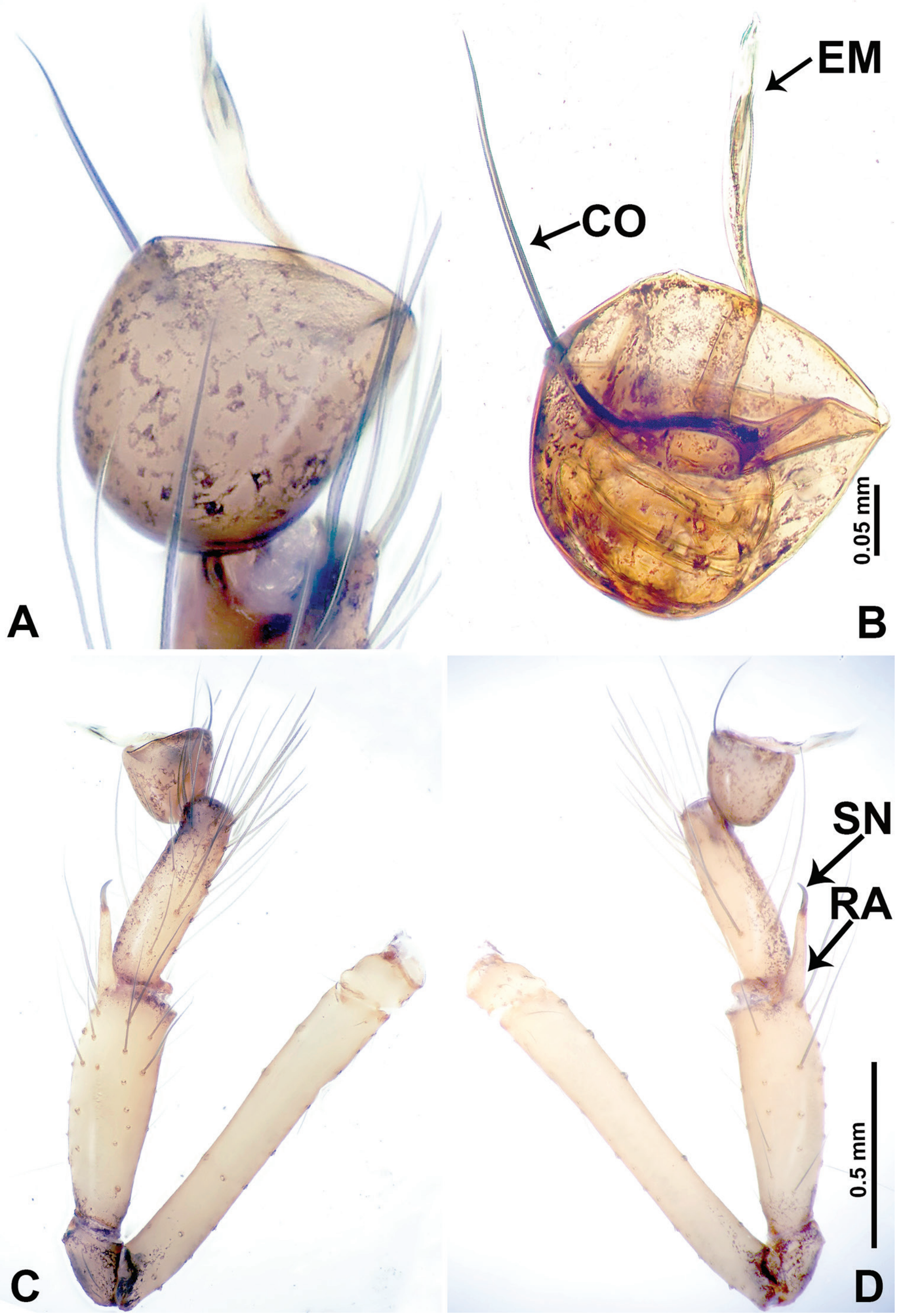

Figure 34. *Leclercera zhamensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, RA = retrolateral apophysis, SN = spine.

bulb brown, semicircle with conductor and embolus arising distally; conductor dark and thin, basally fused with embolus, almost as long as embolus, two times longer than tegulum; embolus laminar-like, almost transparent (Fig. 34B).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera sanjiao sp. nov.

http://zoobank.org/F7DF65E5-B728-4856-A17F-2BDD1D4B4C0D

Figs 35, 55C, 58

Types. ***Holotype*:** ♀ (IZCAS), China, Tibet Autonomous Region, Xigaze, Gyirong County, Zalong Village, 28°22.8650'N, 85°21.1580'E, elevation ca 2715 m, 31.VIII.2014, Y. Li leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "sānjiǎo" (triangle) and refers to the distinct triangular shape of the external genitalia.

Diagnosis. Females of *L. sanjiao* sp. nov. can be distinguished from other congeners by the distinct triangular form of the external genitalia (Fig. 35B) (vs. the absence of triangular external genitalia in congeners), and a pair of transverse linear spermathecae (Fig. 35A) (vs. the absence of linear spermathecae in congeners).

Description. Female. Total length 3.80; carapace 1.20 long, 1.20 wide; abdomen 2.60 long, 1.60 wide. Carapace round and brown, with three longitudinal dark brown bands, median band four times wider than the lateral band (Fig. 35C). Chelicerae brown (Fig. 55C). Clypeus brown, with dark brown band medially. Endites dark brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, dorsum with scattered dark brown spots laterally, with dark brown median stripes (Fig. 35C), antero-ventrally light brown with a distinct triangular external genitalia region, with indistinct dark brown patches posteriorly (Fig. 35D). Legs uniformly brown; measurements: I 17.49 (4.81, 0.50, 5.13, 5.13, 1.92), II 12.90 (3.80, 0.50, 3.60, 3.60, 1.40), III 9.17 (2.88, 0.40, 2.40, 2.40, 1.09), IV 13.67 (4.17, 0.50, 3.75, 3.75, 1.50). Epigastric area (Fig. 35B): triangular pale brown patch with posterior yellowish slit. Endogyne (Fig. 35A): a pair of transverse, linear spermathecae, with the posterior pair curving downwards, slightly longer than the anterior pair; both anterior and posterior pairs with rounded tips and similar in width.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera selasihensis sp. nov.

http://zoobank.org/67E75A89-0332-460F-8968-FC6D89E72FA8

Figs 36, 37, 56I, 58

Types. ***Holotype*:** ♂ (IZCAS), Indonesia, Sumatra, West Sumatra Province, Solok Bukit Selasih Village, 0°46.0400'S, 100°43.1750'E, elevation ca 426 m, 28.V.2014, Z. Yao leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

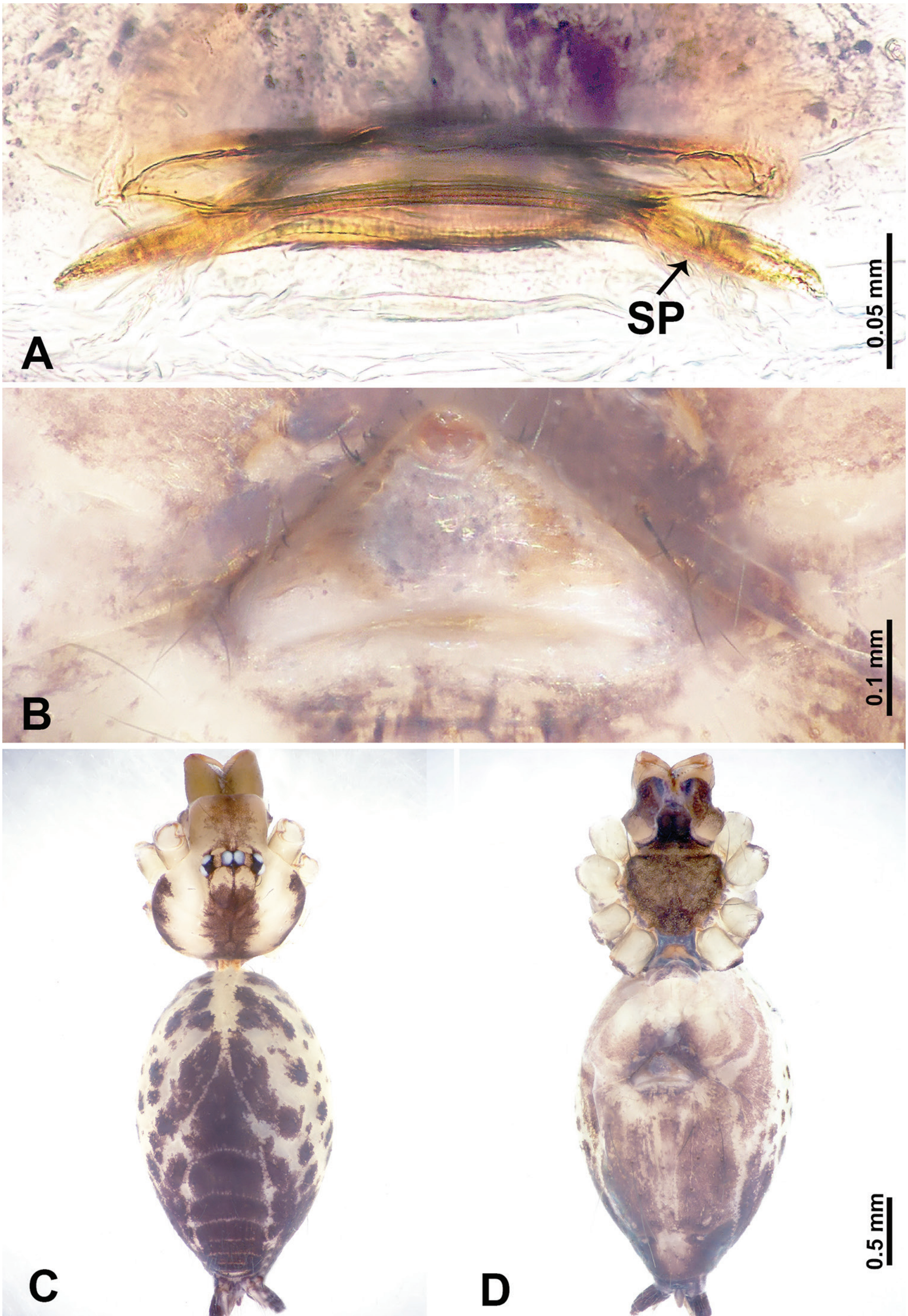

Figure 35. *Leclercera sanjiao* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

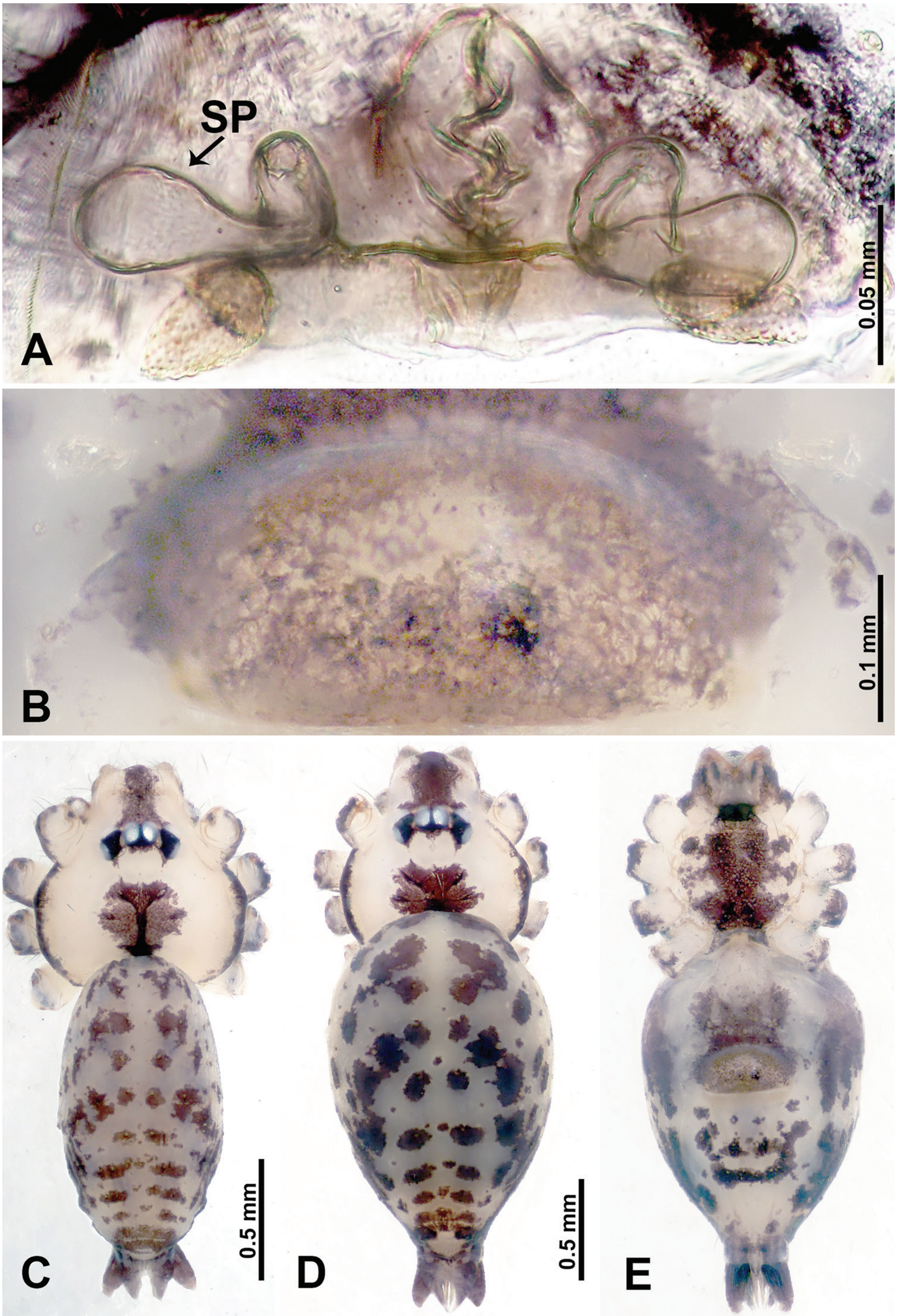

Figure 36. *Leclercera selasihensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

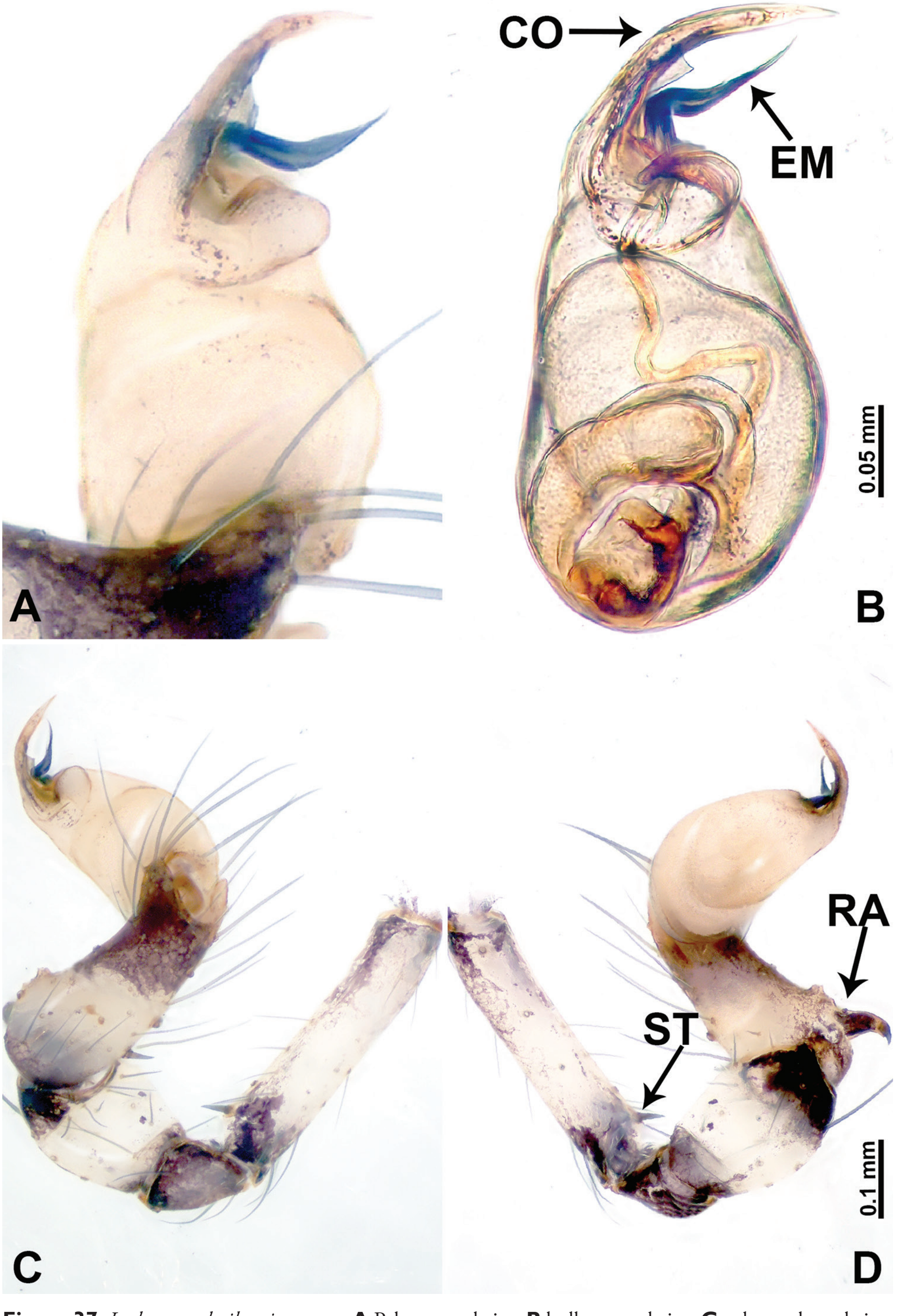

Figure 37. *Leclercera selasihensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, RA = retrolateral apophysis, ST = strong seta.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Diagnostic features of males and females are discussed in the diagnosis of *L. mianqiu* sp. nov.

Description. Male (Holotype). Total length 1.80; carapace 0.70 long, 0.75 wide; abdomen 1.10 long, 0.63 wide. Carapace round and pale brown, with three longitudinal dark brown bands, median band six times wider than lateral band (Fig. 36C). Chelicerae dark brown (Fig. 56I). Clypeus pale brown, dark brown band medially. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown, with lateral pale brown spots. Abdomen elongated, dorsum with complex dark brown spots, antero-ventrally with "V"-shaped dark brown patch and brown ovoid patch, posterior with brown spots forming a ring shape. Legs uniformly brown; measurements: I missing, II 8.43 (2.50, 0.31, 2.34, 2.50, 0.78), III 6.52 (1.88, 0.25, 1.88, 1.88, 0.63), IV 9.56 (2.75, 0.25, 2.81, 2.97, 0.78). Palp (Fig. 37A–D): femur slender, four times longer than patella, anterior with one strong seta prolaterally; patella not swollen, dark purplish; tibia swollen, 1.2 times shorter and two times wider than femur, dark purplish proximally and distally; cymbium two times shorter than femur, dark purplish distally, basally swollen with slightly curved postero-retrolateral apophysis that is almost perpendicular to cymbium (Fig. 37D); bulb light brown, pyriform, with embolus and conductor arising distally; embolus thin and dark, arises medially from tegulum, half the length of, and adjacent to, conductor; conductor arises laterally from tegulum, two times shorter than tegulum, attached with tiny triangular protrusion (Fig. 37B).

Female (Paratype). General features and coloration similar to those of male (Fig. 36D, E). Measurements: total length 1.80; carapace 0.60 long, 0.70 wide; abdomen 1.20 long, 0.86 wide. Leg measurements: I missing, II 6.76 (1.80, 0.25, 1.88, 2.03, 0.80), III 5.10 (1.50, 0.20, 1.30, 1.50, 0.60), IV 7.60 (2.03, 0.20, 2.25, 2.34, 0.78). Epigastric area (Fig. 36B): an elliptical dark brown patch. Endogyne (Fig. 36A): a pair of bean-shaped spermathecae with a strong depression and rounded ends, spiralled duct system medially.

Distribution. Known only from the type locality (Fig. 58).

Leclercera yuanzhui **sp. nov.**

http://zoobank.org/F1620E22-6F83-4C7D-88D7-F5BECD248BB9
Figs 38, 56J, 58

Types. ***Holotype*****:** ♀ (IZCAS), China, Yunnan Province, Wenshan State, Jinping County, mountain around bus station (direction of timber factory), 22°47.6920'N, 103°13.3360'E, elevation ca 1399 m, 14.V.2015, Z. Chen and F. Li leg.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "yuánzhuī" (conical) and refers to the shape of the external genitalia with a genitalic lobe that greatly resembles the shape of a conical flask (Fig. 38B, C).

Diagnosis. Females of *L. yuanzhui* sp. nov. resemble *L. maochong* sp. nov. and *L. shanzi* sp. nov. but can be distinguished by the presence of a protruded genitalic lobe

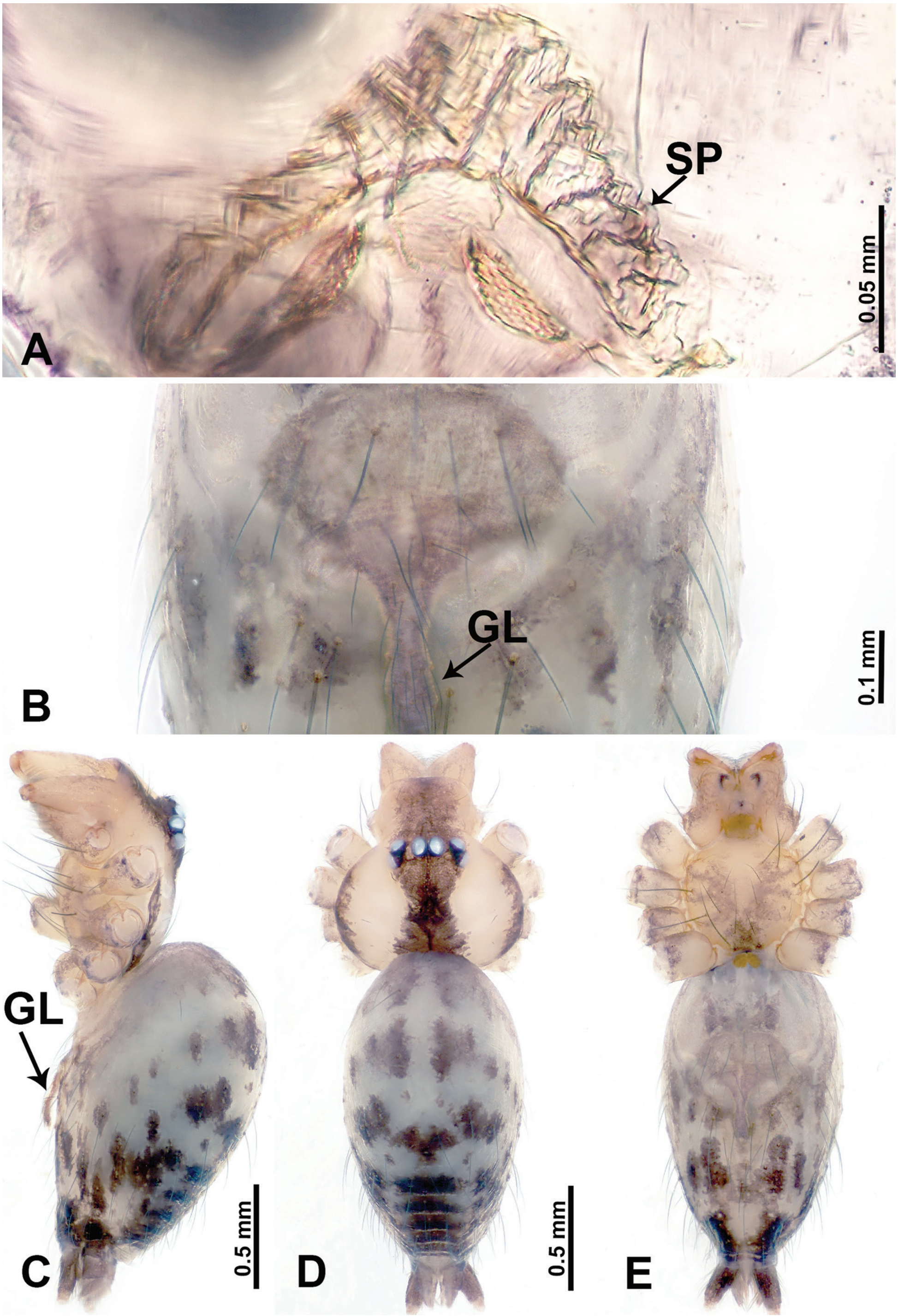

Figure 38. *Leclercera yuanzhui* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habistus, lateral view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviations: GL = genitalic lobe, SP = spermatheca.

(Fig. 38C) (vs. the absence of a genitalic lobe), the presence of a pair of widely separated semi-circular bodies posteriorly (vs. the absence of semi-circular bodies or with circular bodies), and entire spermathecae rather thin and narrow (Fig. 38A) (vs. entire spermathecae rather thick and wide).

Description. Female. Total length 2.20; carapace 0.70 long, 0.90 wide; abdomen 1.50 long, 0.90 wide. Carapace round and brown, with three dark brown longitudinal bands, median band six times wider than lateral band (Fig. 38D). Chelicerae brown (Fig. 56J). Clypeus dark brown medially. Endites brown, light brown basally. Labium brown. Sternum with purplish stripes laterally. Abdomen elongated, dorsum with dark brown spots, posteriorly with dark brown stripes (Fig. 38D), antero-ventrally with conical shaped external genitalia region, with protruded genitalic lobe (Fig. 38C), posterior with complex pattern of dark brown spots. Legs uniformly brown; measurements: I–II missing, III 4.91 (1.41, 0.20, 1.40, 1.20, 0.70), IV 8.08 (2.40, 0.31, 2.40, 2.03, 0.94). Epigastric area (Fig. 38B): inverted triangular brown patch sagging with distinct genitalic lobe. Endogyne (Fig. 38A): pair of spermathecae resembling inverted "V" with loops, posteriorly with a pair of semi-circular bodies.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera paiensis **sp. nov.**

http://zoobank.org/CB98BBAE-D4B3-42A6-975C-1AD98C337991

Figs 39, 56K, 58

Types. ***Holotype*:** ♀ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Mainling County, around Pai Town (about 65km on Gangpai highway), 29°30.7020'N, 94°52.0860'E, elevation ca 3004 m, 5.VIII.2015, J. Wu leg.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Females of *L. paiensis* sp. nov. can be distinguished from other congeners by the presence of a distinct horizontal, thick lip posterior to the external genitalia region (Fig. 39B) (vs. the absence of a thick lip on the external genitalia region in congeners), and twisted, stalked spermathecae with ovoid bases (Fig. 39A) (vs. an absence of twisted, stalked spermathecae in congeners).

Description. Female. Total length 3.20; carapace 1.00 long, 1.20 wide; abdomen 2.20 long, 1.56 wide. Carapace round and brown, with median dark brown band (Fig. 39C). Chelicerae brown (Fig. 56K). Clypeus light brown. Endites light brown. Labium dark brown. Sternum dark brown, delimiting light brown "T"-shape anteriorly. Abdomen elongated, dorsum with indistinct dark brown spots (Fig. 39C), antero-ventrally with a semi-circular dark brown patch followed by horizontal thick lip of external genitalia region, dark brown with complex pattern (Fig. 39D). Legs uniformly brown; measurements: I 9.74 (2.75, 0.40, 3.00, 2.34, 1.25), II 8.66 (2.34, 0.38, 2.66, 2.03, 1.25), III 6.36 (1.80, 0.31, 1.75, 1.50, 1.00), IV 9.00 (2.50, 0.40, 2.66, 2.19, 1.25). Epigastric area (Fig. 39B): dark brown, semi-circular patch with thick horizontal, light

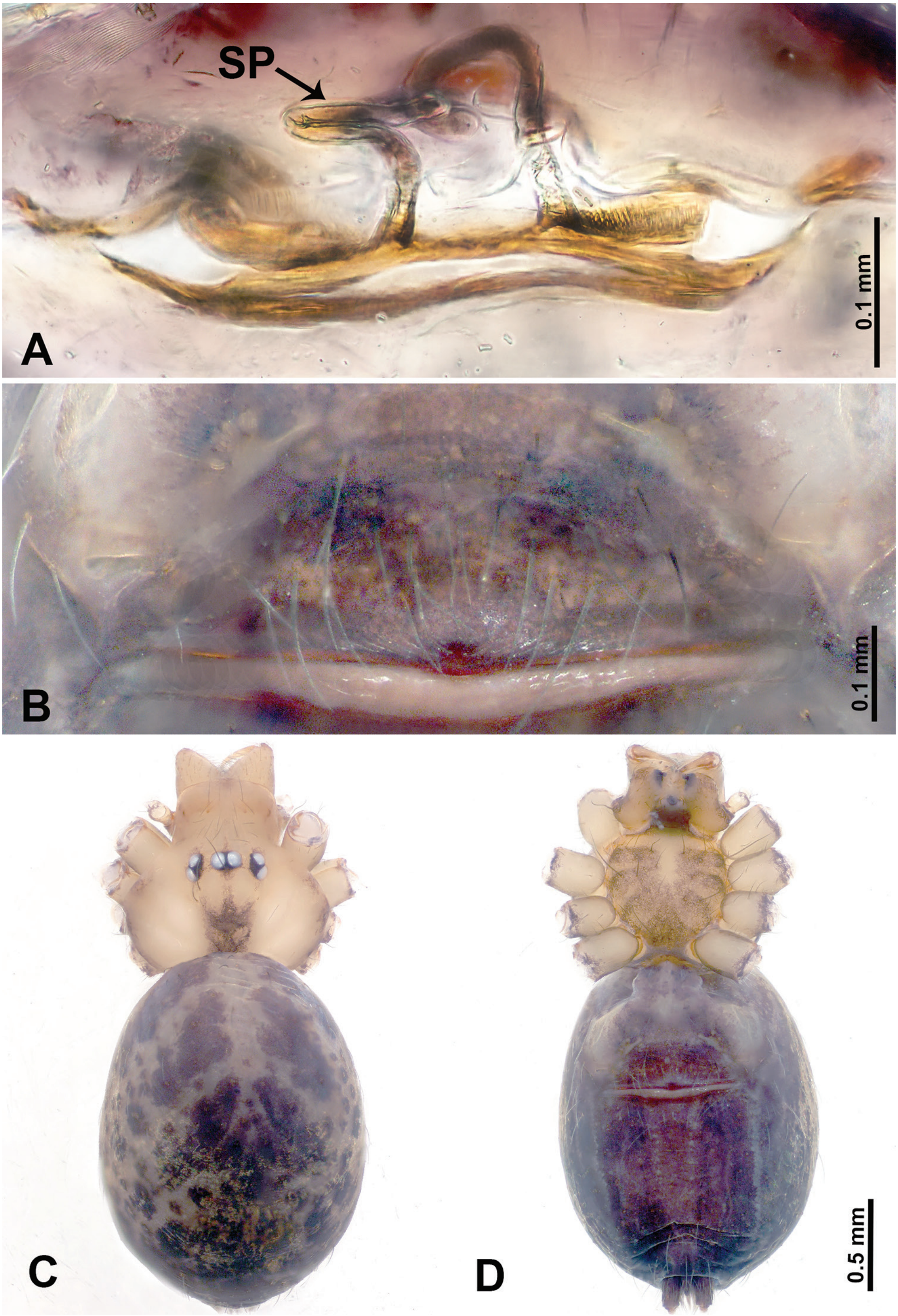

Figure 39. *Leclercera paiensis* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

brown base posteriorly. Endogyne (Fig. 39A): a pair of twisted, stalked spermathecae with ovoid base and posteriorly connected with a wavy duct system.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera zanggaensis **sp. nov.**

http://zoobank.org/459210A3-07D8-4E8A-9A3A-10A234DFF659

Figs 40, 56L, 58

Types. ***Holotype*****:** ♀ (IZCAS), China, Tibet Autonomous Region, Xigaze, Dinggye County, Chentang Town, Zangga Village, 27°51.6307'N, 87°25.4768'E, elevation ca 2219 m, 14.VIII.2017, X. Zhang, Z. Bai leg.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Females of *L. zanggaensis* sp. nov. can be distinguished from other congeners by the presence of right-angled, stalked spermathecae (Fig. 40A) (vs. the absence of right-angled, stalked spermathecae in congeners), and the external genitalia is distinctly depressed medially (Fig. 40B) (vs. the absence of indented external genitalia in congeners).

Description. Female. Total length 3.12; carapace 1.09 long, 1.09 wide; abdomen 2.03 long, 0.80 wide. Carapace round and brown, with median dark brown longitudinal band (Fig. 40C). Chelicerae brown (Fig. 56L). Clypeus dark brown medially. Endites dark brown, light brown basally. Labium dark brown. Sternum with dark brown heart shape. Abdomen elongated, antero-dorsum with pairs of dark brown longitudinal spots, posteriorly with dark brown horizontal stripes (Fig. 40C), antero-ventrally with elliptical external genitalia region, posterior with complex dark brown spots. Legs uniformly brown; measurements: I 13.11 (3.75, 0.31, 3.80, 3.75, 1.50), II–III missing, IV 13.40 (3.75, 0.40, 4.00, 3.75, 1.50). Epigastric area (Fig. 40B): linear light brown patch with distinct indented slit. Endogyne (Fig. 40A): a pair of right-angled, stalked spermathecae, with slightly downward curving blunt ends, vertical parts five times shorter than horizontal parts.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera aniensis **sp. nov.**

http://zoobank.org/62DFCEEF-797A-4766-8EEB-485CDCD80BB9

Figs 41, 42, 57A, 58

Types. ***Holotype*****:** ♂ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Medog County, Medog Town, Beibung Village, road from Jiefang Bridge to Ani Bridge, 30°11.2620'N, 94°19.4180'E, elevation ca 3087 m, 18.VII.2019, X. Zhang, Z. Bai and J. Liu leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

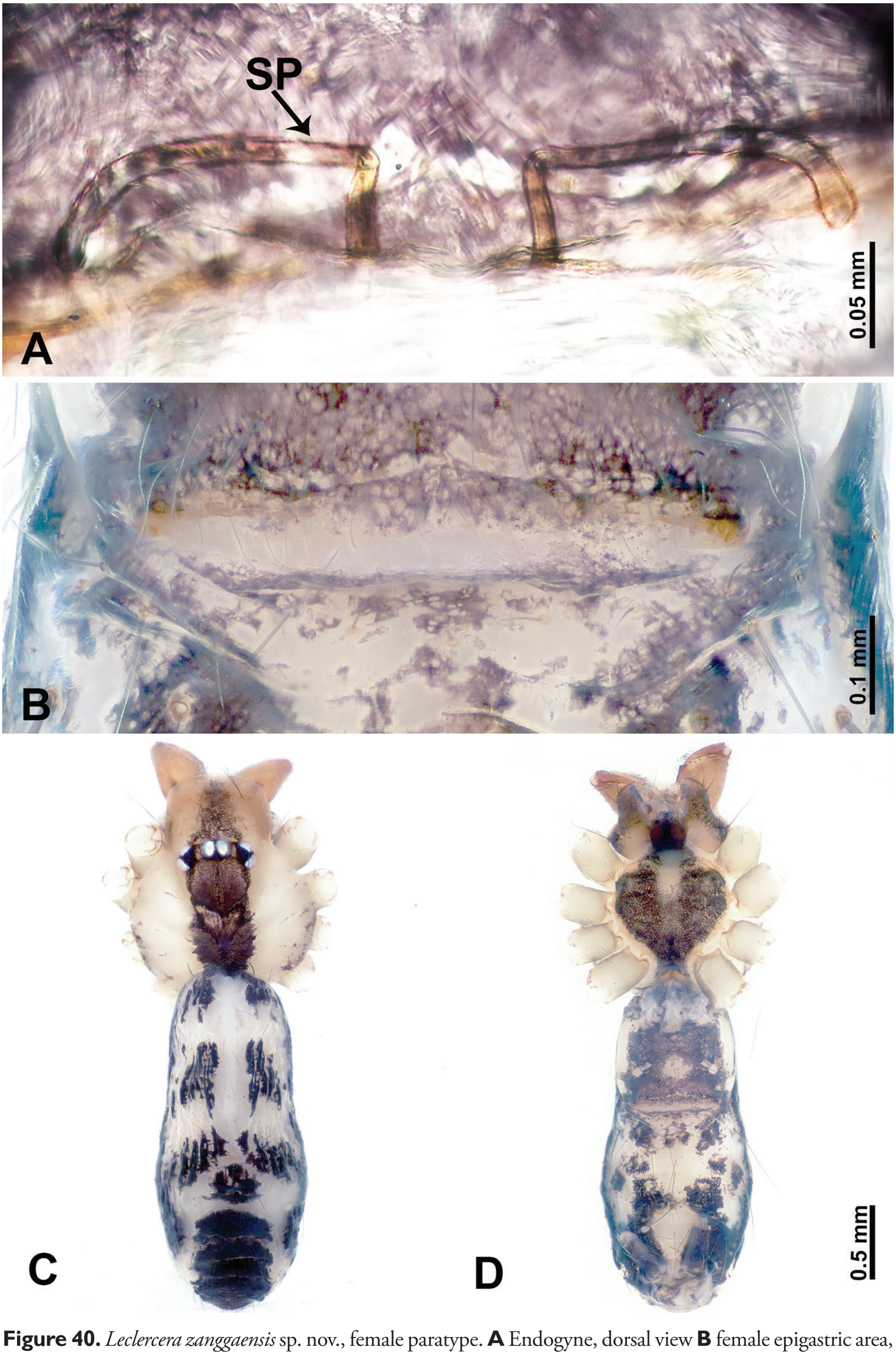

Figure 40. *Leclercera zanggaensis* sp. nov., female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** female habitus, dorsal view **D** female habitus, ventral view. Abbreviation: SP = spermatheca.

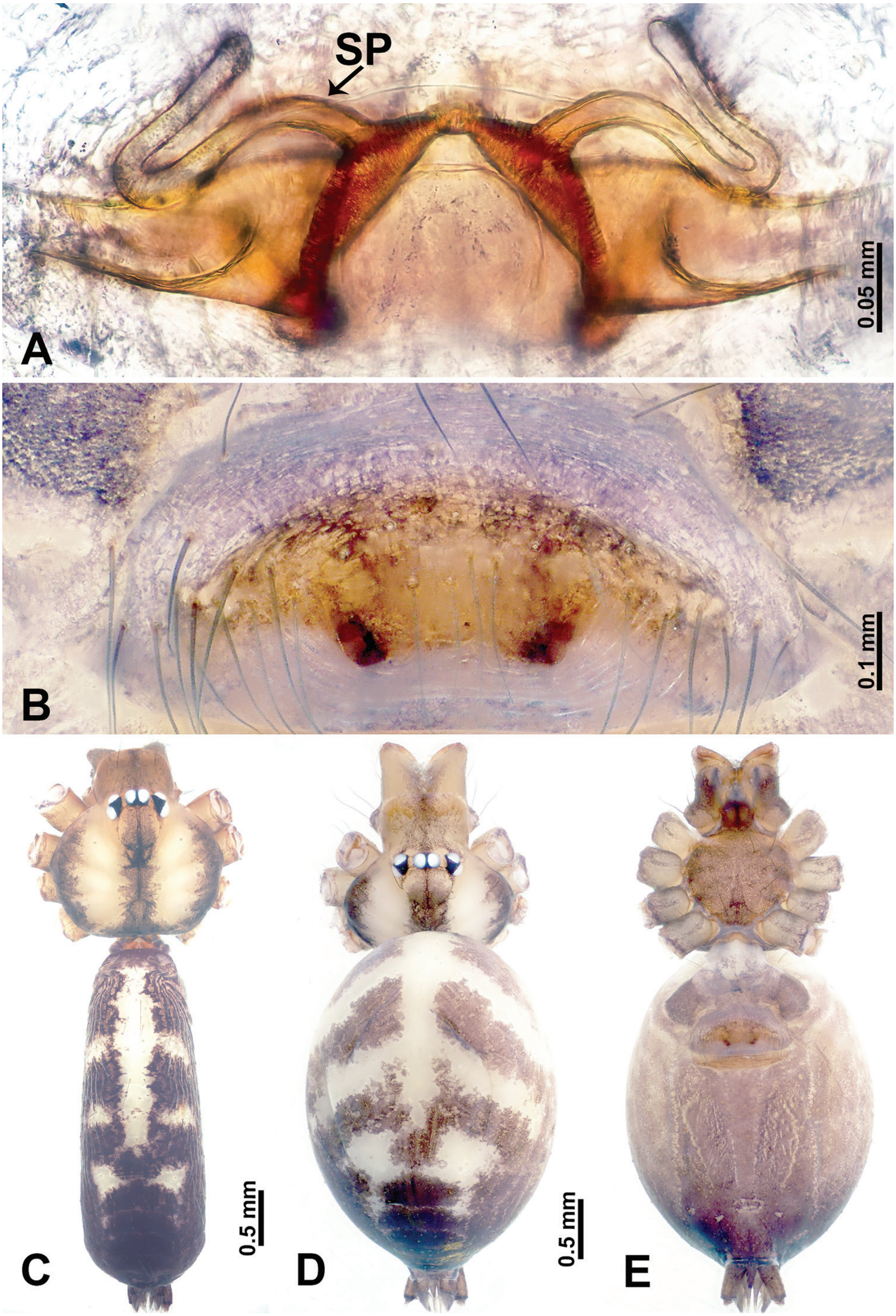

Figure 41. *Leclercera aniensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca

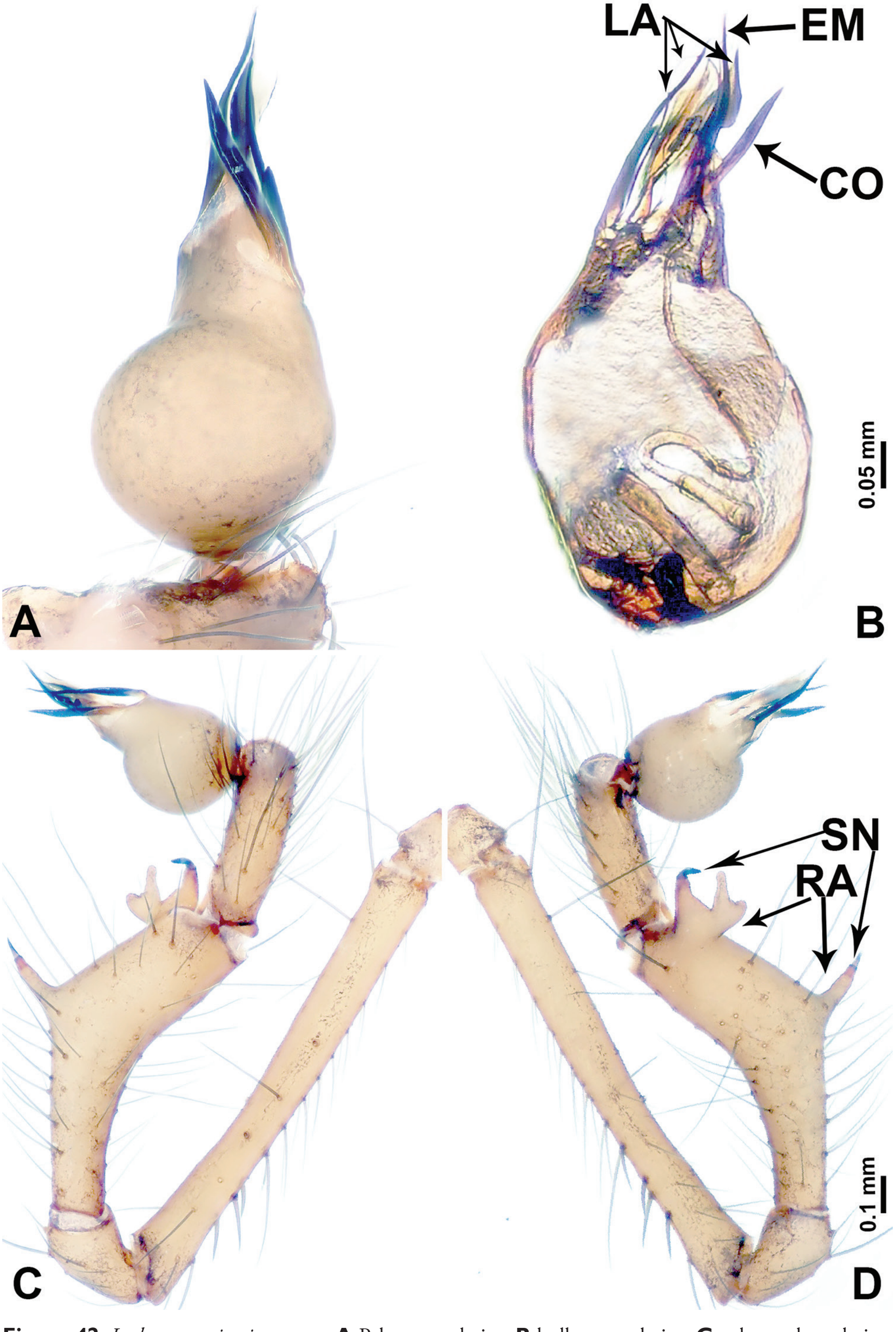

Figure 42. *Leclercera aniensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophyses, RA = retrolateral apophyses, SN = spines.

Diagnosis. Diagnostic features of males and females are discussed in the diagnosis of *L. jiazhongensis* sp. nov.

Description. Male (Holotype). Total length 4.38; carapace 1.38 long, 1.50 wide; abdomen 3.00 long, 1.09 wide. Carapace round and brown, with three dark brown longitudinal bands, median band and lateral bands similar in width (Fig. 41C). Chelicerae brown (Fig. 57A). Clypeus dark brown, darkens anteriorly. Endites dark brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, dorsum with three pairs of dark brown spots laterally, posterior with dark brown horizontal stripes, antero-ventrally with a pair of dark brown square spots laterally, followed by elliptical yellowish spot, posterior with indistinct purplish veined spots. Legs uniformly brown; measurements: I 18.91 (5.45, 0.64, 5.77, 5.13, 1.92), II 16.21 (4.49, 0.50, 4.81, 4.49, 1.92), III 11.50 (3.50, 0.40, 3.20, 3.00, 1.40), IV missing. Palp (Fig. 42A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, resembles isosceles triangle, with two retrolateral apophyses anteriorly and medially (Fig. 42D), anterior apophysis branched and two times wider than the median apophysis, one branch bearing a tiny crooked spine, another branch with a divided protrusion; median apophysis bearing spine three times shorter than apophysis; cymbium three times shorter than femur; bulb brown, pyriform, with embolus, laminar apophysis, and conductor arising distally; embolus black and slender, longest between laminar apophyses and conductor; three laminar apophyses (middle apophysis three times wider than the other two) adjacent to embolus; conductor slightly similar in width to, shorter than, and basally connected to embolus (Fig. 42B).

Female (Paratype). General features and coloration similar to those of male (Fig. 41D, E). Measurements: total length 3.44; carapace 0.94 long, 1.25 wide; abdomen 2.50 long, 1.80 wide. Leg measurements: I 11.73 (3.21, 0.40, 3.50, 3.21, 1.41), II 8.44 (2.40, 0.40, 2.25, 2.19, 1.20), III missing, IV 11.70 (3.40, 0.40, 3.40, 3.00, 1.50). Epigastric area (Fig. 41B): semi-circular patch, outer region pale purple and inner region brownish, with a pair of dark brown dots. Endogyne (Fig. 41A): pair of slightly twisted, upturned, stalked spermathecae with isosceles triangle-shaped receptacles, upturned spermathecae with blunt tips.

Distribution. Known only from the type locality (Fig. 58).

Leclercera renqinensis sp. nov.

http://zoobank.org/517CC264-4972-45A5-9D2B-D8C6E5860AB6

Figs 43, 44, 57B, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Medog County, Medog Town, road to Renqinbeng Temple, 29°18.4260'N, 95°21.5100'E, elevation ca 2036 m, 21.VII.2019, X. Zhang, Z. Bai and J. Liu. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. renqinensis* sp. nov. resemble *L. tudao* sp. nov. but can be distinguished by the presence of four uneven retrolateral apophyses on a swollen tibia,

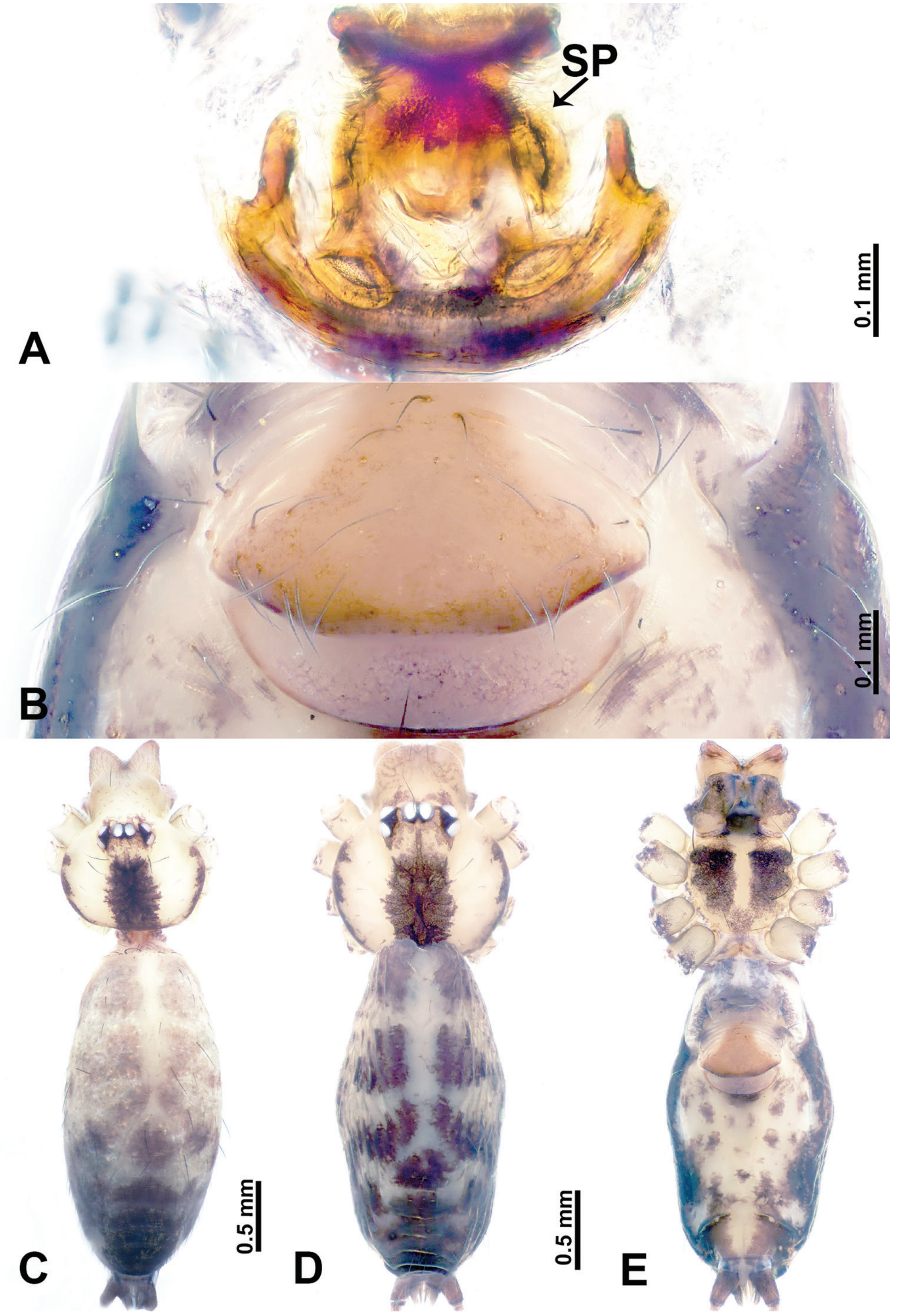

Figure 43. *Leclercera renqinensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

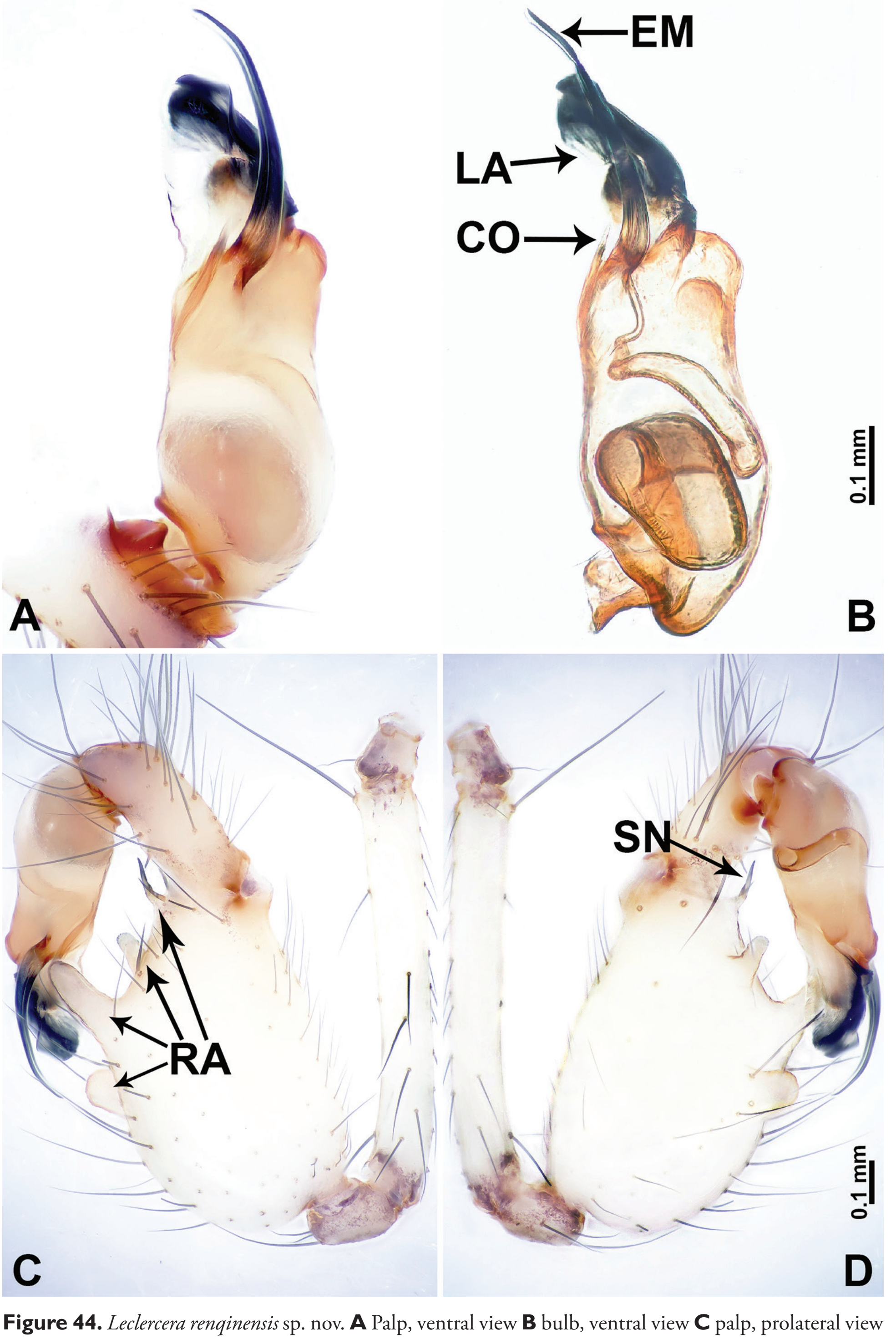

Figure 44. *Leclercera renqinensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophysis, RA = retrolateral apophyses, SN = spine.

with one apophysis bearing a spine (Fig. 44C) (vs. the presence of a spine and three retrolateral apophyses bearing spines on a swollen tibia (Fig. 50C)), tibia swollen pentagonally (Fig. 44C) (vs. tibia swollen triangularly (Fig. 50C)), pyriform bulb rather slender and elongated (Fig. 44B) (vs. pyriform bulb rather plump (Fig. 50B)), a thin strip of the conductor arises at the margins (Fig. 44B) (vs. a wide part of the conductor arises at the margins), laminar apophysis and embolus not attached to each other (Fig. 44B) (vs. embolus attached to laminar apophysis); females can be recognized by having a pair of spermathecae resembling a bow (Fig. 43A) (vs. a pair of stalked spermathecae (Fig. 49A)), external genitalia with triangular orange area (Fig. 43B) (vs. dark brown area (Fig. 49B)).

Description. Male (Holotype). Total length 3.30; carapace 0.96 long, 1.09 wide; abdomen 2.34 long, 1.25 wide. Carapace round and brown, with three dark brown longitudinal bands, median band six times wider than lateral band (Fig. 43C). Chelicerae brown (Fig. 57B). Clypeus pale brown. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown laterally, light brown medially. Abdomen elongated, dorsum with brown spots, posterior with dark brown horizontal stripes, antero-ventrally with distinct triangular orange area, posterior with dark brown bands laterally, scattered brown spots medially. Legs uniformly brown; measurements: I 16.00 (4.25, 0.40, 4.75, 5.00, 1.60), II 11.61 (3.21, 0.40, 3.20, 3.40, 1.40), III 7.71 (2.20, 0.31, 2.20, 2.00, 1.00), IV 12.50 (3.85, 0.40, 3.50, 3.50, 1.25). Palp (Fig. 44A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen pentagonally, 1.2 times shorter and 4 times wider than femur, with four retrolateral apophyses anteriorly (Fig. 44C) (one apophysis bearing a spine, three others with rounded tip, with apophysis one being longest); cymbium three times shorter than femur, brown; bulb brown, pyriform, with embolus, laminar apophysis, and conductor arising distally; embolus black and slender, longer than laminar apophysis and conductor; laminar apophysis with blunt tip, two times wider and not attached to embolus; conductor brown, arising marginally as a thin strip, embolus three times wider and longer than conductor (Fig. 44B).

Female (Paratype). General features and coloration similar to those of male (Fig. 43D, E). Measurements: total length 2.82; carapace 0.94 long, 1.00 wide; abdomen 1.88 long, 1.00 wide. Leg measurements: I 12.65 (2.75, 0.40, 4.00, 4.00, 1.50), II 10.11 (2.80, 0.31, 3.00, 2.80, 1.20), III 9.06 (1.75, 0.31, 3.00, 2.80, 1.20), IV 10.80 (3.00, 0.40, 3.20, 3.00, 1.20). Epigastric area (Fig. 43B): distinct triangular orangeish patch with pale brown crescent at base. Endogyne (Fig. 43A): spermathecae resemble a ribbon knot with a pair of ovoid droplet-shaped marks, receptacles with rounded upturned ends.

Distribution. Known only from the type locality (Fig. 58).

Leclercera shergylaensis **sp. nov.**

http://zoobank.org/5D098902-6A00-480F-91C4-7706C93EECEE

Figs 45, 46, 57C, 58

Types. ***Holotype*****:** ♂ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Shergyla Mountain, 29°33.7980'N, 94°34.2060'E, elevation ca 3764 m, 15.VII.2019, X. Zhang, Z. Bai and J. Liu leg. ***Paratype*****:** 1♀ (IZCAS), same data as holotype.

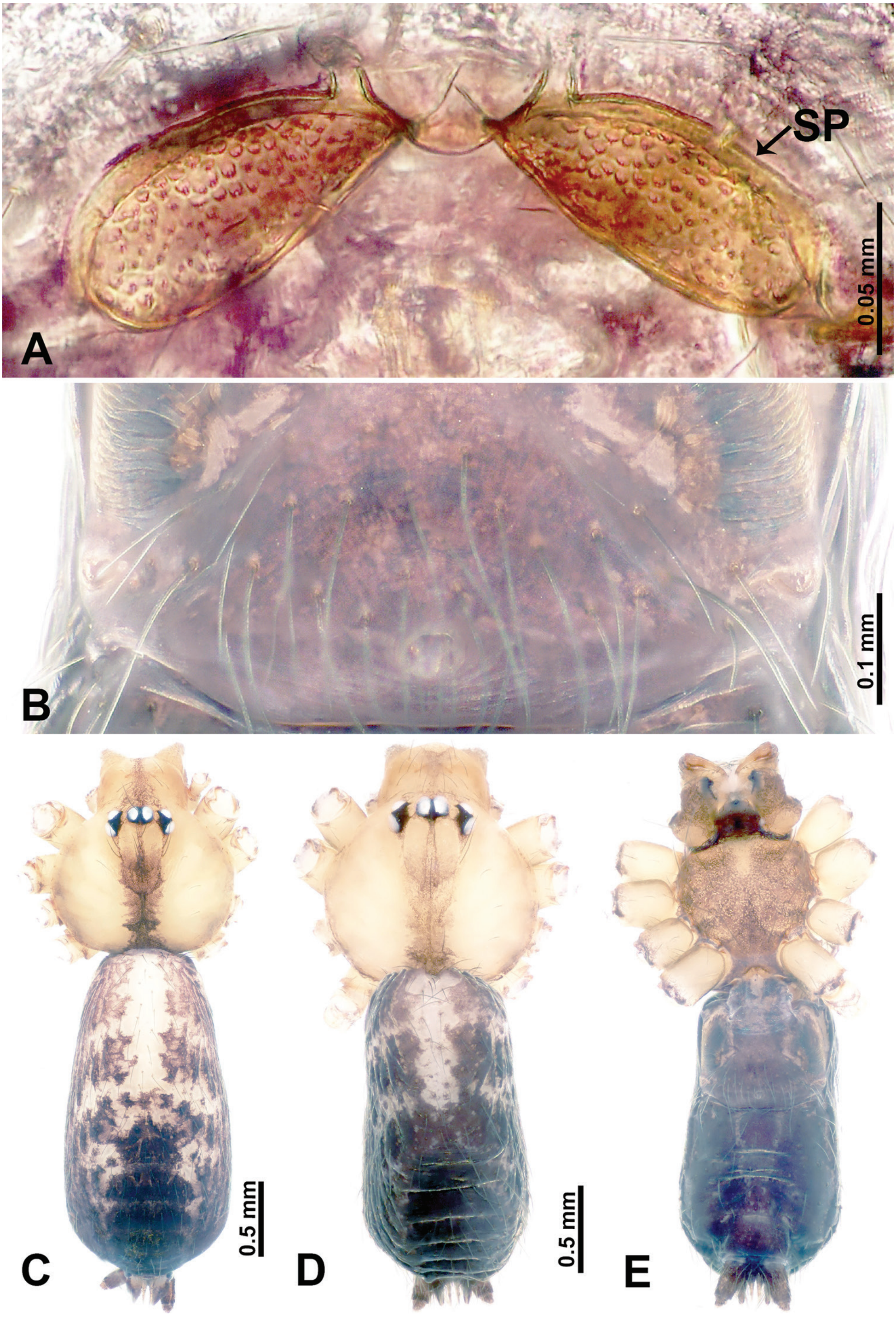

Figure 45. *Leclercera shergylaensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

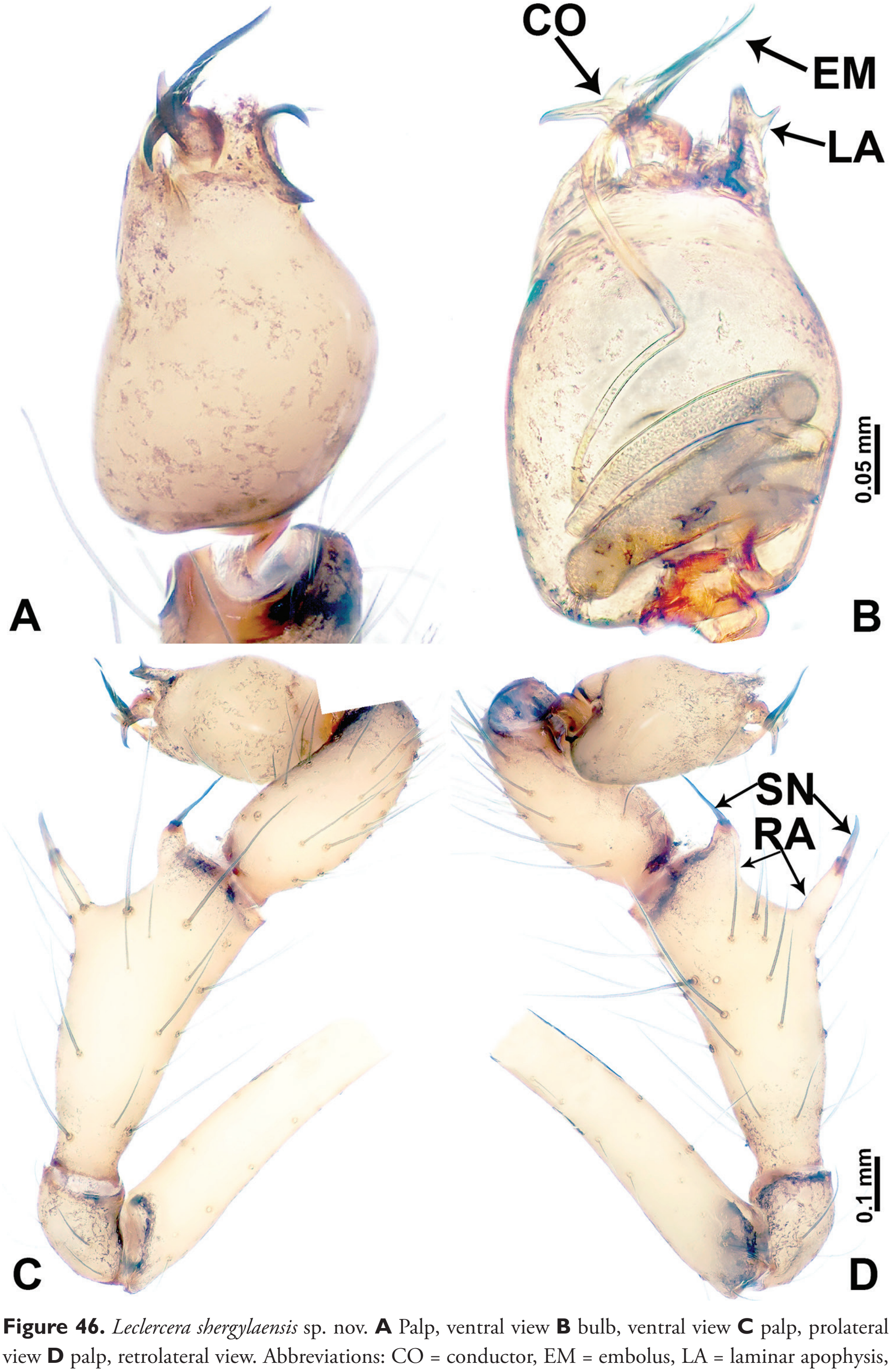

Figure 46. *Leclercera shergylaensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophysis, RA = retrolateral apophyses, SN = spines.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. shergylaensis* sp. nov. resemble *L. pulongensis* sp. nov. and *L. duibaensis* sp. nov. but can be distinguished by the presence of a conductor (Fig. 46B) (vs. absence of a conductor in *L. pulongensis* sp. nov. (Fig. 48B) and *L. duibaensis* sp. nov. (Fig. 52B)), two retrolateral apophyses bearing a spine on the tibia (Fig. 46D) (vs. a prolateral apophysis bearing a hooked spine on the tibia in *L. pulongensis* sp. nov. (Fig. 48C)) and a retrolateral apophysis bearing spine on tibia in *L. duibaensis* sp. nov. (Fig. 52D)), absence of strong setae in both *L. shergylaensis* sp. nov. and *L. duibaensis* sp. nov. (vs. the presence of strong setae on the tibia anteriorly in *L. pulongensis* sp. nov. (Fig. 48D)), and the absence of a bulge on the bulb of both *L. shergylaensis* sp. nov. and *L. pulongensis* sp. nov. (vs. the presence of a bulge on the bulb of *L. duibaensis* sp. nov. (Fig. 52B)), absence of an apophysis on the cymbium in both *L. shergylaensis* sp. nov. and *L. pulongensis* sp. nov. (vs. the presence of a retrolateral apophysis bearing four spines on the cymbium in *L. duibaensis* sp. nov. (Fig. 52D)), and the tibia swollen angularly (Fig. 46C) (vs. tibia roundly swollen in both *L. pulongensis* sp. nov. and *L. duibaensis* sp. nov.).

Description. Male (Holotype). Total length 3.13; carapace 1.00 long, 1.13 wide; abdomen 2.13 long, 1.09 wide. Carapace round and brown, with median dark brown band (Fig. 45C). Chelicerae brown (Fig. 57C). Clypeus pale brown. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown, with short light brown band medially. Abdomen elongated, dorsum with dark brown spots, posterior with dark brown horizontal stripes, antero-ventrally with dark brown inverted fan-shaped pattern medially and kidney-shaped pattern laterally, posterior dark brown with two light vertical traces medially. Legs uniformly brown; measurements: I 9.60 (2.60. 0.40. 3.00, 2.40, 1.20), II 8.94 (2.60, 0.40, 2.50, 2.24, 1.20), III missing, IV 9.20 (2.60, 0.40, 2.80, 2.20, 1.20). Palp (Fig. 46A–D): femur slender, four times longer than patella; patella not swollen; tibia swollen pentagonally, similar length to, and 2 times wider than femur, with two retrolateral apophyses bearing spine (Fig. 46D) (one apophysis on anterior, the other medially on tibia), spine and apophysis similar in length; cymbium two times shorter than femur, dark brown distally; bulb brown, ovate, with embolus, laminar apophysis, and conductor arising distally; embolus thin, two times longer than conductor and laminar apophysis; branched laminar apophysis, two times wider than embolus, adjacent to conductor; conductor branched, with the longer branch longer than laminar apophysis, attached to embolus (Fig. 46B).

Female (Paratype). General features and coloration similar to those of male (Fig. 45D, E). Measurements: total length 2.44; carapace 0.94 long, 1.00 wide; abdomen 1.50 long, 0.88 wide. Leg measurements: I 7.69 (2.24, 0.31, 2.34, 1.80, 1.00), II 6.70 (1.80, 0.31, 2.03, 1.56, 1.00), III 5.29 (1.41, 0.31, 1.38, 1.25, 0.94), IV 6.10 (1.80, 0.31, 2.19, 1.80, 1.00). Epigastric area (Fig. 45B): elliptical dark brown patch with distinct whitish slit. Endogyne (Fig. 45A): a pair of ovoid spermathecae, thickening at margins.

Distribution. Known only from the type locality (Fig. 58).

Leclercera pulongensis sp. nov.

http://zoobank.org/7D2D5BA0-C547-4B26-A3E3-1A7A12FE7C26
Figs 47, 48, 57D, 58

Types. ***Holotype***: ♂ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Mainling County, Pulong Village, 29°16.0980'N, 93°32.5380'E, elevation ca 3335 m, 10.VIII.2019, X. Zhang, Z. Bai and J. Liu leg.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Diagnostic features of males are discussed in the diagnosis of *L. shergylaensis* sp. nov.

Description. Male (Holotype). Total length 2.57; carapace 0.94 long, 1.13 wide; abdomen 1.63 long, 0.90 wide. Carapace round and brown, with dark brown traces marginally and medially (Fig. 47A). Chelicerae brown (Fig. 57D). Clypeus pale brown, with brown traces medially. Endites brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, antero-dorsally with three pairs of dark brown spots laterally, posterior with dark brown horizontal stripes medially, antero-ventrally with pairs of brown kidney-shaped spots laterally, medially with elliptical patch, posterior with indistinct dark brown pattern. Legs uniformly brown; measurements: I 10.00 (3.00, 0.40, 3.00, 2.40, 1.20), II 9.31 (2.75, 0.31, 2.81, 2.19, 1.25), III 6.58 (1.80,

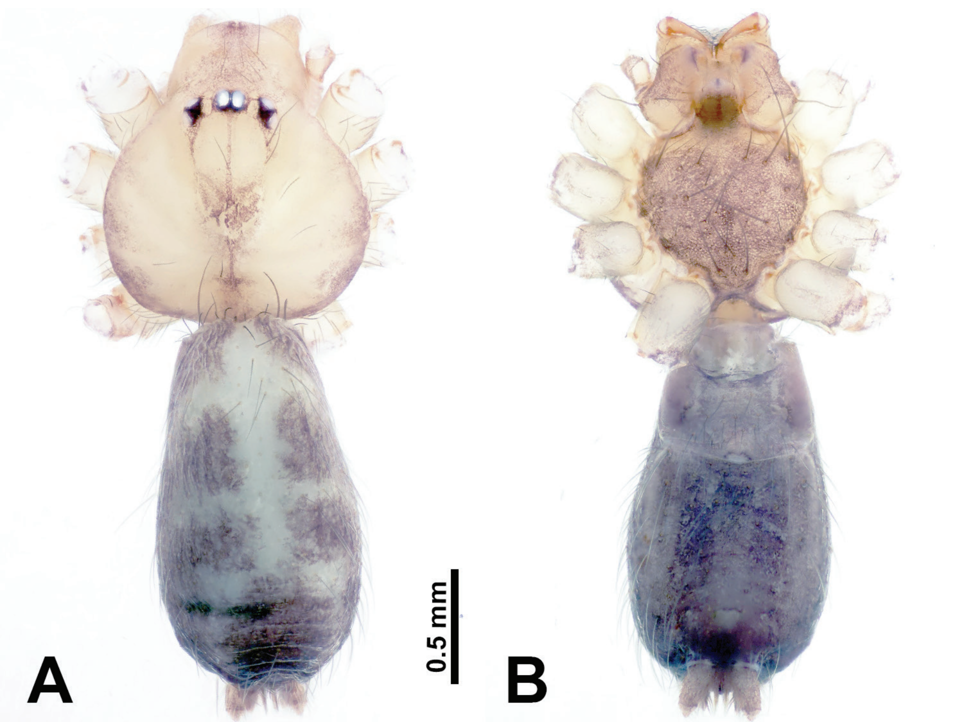

Figure 47. *Leclercera pulongensis* sp. nov., male holotype. **A** Habitus, dorsal view **B** habitus ventral view.

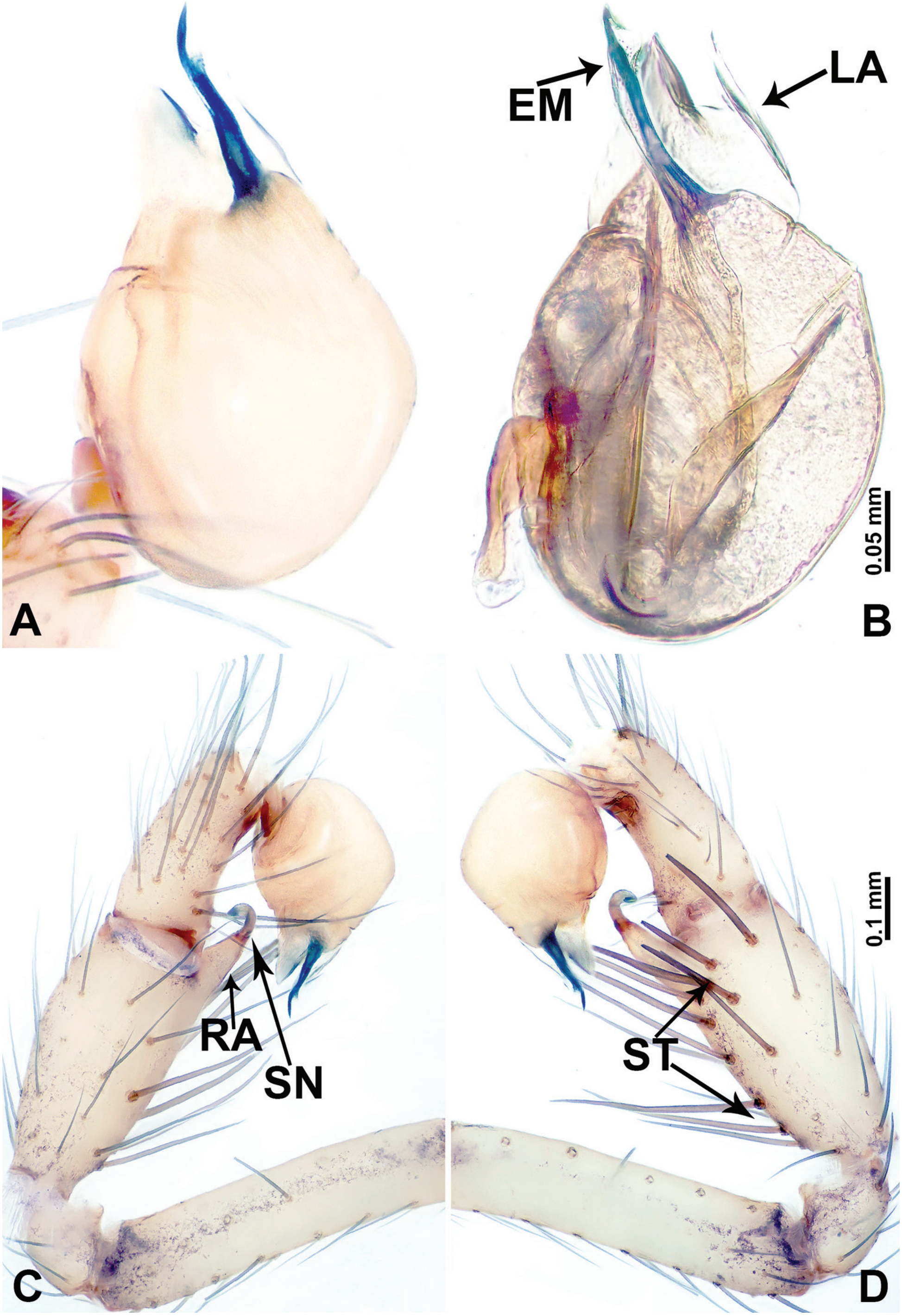

Figure 48. *Leclercera pulongensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: EM = embolus, LA = laminar apophysis, RA = retrolateral apophysis, SN = spine, ST = strong setae.

0.40, 1.88, 1.56, 0.94), IV 9.60 (2.80, 0.40, 2.80, 2.40, 1.20). Palp (Fig. 48A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, 1.2 times shorter and two times wider than femur, with prolateral apophysis bearing a hooked spine anteriorly, and more than 10 strong setae; cymbium 2.5 times shorter than femur; bulb brown, globose, with embolus and laminar apophysis arising distally; embolus thin and black, slightly longer than, and not attached to, laminar apophysis; laminar apophysis branched, with one branch four times wider than the other (Fig. 48B).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera tudao sp. nov.

http://zoobank.org/9514B93C-82C8-4B13-9B64-1A50A42CFF68
Figs 49, 50, 57E, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Tibet Autonomous Region, Xigaze, Nyalam County, Zham Town, road to Guomen, 27°28.7100'N, 85°58.6920'E, elevation ca 2333 m, 10.VII.2019, X. Zhang, Z. Bai and J. Liu leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is a noun in apposition derived from the Chinese pinyin "túdāo" (cleaver) and refers to the structure of the laminar apophysis and embolus together resembling a pair of cleavers (Fig. 50A).

Diagnosis. Diagnostic features of the males are discussed in the diagnosis of *L. renqinensis* sp. nov.

Description. Male (Holotype). Total length 3.13; carapace 1.00 long, 1.10 wide; abdomen 2.13 long, 0.90 wide. Carapace round and pale brown, with three longitudinal dark brown bands, median band five times wider than lateral bands (Fig. 49C). Chelicerae brown (Fig. 57E). Clypeus pale brown, dark brown medially. Endites dark brown, light brown basally. Labium and sternum dark brown. Abdomen elongated, dorsum with pairs of dark brown spots, posterior with dark brown horizontal stripes, ventrum with dark brown band marginally, antero-ventrally with elliptical dark brown patch, posterior with a pair of distinct rectangular dark brown spots. Legs uniformly brown; measurements: I 20.35 (5.45, 2.00, 5.13, 5.77, 2.00), II 12.95 (3.75, 0.40, 3.60, 3.80, 1.40), III 13.35 (3.75, 0.40, 3.80, 4.00, 1.40), IV 8.74 (2.50, 0.31, 2.34, 2.50, 1.09). Palp (Fig. 50A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen, 1.2 times shorter and 2 times wider than femur, with a distinct spine and three retrolateral apophyses bearing spines anteriorly, spines about three times longer than apophysis (Fig. 50C); cymbium three times shorter than femur; bulb brown, globose, with embolus, laminar apophysis, and conductor arising distally; embolus thin and black, adjacent and basally attached to laminar apophysis; laminar apophysis about 8 times wider than embolus, with flat tip, adjacent to conductor but not attached; conductor with rounded tip, similar to laminar apophysis but two times shorter (Fig. 50B).

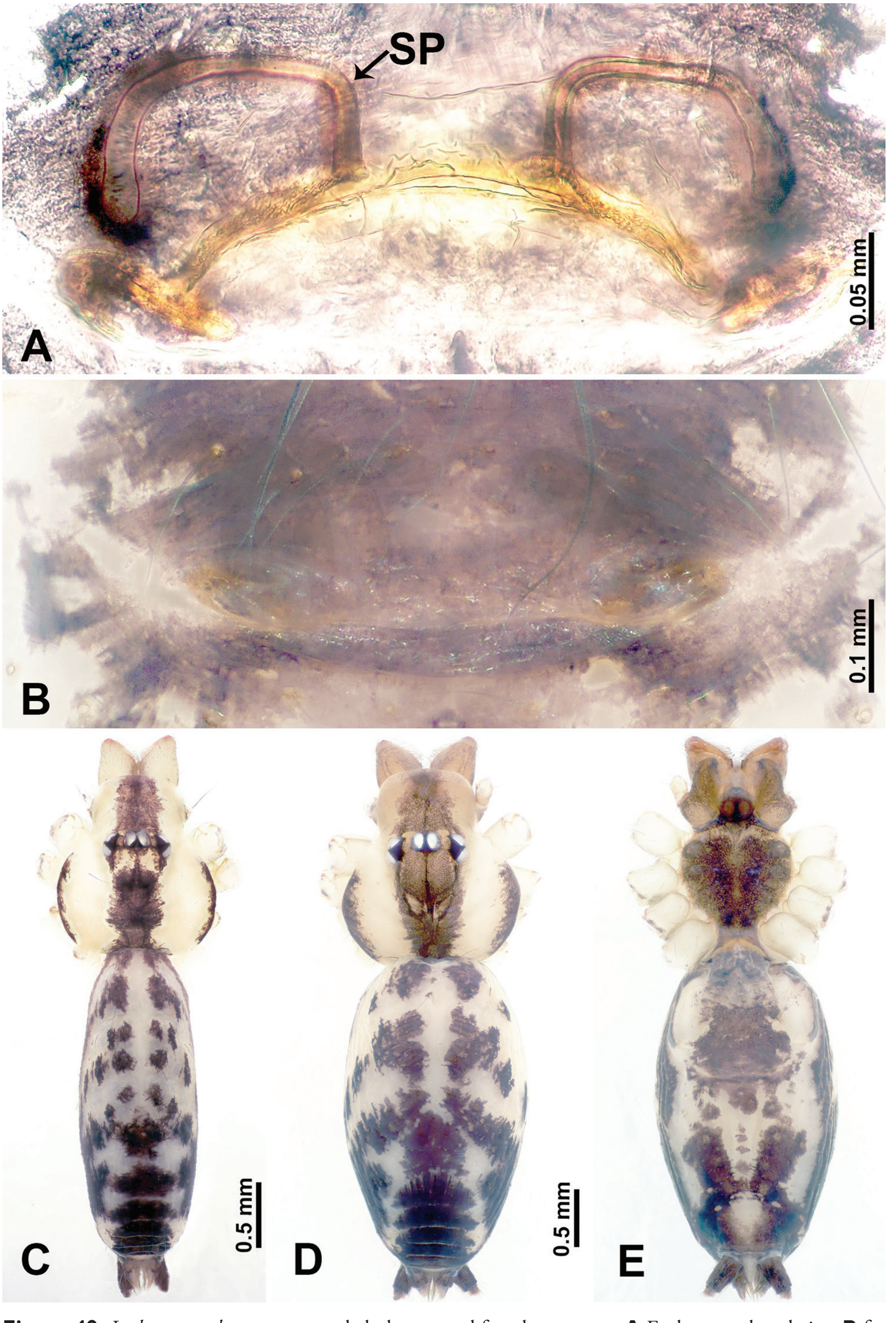

Figure 49. *Leclercera tudao* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

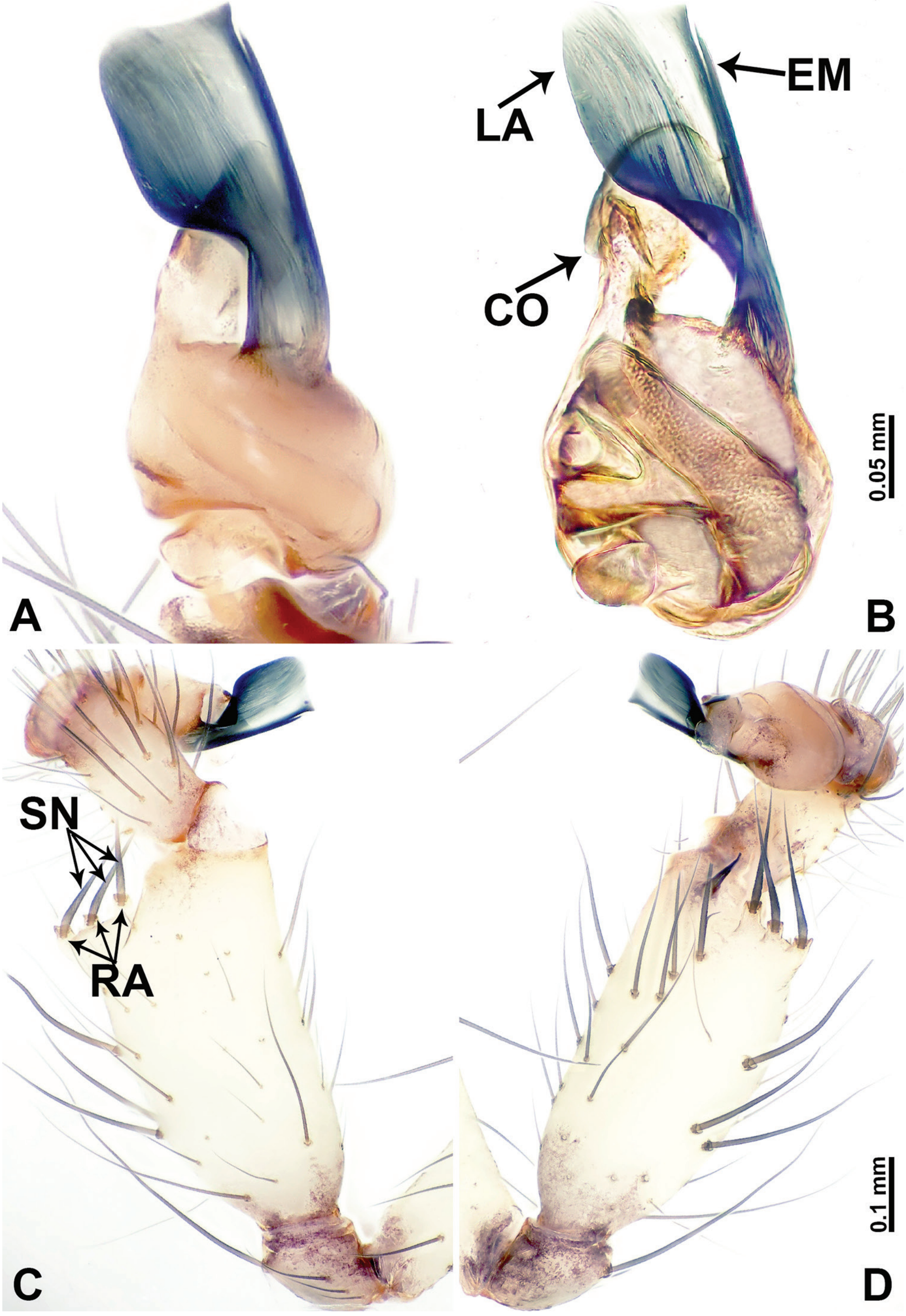

Figure 50. *Leclercera tudao* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophysis, RA = retrolateral apophyses, SN = spines.

Female (Paratype). General features and coloration similar to those of male (Fig. 49D, E). Measurements: total length 3.00; carapace 1.00 long, 1.09 wide; abdomen 2.00 long, 1.25 wide. Leg measurements: I – (4.81, 0.40, 4.75, 4.50, -), II – (3.50, 0.40, 3.60, 3.40, -), III 8.60 (2.40, 0.40, 2.40, 2.20, 1.20), IV – (3.85, 0.40, 3.75, 3.50, -). Epigastric area (Fig. 49B): dark brown patch with yellowish and pale brownish slit. Endogyne (Fig. 49A): a pair of stalked spermathecae, stalks curving downwards, almost forming a pair of perpendicular stalks with rounded tips.

Distribution. Known only from the type locality (Fig. 58).

Leclercera duibaensis sp. nov.

http://zoobank.org/00AE7BE3-89B4-47DA-AA5D-BE3A2813C7A7

Figs 51, 52, 57F, 58

Types. ***Holotype***: ♂ (IZCAS), China, Tibet Autonomous Region, Shannan, Duopozhang Village, Duiba Village, 29°22.2840'N, 91°41.8320'E, elevation ca 4095 m, 14.VIII.2019, X. Zhang, Z. Bai and J. Liu leg.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Diagnostic features of the males are discussed in the diagnosis of *L. shergylaensis* sp. nov.

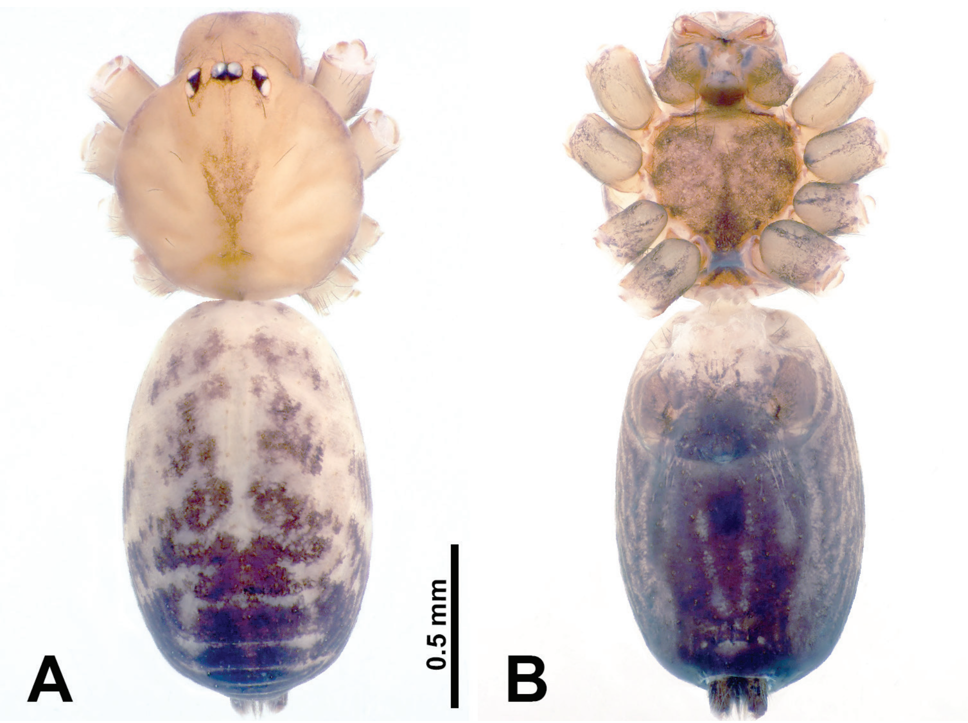

Figure 51. *Leclercera duibaensis* sp. nov., male holotype. **A** Habitus, dorsal view **B** habitus ventral view.

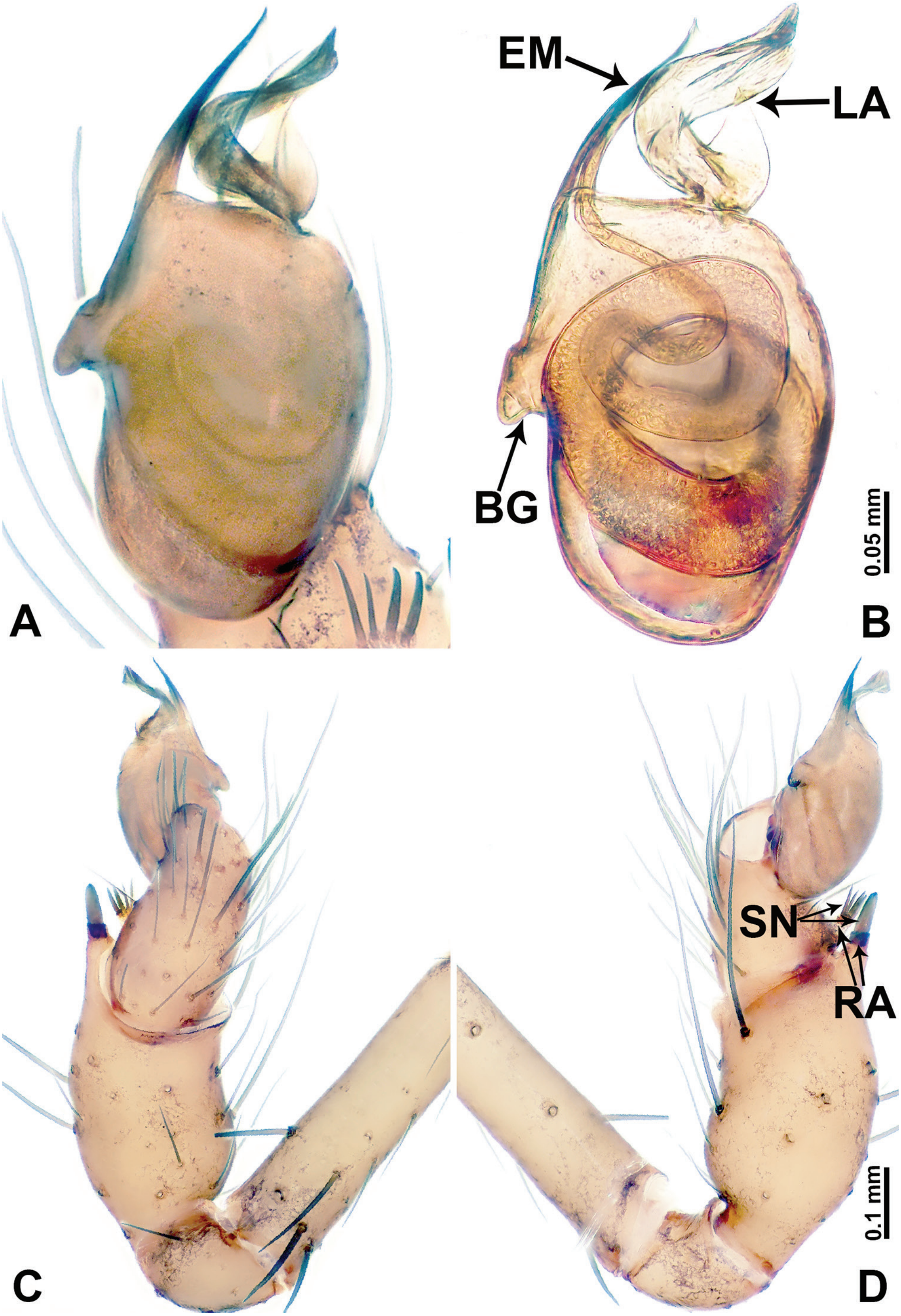

Figure 52. *Leclercera duibaensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: BG = bulge, EM = embolus, LA = laminar apophysis, RA = retrolateral apophyses, SN = spines.

Description. Male (Holotype). Total length 3.60; carapace 1.41 long, 1.40 wide; abdomen 2.19 long, 1.00 wide. Carapace round and brown, with dark brown traces medially (Fig. 51A). Chelicerae brown (Fig. 57F). Clypeus brown. Endites dark brown, light brown basally. Labium dark brown. Sternum dark brown, with light brown "T"-shaped trace anteriorly. Abdomen elongated, antero-dorsally with pairs of dark brown spots laterally, posterior with dark brown horizontal stripes medially, antero-ventrally with pairs of brown, kidney-shaped spots laterally, medially with elliptical patch, posterior with indistinct dark brown vertical patterns. Legs uniformly brown; measurements: I 10.85 (3.85, 0.50, 3.75, 1.75, 1.00), II 10.25 (3.00, 0.50, 3.00, 2.50, 1.25), III 7.39 (2.19, 0.40, 2.00, 1.80, 1.00), IV 12.20 (3.50, 0.50, 4.00, 2.80, 1.40). Palp (Fig. 52A–D): femur slender, three times longer than patella; patella not swollen; tibia swollen, 1.5 times shorter and two times wider than femur, with a retrolateral apophysis bearing a spine anteriorly, spine and apophysis similar in length (Fig. 52D); cymbium two times shorter than femur, with retrolateral apophysis bearing four spines posteriorly, spines and apophysis similar in length (Fig. 52D); bulb brown, ovoid with embolus and laminar apophysis arising distally, presence of a bulge marginally; embolus fine and black, slightly shorter than laminar apophysis; laminar apophysis slightly twisted, forming a "U"-shaped branch, with one branch two times longer than other branch, four times wider than, and not attached to, embolus (Fig. 52B).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 58).

Leclercera jiazhongensis sp. nov.

http://zoobank.org/24C9F76A-CC61-4074-82DF-DF241361C705

Figs 53, 54, 57G, 58

Types. ***Holotype*:** ♂ (IZCAS), China, Tibet Autonomous Region, Nyingchi, Bomê County, Yigong Village, mountain in Jiazhong Village, 30°11.2620'N, 94°19.4180'E, elevation ca 3087 m, 18.VII.2019, X. Zhang, Z. Bai and J. Liu leg. ***Paratype*:** 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Males of *L. jiazhongensis* sp. nov. resemble *L. aniensis* sp. nov. but can be distinguished by the presence of a prolateral apophysis bearing a spine on the tibia (Fig. 54D) (vs. the presence of two retrolateral apophyses, each bearing a spine, on the tibia, where the anterior apophysis is branched and resembles a claw (Fig. 42D)), cymbium similar in length to tibia (vs. cymbium about three times shorter than the tibia), tibia swollen, resembles "D" shape (vs. tibia swollen, resembles isosceles triangle), bulb rather slender and elongated (Fig. 54B) (vs. bulb rather plump and short (Fig. 42B)), and the presence of one laminar apophysis (vs. the presence of three laminar apophyses); females can be distinguished by a pair of long, wavy, stalked spermathecae (Fig. 53A) (vs. a pair of short and upturned stalked spermathecae (Fig. 41A)).

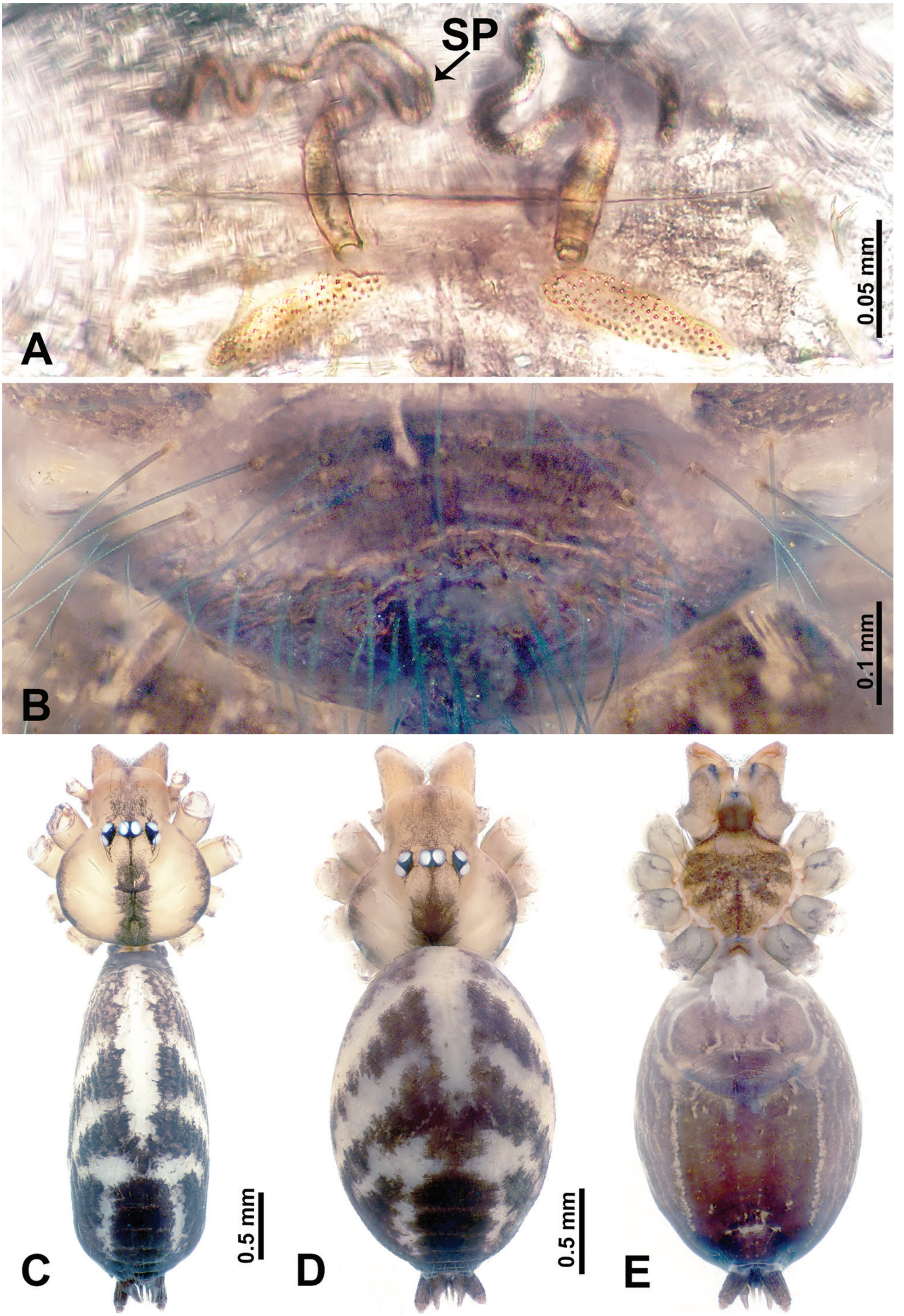

Figure 53. *Leclercera jiazhongensis* sp. nov., male holotype and female paratype. **A** Endogyne, dorsal view **B** female epigastric area, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: SP = spermatheca.

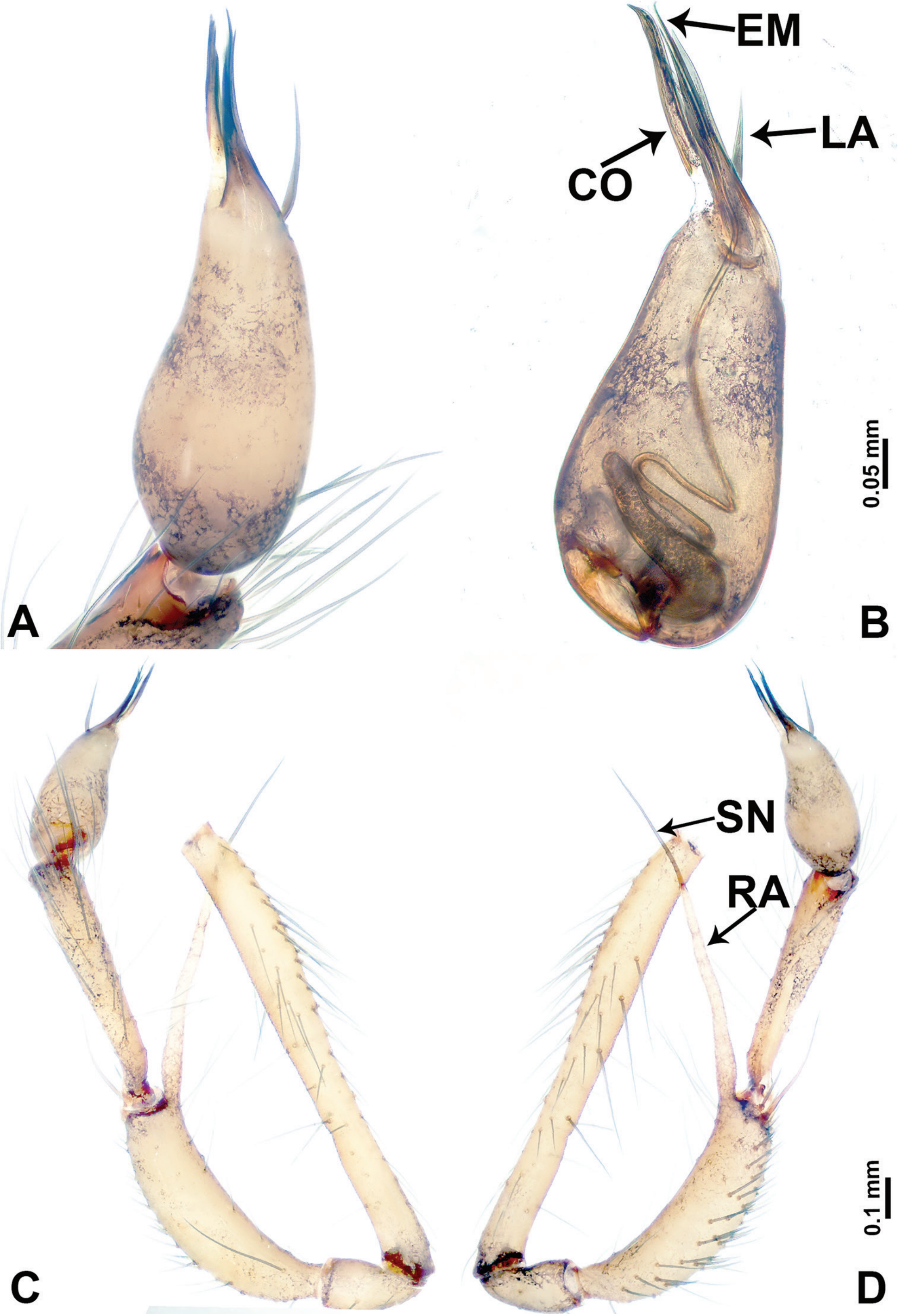

Figure 54. *Leclercera jiazhongensis* sp. nov. **A** Palp, ventral view **B** bulb, ventral view **C** palp, prolateral view **D** palp, retrolateral view. Abbreviations: CO = conductor, EM = embolus, LA = laminar apophysis, RA = retrolateral apophysis, SN = spine.

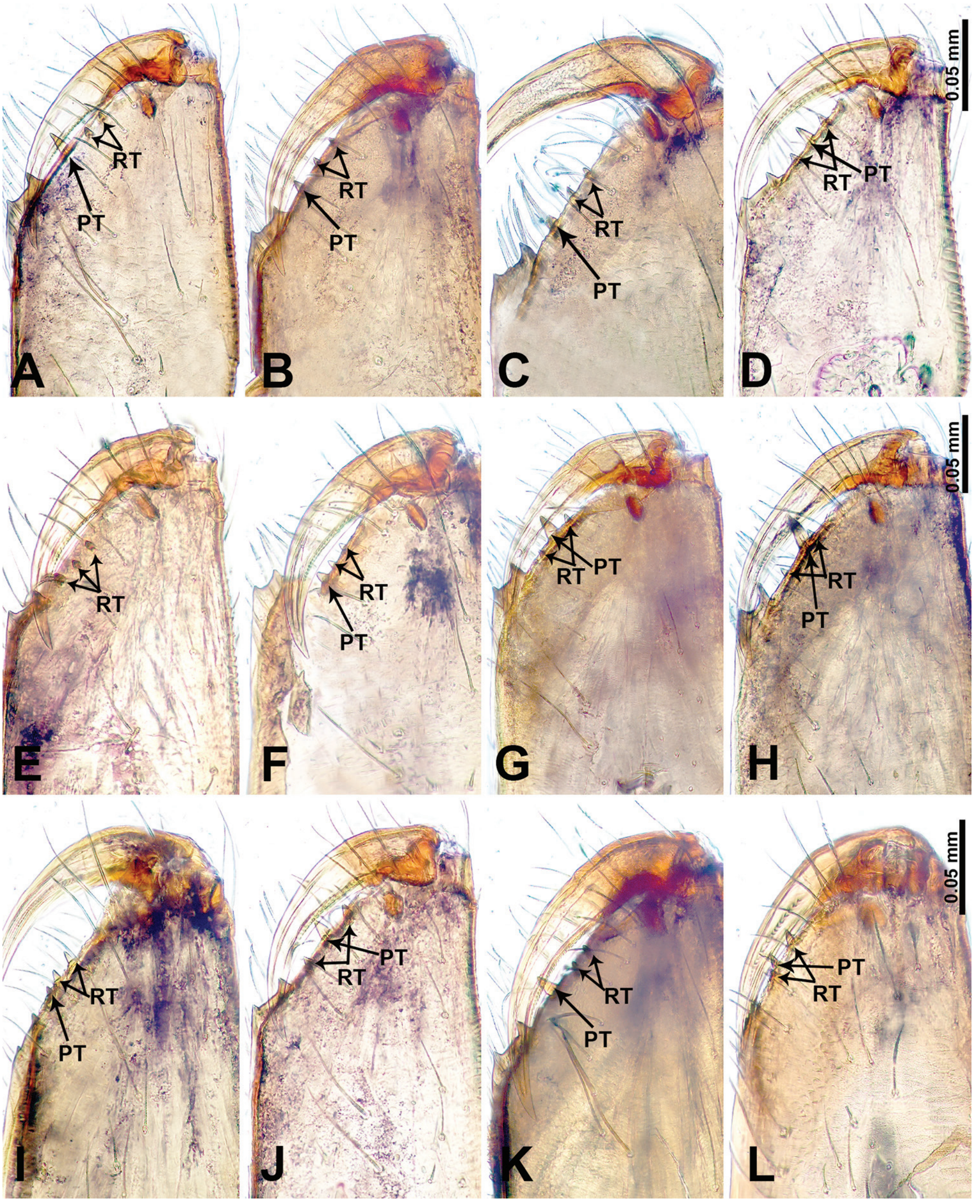

Figure 55. Cheliceral retromargin, posterior view. **A** *Leclercera xiaodai* sp. nov. **B** *L. zhamensis* sp. nov. **C** *L. sanjiao* sp. nov. **D** *L. banensis* sp. nov. **E** *L. jianzuiyu* sp. nov. **F** *L. xiangbabang* sp. nov. **G** *L. maochong* sp. nov. **H** *L. shanzi* sp. nov. **I** *L. yandou* sp. nov. **J** *L. suwanensis* sp. nov. **K** *L. duandai* sp. nov. **L** *L. yanjing* sp. nov. Abbreviations: PT = promargin teeth, RT = retromargin teeth.

Description. Male (Holotype). Total length 3.44; carapace 0.94 long, 1.13 wide; abdomen 2.50 long, 1.13 wide. Carapace round and brown, with three dark brown longitudinal bands, median band four times wider than lateral band (Fig. 53C). Chelicerae brown (Fig. 57G). Clypeus brown, dark brown medially. Endites dark brown, light brown

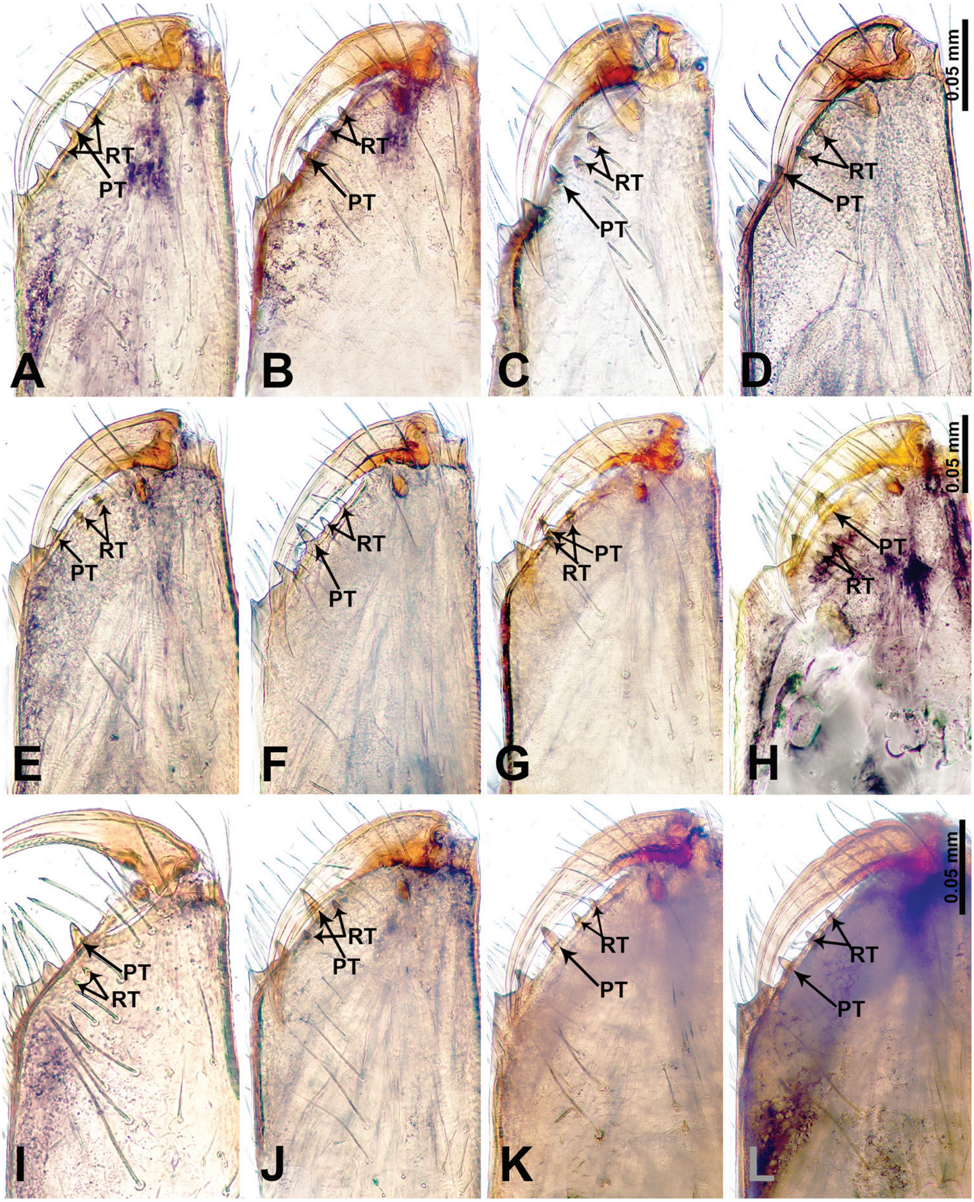

Figure 56. Cheliceral retromargin, posterior view. **A** *Leclercera dumuzhou* sp. nov. **B** *L. ekteenensis* sp. nov. **C** *L. thamkaewensis* sp. nov. **D** *L. yamaensis* sp. nov. **E** *L. thamsangensis* sp. nov. **F** *L. hponensis* sp. nov. **G** *L. lizi* sp. nov. **H** *L. mianqiu* sp. nov. **I** *L. selasihensis* sp. nov. **J** *L. yuanzhui* sp. nov. **K** *L. paiensis* sp. nov. **L** *L. zanggaensis* sp. nov. Abbreviations: PT = promargin teeth, RT = retromargin teeth.

basally. Labium dark brown. Sternum with dark brown stripes. Abdomen elongated, dorsum with three pairs of dark brown spots laterally, posterior with dark brown horizontal stripes, antero-ventrally with a pair of kidney-shaped dark brown spots laterally, followed by elliptical dark brown region, posterior dark brown, delimiting vertical light brown

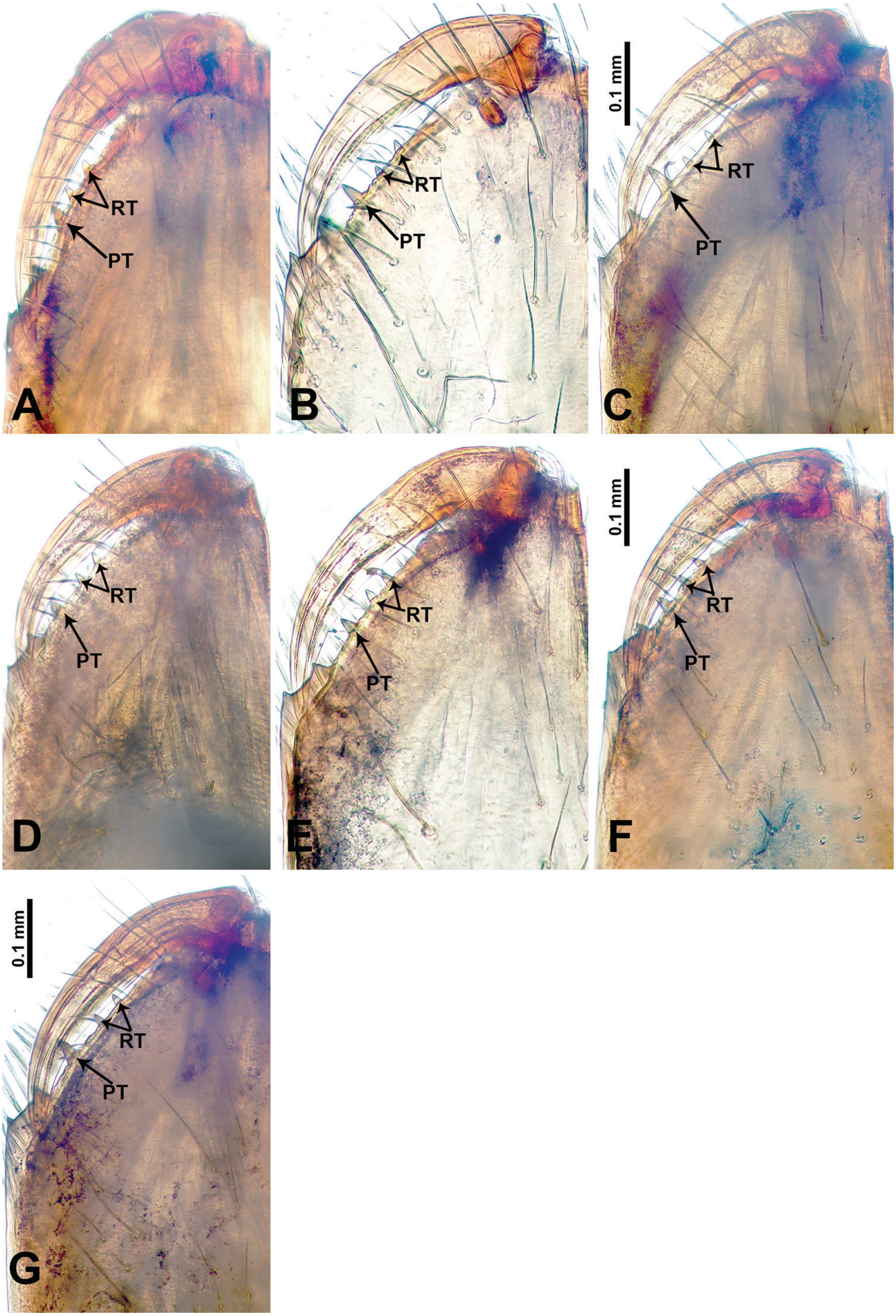

Figure 57. Cheliceral retromargin, posterior view. **A** *Leclercera aniensis* sp. nov. **B** *L. renqinensis* sp. nov. **C** *L. shergylaensis* sp. nov. **D** *L. pulongensis* sp. nov. **E** *L. tudao* sp. nov. **F** *L. duibaensis* sp. nov. **G** *L. jiazhongensis* sp. nov. Abbreviations: PT = promargin teeth, RT = retromargin teeth.

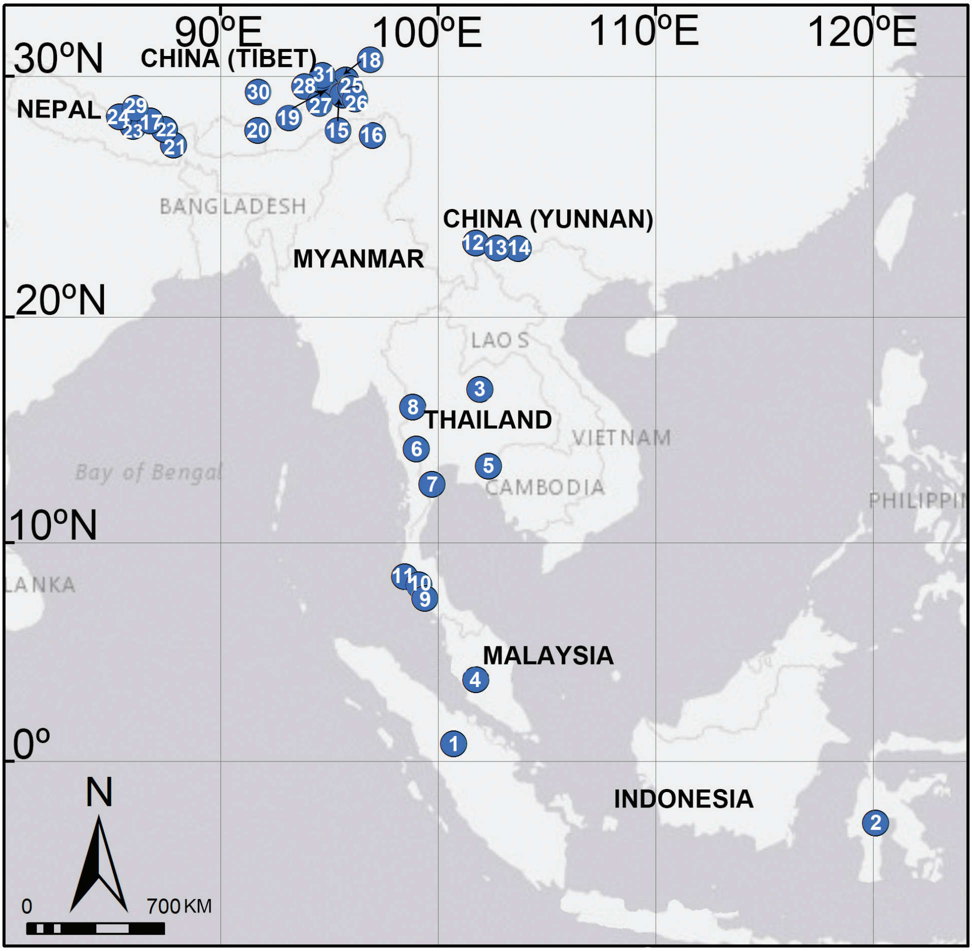

Figure 58. Distribution of new *Leclercera* species in Southeast Asia. **1** *L. selasihensis* sp. nov. **2** *L. mianqiu* sp. nov. **3** *L. thamsangensis* sp. nov. **4** *L. yandou* sp. nov. **5** *L. thamkaewensis* sp. nov. **6** *L. xiangbabang* sp. nov. **7** *L. jianzuiyu* sp. nov. **8** *L. yamaensis* sp. nov. **9** *L. banensis* sp. nov. **10** *L. dumuzhou* sp. nov. **11** *L. suwanensis* sp. nov. **12** *L. maochong* sp. nov. **13** *L. yuanzhui* sp. nov. **14** *L. shanzi* sp. nov. **15** *L. duandai* sp. nov. **16** *L. hponensis* sp. nov. **17** *L. lizi* sp. nov. **18** *L. xiaodai* sp. nov. **19** *L. paiensis* sp. nov. **20** *L. yanjing* sp. nov. **21** *L. ekteenensis* sp. nov. **22** *L. zanggaensis* sp. nov. **23** *L. zhamensis* sp. nov. **24** *L. sanjiao* sp. nov. **25** *L. aniensis* sp. nov. **26** *L. renqinensis* sp. nov. **27** *L. shergylaensis* sp. nov. **28** *L. pulongensis* sp. nov. **29** *L. tudao* sp. nov. **30** *L. duibaensis* sp. nov. **31** *L. jiazhongensis* sp. nov.

lines laterally. Legs uniformly brown; measurements: I 10.84 (2.24, 0.40, 3.60, 3.00, 1.60), II 10.60 (3.00, 0.40, 3.20, 2.75, 1.25), III 7.49 (2.20, 0.40, 2.00. 1.80, 1.09), IV 10.55 (3.00, 0.40, 3.00, 2.75, 1.40). Palp (Fig. 54A–D): femur slender, five times longer than patella; patella not swollen; tibia swollen forming a "D" shape, 2 times shorter and only slightly wider than femur, with a prolateral apophysis bearing spine anteriorly, spine two times shorter than apophysis (Fig. 54D); cymbium two times shorter than femur, similar in length but two times narrower than tibia; bulb brown, pyriform, with embolus, laminar apophysis, and conductor arise distally; embolus black and slender, widest between laminar apophysis and conductor, similar in length to conductor and two times longer than laminar apophysis; laminar apophysis appears to be shortest, basally connected to embolus; conductor alongside embolus, and similar in width to embolus (Fig. 54B).

Female (Paratype). General features and coloration similar to those ofmale (Fig. 53D, E). Measurements: total length 3.00; carapace 1.00 long, 1.00 wide; abdomen 2.00 long, 1.50 wide. Leg measurements: I 10.51 (2.80, 0.31, 3.20, 2.60, 1.60), II 9.35 (2.75, 0.40, 2.75, 2.25, 1.20), III 6.46 (1.75, 0.31, 1.80, 1.60, 1.00), IV 9.32 (2.60, 0.31, 2.66, 2.34, 1.41). Epigastric area (Fig. 53B): semi-circular dark brown patch. Endogyne (Fig. 53A): pair of lengthy, stalked spermathecae with anterior wavy horizontal part and twisted vertical posterior part, both parts with rounded tips, posterior ends with a pair of elliptical bodies.

Distribution. Known only from the type locality (Fig. 58).

Discussion

This study describes 31 new species, yielding a total of 42 species in the genus *Leclercera*. *Leclercera* species are reported for the first time from the Tibet Autonomous Region of China, Malaysia, Indonesia, and Myanmar. The large amount of new species discovered in Tibet (15 new species in this study) are noteworthy. The new Tibetan species occur in close proximity to one another, but this study surprisingly reveals large differences in genital morphology. This is congruent with previous studies of the abundant biodiversity and biological diversification due to the uplift of the Tibetan Plateau (Zhang et al. 2002, Zhao and Li 2017). This study provides a strong case for taxonomic studies in Southeast Asia, especially Tibet. Based on this work and additional observations, we predict that there are additional species in this genus awaiting discovery.

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Notes on the leaf insects of the genus *Phyllium* of Sumatra and Java, Indonesia, including the description of two new species with purple coxae (Phasmatodea, Phylliidae)

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Abstract

Within the last two years, the leaf insects of the genus *Phyllium* of both the islands of Java and Sumatra have been reviewed extensively based on morphological observations. However, cryptic species which cannot be differentiated morphologically may be present among the various populations. Since it has frequently been demonstrated that analyses based on molecular data can bring clarity in such cases, we conducted a phylogenetic analysis based on three genes (nuclear gene 28S and mitochondrial genes COI and 16S) from the *Phyllium* species of these islands. The results show distinct molecular divergence for several populations and suggest the presence of two new cryptic species, morphologically inseparable from *Phyllium hausleithneri* Brock, 1999. From Sumatra, the population originally thought to be a range expansion for *Phyllium hausleithneri*, is now here described as *Phyllium nisus* **sp. nov.**, with the only consistent morphological difference being the color of the eggs between the two populations (dark brown in *P. hausleithneri* and tan in *P. nisus* **sp. nov.**). Further, an additional population with purple coxae from Java was morphologically examined and found to have no consistent features to separate it morphologically from the other purple coxae species. This cryptic species from Java was however shown to be molecularly distinct from the other purple coxae populations from Sumatra and Peninsular Malaysia and is here described as *Phyllium gardabagusi* **sp. nov.** In addition, *Phyllium giganteum* is here officially reported from Java for the first time based on both historic and modern records of male specimens.

Keywords
Cryptic species, molecular phylogeny, phasmid, taxonomy, walking leaf

Introduction

Stick and leaf insects (Phasmatodea) are known for their extreme forms of crypsis by camouflaging themselves as parts of plants, with the majority of forms imitating twigs and exhibiting extremely slender and elongated bodies (Bedford 1978). In contrast, the true leaf insects (Phylliidae) are excellent leaf mimics with extensive lobe-like expansions throughout their bodies and legs, forming a dorso-ventrally flattened body (Figure 1). Leaf similarity is further enhanced by the wing venation of the large female forewings resembling the nerves of angiosperm leaves (Klante 1976). Historically, Phylliidae have been considered to be an early lineage among Phasmatodea branching off from a basal node of the phasmatodean tree of life (Zompro 2004). However, more recent phylogenomic analyses place them as a subordinate lineage among the Euphasmatodea as members of the Old World clade Oriophasmata (Simon et al. 2019). The geographic distribution of the currently described 80+ extant species of Phylliidae (Brock et al. 2019) ranges from as far east as the Seychelles in the Indian Ocean, throughout the Australasian region, to as far west as Fiji in the Southern Pacific (Günther 1953) with extinct members occurring in the Eocene of Germany (Wedmann et al. 2007).

Previous studies have dealt with the Phylliidae of Indonesia in several regional works in the last few years [Wallacea: Cumming et al. 2019; Java: Cumming and Le Tirant 2018; Sumatra: Cumming et al. 2018 and Seow-Choen 2018; Lesser Sunda Islands: Cumming et al. 2018; and West Papua: Brock 2014; and van de Kamp and Hennemann 2014], however, only morphological characters have been reviewed to date. This work reviews the *Phyllium* species of the Indonesian islands of Sumatra and Java using molecular data and identifies two cryptic species which were morphologically inseparable from *Phyllium hausleithneri* in need of formal description.

Materials and methods

Morphological examination

Morphological examinations were done with a Leica ZOOM 2000 stereomicroscope. Measurements of the holotype were conducted to the nearest 0.1 mm using digital calipers. Egg orientation terminology follows Clark (1978). Wing venation terminology follows that of Burt (1932) and Ragge (1955). Type material coloration descriptions are based on photographs of live individuals bred in captivity by Bruno Kneubühler (Switzerland), Tim Van molle (Belgium), and from well preserved dried specimens.

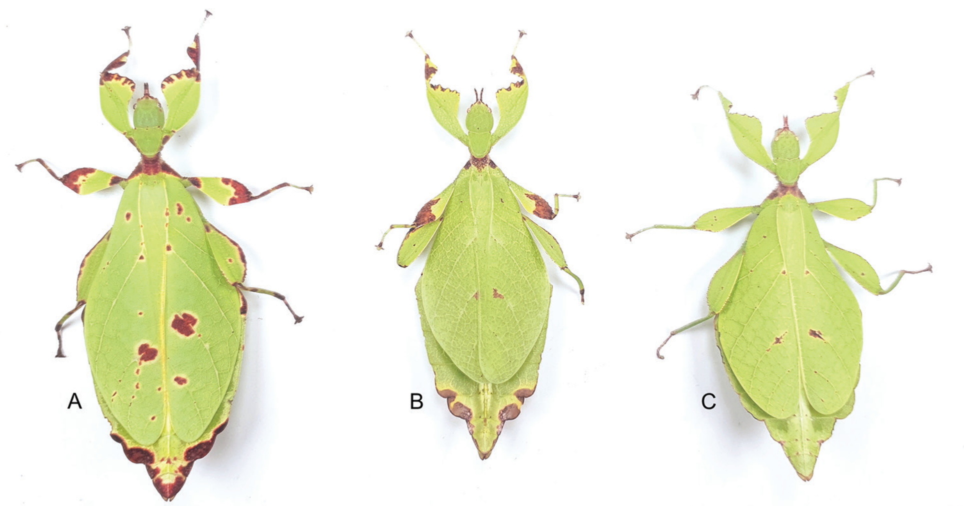

Figure 1. Three female *Phyllium* with purple coxae, dorsal. Bred by Tim Van molle (Rupelmonde, Belgium). **A** *Phyllium hausleithneri* "Tapah, Perak Malaysia" **B** *Phyllium nisus* sp. nov. "Bukit Daun, Sumatra, Indonesia" **C** *Phyllium gardabagusi* sp. nov. "Argopuro, Java, Indonesia".

Abbreviations

The following institutional abbreviations are used herein:

IMQC	Insectarium de Montréal, Montréal, Québec, Canada
MZSF	Strasbourg Zoological Museum, Strasbourg, France
NHMB	Naturhistorisches Museum Basel, Basel, Switzerland
Coll RC	Private collection of Royce T. Cumming, U.S.A.
Coll SLT	Private collection of Stéphane Le Tirant, Canada

The following wing venation abbreviations are used in Figure 10 (listed in order from the anterior to the posterior of the wing):

C	costa
Sc	subcosta
R	radius
R1	first radius
Rs	radial sector
M	media
MA	media anterior
MP	media posterior
Cu	cubitus
CuA	cubitus anterior
CuP	cubitus posterior
Cu+1AA	cubitus fused with first anterior anal)
1AA–7AA	anterior anal veins one through seven
1PA–5PA	posterior anal veins one through five
1A	first anal

Molecular laboratory work and phylogenetic analysis

We selected 18 *Phyllium* specimens that represent all eight species known from Java and Sumatra (see species checklist at the end for more details and Suppl. material 1: Table S1 for specimen data). Outgroups were chosen according to Simon et al. (2019), who recovered Bacillinae as sister taxon to Phylliidae, whereas Anisacanthinae is sister to Bacillinae + Phylliidae, and Aschiphasmatinae forms the sister group to all remaining Euphasmatodea.

One dried hind leg per specimen was soaked in water before removing femoral muscle tissue. Genomic DNA was extracted from the muscle tissue with the Quick-DNA™ Miniprep Plus kit (Zymo Research, Irvine, USA) and eluted in 60 µl elution buffer following the manufacturer's protocol. Using PCR, we amplified the two mitochondrial genes COI and 16S and parts of the nuclear gene 28S using primers described elsewhere (see Suppl. material 2: Table S2). After quality assessment via gel electrophoresis, positive PCR products were purified with Exo-SAP-IT™ (Thermo Fisher Scientific, Waltham, USA) and subsequently Sanger-sequenced (Microsynth Seqlab, Göttingen, Germany). DNA sequences were deposited in GenBank under accession numbers MN364958–MN365012 (Suppl. material 1: Table S1).

Sequences were aligned for each individual gene with ClustalW v. 2.1 (Larkin et al. 2007) implemented in Geneious v. 11.0.5 (http://www.geneious.com). The alignments were trimmed using a custom Perl script and concatenated using FASconCAT (Kück and Meusemann 2010). The phylogenetic tree was inferred in IQ-TREE v. 1.6.8 (Nguyen et al. 2015) using the suggested substitution model GTR+F+G4 (Kalyaanamoorthy et al. 2017) and the ultrafast bootstrap approximation for branch support (Hoang et al. 2017).

Results

Phylogenetic analysis

For the 21 specimens sampled (18 *Phyllium* and three outgroups), we obtained 16 COI, 18 28S, and 21 16S sequences, resulting in a final concatenated dataset comprising 1758 bp (Suppl. material 5 for the supermatrix; Suppl. material 6 for the original tree file). The phylogenetic tree recovers Phylliidae as a monophyletic group with excellent support (Figure 2). Within Phylliidae, some node support values are suboptimal but can be neglected, since our primary objective was to reveal specific species clusters rather than phylogenetic relatedness. Clusters with short branch lengths were collapsed to emphasize the different species. *Phyllium* is divided into two well-supported clades of which one has several representatives with purple coxae (clade B, Figure 2). Within clade B, two lineages are distinctly different from the previously known *P. jacobsoni* and *P. hausleithneri* and are herein described as new species: *Phyllium gardabagusi* sp. nov. and *Phyllium nisus* sp. nov. Three species exhibit purple coxae (*P. gardabagusi*, *P. hausleithneri*, and *P. nisus*) but do not form a monophyletic group. *Phyllium jacobsoni*, with white coxae coloration, is more closely related to *P. gardabagusi*, but with weak support.

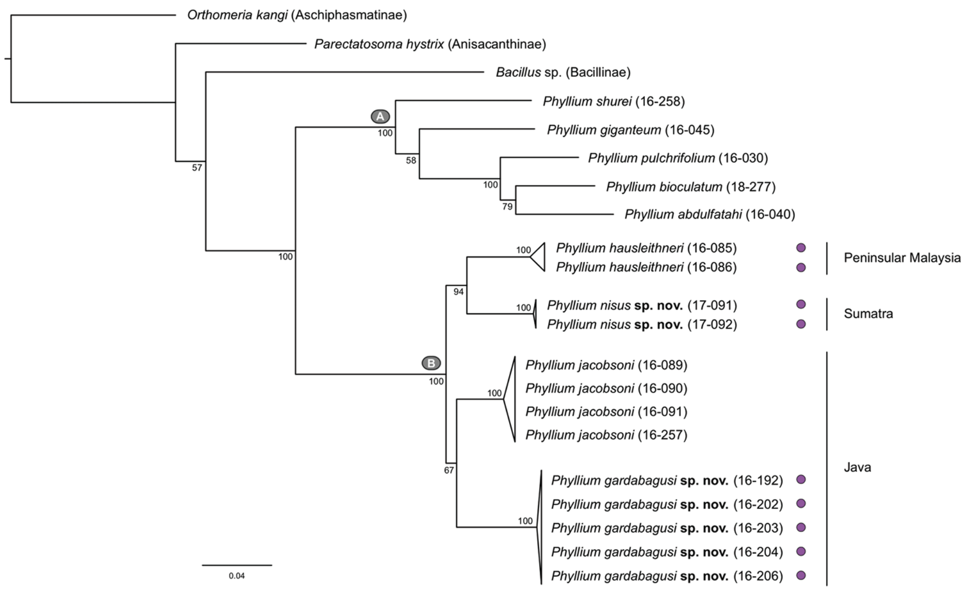

Figure 2. Maximum likelihood tree of 18 *Phyllium* specimens from Java and Sumatra and three outgroup species. The phylogenetic tree was generated with IQ-TREE and rooted with *Orthomeria kangi* (Aschiphasmatinae). Ultrafast Bootstrap support values are given below nodes. Lineages with short branch lengths were collapsed. **A** and **B** depict the two main *Phyllium* clades. Purple circles indicate those species with purple colored coxae.

Systematics

Phyllium (*Pulchriphyllium*) Griffini, 1898

Type species. *Phyllium pulchrifolium* Audinet-Serville, 1838.

Phyllium (*Pulchriphyllium*) *giganteum* Hausleithner, 1984

Figure 3A–E

Distribution. Malaysia: (Peninsular) Perak, Pahang, and Selangor States; (Bornean) Sarawak (Bintulu Division) and Sabah (Pensiangan) States. Indonesia: Sumatra, Bengkulu Province; (Borneo) West Kalimantan Province (Mount Bawang).

Range expansion. Indonesia: West Java Province (Mount Halimun and Mount Gede) (Figure 3 A–C).

Discussion. *Phyllium giganteum* is a widely distributed species ranging from Peninsular Malaysia (the type locality), to Borneo, Sumatra, and most recently Java, Indonesia, the furthest south this species is currently known to occur (Cumming et al. 2018) (Figure 4).

As a morphologically variable species with regards to abdominal shape and coloration (Cumming et al. 2018), numerous morphological aspects have been reviewed

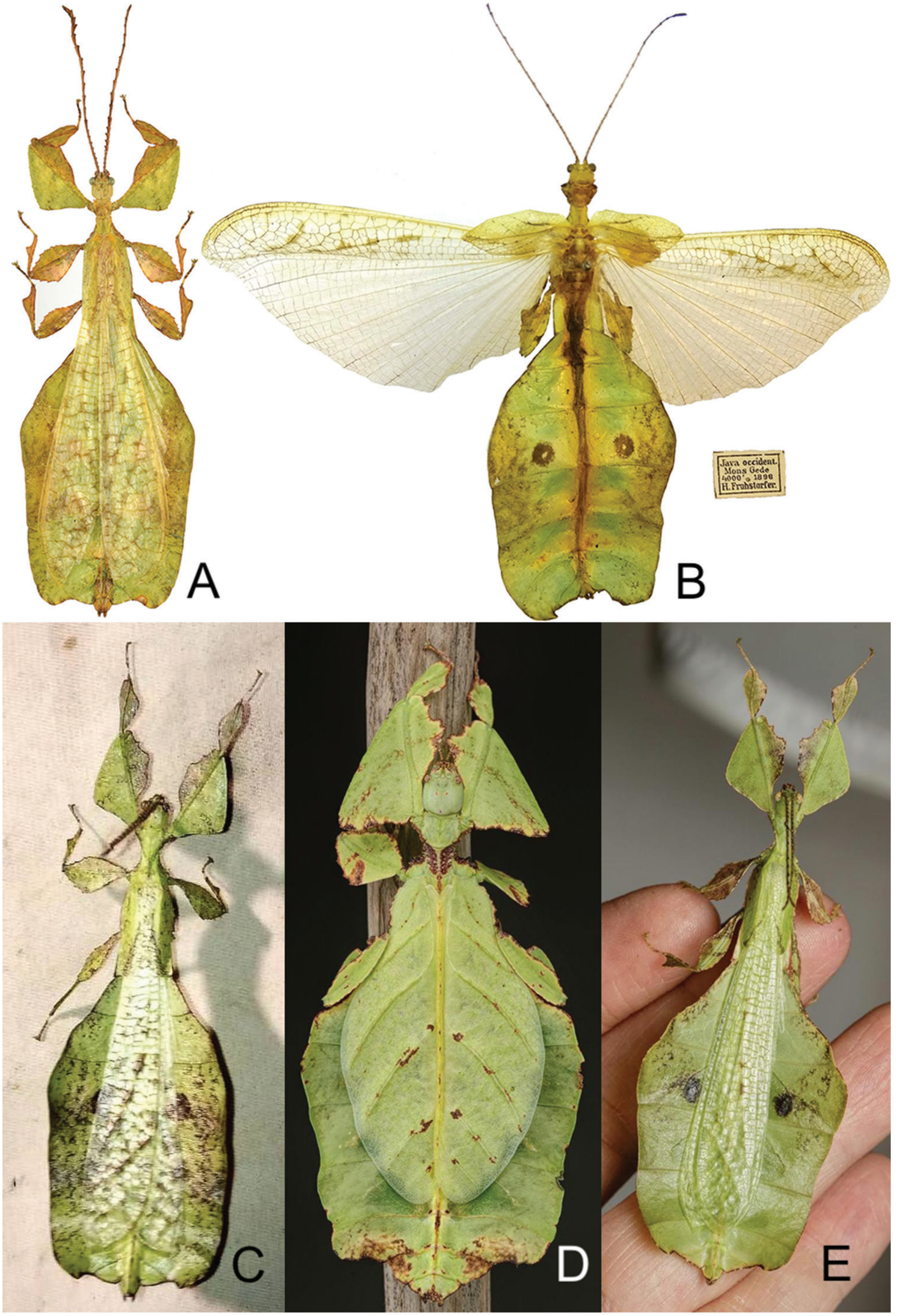

Figure 3. *Phyllium giganteum*. **A, B** Dorsal view of male *Phyllium giganteum* from Java, Indonesia **C–E** live *Phyllium giganteum* **A** male from Mount Halimun, West Java, Coll SLT **B** antique male from the MZSF collection from Mount Gede, West Java, collected by Fruhstorfer in 1898 **C** wild male photographed by Maman Cahyana (Indonesia) while out collecting at night on Mount Halimun, West Java **D** captive bred female and **E** captive bred male bred by Bruno Kneubühler, stock origin Perak, Malaysia.

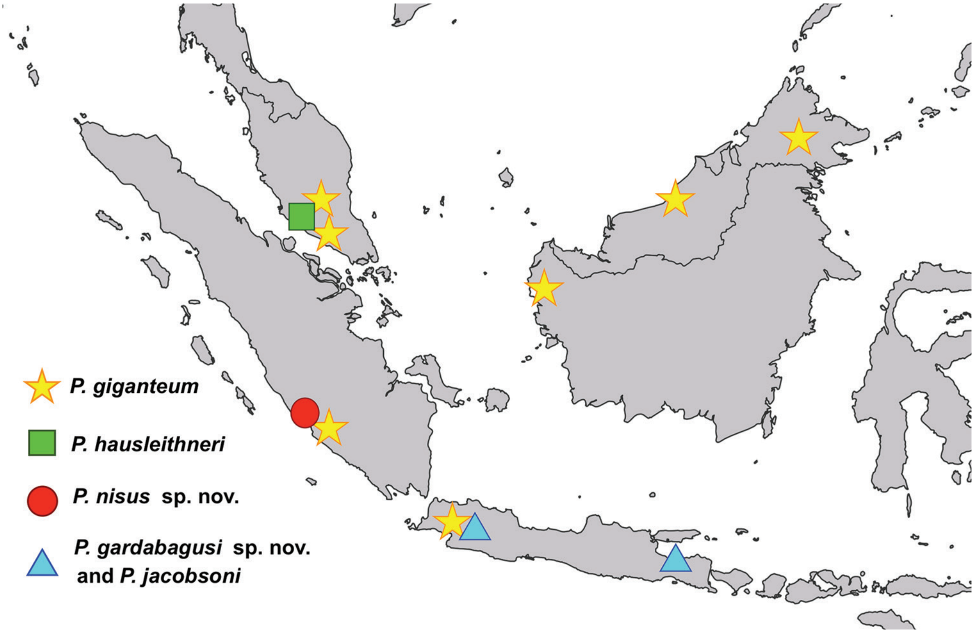

Figure 4. Distribution map for *Phyllium giganteum* (Borneo, Peninsular Malaysia, Sumatra, and Java), *Phyllium hausleithneri* (Peninsular Malaysia), *Phyllium nisus* sp. nov. (Sumatra), and *Phyllium gardabagusi* sp. nov. (Java) and *Phyllium jacobsoni* (Java).

across all known populations (including the several recently examined Javan specimens) with no consistent feature allowing morphological separation of any one population from the others. Future molecular studies based on a comprehensive taxon sampling throughout the *Phyllium giganteum* range might provide evidence of genetic differences between populations of this widely distributed lineage. Unfortunately, given that our current review is solely based on adult morphology we have no basis to separate the widely distributed *Phyllium giganteum* into subspecies, assuming such a distinction is warranted.

Phyllium (*Phyllium*) Linnaeus, 1758

Type species. *Gryllis* (*Mantis*) *siccifolius* Linnaeus, 1758.

Phyllium (*Phyllium*) *jacobsoni* Rehn & Rehn, 1934

Figure 5A–E

Distribution. Indonesia: Eastern Java (Nongkodjadjar [type locality]); Eastern Java, Mt. Argopuro; Western Java, Mt. Halimun (Figure 4).

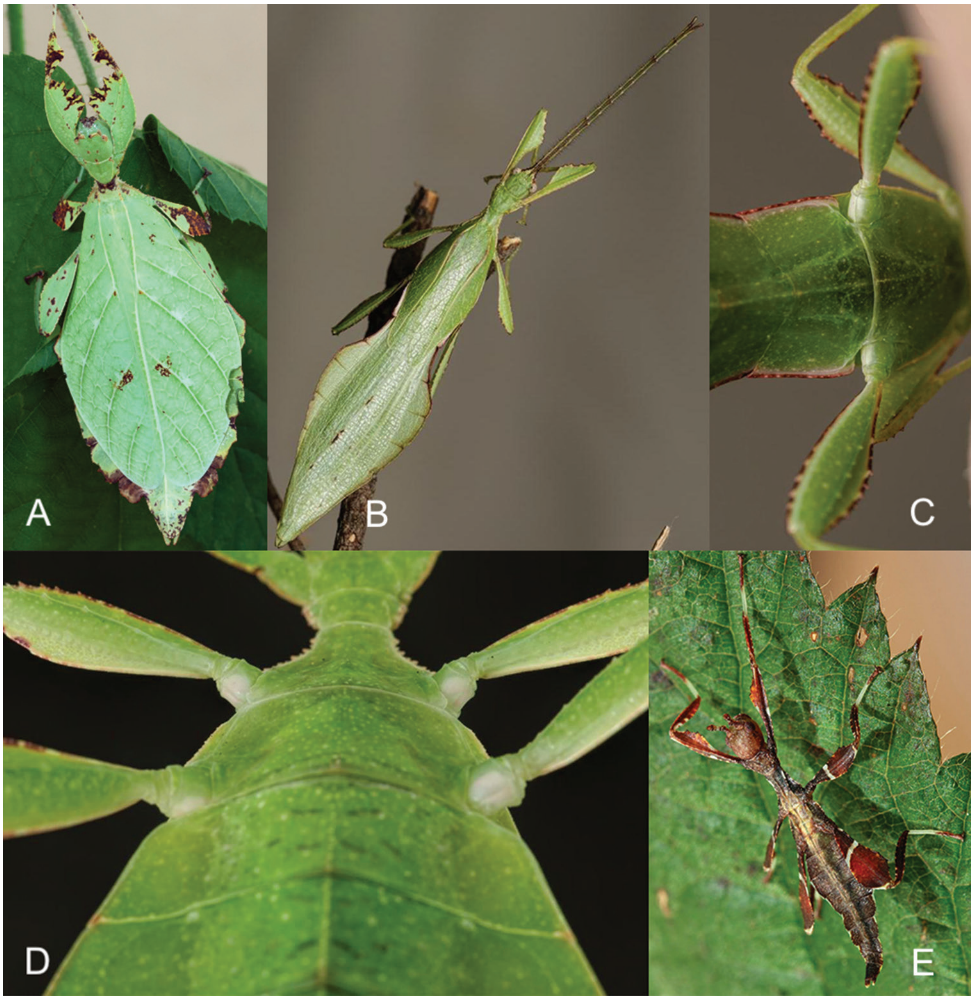

Figure 5. *Phyllium jacobsoni* live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** Female **B** male **C** male ventral view of coxae **D** female ventral view of coxae **E** freshly hatched nymph.

Discussion. With the description of the very morphologically similar *Phyllium gardabagusi* sp. nov., also from Java, the numerous localities noted within Hennemann et al. (2009) cannot be confirmed as *Phyllium jacobsoni.* This is because the only clear morphological feature to differentiate between these two populations is the coxae color, which can fade in specimens which were not well preserved. Therefore, we only list the localities where we have been able to confirm specimens as *Phyllium jacobsoni*. Nevertheless, with this species confirmed from both West and East Java, it is likely the species is found throughout the island.

Differentiation. This is the only species in the clade that can easily be differentiated morphologically from other clade members. The coxae color in *P. jacobsoni* is white (see

Table 1. Morphological features compared between the members of clade B. Key: [a] As noted in Hennemann et al. (2009). [b] 75 mm for *Phyllium jacobsoni* is noted from personal communication with Bruno Kneubühler who bred *P. jacobsoni* from the type locality of Nongkodjadjar, East Java. [c] Größer (2008) lists *P. hausleithneri* as having 44–46 teeth, and Hennemann et al. (2009) note 44–48 teeth. [d] As noted in Cumming et al. (2018). [e] Only counted on paratype specimens Coll RC 16-203 and Coll RC 18-418.

Feature	*Phyllium jacobsoni*	*Phyllium hausleithneri*	*Phyllium nisus* sp. nov.	*Phyllium gardabagusi* sp. nov.
Distribution	Java	Peninsular Malaysia	Sumatra	Java
Female length [mm]	63.5–75.0[a/b]	74.6–82.8	70.3–79.3	68.4–77.3
Male length [mm]	42.5–56.5[a]	55.8–57.8	51.4–56.1	50.0–50.5
Number of teeth on the *pars stridens* of antennomere III in females	40[a]	44–48[c]	37–44[d]	34–39[e]
Egg color	Tan to medium brown	Dark, rich brown	Pale tan to medium brown	Pale brown to medium brown
Coxae color	White	Purple	Purple	Purple

Figure 5C, D) compared to a distinct and dark purple in the other three clade members (Table 1). This purple color is easier to view in females and can only be faintly seen on very well preserved or live males. In any discolored male it is impossible to differentiate the species by looking at the coxae because the white and faint purple color do not preserve well and cannot be differentiated on poor quality specimens. It is fortunate that the holotype for *Phyllium jacobsoni* is a female specimen as it can clearly be seen on the holotype female that this was not the sympatric species *Phyllium gardabagusi* sp. nov. with purple coxae and is instead a specimen with white coxae which defines *Phyllium jacobsoni.*

On average *P. jacobsoni* tend to be smaller individuals, but as with the other species in the clade there were significant outliers that made the range of sizes overlap with the other species significantly (Table 1). *Phyllium jacobsoni* newly hatched nymphs (Figure 5E) appear to be the most variable in coloration of the four clade B members. *Phyllium jacobsoni* overall coloration ranges from reddish brown to dark brown (in the other three members dark brown to black), and on *P. jacobsoni* the white transverse band on the meso- and metafemora can be a solid line (like in the other three clade B species) or can occasionally be a broken white line (but this is a less common form).

***Phyllium* (*Phyllium*) *hausleithneri* Brock, 1999**

Figure 6A–E

Distribution. Malaysia: (Peninsular) Perak and Pahang states (Figure 4).

Unconfirmed distributions:

Malaysia: Selangor State, Bukit Kutu. This record was noted as *Phyllium siccifolium* in Brock (1999) and treated as a smooth abdominal form of *P. hausleithneri* in Hennemann et al. (2009), however, without examining the specimen in question it is best to leave this as an unconfirmed record. This is because the morphologically similar

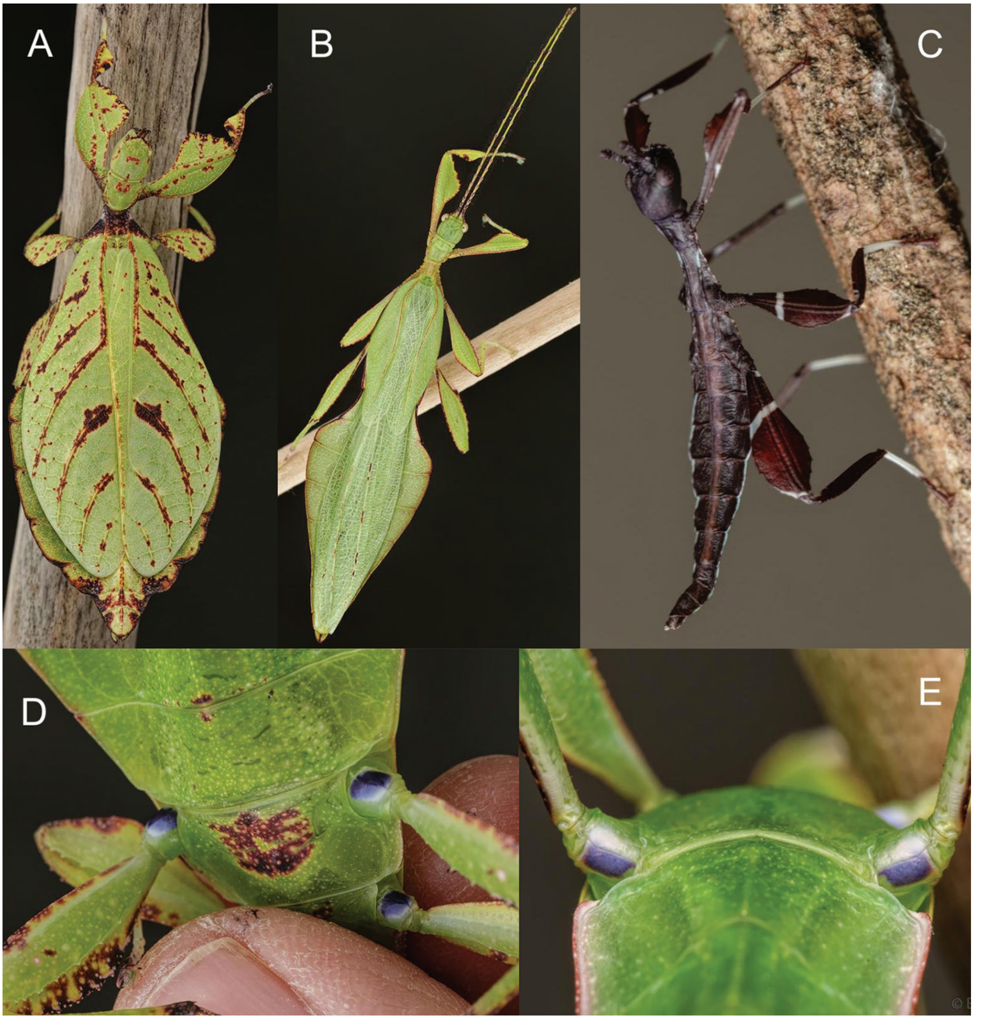

Figure 6. *Phyllium hausleithneri* live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** Female **B** male **C** freshly hatched nymph **D** female ventral view of purple coxae **E** male ventral view of purple coxae.

Phyllium rubrum Cumming, Le Tirant, & Teemsma, 2018 is also found in Peninsular Malaysia and has in the past been considered a form of *P. hausleithneri*. *Phyllium rubrum* can be differentiated from *Phyllium hausleithneri* by the larger size (90.0 mm or larger in female *P. rubrum* and 74.6–82.8 mm in *P. hausleithneri*) and coxae color (red/orange in *P. rubrum* and purple in *P. hausleithneri*). Brock (1999) lists this Selangor State record as *Phyllium siccifolium* and notes that females from Peninsular Malaysia are ranging in size from 77.0 to 92.0 mm in length which encompasses the range of sizes of both these species. Therefore, without examining the specimen from Bukit Kutu, we must treat this identification as tentative until it can be confirmed as *P. hausleithneri* or *P. rubrum*.

Singapore: Seow-Choen (2017) listed this species, but gave no actual specimen records, and his included photos were stated as coming from Tapah Hills, Perak, Malaysia, so we are unsure of the basis for the inclusion. He could have been referencing to a specimen listed in Klante (1976) from Singapore ("Bukit Timah rd."; incorrectly identified as *Phyllium woodi* Rehn & Rehn, 1934), which Klante noted as being 75.0 mm in length, matching the size range of *P. hausleithneri* and not *P. rubrum*. But with so many errors in identification over the years we do not include this record in our confirmed distribution for this species yet and wait until additional material is collected and confirmed from Singapore.

Discussion. This species has been in the phasmid breeding community for many years (Figure 6A–E), with most of those years being sold erroneously as *Phyllium siccifolium* which has led to much of the confusion surrounding this species. To help clear up confusion, the morphological variations and numerous misidentifications were presented in the discussion of *Phyllium hausleithneri* in Hennemann et al. (2009). *Phyllium hausleithneri* from Peninsular Malaysia was morphologically compared extensively to *P. nisus* sp. nov. in Cumming et al. (2018) before it was realized that *P. nisus* sp. nov. was an undescribed sister species. Newly hatched nymphs of *P. hausleithneri* (Figure 6C) cannot be distinguished from the two new species from within clade B described below as their coloration falls within their observed variation.

Description of new species

***Phyllium* (*Phyllium*) *nisus* sp. nov.**
http://zoobank.org/7FE8BB94-1E94-4337-BA9C-3DA2A1224DFF
Figures 7A–E, 8A–E, 9C–D, 10A, 13A

Type material. Holotype: ♀, Indonesia: Sumatra, Bengkulu Prov., Bengkulu District, Besuki Village: IV.2017, Local Collector. Deposited in the Montreal Insectarium type collection (Coll RC 18-157) (Figure 13A). Paratypes: of 128 ♀♀, 36 ♂♂, and 39 eggs are deposited in the collections of Royce T. Cumming, Stephane Le Tirant, Oskar V. Conle, the Bogor Zoology Museum, and the Montreal Insectarium (see Suppl. material 3: Table S3 for details).

Discussion. This population has been available within the phasmid breeding community for a number of years under the name *Phyllium* sp. "Bukit Daun" and has been noted as a reasonably easy species to breed in captivity (Figures 7A–E, 8A–E).

This population has already undergone extensive morphological scrutiny in Cumming et al. (2018) where no significant morphological features were identified between the Peninsular Malaysia and Sumatran populations to allow visual separation based on adults alone. The only consistent visible feature between the two populations is the color of the eggs, with *Phyllium hausleithneri* from Peninsular Malaysia having dark brown eggs (Figure 9A, B) and *Phyllium nisus* sp. nov. with pale tan eggs (Figure 9C, D). The only closely related species which can consistently be morphologically separated is

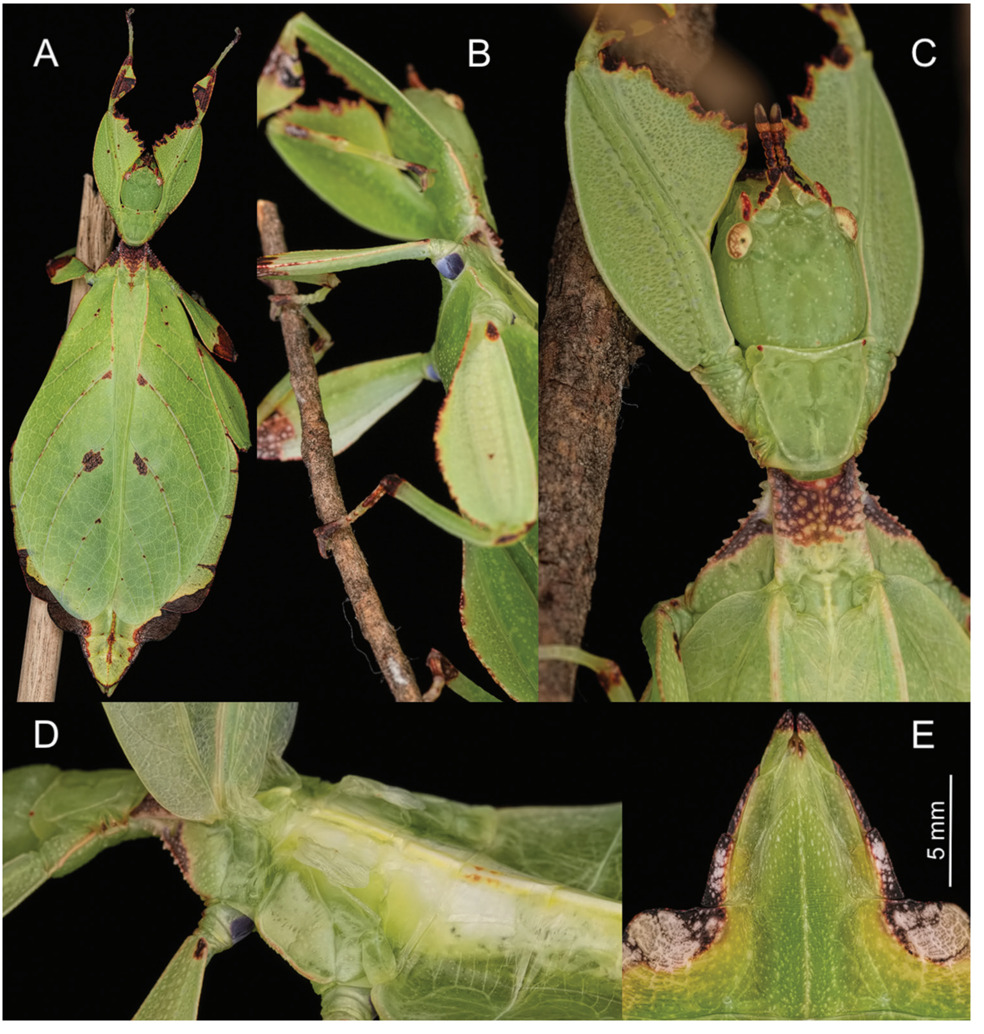

Figure 7. Female *Phyllium nisus* sp. nov. live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** dorsal view **B** ventral view of purple coxae **C** dorsal head and thorax details **D** tegmina held open to show exposed underdeveloped alae **E** ventral genitalia details.

Phyllium jacobsoni by coxae color (white in *P. jacobsoni*, Figure 5C, D, and purple in *P. nisus* sp. nov., Figures 7B, 8D). Newly hatched nymphs of *P. nisus* sp. nov. (Figure 8E) cannot be differentiated from the dark form of *P. jacobsoni* or the average *P. hausleithneri* nymphs, and their identical morphology helps to illustrate their shared common ancestry.

Phyllium nisus sp. nov. is possibly the species referred to in Klante (1976) from Sumatra, which he erroneously attributed to *Phyllium woodi* Rehn & Rehn, 1934. The specimen he examined was rather large at 79.0 mm, which falls within the observed range of *Phyllium nisus* sp. nov. (see Table 1), and, based on the prominent profemoral interior lobe teeth, this specimen could be a large major form of *Phyllium nisus* sp. nov.

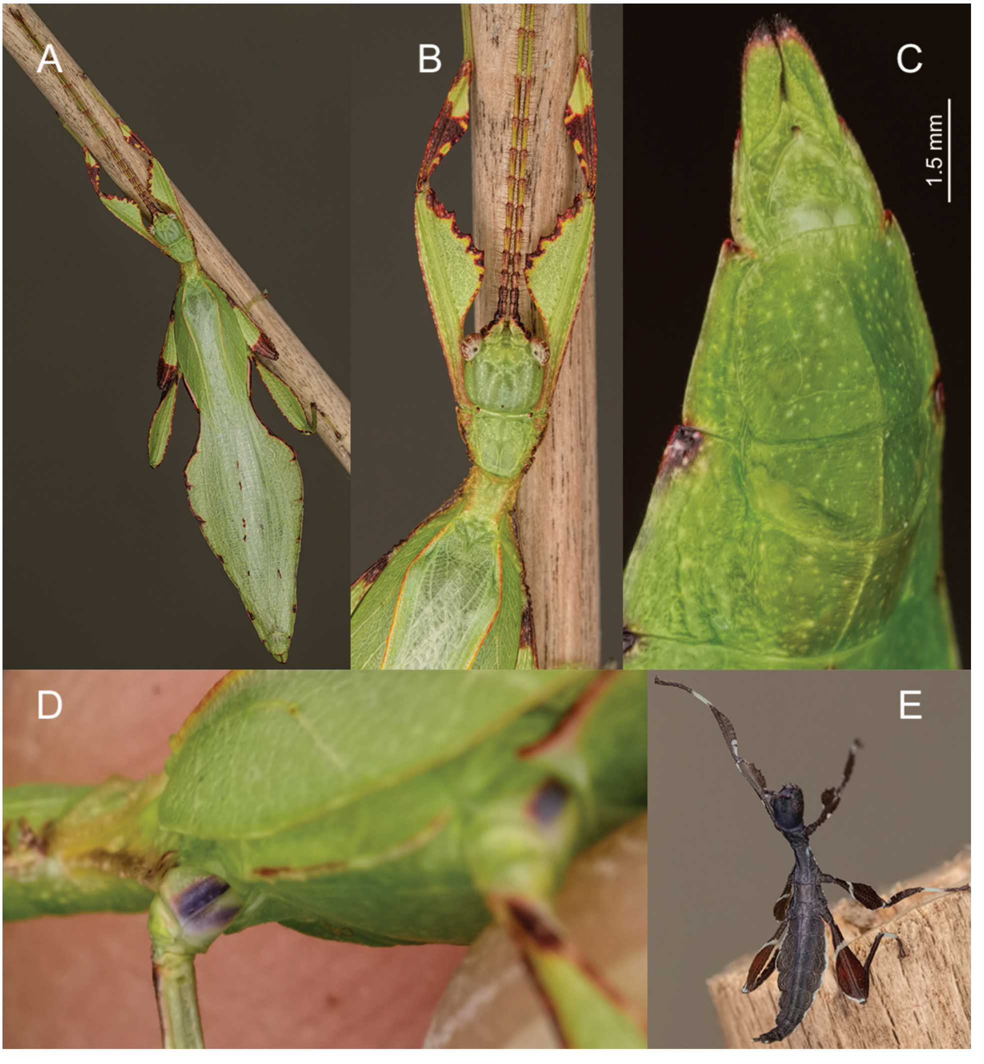

Figure 8. Male *Phyllium nisus* sp. nov. live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** Dorsal view **B** dorsal head and thorax details **C** ventral genitalia details **D** ventral view of purple coxae **E** freshly hatched nymph.

female. However, without examining this specimen in person we are not confident in attributing this specimen to *Phyllium nisus* sp. nov. due to the cryptic nature of congenerics and therefore must leave this historic record at speculation. For full morphological measurements see Suppl. material 3: Table S3. Fortunately, a sizeable series of bred paratype specimens were examined thus allowing adequate description of the average adults and egg coloration. Coloration of the overall body was rather variable as discussed below, but the coxae and egg coloration showed little variation between individuals and we consider these colors as a reliable feature for differentiation.

Description. Female. ***Coloration.*** Individuals are always a vibrant pale green with varying degrees of reddish or grayish brown coloration on specific regions of the body (Figures 1B, 7A). On the lightest colored individuals, no brown markings are present, with even the antennae a pale color similar to the shade of green on the head capsule (see the holotype female in Figure 13A for an example of a female without brown markings). In individuals which are more colored, the areas which are most frequently with these brown markings are the antennae, frontal convexity, protibiae, profemoral interior lobe, prescutum, mesopleurae (Figure 7C), small interior patches of brown on the tegmina, and the terminal abdominal segments VII–X margins (Figure 7A). On intermediate colored individuals, these features can be a third to half colored with brown, and in darker individuals these features are always at least half colored with some features almost completely colored with brown. Compound eyes are generally paler than the head capsule and usually of a yellow coloration with slight tan striping (Figure 7A). Meso- and metacoxae ventrally always with a dark blue to purple coloration which is only visible when the legs are bent forward (Figure 7B).

Morphology. *Head.* Head capsule about as long as wide, vertex with granulation throughout the surface, some more closely spaced than others (Figure 7C). The posteromedial tubercle is broader and taller than any other nodes, on the head. Frontal convexity broad and about as long as the first antennomere, and with slight granulation on the dorsal surface and several setae present which are longer than any setae on the antennae. Compound eyes only slightly protruding from the head capsule, but are significantly large, taking up about one fourth of the length of the lateral head capsule margins (Figure 7C). Ocelli absent. Antennal fields slightly wider than and about as long as the length of the first antennomere. *Antennae.* Antennae consisting of nine segments, with the terminal segment about the same length as the preceding two segments' lengths combined (Figure 7C). Antennomeres I–VII sparsely marked with small transparent setae, the terminal two antennomeres are covered in stout, brown setae. The *pars stridens* of antennomere III has 37–44 teeth. *Thorax.* Pronotum with gently concave anterior margin and nearly straight lateral margins, which converge to a straight posterior margin that is half the width of the anterior margin (Figure 7C). Pronotum anterior margin with small lateral defensive spray gland openings (no detectable defensive spray has been noted for these while in breeding however). The pronotum surface is marked with only minimal small granulation, with only a prominent pit in the center, and slight furrows anterior and lateral to the pit (Figure 7C). The pronotum has a prominent anterior rim and weakly formed lateral and posterior rims, all of which have only slight granulation (Figure 7C). Prosternum and the mesosternum with stout and numerous nodes, those on the anterior half of the mesosternum on the sagittal plane are slightly larger than those on the prosternum. Metasternum with short granulation throughout the entire surface. Prescutum as long as wide or occasionally slightly longer than wide, but never wider than long (Figure 7C). Lateral rims with nine to eleven lumpy node-like tubercles ranging in size from small to medium with small granulation present throughout the length interspersed with the tubercles (Figure 7C). Prescutum anterior rim prominent but not strongly protruding, with a distinct singular tubercle with the remainder of the rim relatively smooth (Figure 7C). Prescutum crest (excluding the tubercle of the anterior rim) with four to five distinct but not large nodes evenly spaced and nearly uniform in size, or with the anterior most node slightly larger than the rest. The Prescutum crest is not prominently protruding because the smooth surface of the Prescutum rises up to it, making the crest not much more than the nodes along the sagittal plane (Figure 7C). Mesopleurae beginning near the anterior margin of the Prescutum and evenly diverging; lateral margin with eight to eleven tubercles which are largest on the anterior end and steadily decreasing in size as they reach the posterior, eventually no larger than nodes (Figure 7C). Some of the largest tubercles have slightly granular surfaces or granulation at the base. Face of the mesopleurae with granulation throughout, and with two notable divots, one on the anterior third and one nearer the posterior third (Figure 7C). *Wings.* Tegmina length variable, ranging in length from halfway through abdominal segment VII to at most reaching about three quarters of the way into segment VIII. Tegmina venation is rather stable between individuals (Figure 10A). The subcosta (Sc) is the first vein in the forewing and bends inward away from the anterior margin. The radius (R) spans the central portion of the forewing with two subparallel branched veins; radius 1 (R1) terminates anterior to the widest medial expansion of the tegmina, and the radial sector (Rs) terminates posterior to the widest medial expansion, therefore the R1 and Rs occupy the majority of the center of the wing. There is a weak continuation of the radius following the prominent Rs branching which continues on as a short and thinner R–M crossvein that does not appear to solidly connect the two veins fading as it reaches the media. The media (M) is simply bifurcate with both the media anterior (MA) and media posterior (MP) terminating close to the posterior fourth of the wing. The cubitus (Cu) is also bifurcate, branching near the posterior fifth of the wing into the cubitus anterior (CuA) and cubitus posterior (CuP) which both terminate at or very near the wing posterior apex. The first anal vein (1A) is simple and fuses with the cubitus early on, only slightly past the branching distance of the R1 from R (Figure 10A). Alae rudimentary, only about 4.0 mm in length (Figure 7D). *Abdomen.* Abdominal shape quite variable, with the only consistent feature being segments II through the anterior two thirds of IV diverging, with the posterior third of segment IV the widest segment. Segments V through VIII are variable and can have perfectly straight margins (giving the abdomen a smooth spade shaped appearance, similar to the holotype female in Figure 13A) or strongly lobed margins (like in Figure 1B). Between these two extremes there are all possible forms/degrees of lobed margins with the forms continuous, not discrete. Segments IX and X are notably narrower than the previous segments and converge uniformly without lobes to the rounded apex. *Genitalia.* Subgenital plate starts at the anterior margin of segment VIII, is broad, and extends halfway to three quarters into segment X, ending in a fine point (Figure 7E). Gonapophyses are long and slender, reaching or very slightly exceeding the apex of abdominal segment X (Figure 7E). Cerci flat, not strongly cupped, with a granular surface and few detectable setae (Figure 7E). *Legs.* Profemoral exterior lobes narrow and smoothly arcing from end to end without a strongly notable angle, narrower than the width of the interior lobe (Figure 7C).

Edge of the profemoral exterior lobe smooth without notable granulation or teeth (Figure 7C). Profemoral interior lobe wider than the exterior and with a right angle or slightly obtuse angle and marked with four to five teeth (Figure 7C). These teeth have a slightly wider gap in the center, and are variable in size ranging from small serrate teeth to larger angular teeth (Figure 7C). Generally, the size of the teeth is paralleled by the size of the abdominal lobes but not always. Mesofemoral exterior lobe arcs from end to end but is slightly weighted towards the distal half and marked with one to three small serrate teeth distributed on the distal half only. Interior and exterior lobes can be of similar width, or interior lobe can be slightly thinner. Mesofemoral interior lobe arcs end to end with five to six small serrate teeth only on the distal half of the arc which is slightly wider than the proximal half of the arc. Metafemoral interior lobe arcs end to end and has five to six serrate teeth on the distal half of the lobe. Metafemoral exterior lobe is thin and smooth, hugging the metafemoral shaft and generally with no teeth but occasionally with one to two at the distal most edge. Protibiae lacking an exterior lobe. Protibiae interior lobe spans the entire length of the protibiae and can be one and a half to two times the width of the protibiae shaft itself. The lobe is distinctly triangular and can be nearly evenly distributed or slightly wider on the distal half. Mesotibiae and metatibiae lacking exterior and interior lobes.

Male. ***Coloration.*** Overall coloration pale green throughout with variable patches of brown to reddish coloration (Figure 8A). Compound eyes are generally paler than the head capsule and of a yellow coloration with slight tan striping (Figure 8B). The antennae are darker in color, with each segment exhibiting a slight green in addition to brown towards the apex of each segment, which gives the antennae an overall striped appearance of green and brown (Figure 8B). Males can be completely green lacking any brown coloration except slight brown markings on the protibial interior lobe, or they can range to the other extreme with brown markings on protibial, profemoral, and mesofemoral lobes along with the margins of the metafemoral lobes and the margin of the abdomen (Figure 8A). Meso- and metacoxae ventrally with a pale to dark purple and white coloration (Figure 8D). The coloration on the mesocoxae is generally darker and easier to distinguish than the purple on the metacoxae, which is only a faint purple hue on a mostly white surface.

Morphology. *Head.* Head capsule longer than wide, with a vertex that is nearly completely smooth or in some individuals there can be two or three small nodes near the posteromedial tubercle (Figure 8B). Frontal convexity stout with sparse thin setae. The posteromedial tubercle is not broad but is distinctly raised from the head capsule. Compound eyes large and bulbous, taking up over one third of the head capsule lateral margins (Figure 8B). Three ocelli moderately developed located between and slightly posterior to the compound eyes. Antennal fields as wide and as long as the scapus. *Antennae.* Antennae (including the scapus and pedicellus) consists of 23 segments, all segments except the scapus and pedicellus and terminal four segments are covered in dense setae that are as long as or longer than the antennae segment is wide. The terminal four segments are covered in dense short setae and the scapus and pedicellus are nearly completely bare. *Thorax.* Pronotum with anterior margin distinctly concave and lateral margins that are slightly convex and converging to a straight posterior margin that is slightly more than half the width of the anterior rim (Figure 8B). Anterior margin of the pronotum has a distinct rim, lateral margins have moderate rims, and the posterior margin lacks a rim (Figure 8B). Face of the pronotum is marked by a distinct furrow and pit in the center, a smooth surface, and three distinct pits along the anterior margin (Figure 8B). Prosternum is granulose throughout with small nodes of even size and spacing. Mesosternum surface marked with more prominent nodes, with the largest along the sagittal plane and more strongly on the anterior margin, posterior margin with less prominent and small nodes. Prescutum longer than wide, with lateral margins slightly converging to the posterior (Figure 8B). Lateral rims with eight to nine tubercles of varying size, some prominent but others rather small and not much more prominent than nodes (Figure 8B). Prescutum crest along the sagittal plane with four to five small nodes of uniform size and spaced throughout the length. The surface of the prescutum rises up to meet the crest with a face that is smooth (Figure 8B). Prescutum anterior margin marked with a tubercle, which is only about two times larger than any of the other nodes along the crest. Mesopleurae not notably wide and diverge almost uniformly along the entire length, diverging slightly more prominently at the posterior margin (Figure 8B). Lateral margin with four to five major tubercles throughout the length, and between six and nine smaller minor tubercles interspersed throughout. Each tubercle is marked by either a single stiff, short setae or with as many as three setae. Face of the mesopleurae slightly wrinkled and with two faint divots, one on the anterior third and one on the posterior third. Tegmina moderate length, extending halfway to three quarters the way through abdominal segment III. *Wings.* Tegmina wing venation (see Figure 10B for general venation found in the species of this clade): the subcosta (Sc) is the first vein and terminates the earliest, about one third of the way through the overall tegmina length. The radius (R) spans the entire length of the tegmina with the radius 1 (R1) branching just anterior to the middle and terminating just posterior to the middle of the wing with the radial sector (Rs) terminating nearly at the wing apex. The media (M) also spans the entire length of the tegmina with the media posterior (MP) branching off slightly posterior to the middle and terminating promptly. The cubitus (Cu) terminates past the midline upon meeting the media posterior. The first anal (1A) vein terminates upon reaching the cubitus near the midline. Alae well developed in an oval fan configuration, long, reaching to the anterior margin of abdominal segments IX or X. Alae wing venation (see Figure 10B for general venation found in the species of this clade): the costa (C) is present along the entire foremargin giving stability to the wing. The subcosta (Sc) is short, spanning less than a third of the wing length and is mostly fused with the radius in the beginning but terminates when it meets the costa. The radius (R) spans the entire wing and branches approximately a third of the way through into the radius 1 (R1) and radial sector (Rs) which run nearly parallel through most of their length until they terminate at the wing apex near each other but not touching. The media (M) branches early (only about a sixth of the way through the wing into the media anterior (MA) and the media posterior (MP) which run parallel with each other throughout the central two thirds of the wing until the media posterior fuses with the media anterior which eventually fuses with the above radial sector about one sixth of the way from the wing apex. The cubitus (Cu) runs unbranched and terminates at the wing apex. Of the anterior anal veins, the first anterior anal (1AA) fuses with the cubitus near the point where the media branches into the media anterior and media posterior and then the first anterior anal branches from the cubitus three fifths of the way through the wing length where it uniformly diverges from the cubitus until it terminates at the wing margin. The anterior anal veins two through seven (2AA–7AA) have a common origin and run unbranched in a folding fan pattern of relatively uniform spacing to the wing margin. The posterior anal veins (1PA–5PA) share a common origin separate from the anterior anal veins and run unbranched to the wing margin with slightly thinner spacing than the anterior anal veins. *Abdomen.* Abdominal segments II slightly converging, III through the anterior two thirds of segment IV diverging to the widest portion. The posterior of IV through V either almost parallel sided or converging, and segment VI through X uniformly converging (Figure 8A). *Genitalia.* Poculum broad, and ends in a straight margined apex that slightly passes the anterior margin of segment X (Figure 8C). Cerci long and slender, extending from under the anal abdominal segment, slightly cupped, covered in a granulose surface and numerous short setae (Figure 8C). Vomer broad and stout with straight sides evenly converging, and a thick single apical hook which hooks upwards into the paraproct (Figure 8C). *Legs.* Profemoral exterior lobe one third to two thirds the width of the interior lobe, hugging the curve of the profemoral shaft and marked with a granular margin and fine small setae but no notable teeth (Figure 8B). Profemoral interior lobe roundly triangular and marked with five teeth which can be small and serrate or larger and triangular in more prominent individuals (Figure 8B). Mesofemoral exterior lobe arcs end to end, but is significantly weighted on the distal half which is marked with one to two serrate teeth, and the proximal half that is rather thin. Mesofemoral interior lobe is slightly thinner than the exterior lobe, is broader on the distal end and is marked with five to six small serrate teeth. Metafemoral exterior lobe lacks dentition, and has a straight margin along the metafemoral shaft. Metafemoral interior lobe smoothly arcs end to end with seven to eight small serrate teeth on the distal half. Protibiae lacking exterior lobe, interior lobe reaching end to end in a smooth evenly weighted triangle only one to one and a half times as wide as the protibial shaft (Figure 8B). Meso- and metatibiae simple, lacking lobes completely.

Eggs. The lateral surfaces are flattened and the dorsal surface is slightly convex, which gives the egg a slight bend (Figure 9C, D). When viewed from the lateral aspect, the anterior width of the capsule is the narrowest, with the width slightly increasing steadily to the posterior, but only slightly so (Figure 9C). When viewed from the lateral aspect, the dorsal margin has long feather-like pinnae with single or double branching tips along almost the entire length with occasionally some individuals with the anterior most area lacking these long pinnae, the posterior margin also has these long pinnae (Figure 9C). The ventral margin lacks these long feather-like pinnae on the edges, but instead has a row of slightly shorter pinnae along the posterior half of the ventral surface sagittal plane with those at the posterior the largest followed by pinnae

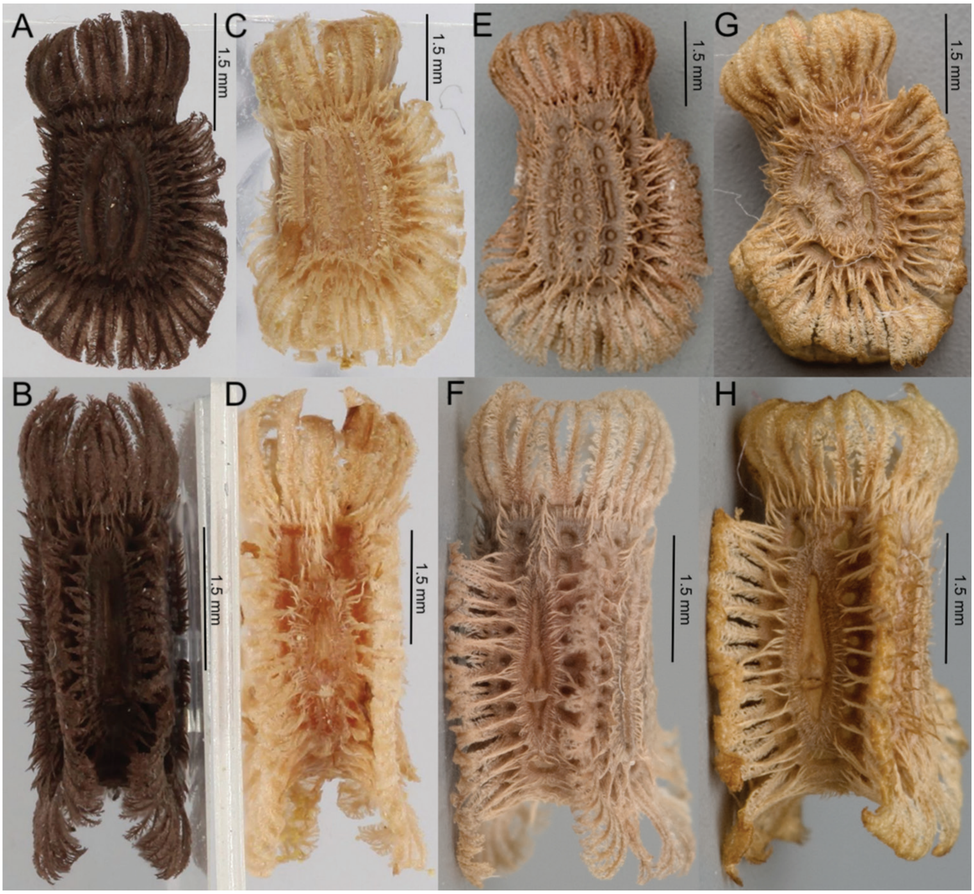

Figure 9. Eggs from the four species in clade B. **A** *Phyllium hausleithneri*, lateral view (Coll RC 18-002) **B** micropylar plate view (Coll RC 18-003), note that this individual exhibits a slightly longer micropylar plate than average which makes it appear longer than the other clade members, this is simply the upper limit of the morphological variation **C** *Phyllium nisus* sp. nov., lateral view (Coll RC 17-380) **D** micropylar plate view (Coll RC 17-377) **E** *Phyllium gardabagusi* sp. nov., lateral view **F** micropylar plate view **G** *Phyllium jacobsoni*, lateral view **H** micropylar plate view. Photos **E–H** courtesy of Bruno Kneubühler.

steadily decreasing in length as they reach the anterior which lacks these sagittal pinnae (Figure 9C). Lateral surfaces with three rows of bald impressions, with the space between densely covered with short carpet-like pinnae (Figure 9C). These three rows of impressions are variable between individuals, but the most common is that the three bald rows are continuous, not broken into smaller bald impressions, however, some individuals have been observed as having the bald impressions slightly broken up into smaller portions. Micropylar plate ranging from two thirds to four fifths of the overall dorsal surface length, with the thickest portion the center or slightly off center towards the micropylar cup (Figure 9D). Micropylar plate teardrop shaped, with most of the width as wide as the micropylar cup (Figure 9D). Micropylar cup of moderate size and

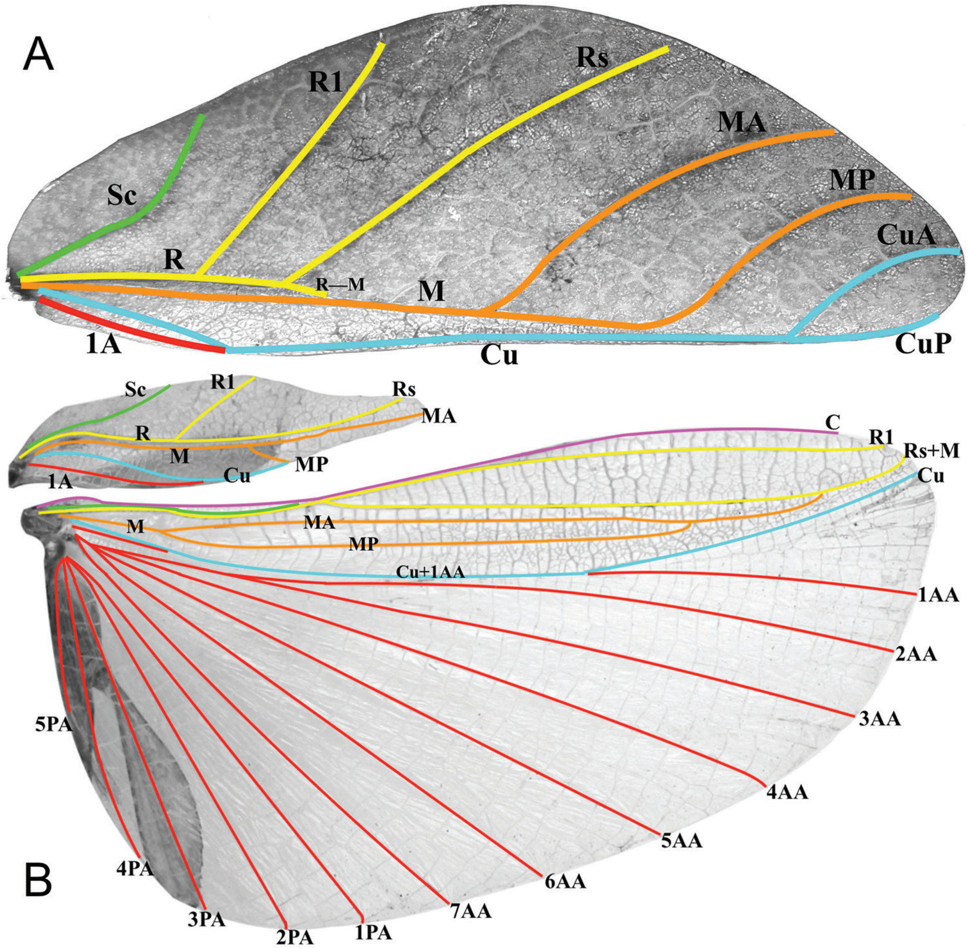

Figure 10. Representative female and male tegmina and alae wing venation present in our molecularly identified Clade B (see Figure 2), which is present in the new species *Phyllium gardabagusi* sp. nov. and *Phyllium nisus* sp. nov. **A** Female tegmina illustrated here is a *Phyllium nisus* sp. nov. (Coll RC 17-107) **B** male tegmina and alae illustrated here is a *Phyllium hausleithneri* (Coll RC 16-087). Abbreviations used: **C** (costa); **Sc** (subcosta); **R** (radius); **R1** (radius 1); **Rs** (radial sector); **R–M** (radius and medial crossvein); **M** (media); **MA** (media anterior); **MP** (media posterior); **Cu** (cubitus); **CuA** (cubitus anterior); **CuP** (cubitus posterior); **Cu+1AA** (cubitus and first anterior anal); **1A** (first anal); **1AA–7AA** (first through seventh anterior anal); **1PA–5PA** (first through fifth posterior anal).

placed on the posterior quarter of the capsule (Figure 9D). Operculum slightly ovular, with the outer margin with a row of pinnae similar to those along the posterior edge of the capsule, rarely forked, almost always with a single prominent end. Overall color light tan (Figure 9C, D).

Measurements including the extended pinnae [mm]. Length (including operculum) 6.2–6.5 mm, maximum width of capsule when viewed from lateral aspect 3.6–3.8 mm, length of micropylar plate 2.5–2.6 mm.

Newly hatched nymphs. General color throughout the body (including head and antennae) is dark brown to black (Figure 8E). Margins of the abdomen are white. Meso- and metafemora with a continuous transverse white band on the proximal third; a small white spot on the interior lobe proximal margin; and a thin white crescent on the distal exterior lobe margin. Profemora dark brown to black, except for near the proximal third where there can be small white spots on each side of the profemoral shaft, but not a solid transverse white band. Tibiae on all legs the same dark brown to black as the rest of the body but with faint two to three tan spots on all of the interior margins on the proximal third, or more clearly white than tan on the protibial interior lobe. Basitarsi are white and remaining tarsal segments are tan to dark brown.

Etymology. Noun, Greek in origin, Νῖσος. Named after Nisus, king of Megara, who had a single purple lock of hair that, for as long as it was not cut, guaranteed him life and possession of his kingdom. We felt that this homage was fitting to the purple-haired king as this species has the singular purple feature (coxae) which is unique among the Phylliidae with only the species in this clade known to have purple coxae.

***Phyllium* (*Phyllium*) *gardabagusi* sp. nov.**

http://zoobank.org/81385867-BCE0-4D79-8372-3CF5A9E5C32C
Figures 9 E, F, 11 A–E, 12 A–E, 13B

Type material. Holotype: ♀: Indonesia: West-Java, Mt. Halimun: August 2014. Deposited in the Montreal Insectarium type collection (Coll RC 16-202) (Figure 13B). Paratypes of 23 ♀♀, 18 ♂♂, and 50 eggs are deposited in the collections of Royce T. Cumming, Stephane Le Tirant, Oskar V. Conle, and Maxime Oritz (see Suppl. material 3: Table S3 for details).

Discussion and differentiation. This population has also recently entered the phasmid breeding community under the culture name of *Phyllium* sp. "Argopuro, Blue-coxae" (Figures 11 A–E, 12 A–E). This was another population which the authors examined extensively looking for consistent morphological differences but due to the significant intraspecies variation within all members of this clade, no useful feature could be found to separate *P. gardabagusi* sp. nov. from either *P. hausleithneri* or *P. nisus* sp. nov. The only closely related species which can consistently be morphologically separated is *Phyllium jacobsoni* because of the coxae color (white in *P. jacobsoni* Figure 5C, D and purple in *P. gardabagusi* sp. nov. Figures 11C, 12B). For full morphological measurements see Suppl. material 4: Table S4. Fortunately, a sizeable series of bred paratype specimens were examined thus allowing adequate description of the average adults and egg coloration. Coloration of the overall body was rather variable as discussed below, but the coxae and egg coloration showed little variation between individuals and we feel these colors are a reliable feature for differentiation. Newly hatched nymphs of *P. gardabagusi* sp. nov. (Figure 12E) cannot be differentiated from dark form *P. jacobsoni* or normal *P. hausleithneri* nymphs, and their identical morphology helps to illustrate their shared common ancestry.

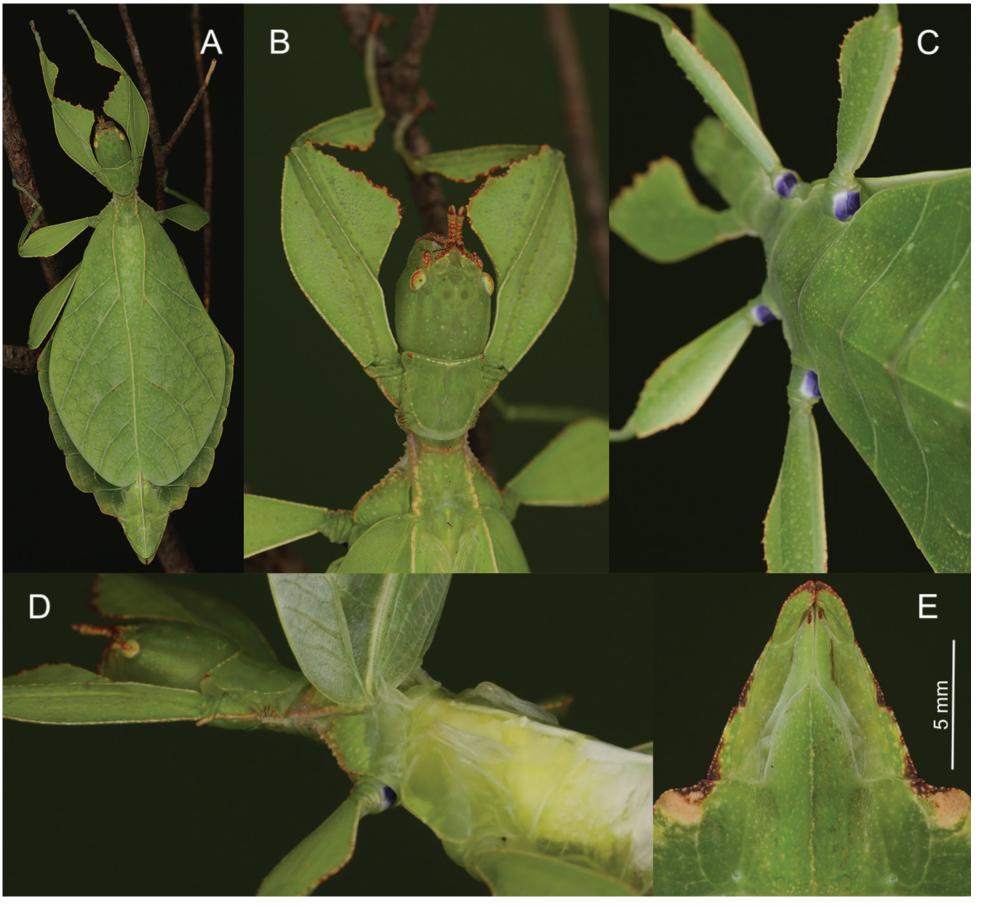

Figure 11. Female *Phyllium gardabagusi* sp. nov. live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** Dorsal view **B** dorsal head and thorax details **C** ventral view of purple coxae **D** tegmina held open to show exposed underdeveloped alae **E** ventral genitalia details.

Description. Female. ***Coloration.*** Specimens are always a vibrant pale green with varying degrees of reddish or grayish brown coloration more common on specific regions of the body. On the lightest colored individuals, no brown markings are present, with even the antennae a pale color similar to the shade of green seen on the head capsule (Figure 11A). Some lightly colored individuals have brown antennae and slight brown margins on the profemoral and protibial interior lobes and the thorax, with little to no brown coloration on the rest of the individual (Figure 1C). In individuals which are more colored, protibial interior lobes, profemoral interior lobes, mesofemoral lobes, and metatibial lobes can be a third to half colored with brown (Figure 13B). No individuals with strong brown coloration have been seen so far, but with such variable individuals it would not be surprising if this species also had individuals with darker brown coloration. Compound eyes are generally paler than the head capsule and usually of a yellow coloration with slight tan striping (Figure 11B). Meso- and metacoxae ventrally always with a royal purple coloration with a white margin which can only be viewed when the legs are bent forward (Figure 11C).

Morphology. *Head.* Head capsule about as long as wide, vertex with granulation throughout the surface, some more closely spaced than others (Figure 11B). The posteromedial tubercle is broader and taller than any other nodes, on the head. Frontal convexity broad and about as long as the first antennomere, and with slight granulation on the dorsal surface and several setae present which are longer than any setae on the antennae. Compound eyes only slightly protruding from the head capsule, but are significantly large, taking up about one fourth of the length of the lateral head capsule margins (Figure 11B). Ocelli absent. Antennal fields slightly wider than and about as long as the length of the first antennomere. *Antennae.* Antennae consisting of nine segments, with the terminal segment about the same length as the preceding segment or slightly longer (Figure 11B). Antennomeres I–VII sparsely marked with small transparent setae, the terminal two antennomeres are covered in stout, brown setae. The *pars stridens* of antennomere III on examined paratypes have 34–39 teeth. *Thorax.* Pronotum with gently concave anterior margin and nearly straight lateral margins, which converge to a straight posterior margin that is half the width of the anterior margin (Figure 11B). Pronotum anterior margin with small lateral defensive spray gland openings (no detectable defensive spray has been noted for these while in breeding) (Figure 11B). The pronotum surface is marked with only minimal small granulation, with only a prominent pit in the center, and slight furrows anterior and lateral to the pit (Figure 11B). The pronotum has a prominent anterior rim and weakly formed lateral and posterior rims, all of which have only slight granulation (Figure 11B). Prosternum and the mesosternum with stout and numerous nodes, those on the anterior half of the mesosternum on the sagittal plane are slightly larger than those on the prosternum. Metasternum with short granulation throughout the entire surface. Prescutum as long as wide or occasionally slightly longer than wide, but never wider than long (Figure 11B). Lateral rims with eight to eleven lumpy node-like tubercles ranging in size from small to medium with small granulation present throughout the length interspersed with the tubercles (Figure 11B). Prescutum anterior rim prominent but not strongly protruding, with a distinct singular tubercle with the remainder of the rim relatively smooth or occasionally with slight granulation (Figure 11B). Prescutum crest (excluding the tubercle of the anterior rim) with four to five distinct but not large nodes evenly spaced and nearly uniform in size or with the anterior most node slightly larger than the rest (Figure 11B). Prescutum crest is not prominently protruding because the smooth surface of the prescutum rises up to it, making the crest not much more than the nodes along the sagittal plane (Figure 11B). Mesopleurae beginning near the anterior margin of the prescutum and evenly diverging; lateral margin with eight to eleven tubercles which are largest on the anterior end and steadily decreasing in size as they reach the posterior, eventually no larger than nodes (Figure 11B). Some of the largest tubercles have slightly granular surfaces or granulation at the base (Figure 11B). Face of the mesopleurae with granulation throughout, and with two notable divots, one on the anterior third and one nearer the posterior third. *Wings.* Tegmina length variable, ranging from halfway through abdominal segment VII to at most reaching about one third of the way into segment VIII. Tegmina venation is rather stable between individuals (see Figure 10A for an example of the venation found in this species). The subcosta (Sc) is the first vein in the forewing and bends inward away from the anterior margin. The radius (R) spans the central portion of the forewing with two subparallel branched veins; radius 1 (R1) terminates anterior to the widest medial expansion of the tegmina, and the radial sector (Rs) terminates posterior to the widest medial expansion, therefore the R1 and Rs occupy the majority of the center of the wing. There is a weak continuation of the radius following the prominent Rs branching which continues on as a short and thinner R–M crossvein that does not appear to solidly connect the two veins fading as it reaches the media. The media (M) is simply bifurcate with both the media anterior (MA) and media posterior (MP) terminating close to the posterior fourth of the wing. The cubitus (Cu) is also bifurcate, branching near the posterior fifth of the wing into the cubitus anterior (CuA) and cubitus posterior (CuP) which both terminate at or very near the wing posterior apex. The first anal vein (1A) is simple and fuses with the cubitus early on, only slightly past the branching distance of the R1 from R. Alae rudimentary, only about 4.0 mm in length (Figure 11D). *Abdomen.* Abdominal shape quite variable, with the only consistent feature being segments II through the anterior two thirds of IV diverging, with the posterior third of segment IV the widest segment. Segments V through VIII are variable and can have perfectly straight margins (giving the abdomen a smooth spade shaped appearance, Figure 13B) or lobed margins (Figure 11A). Between these two extremes there are all possible forms/degrees of lobed margins with the forms continuous, not discrete. Segments IX and X are notably narrower than the previous segments and converge uniformly without lobes to the rounded apex. *Genitalia.* Subgenital plate starts at the anterior margin of segment VIII, is broad, and extends halfway to three quarters into segment X, ending in a fine point (Figure 11E). Gonapophyses are long and slender, reaching or very slightly exceeding the apex of abdominal segment X (Figure 11E). Cerci flat, not strongly cupped, with a granular surface and few detectable setae (Figure 11E). *Legs.* Profemoral exterior lobes narrow and smoothly arcing from end to end without a strongly notable angle, narrower than the width of the interior lobe (Figure 11B). Edge of the profemoral exterior lobe smooth without notable granulation or teeth (Figure 11B). Profemoral interior lobe wider than the exterior and with a right angle or slightly obtuse angle and marked with four to five teeth (Figure 11B). These teeth have a slightly wider gap in the center, and are variable in size ranging from small serrate teeth to larger angular teeth (Figure 11B). Generally, the size of the teeth is paralleled by the size of the abdominal lobes but not always. Mesofemoral exterior lobes arc from end to end but are slightly weighted towards the distal half and marked with one to three small serrate teeth distributed on the distal half only. Interior and exterior lobes can be of a similar width, or interior lobe can be slightly thinner. Mesofemoral interior lobe arcs end to end with five to six small serrate teeth only on the distal half of the arc which is slightly wider than the proximal half of the arc. Metafemoral interior lobe arcs end to end and has five to six serrate teeth on the distal half of the lobe. Metafemoral exterior lobe is thin and smooth, hugging the metafemoral shaft and generally with no teeth but occasionally with one to two at the distal most edge. Protibiae lacking an exterior lobe. Protibial interior lobe spans the entire length of the protibiae and can be one and a half to two times the width of the protibiae shaft itself. The lobe is distinctly triangular, and the lobe can be evenly distributed on the proximal and distal halves or the lobe can be slightly wider on the distal half. Mesotibiae and metatibiae lacking exterior and interior lobes.

Male. ***Coloration.*** Overall coloration pale green throughout with some veins and nodes a lighter yellow color (Figure 12A). Compound eyes are generally paler than the head capsule and usually of a yellow coloration with slight tan striping (Figure 12C). The antennae are darker in color, with each segment exhibiting a slight green in addition to brown towards the apex of each segment, which gives the antennae an overall striped appearance of green and brown. Nearly all observed males were completely green lacking any brown coloration except occasionally slight brown markings on the protibial interior lobe. The only consistent brown feature was the margin of abdominal segments II–IV, and the margins of the mesofemoral lobes which have a tan to brown color. Meso- and metacoxae ventrally with a pale purple and white coloration (Figure 12B). The coloration on the mesocoxae is generally darker and easier to distinguish than the purple on the metacoxae, which is only a faint purple hue on a mostly white surface.

Morphology. *Head.* Head capsule longer than wide, with a vertex that can be nearly completely smooth with two or three small nodes near the posteromedial tubercle or with slight granulation throughout the surface (Figure 12C). Frontal convexity with thin pale setae. The posteromedial tubercle is not broad but is distinctly raised from the head capsule. Compound eyes large and bulbous, taking up over one third of the head capsule lateral margins (Figure 12C). Three ocelli moderately developed located between and slightly posterior to the compound eyes. Antennal fields as wide and as long as the scapus. *Antennae.* Antennae (including the scapus and pedicellus) consists of 23 segments, all segments except the scapus and pedicellus and terminal four segments are covered in dense setae that are as long as or longer than the antennae segment is wide. The terminal four segments are covered in dense short setae and the scapus and pedicellus are nearly completely bare. *Thorax.* Pronotum with anterior margin distinctly concave and lateral margins that are slightly convex and converging to a straight posterior margin that is slightly more than half the width of the anterior rim (Figure 12C). Anterior margin of the pronotum has a distinct rim, lateral margins have moderate rims, and the posterior margin lacks a rim (Figure 12C). Face of the pronotum is marked by a distinct furrow and pit in the center, a smooth surface, and three distinct pits along the anterior margin (Figure 12C). Prosternum is granulose throughout with small nodes of even size and spacing. Mesosternum surface marked with more prominent nodes, with the largest along the sagittal plane and more strongly on the anterior margin, posterior margin with less prominent and small nodes. Prescutum longer than wide, with lateral margins slightly converging to the posterior (Figure 12C). Lateral rims with eight to nine tubercles of varying size, some prominent but other rather small and not much more prominent than nodes (Figure 12C). Prescutum crest along the sagittal plane with three to four small nodes of uniform size and spaced

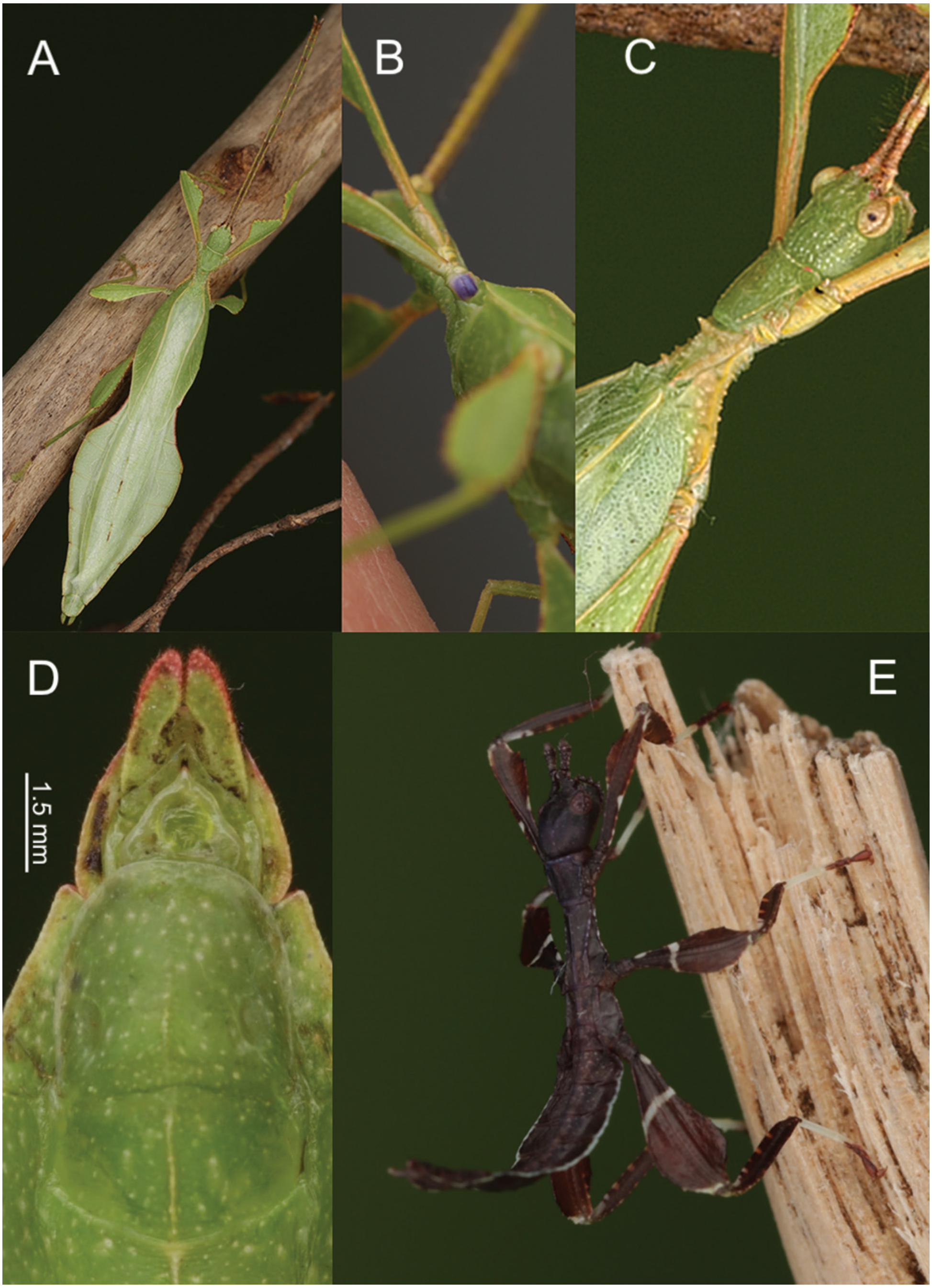

Figure 12. Male *Phyllium gardabagusi* sp. nov. live captive bred individuals, photos courtesy of Bruno Kneubühler. **A** Dorsal view **B** ventral view of purple coxae **C** dorsolateral, head and thorax details **D** ventral genitalia details **E** freshly hatched nymph.

throughout the length (Figure 12C). The surface of the prescutum rises up to meet the crest with a face that is smooth. Prescutum anterior margin marked with a tubercle, which is only about two times larger than any of the other nodes along the crest (Figure 12C). Mesopleurae not notably wide and diverge almost uniformly along the entire length, diverging slightly more prominently at the posterior margin (Figure 12C). Lateral margin with five to six major tubercles throughout the length, and between five and seven smaller minor tubercles interspersed throughout (Figure 12C). Each tubercle is marked by either a single stiff, short setae or with as many as three setae. Face of the mesopleurae slightly wrinkled and with two faint divots, one on the anterior third and one on the posterior third (Figure 12C). *Wings.* Tegmina moderate length, extending three quarters the way through abdominal segment III. Tegmina wing venation (see Figure 10B for general venation found in the species of this clade): the subcosta (Sc) is the first vein and terminates the earliest, about one third of the way through the overall tegmina length. The radius (R) spans the entire length of the tegmina with the radius 1 (R1) branching just anterior to the middle and terminating just posterior to the middle of the wing with the radial sector (Rs) terminating nearly at the wing apex. The media (M) also spans the entire length of the tegmina with the media posterior (MP) branching off slightly posterior to the middle and terminating promptly. The cubitus (Cu) terminates past the midline upon meeting the media posterior. The first anal (1A) vein terminates upon reaching the cubitus near the midline. Alae well developed in an oval fan configuration, long, reaching to the anterior margin of abdominal segment X. Alae wing venation (see Figure 10B for general venation found in the species of this clade): the costa (C) is present along the entire foremargin giving stability to the wing. The subcosta (Sc) is short, spanning less than a third of the wing length and is mostly fused with the radius in the beginning but terminates when it meets the costa. The radius (R) spans the entire wing and branches approximately a third of the way through into the radius 1 (R1) and radial sector (Rs) which run nearly parallel through most of their length until they terminate at the wing apex near each other but not touching. The media (M) branches early (only about a sixth of the way through the wing into the media anterior (MA) and the media posterior (MP) which run parallel with each other throughout the central two thirds of the wing until the media posterior fuses with the media anterior which eventually fuses with the above radial sector about one sixth of the way from the wing apex. The cubitus (Cu) runs unbranched and terminates at the wing apex. Of the anterior anal veins, the first anterior anal (1AA) fuses with the cubitus in line with the branching of the media into the media anterior and media posterior and then the first anterior anal branches from the cubitus three fifths of the way through the wing length where it uniformly diverges from the cubitus until it terminates at the wing margin. The anterior anal veins two through seven (2AA–7AA) begin from a common origin and run unbranched in a folding fan pattern of relatively uniform spacing to the wing margin. The posterior anal veins (1PA–5PA) share a common origin separate from the anterior anal veins and run unbranched to the wing margin with slightly thinner spacing than the anterior anal veins. *Abdomen.* Abdominal segments II slightly converging, III through the anterior two thirds of segment IV diverging to the widest portion (Figure 12A). The posterior of IV through V either almost parallel sided or converging, and segment VI through X uniformly converging (Figure 12A). *Genitalia.* Poculum broad and ends in a straight margined apex that slightly passes the anterior margin of segment X (Figure 12D). Cerci long and slender, extending from under the anal abdominal segment, slightly cupped, covered in a granulose surface, and numerous short setae (Figure 12D). Vomer broad and stout with straight sides evenly converging, and a thick single apical hook which hooks upwards into the paraproct (Figure 12D). *Legs.* Profemoral exterior lobe one third the width of the interior lobe, hugging the curve of the profemoral shaft and marked with a granular margin and fine small setae but no notable teeth. Profemoral interior lobe roundly triangular and marked with five serrate teeth with a larger gap between the middle two. Mesofemoral exterior lobe arcs end to end but is significantly weighted on the distal half which is marked with one to two serrate teeth, and the proximal half that is rather thin. Mesofemoral interior lobe is slightly thinner than the exterior lobe, is broader on the distal end and is marked with five to six small serrate teeth. Metafemoral exterior lobe lacks dentition, and with a straight margin along the metafemoral shaft. Metafemoral interior lobe smoothly arcs end to end with eight to nine small serrate teeth on the distal half. Protibiae lacking exterior lobe, interior lobe reaching end to end in a smooth evenly weighted triangle only one to one and a half times as wide as the protibial shaft. Meso- and metatibiae simple, lacking lobes completely.

Eggs. The lateral surfaces are flattened and the dorsal surface is slightly convex, which gives the egg a slight bend (Figure 9E). When viewed from the lateral aspect, the anterior width of the capsule is the narrowest, with the width slightly increasing steadily to the posterior, but only slightly so (Figure 9E). When viewed from the lateral aspect; the dorsal margin has long feather-like pinnae with single or double branching tips along three quarters to almost the entire length of the margin, with the anterior quarter occasionally lacking these long pinnae, the posterior margin also has these long pinnae (Figure 9E). The ventral margin lacks these long feather-like pinnae on the edges, but instead has a row of slightly shorter pinnae along the ventral surface sagittal plane with those at the posterior the largest followed by pinnae steadily decreasing in length as they reach the anterior which culminates in a narrow area at the anterior without pinnae near the operculum (Figure 9E). Lateral surfaces with three rows of bald impressions, with the space between densely covered with short carpet-like pinnae (Figure 9E). These three rows of impressions are variable between individuals, ranging from broken into numerous small patches, or with a majority of each impression continuous throughout its length (Figure 9E). Micropylar plate ranging from two thirds to four fifths of the overall dorsal surface length, with the thicker end situated towards the posterior half (Figure 9F). Micropylar plate in a slight teardrop shape, with most of the width as wide as the micropylar cup (Figure 9F). Micropylar cup of moderate size and placed on the posterior quarter of the capsule (Figure 9F). Operculum slightly ovular, with the outer margin with a row of pinnae similar to those along the posterior edge of the capsule, rarely forked, almost always with a single prominent end. Overall color light to medium brown (Figure 9E, F).

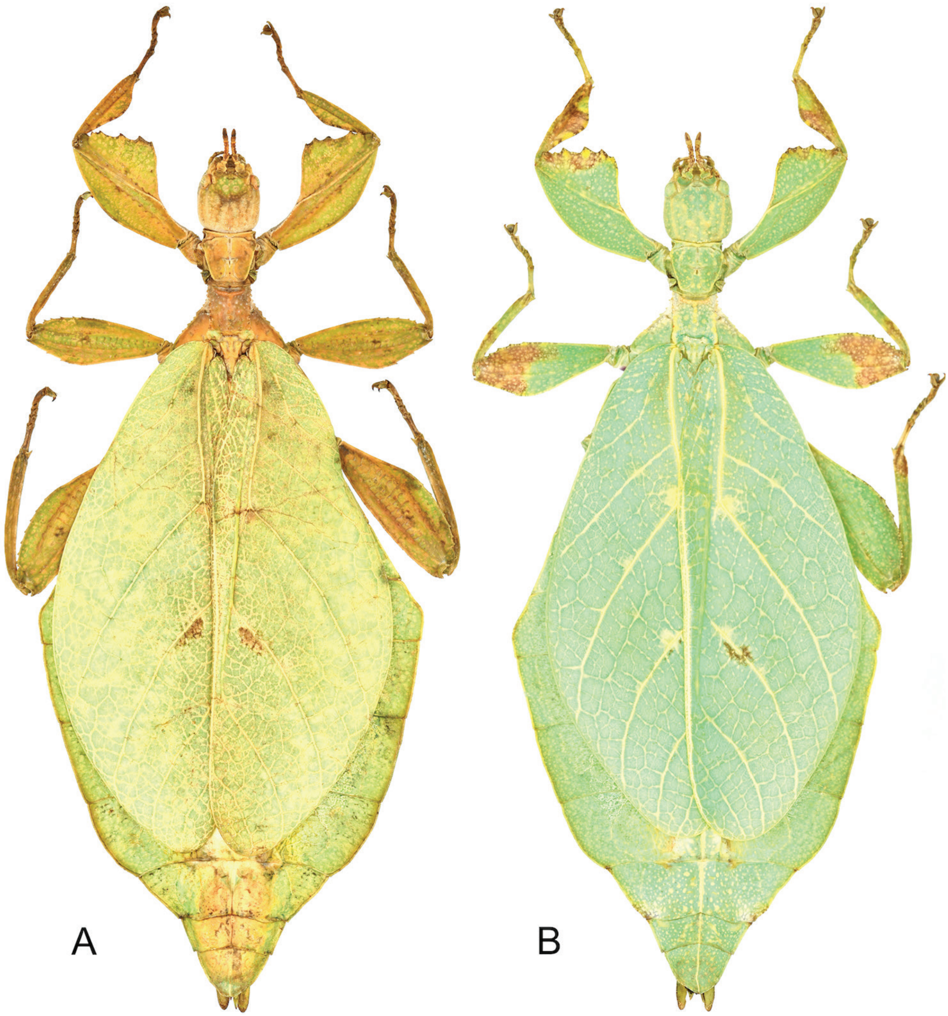

Figure 13. Holotypes for the two new *Phyllium* species described herein. **A** *Phyllium* (*Phyllium*) *nisus* sp. nov. from Sumatra, Indonesia **B** *Phyllium* (*Phyllium*) *gardabagusi* sp. nov. from Java, Indonesia.

Measurements including the extended pinnae [mm]. Length (including operculum) 5.6–5.7, maximum width of capsule when viewed from lateral aspect 4.0–4.3 mm, length of micropylar plate 2.5–2.6 mm.

Newly hatched nymphs. General color throughout the body (including head and antennae) is dark brown to black (Figure 12E). Margins of the abdomen are white. Meso- and metafemora with a continuous transverse white band on the proximal third; a small white spot on the interior lobe proximal margin; and a thin white crescent on the distal exterior lobe margin. Profemora dark brown to black, except for near the proximal third where there can be small white spots on each side of the profemoral shaft, but not a solid transverse white band. Tibiae on all legs the same dark brown to black as the rest of the body but with faint two to three tan spots on all of the interior margins on the proximal third, or more clearly white than tan on the protibial interior lobe. Basitarsi are white and remaining tarsal segments are tan to dark brown.

Etymology. Patronym, named after Garda Bagus (Java, Indonesia) who has helped to collect and rear several *Phyllium* species over the years and who has been instrumental in getting these established in the phasmid breeding community.

Checklist of species known from Sumatra and Java

The distribution is indicated by (S) for Sumatra; (J) for Java; or (S, J) for both islands.

Phyllium (*Pulchriphyllium*) *giganteum* Hausleithner, 1984 (S, J)
Phyllium (*Pulchriphyllium*) *pulchrifolium* Audinet-Serville, 1838 (S, J)
= *magdelainei* Lucas, 1857
Phyllium (*Pulchriphyllium*) *bioculatum* Gray, 1832 (S)
Phyllium (*Pulchriphyllium*) *abdulfatahi* Seow-Choen, 2017 (S)
Phyllium (*Pulchriphyllium*) *shurei* Cumming and Le Tirant, 2018 (J)
Phyllium (*Phyllium*) *jacobsoni* Rehn & Rehn, 1934 (J, Sumatran record presented in Seow-Choen (2017) is unconfirmed. Seow-Choen cites this record based on a single male specimen collected in 1936 from the NHMB collection. Unfortunately, due to old age and poor preservation of the specimen, the coxae color is faded removing the only easy and reliable currently known morphological method for differentiation. Hopefully further exploration on Sumatra can reveal if in fact *P. jacobsoni* is present or if this was simply a *P. nisus* sp. nov. male with the coxae color faded.)
Phyllium (*Phyllium*) *nisus* sp. nov. (S) (holotype Figure 13A)
Phyllium (*Phyllium*) *gardabagusi* sp. nov. (J) (holotype Figure 13B)

Erroneous records

Phyllium (*Phyllium*) *hausleithneri* Brock, 1999. Only known from Peninsular Malaysia; the population from Sumatra discussed in Cumming et al. (2018) is now known as *Phyllium nisus* sp. nov., sister species to *Phyllium hausleithneri*.

Phyllium (*Pulchriphyllium*) *mannani* Seow-Choen, 2017. This species was erroneously recorded from Sumatra based on a male *Phyllium bioculatum* Gray, 1832 specimen from the NHMB collection and published in Seow-Choen (2018). Features which differentiate *P. bioculatum* from *P. mannani* are as follows:

1 Antennae length, *P. mannani* = 18–21 mm (shorter or same length as tegmina when at rest along the dorsal surface), *P. bioculatum* = 26–28 mm (antennae always longer than tegmina).
2 Tegmina length, *P. mannani* = 14–15.5 mm, *P. bioculatum* = 11–11.5 mm.

3 Widest abdominal segment, *P. mannani* = segment VI, *P. bioculatum* = segment V.
4 Protibial exterior lobe, *P. mannani* = nearly absent, only a slight sliver, *P. bioculatum* = distal end notably wider than the remainder of the length.
5 Mesofemoral exterior lobe shape, *P. mannani* = V-shaped, *P. bioculatum* = U-shaped.

To date no records of *Phyllium mannani* from Sumatra are known to exist, and based on the above morphological characters, the specimen in the NHMB keys out as a *Phyllium bioculatum* male.

Discussion

Our molecular results reveal that the two Javan species are the sister group of the Sumatran and Peninsular Malaysian sister species, *Phyllium nisus* and *Phyllium hausleithneri*, respectively. Although we were able to examine an extensive range of specimens for all three species with purple coxae, their wide range of morphological variation has not allowed reliable external morphological differentiation. There is however the possibility of internal genitalia structures which might allow morphological differentiation, but despite dissection of several individuals no such structures could be identified. With all purple coxae species morphologically inseparable as adults, only the eggs of *P. nisus* and *P. hausleithneri*, can be distinguishable by their coloration (dark brown in *P. hausleithneri* Figure 9A and tan in *P. nisus* sp. nov. Figure 9C). Sumatran *P. nisus* sp. nov. was considered a range expansion of *P. hausleithneri* from Peninsular Malaysia (Cumming et al. 2018) but both species are now inferred as separate species and sister taxa with good support (Figure 2). Our molecular results illustrate the value of molecular data compared to traditional morphological taxonomic work as based on our two newly described cryptic species, which would have remained undescribed otherwise.

The significance of wing venation traits for Phylliidae systematics has been emphasized before (Bradler 2009), and we found the fusion of the MA and MP towards the apex of the male hind wing and the subsequent fusion with Rs (Figure 10B) to be an apomorphic (derived) trait of the *Phyllium* clade B. In the females of this clade the tegmina exhibit a conspicuous short vein that connects Rs with M (approximately at one third of the wing length, Figure 10A, noted as R–M in our figure). This vein was mentioned and depicted by Klante (1976: figs 11, 12) for the erroneously identified *P. woodi* (see above) and might constitute another derived trait of taxonomic value for this clade. To corroborate these assumptions a thorough comparison of the wing venation across the whole Phylliidae is necessary, which is beyond the scope of the current contribution and will become the subject in more comprehensive future studies.

The purple coxae coloration observed in *P. hausleithneri* and the two newly described species *P. gardabagusi* and *P. nisus* is likely a homologous trait between these three taxa, given their close relationship as recovered here (Figure 2), which originated in the last common ancestor of clade B. The absence of purple coxae coloration in *P. jacobsoni*, which is nested within clade B, could be the result of secondary loss. Although the assumption of two independent origins of purple coxae is equally parsimonious as one gain and one loss, requiring two steps each, we favor a single origin of this unique trait. Considering the low node support, we cannot exclude a sister relationship of *P. jacobsoni* to *P. gardabagusi* + *P. hausleithneri* + *P. nisus* and, consequently, a single origin of purple coloration without secondary loss. Vibrant coxae colors are rare among leaf insects, such as orange for *Phyllium rubrum* Cumming et al., 2018 or black for *Phyllium gantungense* Hennemann et al., 2009 and obviously serve some unidentified purpose. Leaf insects, as most phasmatodeans, rely on camouflage with reduced diurnal activity to minimize the risk of detection. If their camouflage fails, phasmatodeans often have elaborate secondary defenses to deploy, for instance deimatic behavior that involves the sudden display of striking coloration in several species from the hind wings (Bedford 1978). In some taxa these vibrant colors associated with startle displays stem from membranes, for instance, the turquoise coloration between the sclerites on the venter of the metathorax and proximal abdomen of *Haaniella echinata* (Hennemann et al. 2016). Suddenly revealing visual cues during deimatic behavior is thought to stop a predator's attack or make it pause long enough for the insect to escape (Umbers et al. 2015). We tentatively speculate that Phylliidae also use their vibrantly colored coxal membrane for defense purpose, but we lack behavioral observations supporting this assumption.

Outlook

The present study is a first step towards understanding the phylogeny, taxonomy, historical biogeography, and evolution of leaf insects. Preliminary molecular data indicated that the leaf insect genera *Phyllium* and *Chitoniscus* both do not form monophyletic groups (Buckley et al. 2009; Bradler et al. 2015; Robertson et al. 2018). Thus, the Phylliidae are in need of a thorough taxonomic revision based on robust phylogenetic background information. As discussed in our interpretation of the molecular analyses, some of the branches lack strong support values, therefore we cannot at this time present a fully reliable interpretation of their phylogenetic relationships within the two clades. Hopefully, with additional genetic data included and an enhanced taxon sampling in future works, we expect a more robust phylogeny to emerge.

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Supplementary material 1

Table S1. GenBank accession numbers for 55 sequences from *Phyllium* specimens, including sex, type designation, specimen collection code, and collection data

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Link: https://doi.org/10.3897/zookeys.913.49044.suppl1

Supplementary material 2

Table S2. Primers and corresponding information for genes used in this study

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Link: https://doi.org/10.3897/zookeys.913.49044.suppl2

Supplementary material 3

Table S3. Measurements of *Phyllium nisus* sp. nov., holotype female, para- type males and females

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Explanation note: All measurements made to the nearest 0.1 mm. Measurements for paratypes are given with a minimum to maximum range. *Including cerci and head, excluding antennae. **Only one female specimen [Coll RC 16-203] had the alae exposed to measure.

Link: https://doi.org/10.3897/zookeys.913.49044.suppl3

Supplementary material 4

Table S4. Measurements of *Phyllium gardabagusi* sp. nov., holotype female, paratype males and females

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Explanation note: All measurements made to the nearest 0.1 mm. Measurements for paratypes are given with a minimum to maximum range. *Including cerci and head, excluding antennae. **Only one female specimen [Coll RC 16-203] had the alae exposed to measure.

Link: https://doi.org/10.3897/zookeys.913.49044.suppl4

Supplementary material 5

File S1. Concatenated supermatrix of COI, 28S, and 16S sequences from the 21 specimens sampled (18 Phyllium and three outgroups)

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Explanation note: Supermatrix of 16 COI, 18 28S, and 21 16S sequences from the 21 specimens sampled (18 *Phyllium* and three outgroups).

Link: https://doi.org/10.3897/zookeys.913.49044.suppl5

Supplementary material 6

File S2. Original newick-formatted tree file inferred from COI, 28S, and 16S using IQ-TREE

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Explanation note: Original tree file based on 16 COI, 18 28S, and 21 16S sequences.

Link: https://doi.org/10.3897/zookeys.913.49044.suppl6

Supplementary material 7

File S3. Deposition of paratype material for *Phyllium* (*Phyllium*) *gardabagusi* sp. nov. and *Phyllium* (*Phyllium*) *nisus* sp. nov.

Authors: Royce T. Cumming, Sarah Bank, Stephane Le Tirant, Sven Bradler

Link: https://doi.org/10.3897/zookeys.913.49044.suppl7

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RESEARCH ARTICLE

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A new species of *Glyptapanteles* Ashmead (Hymenoptera, Braconidae, Microgastrinae) within *Macrobrochis gigas* (Lepidoptera, Arctiidae, Lithosiidae) in Fujian, China

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Abstract

The south-east coastal area of Fujian, China, belongs to the Oriental Realm, and is characterized by a high insect species richness. In this work, a new species of Hymenopteran parasitoid, *Glyptapanteles gigas* Liang & Song, **sp. nov.** found in Jinjiang within hosts of caterpillars *Macrobrochis gigas* (Lepidoptera: Arctiidae), is described and illustrated, with differences from similar species. Additionally, we presumed that both parasitoid and host species play very important role in the coevolution and tritrophic interaction between plants, phytophagous insects, and their parasitoids, because these insects probably broke the sporangia and made contributions to their colonization, or some spores were spread for long distances by adult moths after their emergence, or some parasitoids were attracted by the eggs and larvae of these caterpillars, which was also thought to be helpful to spread of spores.

Keywords

Glyptapanteles, *Macrobrochis gigas*, new species, Oriental Realm, parasitoid

Introduction

In an agricultural ecosystem, insect parasitoids play very important roles in the trophic networks and attract much research for their potential in biological control (Godfray 1994), especially as some species have largely been reared artificially and then released in the fields to suppress the pest populations (Liang et al. 2015). Each species kills and lives at the expense of host as a result of its development after ovipositing its egg within or on the surface of the host (Eggleton and Gaston 1990; Rachel et al. 2016). There are an estimated 60000 species of insect parasitoids belonging to the Hymenoptera (Lasalle and Gauld 1993), encompassing thousands of species specifically or generally attacking host eggs, larvae, or pupae of Lepidoptera (Shenefelt 1973; Clausen 1978; Shaw 1983; Chen and Wu 1994; Chen and Ji 2003; Traugott et al. 2006; Daane et al. 2013; Daciana et al. 2016), which would be alternative biological control agents to suppress populations of caterpillars. Previous taxonomic works have provided species identification and great contributions to potential agents of biological control. In this work, we described a new species of the genus *Glyptapanteles* Ashmead from the south and east coastal line (24°30'-24°54' North) in Fujian, China, emerged from its host caterpillar species *Macrobrochis gigas* (Walker, 1856) (Lepidoptera: Arctiidae) (Walker 1965). This caterpillar feeds on mosses growing on the trunks of trees.

Materials and methods

Field sampling

During field surveys for wasps parasitizing *M. gigas*, we discovered a new species of *Glyptapanteles* Ashmead, 1904 (Braconidae, Microgastrinae) associated with the caterpillars feeding specifically on mosses. This new species was found in the summers of 2015-2016 from Linyuan town (N24°44'40.42", E118°30'55.65") and Yonghe town (N24°42'57.34", E118°35'10.42") in Jinjiang, Fujian, south and east coastal areas of China. Braconidae parasitoids of *M. gigas* were sampled using two methods: (1) ectoparasitic cocoons of parasitoids coupled with mummies of host larvae were collected from the trunks of trees; (2) and some living larvae at different instar stages were collected every ten days and reared with mosses indoor to obtain the specimens of parasitoid species. Hymenopteran parasitoids were then sorted and identified.

Morphological diagnosis

Parasitoid adult specimens were cleared up and mounted in Canada Balsam or in Euparal® for measurement of appendages under a stereomicroscope (LEICA 205C, Germany). All figures were made using Leica Application Suite (LAS V 4.0) software. One female paratype specimen was sputter gold-coated and examined using a Jeol JSM – 6380 LV Scanning Electron Microscope. For identification of the subfamily Microgastrinae, see van Achterberg (1990, 1993); for references to the genus and other genera mentioned in this paper, see Yu et al. (2016). Morphological terminology follows van Achterberg (1988, 1993) and Eady (1974), including the abbreviations for the wing venation. TI stands for first metasomal tergite, TII for the second tergite, etc.

The types of the newly described species are deposited in the collection of the Parasitoid Wasp Museum of the Institute of Beneficial Insects, College of Plant Protection, Fujian Agriculture and Forestry University (**FAFU**), Fuzhou, China.

Abbreviations used in this paper are as follows:

POL Postocellar line (minimum distance between posterior ocelli)
OD Posterior ocellus maximum diameter
OOL Ocular-ocellar distance (minimum distance between posterior ocellus and eye).

Systematics

Glyptapanteles was originally described in 1904 (Ashmead 1904), then segregated from *Apanteles* genus by Ashmead, but Muesebeck (1920, 1922) subsumed *Glyptapanteles* again into *Apanteles* (Whitfield et al. 2002b). Later, Nixon (1965, 1973) did not recognize *Glyptapanteles* as a valid genus in his reclassification of Microgastrinae, but finally, it was accepted as a distinct genus in 1981 (Arias-Penna et al. 2019).

Glyptapanteles is a cosmopolitan group of hyper-diverse parasitoid species, which occur in all faunal regions (Whitfield et al. 2018) worldwide including Australia (Austin and Dangerfield 1992), Ecuador (Whitfield et al. 2002), China (Chen and Song 2004; Zeng et al. 2007), Greece (Papp 2007), Croatia, Bosnia and Macedonia (Papp 2009), India (Sathe and Dawale 1999; Gupta and Pereira 2012; Gupta and Fernández-Triana and Ward 2014; Gupta et al. 2011, 2016), and remains taxonomically challenging worldwide due to its highly specious nature, morphological similarity amongst species and negligible host records. Recent specimens from Neotropical regions indicates this genus has the most diverse species within Microgastrinae containing *Glyptapanteles*, *Apanteles* Förster, and *Diolcogaster* Ashmead (Whitfield et al. 2018). *Glyptapanteles* has a broad habitat of ecological distribution range from 90 m to 2,800 m elevation, attacking 35 host species.

Until 2018, more than 122 species were described worldwide (Yu et al. 2016, Gupta et al. 2016), then 136 new species of *Glyptapanteles* from Costa Rica and Ecuador were described (Arias-Penna et al. 2019). Unfortunately, hundreds of species of *Glyptapanteles* remain undescribed.

The female hypopygium is evenly sclerotized from side to side, never with a series of parallel longitudinal creases. Ovipositor sheath short and mostly concealed by hypopygium, its length not more than half of the hind tibia (rarely longer, but if so, hypopygium is large and acutely pointed, concealing most of the ovipositor), sheaths dagger-shaped with only a few setae concentrated near the apex. Petiole on T1 never wider at the apex, the sides either gradually converging distally or parallel and strongly rounded to the apex. The median area on T2 broadening distally and often subtrapezoidal or truncate-trapezoidal, sometimes lateral grooves delimiting the median area are lost among many diverging aciculations and sometimes do not reach the proximal edge of T3; T3 always smooth. Propodeum usually completely or mostly smooth, but often with coarsely sculpture covering all or part of the surface; rarely with a median longitudinal carina, but never with even a trace of the areola. Fore wing with r-m vein absent, so that the small areolet is open distally. Distal half of margin of vannal lobe of hind wing convex or flattened, with or without a fringe of setae. The anterior furrow of metanotum flattened (without sublateral setiferous projections) and glabrous; scutellar phragma exposed or concealed (Mason 1981).

Glyptapanteles gigas Liang & Song, sp. nov.

http://zoobank.org/9A8DD22D-499D-4BA2-B0B0-3504E9C12774

Distribution. Linyuan town (N24°44'40.42", E118°30'55.65") and Yonghe town (N24°42'57.34", E118°35'10.42") in Jinjiang, Fujian, south and east coastal areas of China.

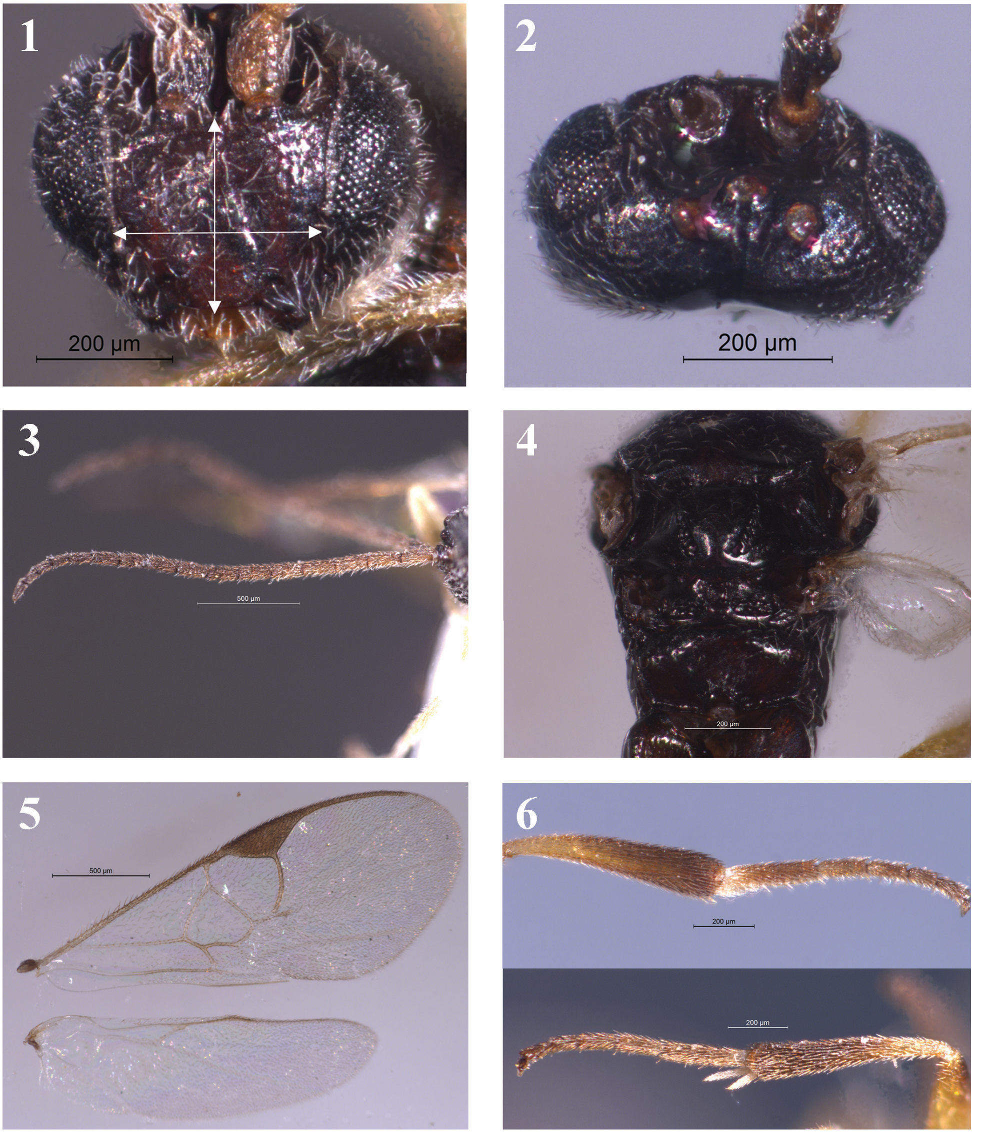
Etymology. The specific epithet is derived from the scientific name of its host *M. gigas.* Gender is masculine.

Description. Female (holotype). Body length 2.1 mm, fore wing length 2.3 mm.

Head. In anterior view, head approximately orbicular-ovate with antennal sockets slightly above middle level of eyes; face slightly convex, finely punctate associated with long hairs, ratio of FH:FW being 2.0: 2.6 (Fig. 1); eyes covered setae; inner margin of eyes slightly constricted towards clypeus. Transverse in dorsal view, 2.3 times as wide as long, 0.9 times as wide as width of mesoscutum. Ocelli large, arranged in a low triangle, posterior tangent of anterior ocellus approaching posterior ocelli. POL: OD: OOL= 0.7: 0.3: 0.8 (Fig. 2). Vertex almost smooth, with fine sparse setae; temple feebly punctate, with dense long setae; occiput smooth, slightly concave. Antenna longer than body in ratio of 10.0:7.9 (Fig. 3); flagellomeres thin, with short bristles, most flagellomeres with placodes arranged regularly in two ranks excerpt for last four or five flagellomeres. Flagellomere ratios: 2 L/W = 2.8, 8 L/W = 2.7, 14 L/W = 1.7, L 2/14 = 1.9, W 2/14 = 1.2. F12-15 tightly connected.

Mesosoma (Fig. 4). Side of pronotum with both a dorsal and a ventral carinate groove. Mesoscutum relatively flat, sparsely punctate with thin setose, relatively smooth near scutellar sulcus; notauli hardly exist. Scutellar sulcus relatively wide and deep, slightly curved; disc of scutellum smooth all over, approximately a low triangle in its shape. Propodeum relatively flat and smooth, horizontally rectangle, not inclined rear surface and no median longitudinal carina.

Wings (Fig. 5). Forewing with areolet open, vein r slightly inner oblique emitted from middle of pterostigma; r and 2-SR meeting at a circular arc and hardly distinguish from each other; 2-SR: r: width of pterostigma = 0.6: 0.8: 0.9; vein 1-R1 1.8 times as long as pterostigma, pterostigma 2.0 times as long as wide. 1-CU1:2-CU1:m-cu= 0.6: 1.0: 0.7. Hind wing narrow, vein cu-a slightly incurved, vannal lobe slightly convex with a few hairs.



Figures 1–6. *Glyptapanteles gigas* Liang & Song, sp. nov. **1** Head approximately orbicular-ovate; face slightly convex with long hairs, FH: FW = 2.0: 2.6 **2** Head. 2.3 times as wide as long. Ocelli large, arranged in a low triangle. POL: OD: OOL= 0.7: 0.3: 0.8 **3** Antenna longer than body (10.0: 7.9); Flagellomere proportions: 2 L/W = 2.8, 8 L/W = 2.7, 14 L/W = 1.7, L 2/14 = 1.9, W 2/14 = 1.2. F12-15 tightly connected **4** Mesosoma. Note that notauli hardly exist. Propodeum relatively flat and smooth, horizontally rectangle, no median longitudinal carina **5** Wings. Forewing with areolet open; r and 2-SR meeting at a circular arc; 2-SR: r: width of pterostigma = 0.6: 0.8: 0.9. 1-CU1:2-CU1:m-cu = 0.6: 1.0: 0.7. **6** Legs. Hind coxa large, near to T3. Hind tibia approximately 0.95 times as long as hind tarsa; inner hind tibial spurs longer than outer one and about half of hind basitarsus.

Legs (Fig. 6). Slender. Hind coxa large, near to T3, compressed, almost smooth and shiny, scattered with weak granular on upper surface. Hind tibia approximately 0.95 times as long as hind tarsi; inner hind tibial spurs longer than outer one and about half of hind basitarsus. Fore distitarsus with a feeble spine.

Metasoma. T1 smooth, 1.9 times as long as its greatest width, slightly parallel on both sides, gradually in general converging apically and rounded to apex, base broad depression concave, narrowed toward the end (Fig. 7). T2 approximately scalariform, the central area inconspicuous with apical width slightly long than central length, T3 1.1 times as wide as long, slightly longer than T2 (Fig. 8). All tergites almost smooth and polished, scattered with feeble setae. Ovipositor short, ovipositor sheath, about equal to length of the 2^{th} hind tarsus with a few hairs on tip (Fig. 9). Hypopygium, evenly sclerotized.

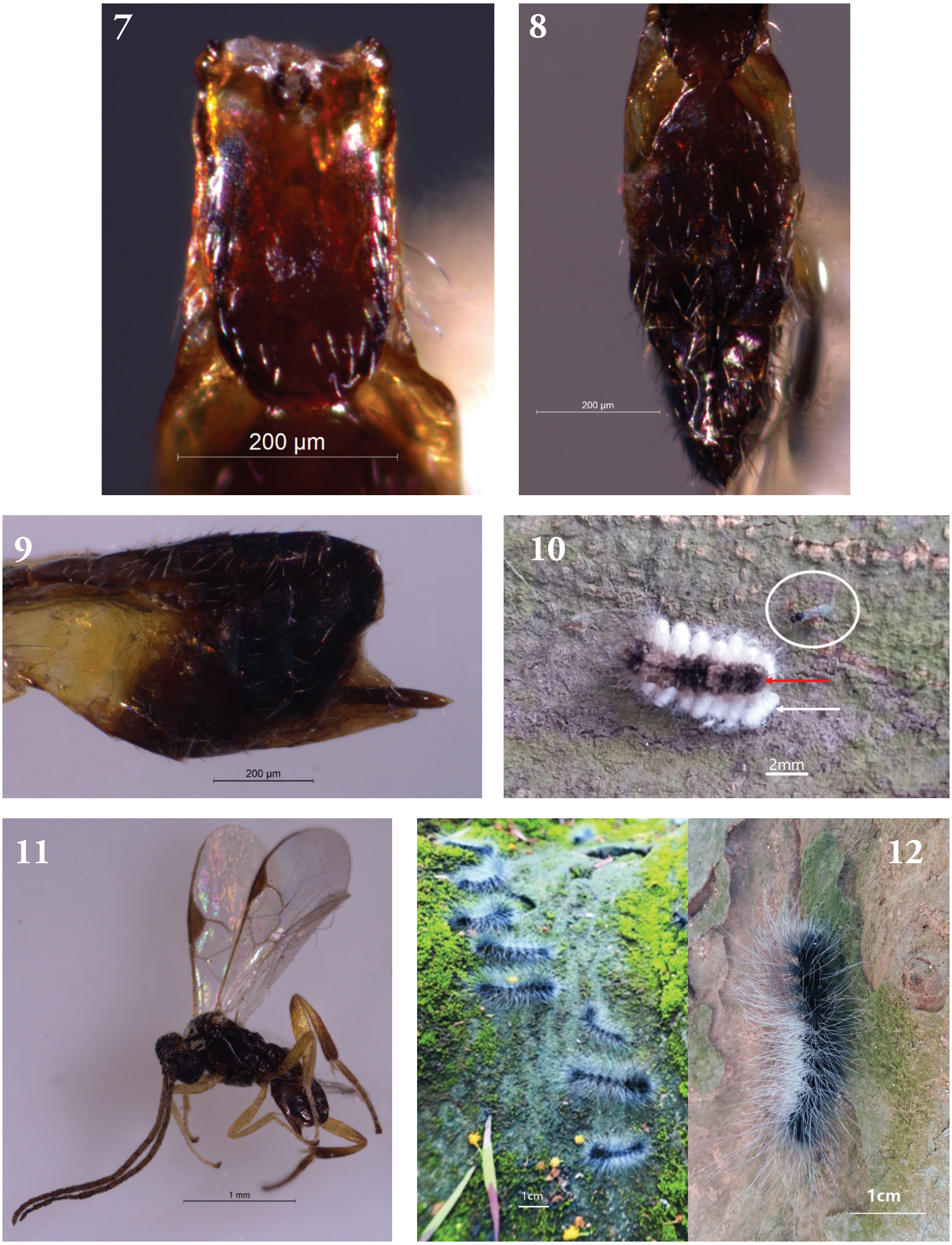
Color. Adult body mostly black (Fig. 10). Antennae black brown; maxillary palps, labial palps, legs yellow, except for most coxae black brown; most hind tibiae and hind tarsus infuscate. Pterostigma dark brown and semi-transparent, most veins pale yellowish. T1 reddish yellow-brown and transparent.

Male. Antenna longer than body (10.0: 7.0), the rest same as female.

Remarks. This new species is closely related to *Glyptapanteles phragmataeciae* (You & Zhou, 1990), but it is easily distinguished from it based on T1 slightly parallel on both sides, gradually in general converging apically and rounded to apex (T1 cuneiform); antenna longer than body (antenna shorter than body); vein 1-R1 1.8 times as long as pterostigma (vein 1-R1 1.0 times as long as pterostigma); inner hind tibial spurs longer than outer one and about half of hind basitarsus (inner hind tibial spurs as long as outer one and shorter than half of hind basitarsus).

Hosts

The parasitoid of genus *Glyptapanteles* mostly attacks lepidopteran caterpillars, of which very few species attacks insects of Coleoptera (Nixon 1976; Papp 1990; Smetacek 2008; Tobias 1971, 1976, 1986; Whitfield 1985, 1995, 1997; Whitfield and Wagner 1991; Wilkinson 1936, 1940). Here, we collected parasitoids specimen from caterpillars of *Macrobrochis gigas* Walker (Fig. 11) between 2015-2016 in China, and they occurred in Guangdong, South China (Fang 1985; Taiwan 2019; Mell 1938; Dubatolov et al. 2012; Liu 2005), India, Sikkim, Bhutan, Nepal, Bangladesh, Indonesia (Fang 2000). Taxonomically, it belongs to the family Arctiidae (Telenga 1955; Papp 1983a, 1983b; Fernández-Triana 2014; Dubatolov et al. 2012), and was firstly recorded and described as a new genera and species in 2001. Biologically, the host insects have one generation per year, and larvae feed on the mosses (Fig. 12) growing on the trunks of masson pines (*Pinus massoniana* Lamb.), litchis (*Litchi chinensis* Sonn.), longans (*Dimocarpus longan* Lour.), coast oak (*Casuarina equisetifolia* Forst.), waxberries (*Myrica rubra* Sieb.et Zucc), eucalyptus (*Eucalyptus grandis* × *urophylla*), *Acacia confusa* Merr., and loquats (*Eriobotrya japonica* (Thunb.) Lindl) from April to June, and the moths prefer the flowers after they emerge at the end of July in South China.



Figures 7–12. 7–10 *Glyptapanteles gigas* Liang & Song, sp. nov. **7** metasoma. T1 smooth, 1.9 times as long as its greatest width, slightly parallel on both sides, base broad depression concave, narrowed toward the end **8** T2 approximately scalariform, the central area inconspicuous with apical width slightly long than central length. T3 1.1 times as wide as long, slightly longer than T2 **9** ovipositor short, ovipositor sheath short, about equal to length of the 2th hind tarsus **10** body mostly black. Antennae black brown. **11** Parasitized larva of *M. gigas,* cocoons and *adult* of *G. gigas*. White ellipse indicating adult of parasitoid. Red and white arrows indicating parasitized larva and cocoons of parasitoid respectively. **12** Unparasitized larvae of the host *M. gigas.*

Discussion

In this work, *G. gigas* sp. nov. found in Jinjiang parasitizing caterpillars of *M. gigas* is described and illustrated, and differences from similar species that may parasitize the moss caterpillars are provided. There are 171 species of Lithosiini (Lepidoptera: Erebidae) recorded in China (Fang 1982; Liu 1989; Dubatolov et al. 2012), the majority of which can be found in the rainforests and shrubs on mountaintops, and associated with an abundant food of mosses and lichens found growing on rocks and trees (Liu 1989). Unfortunately, very few parasitoid species are known from those lepidopteran species, partially because host caterpillars usually have an ecological function rather than cause economic losses, and therefore attract very little attention by entomologists; moreover, little is known regarding the trophic relationships and ecological interactions between these phytophagous insects and their host bryophytes (Wang and Luo 2001; Davidson et al. 1989). In fact, some species of bryophytes such as *Brachythecium rutabulum* (Jacek and Adam 2018), *Mnium hornum*, *Trichocoleopsis cacculatta*, *Chiloscyphus polyanthus*, *Wiesnerella denudata*, *Frullania dilatata*, *F. tamarisci*, and *Gymnocolea inflata* were reported to produce a variety of toxic chemicals which repel caterpillars such as *Spodoptera littoralis* and Limacodidae (Asakawa 1990a, 1990b, 1994; Davidson et al. 1989; Shang and Yan 2014). Some other caterpillars found in these relatively ancient habitats have a long co-evolving interaction between insects and lower host bryophytes (Ren et al. 2008).

The moth is possibly involved in a mimicry relationship with *Eterusia aedea* (Linnnaeus, 1763) (Lepidoptera, Zygaenidae) (Fang 2000), which feeds on woody plants of the families Ebenaceae, Fagaceae, Euphorbiaceae, Rosaceae, and Rutaceae, many of which have pyrrolizidine as their main defensive chemical substance (Dubatolov et al. 2012). This phenomenon is similar to that of bracken ferns, which are consumed by some insect species (Hummel et al. 2008; Smart and Hughes 1973; Balick et al. 1978; Ottosson and Anderson 1983), such as Noctuidae, Tenthredinidae, and *Pteris* spp. (Shang and Yan 2014). Actually, there are some toxic substances within mosses of *Brachythecium rutabulum* and *Mnium hornum*, such as oxalic acid (Gerson 1982), phenolic compounds and ferulic acid, cumaric acids, and gallic acid (Davidson et al. 1989).

On the other hand, we assume this new species and their hosts may play an important ecological role in their trophic interaction between host plants and insects (Wu and Lou 2007). The larva of *M. gigas* is characterized by red crochets and long hairy non-poisonous seta instead of venomous seta. Fortunately, these larvae specifically feed on mosses up and down the trunk on rocks rather than on trees or crops, which probably breaks the sporangia and spreads the spores (Shang and Yan 2014); additionally, some spores may be also spread for a long distance by adult moths after their emergence and, some parasitoids will be attracted by the host eggs or larvae, which may also help the spread of spores. Therefore, we presume that specific interactions were involved in the host plant-herbivore-parasitoid system based on the adaptive strategies and coevolution of tritrophic interactions among *G. gigas*, *M. gigas*, and the mosses.

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Re-examination of the Chinese record of *Opisthotropis maculosa* (Squamata, Natricidae), resulting in the first national record of *O. haihaensis* and description of a new species

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Abstract

The taxonomic status of the previous record of *Opisthotropis maculosa* Stuart & Chuaynkern, 2007 from Guangdong and Guangxi, southern China, is revised based on the comparison of morphological and molecular data collected from the Chinese specimens and the holotype of *O. maculosa* from Thailand and *O. haihaensis* Ziegler, Pham, Nguyen, Nguyen, Wang, Wang, Stuart & Le, 2019 from Vietnam. Results reveal that the population from Shiwandashan Nature Reserve in southern Guangxi, China belongs to *O. haihaensis*, and represents the first national record for China; the populations from western Guangdong

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and southeastern Guangxi are described as a new species, *Opisthotropis hungtai* **sp. nov.** We suggest that *O. maculosa* should be removed from the Chinese herpetofauna checklist. The new national record of *O. haihaensis* and the description of the new species bring the total number of *Opisthotropis* to 13 in China.

Keywords
New national record, *Opisthotropis hungtai* sp. nov., southern China, taxonomy

Introduction

The genus *Opisthotropis* Günther, 1872 currently comprises 23 known species, and has spread widely throughout southern China and mainland of Southeast Asia, eastward to the Ryukyu Archipelago, southward to Sumatra and the Philippines (Ziegler et al. 2008; David et al. 2011, 2015; Yang et al. 2013; Teynié et al. 2014; Wang et al. 2017a, b). Currently, 12 species of the genus have been documented in China: *O. andersonii* (Boulenger, 1888), *O. cheni* Zhao, 1999, *O. guangxiensis* Zhao, Jiang & Huang, 1978, *O. jacobi* Angel & Bourret, 1933, *O. kuatunensis* Pope, 1928, *O. lateralis* Boulenger, 1903, *O. latouchii* (Bouleger, 1899), *O. laui* Yang, Sung & Chan, 2013, *O. maculosa* Stuart & Chuaynkern, 2007, *O. maxwelli* Boulenger, 1914, *O. shenzhenensis* Wang, Guo, Liu, Lyu, Wang, Luo, Sun & Zhang, 2017, and *O. zhaoermii* Ren, Wang, Jiang, Guo & Li, 2017. *O. balteata* (Cope, 1895) was recently transferred from the genus *Opisthotropis* to the genus *Trimerodytes* Cope, 1895 (Ren et al. 2019). Most species of the genus have been well recognized on the basis of phylogenetic and morphological analyses from the type series or topotypic specimens, especially in mainland China and northern Indochina (Ren et al. 2017; Wang et al. 2017; Ziegler et al. 2019). Nevertheless, the taxonomic statuses of several congeners remain unresolved, for instance, the records of *O. maculosa* from Guangdong and Guangxi in southern China (Yang et al. 2011).

Opisthotropis maculosa was originally described based on a single male specimen from northern Thailand (Fig. 1, site 6). Subsequently, it was reported based on morphological identifications in Guangdong (Fig. 1, sites 1, 2) and Guangxi (Fig. 1, sites 3, 4) in southern China (Yang et al. 2011), and northern Vietnam (Fig. 1, site 5) (Nguyen et al. 2018). Although some minor morphological differences among Chinese, Vietnamese and Thai populations were acknowledged in these publications, molecular data only became available recently, which lead to the resolution of the taxonomic statuses of the Vietnamese and Chinese records of *O. maculosa*. The Vietnamese record of *O. maculosa* was described as a distinct species, *O. haihaensis* Ziegler, Pham, Nguyen, Nguyen, Wang, Wang, Stuart & Le, 2019, by comparing the molecular and morphological data with the holotype of *O. maculosa* (Ziegler et al. 2019). In addition, their results also pointed out that the population of *O. maculosa* from Heishiding Nature Reserve in Guangdong, southern China may represent another distinct lineage.

In the present study, the *Opisthotropis* specimens from Guangdong and Guangxi, southern China previously recorded as *O. maculosa*, were re-examined using an integra-

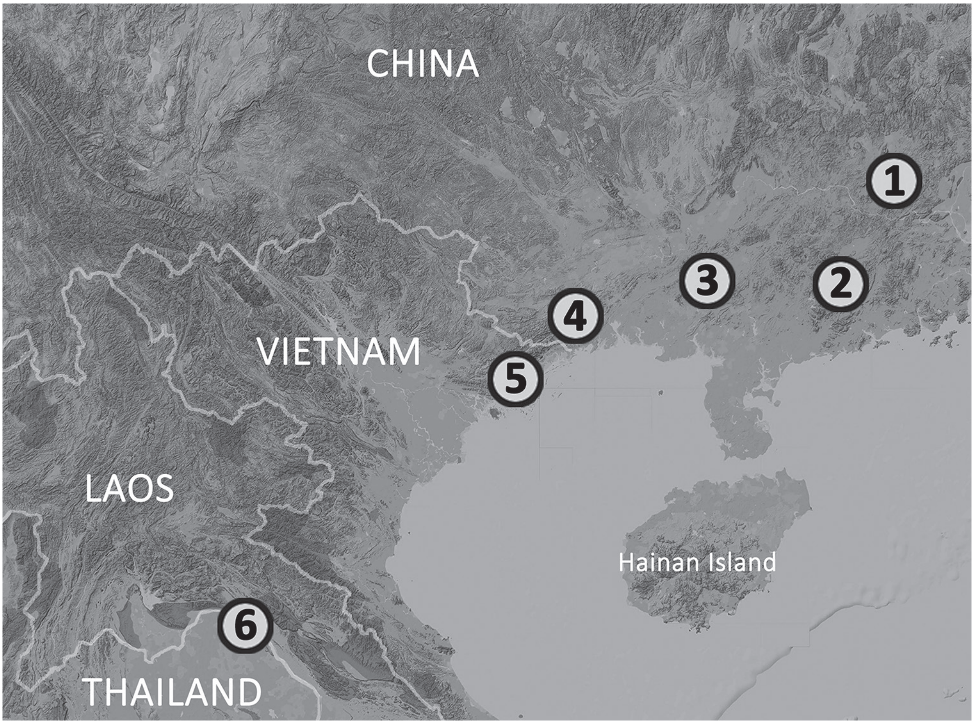

Figure 1. Collection localities of *Opisthotropis hungtai* sp. nov. (**1** the type locality, Heishiding Nature Reserve, Guangdong, China **2** Dawuling Forestry Station, Guangdong, China **3** Mt. Wuhuang, Guangxi, China), *O. haihaensis* (**4** Shiwandashan Nature Reserve, Guangxi, China **5** the forest near Tai Chi Village, Quang Ninh, Vietnam) and *O. maculosa* (**6** Phu Wua Wildlife Sanctuary, Nong Khai, Thailand), respectively.

tive taxonomic approach, by combining results from both morphological and molecular analyses. In particular, morphological comparisons among the Chinese '*O. maculosa*', the true *O. maculosa* from Thailand and the recently described *O. haihaensis* from Vietnam were undertaken in detail. The results demonstrate that the populations from southeastern Guangxi and western Guangdong represent a distinct taxon, which is described as a new species; the population from southern Guangxi is identified as *O. haihaensis*.

Material and methods

Morphometrics

Morphological examinations were performed on the holotype of *Opisthotropis haihaensis*, specimens reported as *O. maculosa* by Yang et al. (2011), and several other newly collected specimens. The collection information is given in the taxonomy accounts below. All specimens were fixed in 10 % buffered formalin and later transferred to 70 % ethanol for preservation, and deposited in the Museum of Biology, Sun Yat-sen

University (**SYS**), Kadoorie Farm and Botanic Garden (**KFBG**), and Institute of Ecology and Biological Resources, Hanoi, Vietnam (**IEBR**).

Measurements followed Wang et al. (2017) and Ziegler et al. (2019) and were taken with digital calipers to the nearest 0.1 mm. These measurements were as follows:

TL total length (from tip of snout to tip of tail);
SVL snout-vent length (from tip of snout to posterior margin of cloacal plate);
TaL tail length (from posterior margin of cloacal plate to tip of tail).

Scalation features and their abbreviations are as follows: preoculars (**PrO**); postoculars (**PtO**); supralabials (**SPL**); infralabials (**IFL**); temporals (**TMP**); ventral scales (**V**); subcaudals (**SC**); dorsal scale rows (**DSR**) were counted at one head length behind head, at midbody, and at one head length before vent, respectively. Bilateral scale counts were given as left/right.

Maxillary teeth counts (**MT**) were determined by subequal teeth or sockets on right upper maxilla, and sex was determined by dissection or by the presence/absence of everted hemipenis.

Phylogenetic analyses

The mitochondrial cytochrome *b* (CYTB) gene was used for molecular analyses. Two new samples from Mt. Wuhuang, southeastern Guangxi and Shiwandashan Nature Reserve, southwestern Guangxi, were included in our study. DNA extraction, PCR amplification and sequencing followed the protocol employed by Wang et al. (2017). In addition, 31 *Opisthotropis* and two outgroup sequences (following Ziegler et al. 2019) were attained from GenBank for the phylogenetic analysis (Table 1).

Amino acid sequences for the CYTB gene of all samples were first aligned using Clustal W with default parameters. After checking the alignment to make sure that there was no stop or error codon, the amino acid sequence dataset was transformed to a nucleotide sequence dataset. We then applied JModelTest v2.1.2 on the nucleotide sequence dataset under Akaike and Bayesian information criteria to determine the best-fit nucleotide substitution model. The dataset was analyzed using maximum likelihood (ML) in RaxmlGUI 1.3 (Silvestro and Michalak 2012) and Bayesian inference (BI) in MrBayes 3.2 (Ronquist et al. 2012) with the GTR + I + G model. For ML analysis, a bootstrap consensus tree inferred from 1000 replicates was used to represent the evolutionary history of the taxa analyzed. Branches reproduced in less than 50% of bootstrap replicates were collapsed. For BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for ten million iterations and sampled for every 1000th iteration. The first 25% of samples were discarded as burn-in. Convergence of the Markov Chain Monte Carlo simulations was assessed using Tracer v.1.4 (http://tree.bio.ed.ac.uk/software/tracer/). We also calculated pairwise sequence divergence based on uncorrected *p*-distance using MEGA 6.06 (Tamura et al. 2013).

Table 1. Localities, voucher information, and GenBank numbers for all samples used in this study.

ID	***Opisthotropis* Species**	**Voucher No.**	**Collection locality**	**Genbank No.**
1	*Opisthotropis hungtai* sp. nov.	SYS r000538 (Paratype)	CHINA: Guangxi: Mt. Wuhuang	MN890018
2	*Opisthotropis hungtai* sp. nov.	SYS r000946 (Holotype)	CHINA: Guangdong: Heishiding Nature Reserve	KY594748
3	*O. andersonii*	SYS r001423 (Topotype)	CHINA: Hongkong: Tai Tam	KY594730
4	*O. andersonii*	SYS r001424 (Topotype)	CHINA: Hongkong: Tai Mo Shan	KY594731
5	*O. cheni*	YBU071040 (Topotype)	CHINA: Hunan: Mangshan Nature Reserve	GQ281779
6	*O. cheni*	SYS r001422	CHINA: Guangdong: Shimentai Nature Reserve	KY594741
7	*O. daovantieni*	ROM FS39306	VIETNAM	MK941140
8	*O. durandi*	NCSM 80739	VIETNAM	MK941137
9	*O. guangxiensis*	GP746	CHINA: Guangxi	GQ281776
10	*O. haihaensis*	IEBR A.2016.34 (Holotype)	VIETNAM: Quang Ninh: Hai Ha District	MK991139
11	*O. haihaensis*	SYS r000537	CHINA: Guangxi: Shiwandashan Nature Reserve	MN890017
12	*O. jacobi*	IEBR 4329	VIETNAM: Vinh Phuc: Tam Dao	MG545601
13	*O. jacobi*	ZFMK 100818	VIETNAM: Vinh Phuc: Tam Dao	MG545602
14	*O. kuatunensis*	SYS r001008	CHINA: Fujian: Shanghang County	KY594746
15	*O. kuatunensis*	SYS r001081	CHINA: Guangdong: Mt. Wutong	KY594747
16	*O. laui*	SYS r001161	CHINA: Guangdong: Shangchuan Island	KY594738
17	*O. laui*	SYS r001170	CHINA: Guangdong: Shangchuan Island	KY594739
18	*O. lateralis*	SYS r000951	CHINA: Guangdong: Heishiding Nature Reserve	KY594743
19	*O. lateralis*	SYS r001080	CHINA: Guangdong: Mt. Wutong	KY594744
20	*O. lateralis*	–	CHINA: Guangxi	GQ281782
21	*O. latouchii*	SYS r000670 (Topotype)	CHINA: Fujian: Mt. Wuyi	KY594742
22	*O. latouchii*	GP647	CHINA: Fujian	GQ281783
23	*O. maculosa*	FMNH 265798 (Holotype)	THAILAND: Nong Khai: Phu Wua Wildlife Sanctuary	MK991138
24	*O. maxwelli*	SYS r000841	CHINA: Guangdong: Nan'ao Island	KY594736
25	*O. maxwelli*	SYS r001053	CHINA: Fujian: Huboliao Nature Reserve	KY594737
26	*O. shenzhenensis*	SYS r001018 (Holotype)	CHINA: Guangdong: Mt. Wutong	KY594727
27	*O. shenzhenensis*	SYS r001021 (Paratype)	CHINA: Guangdong: Mt. Sanzhoutian	KY594728
28	*O. shenzhenensis*	SYS r001032 (Paratype)	CHINA: Guangdong: Mt. Tiantou	KY594729
29	*O. voquyi*	ZFMK 100819 (Paratype)	VIETNAM: Bac Giang: Tay Yen Tu Nature Reserve	MG451049
30	*O. voquyi*	ZFMK 100820 (Paratype)	VIETNAM: Bac Giang: Tay Yen Tu Nature Reserve	MG451050
31	*O. zhaoermii*	CIB109998 (Paratype)	CHINA: Hunan: Guzhang County	MG012799
32	*O. zhaoermii*	CIB109999 (Holotype)	CHINA: Hunan: Guzhang County	MG012800
33	*O. zhaoermii*	CIB110000 (Paratype)	CHINA: Hunan: Guzhang County	MG012801
Outgroups				
34	*Aspidura drummondhayi*	RS-M	SRI LANKA: Nuwara Eliya	KC347455
35	*Aspidura trachyprocta*	RS-134	SRI LANKA: Nuwara Eliya	KC347458

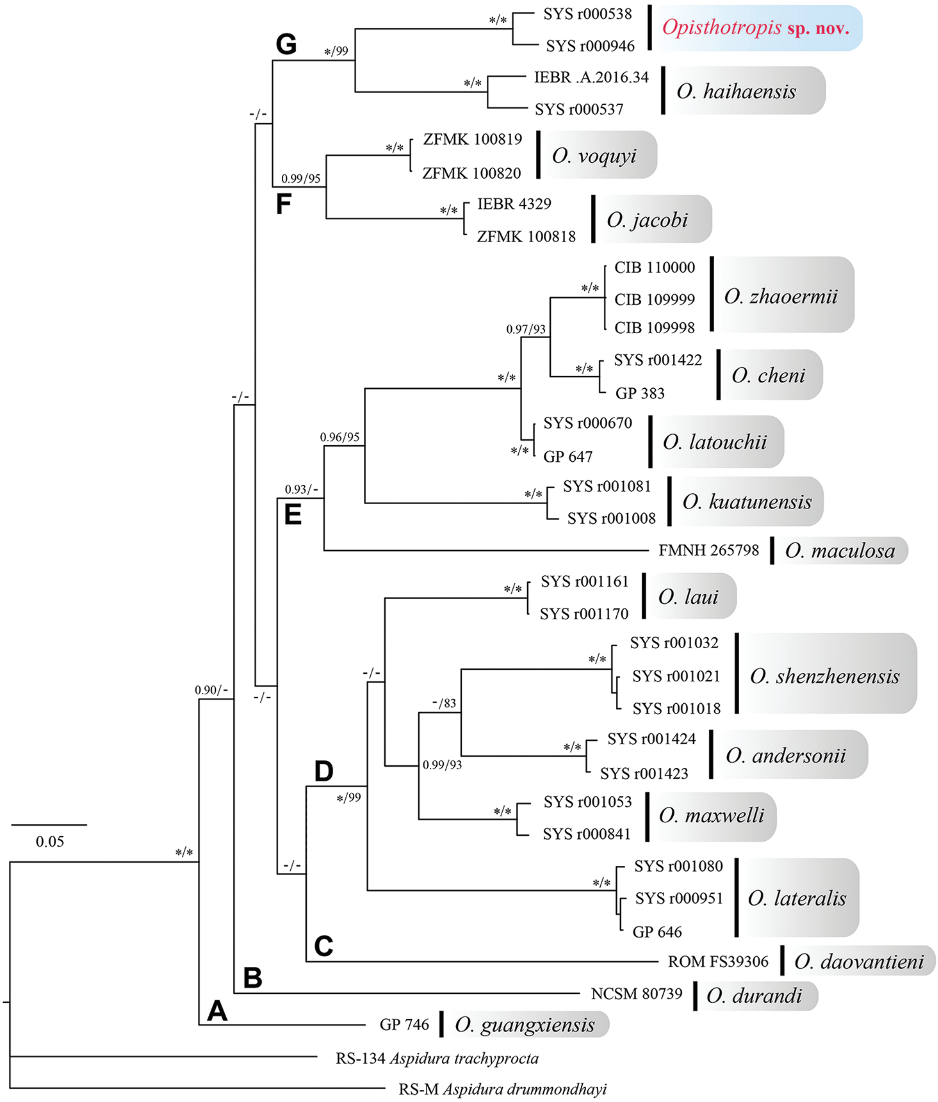

Figure 2. Bayesian Inference and Maximum Likelihood phylogenies. The Bayesian posterior probabilities (BPP) > 0.90 and the bootstrap supports for Maximum Likelihood analysis (BS) > 80 were retained.

Results

The CYTB nucleotide sequence matrix contained 1059 characters without insertion-deletions. The MP and BI analyses produced essentially identical topologies, which were integrated in Fig. 2. Major nodes of the tree were sufficiently supported, with Bayesian posterior probabilities (BPP) > 0.90 and bootstrap supports (BS) for maximum likelihood analysis > 80. Uncorrected *p*-distances among *Opisthotropis* species based on the CYTB gene are shown in Table 2.

Table 2. Uncorrected *p*-distances among *Opisthotropis* species based on partial mitochondrial CYTB gene.

Part 1	**ID**	**1–2**	**3–4**	**5–6**	**7**	**8**	**9**	**10–11**	**12–13**	**14–15**
Opisthotropis hungtai sp. nov.	**1–2**	2.8								
O. andersonii	**3–4**	18.4–19.4	0.9							
O. cheni	**5–6**	20.3–20.8	20.4–21.0	0.5						
O. daovantieni	**7**	22.5–23.0	18.8	21.1–21.2	–					
O. durandi	**8**	20.3	20.3–20.5	21.4–21.6	20.8	–				
O. guangxiensis	**9**	18.0–18.6	16.7	18.9–19.3	21.0	17.9	–			
O. haihaensis	**10–11**	14.7–15.3	18.2–18.7	18.1–18.4	21.6–22.3	19.8–20.1	16.5–16.6	4.6		
O. jacobi	**12–13**	15.9–16.7	18.2–19.0	16.9–17.3	19.3–19.5	18.0–18.2	15.4–15.6	15.8–16.3	0.4	
O. kuatunensis	**14–15**	18.1–19.2	19.0–19.5	15.9–16.5	20.7–21.5	20.2	18.3–18.4	18.9–19.7	17.3–17.6	1.1
O. laui	**16–17**	17.5–19.4	13.6–14.2	19.3–19.6	21.4–21.5	20.9–21.1	18.9–19.0	17.6–18.8	17.8–18.0	19.2–19.6
O. lateralis	**18–20**	20.7–22.2	16.5–16.7	17.9–18.3	22.2–22.8	19.9–20.0	19.3–19.6	18.3–18.6	20.3–20.7	19.0–19.4
O. latouchii	**21–22**	19.3–19.5	18.6–19.0	5.3–5.4	20.1	20.3	17.9	17.7–18.6	16.9–17.0	15.6–16.0
O. maculosa	**23**	21.1	21.7–21.9	20.9	22.2	19.4	18.4	18.8–20.4	18.2–18.3	19.2–19.3
O. maxwelli	**24–25**	16.8–17.7	13.0–13.7	18.4–19.3	20.9–21.6	20.0–20.9	17.9–20.3	17.3–18.6	17.4–18.7	17.7–18.3
O. shenzhenensis	**26–28**	18.8–19.1	12.0–12.5	19.9–20.4	21.8–22.2	20.7–21.3	18.9–19.2	20.2–20.8	18.5–18.9	20.1–21.2
O. voquyi	**29–30**	17.0–17.3	16.2–16.5	16.3–16.8	19.7–19.9	17.6–17.7	14.9–15.0	15.0	10.9–11.5	18.0–18.2
O. zhaoermii	**31–33**	19.6–20.0	18.3–18.7	5.9	21.2	20.8	18.4	17.9–18.1	16.1	16.8–17.0
Part 2	**ID**	**16–17**	**18–20**	**21–22**	**23**	**24–25**	**26–28**	**29–30**	**31–33**	
O. laui	**16–17**	0.1								
O. lateralis	**18–20**	17.1–17.8	0–0.9							
O. latouchii	**21–22**	18.9–19.1	18.3–18.4	0						
O. maculosa	**23**	22.2–22.3	20.6–20.8	20.1	–					
O. maxwelli	**24–25**	12.8–13.4	15.0–16.1	18.0–18.5	20.6–20.9	1.5				
O. shenzhenensis	**26–28**	15.8–16.3	16.2–17.0	18.8–19.2	21.5–21.7	11.8–12.8	0–0.7			
O. voquyi	**29–30**	15.3–15.5	16.6–16.7	16.0–16.1	18.9–19.0	16.4–17.6	17.0–17.2	0.1		
O. zhaoermii	**31–33**	19.1–19.3	18.5–18.6	5.4	20.6	17.6–18.3	18.6–18.8	16.4–16.6	0	

In our phylogenetic tree, all samples of the genus *Opisthotropis* clustered in a monophyletic group with high nodal supports (BPP 1.00 and BS 100), and can be divided into seven clades, although the relationships among these clades were unresolved. *Opisthotropis daovantieni* Orlov, Darevsky & Murphy, 1998, *O. durandi* Teynié, Lottier, David, Nguyen & Vogel, 2014 and *O. guangxiensis* formed three monotypic clades, respectively. *Opisthotropis andersonii*, *O. lateralis*, *O. laui*, *O. maxwelli*, and *O. shenzhenensis* were grouped in clade D (BPP 1.00 and BS 99). Clade E (BPP 0.93) contained *O. cheni*, *O. kuatunensis*, *O. latouchii*, the true *O. maculosa*, and *O. zhaoermii*. The sister species *O. jacobi* and *O. voquyi* Ziegler, David, Ziegler, Pham, Nguyen & Le, 2018 constituted clade F (BPP 0.99 and BS 95).

Within clade G (BPP 1.00 and BS 99), the *Opisthotropis* sample (SYS r000537) from Shiwandashan Nature Reserve, southern Guangxi, was placed with the holotype of *O. haihaensis* from northeastern Vietnam, with high node support values (BPP 1.00 and BS 100) and moderate genetic distance (*p*-distance 4.6%). The detailed morphological examination suggests that they represent individuals of the same species. Thus, we herein revise the identification of the specimen as *O. haihaensis*, and report it as a new national record for China.

Besides, the *Opisthotropis* samples from Mt. Wuhuang, southeastern Guangxi and Heishiding Nature Reserve, western Guangdong, were reconstructed as a monophyletic clade with strong nodal supports (BPP 1.00 and BS 100) and small genetic distance (*p*-distance 2.8%). The populations should be considered as a distinct taxon, which is sister to *O. haihaensis*. These specimens show almost no morphological differences from those collected at Dawuling Forestry Station, western Guangdong, which is located in the same mountain belt as Heishiding Nature Reserve. Therefore, we describe these specimens as a new species, *Opisthotropis hungtai* sp. nov.

Taxonomy accounts

Opisthotropis haihaensis Ziegler, Pham, Nguyen, Nguyen, Wang, Wang, Stuart & Le, 2019

Figures 3, 5A

Chresonymy. *Opisthotropis maculosa* Stuart & Chuaynkern, 2007: Yang et al. (2011) (part); Nguyen et al. (2018).

Holotype. IEBR A.2016.34 [Field No. QN 2016.91], adult female, from the forest near Tai Chi Village, Quang Son Commune, Hai Ha District, Quang Ninh Province, 950 m asl., Vietnam [exact locality and coordinates not provided owing to threat from collection for the pet trade (Ziegler et al. 2019)], collected by Cuong The Pham and Tan Van Nguyen on 9 May 2016.

Specimens examined (N = 1). SYS a000537, adult female, collected by Qing Du and Jian-Huan Yang on 10 July 2009 from Shiwandashan Nature Reserve [exact coordinates not provided owing to threat from collection for the pet trade], Shangsi County, Qinzhou City, Guangxi Zhuang Autonomous Region, 493 m a.s.l., P.R. China.

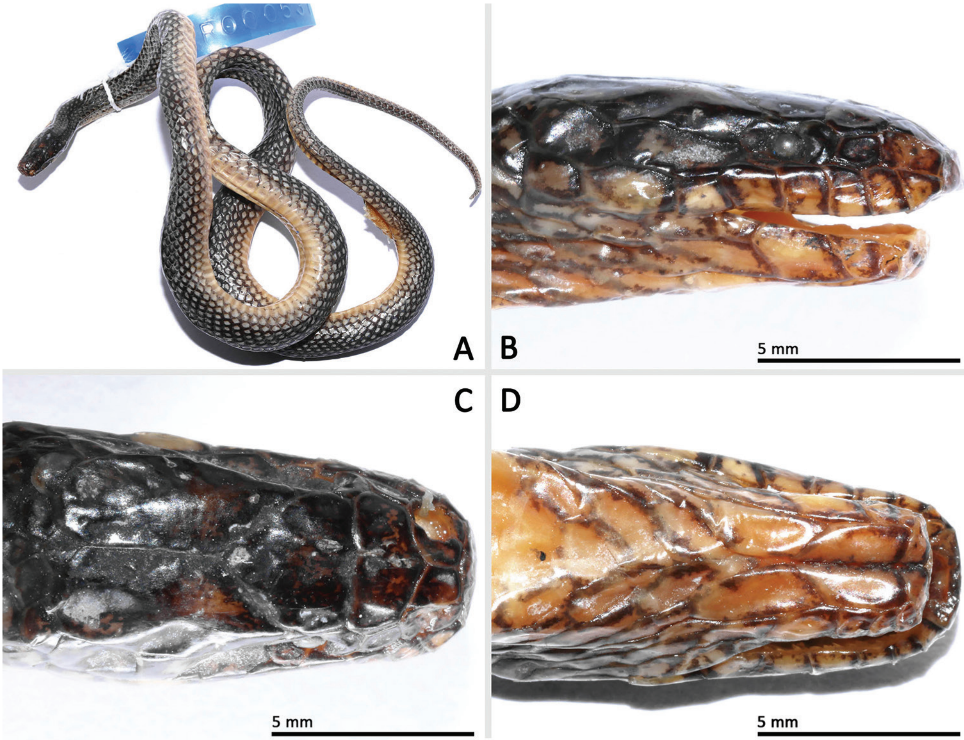

Figure 3. Morphological features of *Opisthotropis haihaensis* (SYS r000537) from Shiwandashan Nature Reserve, Guangxi, China. **A** Habitus view **B–D** close-up of head scales. Photos by Jian Wang.

Etymology. According to the original description, the specific name "*haihaensis*" refers to the type locality of this species, Haiha District (Quang Ninh Province) in Vietnam. As this species is currently reported in China, we suggest its Chinese name "Hai He Hou Leng She (海河后棱蛇)", derived from its scientific name.

Variation. Measurements, scalation and body proportions of the two specimens are listed in Table 3. The specimen from China conforms to the holotype from Vietnam except for: (1) a shorter body size: snout-vent length 391.3 mm, tail length 108.9 mm (vs. SVL 396 mm, Tal 113 mm in the holotype); (2) a higher number of postoculars: PtO 2 (vs. PtO 1 in the holotype); (3) a lower number of maxillary teeth: MT 22 (vs. MT 24 in the holotype); (4) a lower number of ventrals: V 164+2 (vs. V 169+2 in the holotype); (5) a lower number of subcaudals: SC 75 (vs. SC 79 in the holotype); and (6) tail scales indistinctly keeled (vs. tail scales smooth in the holotype).

Revision of original diagnosis. *Opisthotropis haihaensis* is characterized by the combination of the following characters: (1) TL 500.2–509 mm in adult females, (2) tail relatively long, TaL/TL 0.22, (3) internasal not in contact with loreal, prefrontal not touching supraocular, frontal touching preocular, (4) one preocular, one or two postocular(s), (5) temporals 1+1, (6) supralabials eight, fourth and fifth in contact with eye, (6) 22–24 maxillary teeth, (7) anterior pair of chin shields longer than posterior

Table 3. Measurements, scale counts and body proportions of *Opisthotropis haihaensis* and *Opisthotropis hungtai* sp. nov.

Species	***O. haihaensis***		***Opisthotropis hungtai* sp. nov.**							
No.	IEBR A.2016.34	SYS r 000537	SYS r 000720	SYS r 001350	SYS r 001525	SYS r 001515	SYS r 000946	SYS r 000538	SYS r 002017	KFBG 2002.01
Locality	Haiha	Shiwandashan	Heishiding	Heishiding	Heishiding	Dawuling	Heishiding	Mt. Wuhuang	Dawuling	Dawuling
Sex	Female	Female	Female	Female	Female	Female	Male	Male	Male	Male
TL	509	500.2	511	470.2	393.2	435.9	501.2	464.3	366	483.5
SVL	396	391.3	431	383	312	337.9	401.6	343.6	318	373.1
TaL	113	108.9	80 (broken)	87.2	81.2	98	99.6	120.7	48 (broken)	110.4
TaL/SVL	0.22	0.22	broken tail	0.19	0.21	0.22	0.20	0.26	broken tail	0.23
DSR	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15
MT	24	22	17	16	17	18	16	17	18	18
PrO	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
PtO	1/1	2/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
SPL	8 (3–2–3)	8 (3–2–3)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)	7 (3–2–2)
IFL	8/8	8/8	7/7	7/7	7/7	8/8	7/7	8/8	8/9	8/8
TMP	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1	1+1/1+1
V	169	164	168	170	170	175	170	189	180	172
SC	79	75	56 (broken)	69	70	84	76	98	37 (broken)	83

pair; (8) ventrals 164–169 (+ 2 preventrals), (9) subcaudals 75–79, (9) nasal cleft pointing to the first supralabial, (10) body scales in 15–15–15 rows, (11) body scales smooth, tail scales smooth or indistinctly keeled, (12) chin shields yellow with brownish black mottling, and (13) body and tail dorsum dark, each with a light yellow spot per scale.

Coloration in life (SYS r000537). Eye black; scales on dorsal surface of head glossy black with scattered yellow flecking; chin shields yellow with brownish black mottling; body and tail glossy black with iridescence above, with single yellow spot on each scale, yellow spots becoming larger on sides of body; ventrals yellow with brownish black lateral margins and scattered brown flecks; subcaudals yellow with brownish black anterior and lateral margins in both specimens.

Coloration in preservation (SYS r000537). Ground color of upper head and body surface dark brown, that of venter yellowish-beige. Dorsal scales each with light blotch in the center. Dorsal tail scales likewise with light central blotches. Dorsal head surface in part with indistinct light mottling. Anterior supralabials with large light mottling. Infralabials, chin shields and smaller throat scales anterior to ventrals yellowish-beige with dark brown mottling per scale. Belly with few, scattered dark flecks on sides. Outermost edges of light ventrals brown. Ground color of subcaudals brown with transversally enlarged light blotches at each scale end.

Distribution and habits. *Opisthotropis haihaensis* is currently known from its type locality, the forest near Tai Chi Village (ca 950 m a.s.l.), Quang Ninh, northern Vietnam, and Shiwandashan Nature Reserve (ca 500 m a.s.l.), southwestern Guangxi, southern China. The straight-line distance between the two localities is approximately 150 kilometers, indicating that the distribution area of this species is the mountain region on the border between China and Vietnam.

The holotype was found at night in a small rocky stream at 21:30h. The surrounding habitat was secondary evergreen forest consisting of small hardwoods, bamboo, and shrubs. The air temperature was 24–29 °C and the relative humidity was 65–88%. The holotype revealed to be an adult female, as dissection showed up to 16.5 mm long eggs and the oviducts were folded, indicating that eggs had already been laid (Ziegler et al. 2019). Besides, the other specimen, SYS r000537, was collected from a rocky stream (about 8 m wide and 0.3 m deep at the collecting site) running through well-preserved, dense deciduous forests. The collected individual was spotted swimming at night and swiftly hiding under stones when disturbed.

Opisthotropis hungtai sp. nov.

http://zoobank.org/A0FC2C8F-866B-4D81-9237-1E42942711AA
Figures 4, 5B, 6

Chresonymy. *Opisthotropis maculosa* Stuart & Chuaynkern, 2007: Yang et al. (2011) (part); Wang et al. (2017a), Ren et al. (2019).

Holotype. SYS r000946, adult male, collected by Jian Zhao on 2 September 2014 from Heishiding Nature Reserve [exact coordinates not provided owing to threat

Figure 4. Morphological features of the adult male holotype SYS r00946 of *Opisthotropis hungtai* sp. nov. **A** Habitus view in life **B** habitus view in preservative **C** close-up of mid-dorsal body **D–E** close-up of head scales. Photos by Jian Zhao and Jian Wang.

from collection for the pet trade, same as paratypes], Fengkai County, Zhaoqing City, Guangdong Province, 300 m a.s.l., P.R. China.

Paratypes (N = 7). Adult female SYS r001350 collected by Zhi-Tong Lyu on 15 August 2015, adult female SYS r000720 collected by Ying-Yong Wang on 28 June 2012, and adult female SYS r001525 collected by Zhi-Tong Lyu and Ying-Yong Wang on 1 July 2016, from the same locality as the holotype. Adult male KFBG 2002.01 collected by Zhi Xiao on 2 July 2002, adult male SYS r002017 collected by Jian Wang on 14 June 2018, and adult male SYS a001515 collected by Jian Wang on 8 July 2017, all from Dawuling Forestry Station, Xinyi City, Maoming City, Guangdong Province, ca 1150 m a.s.l., P.R. China. Adult male SYS a000538, collected by Qing Du and Runlin Li on 14 July 2009 from Mt. Wuhuang, Pubei County, Qinzhou City, Guangxi Zhuang Autonomous Region, ca 360 m a.s.l., P.R. China.

Etymology. The species name "*hungtai*" refers to Professor Hung-Ta Chang (=Hong-Da Zhang, 张宏达), an outstanding botanist, who established the Tropical and Subtropical Forest Ecosystem Experimental Center in Heishiding Nature Reserve, promoting the development of ecological research in southern China. We suggest the English common name Hung-Ta Chang's mountain Keelback and the Chinese name Zhang Shi Hou Leng She (张氏后棱蛇).

Diagnosis. *Opisthotropis hungtai* sp. nov. is characterized by the following combination of characters: (1) TL 464.3–501.2 mm in adult males, 393.2–511 mm in females, (2) tail moderate, TaL/TL 0.20–0.26 in males, 0.19–0.22 in females, (3) internasal not in contact with loreal, prefrontal not touching supraocular, frontal touching preocular, (4) one preocular, one or two postocular(s), (5) temporals 1+1, (6) supralabials seven, the fourth and fifth in contact with eye; (6) maxillary teeth 16–18, (7) anterior pair of chin shields longer than or equal to posterior pair; (8) ventrals 170–189 (+ 2 preventrals) in males, 168–175 (+ 2 preventrals) in females, (9) subcaudals 76–98 in males, 69–84 in females, (9) nasal cleft pointing to the second supralabial, (10) body scale in 15–15–15 rows, (11) body scales smooth, tail scales smooth or indistinctly keeled, (12) chin shields yellow with brownish black mottling, and (13) body and tail dorsum dark, each with a light spot per scale.

Comparisons. *Opisthotropis hungtai* sp. nov. is compared with *O. maculosa* and *O. haihaensis*, which share a very similar appearance. Measurements, scalation and body proportions of *O. haihaensis* and *Opisthotropis hungtai* sp. nov. are listed in Table 3.

Opisthotropis hungtai sp. nov. differs from *O. maculosa* by prefrontal not touching supraocular (vs. prefrontal touching supraocular in *O. maculosa*), by frontal touching preocular (vs. frontal not touching preocular in *O. maculosa*), by fourth and fifth supralabials in contact with eye (vs. fourth supralabial in contact with eye in *O. maculosa*), by anterior pair of chin shields longer than or equal to posterior pair (vs. anterior pair of chin shields shorter than posterior pair in *O. maculosa*), by a higher number of subcaudals, 76–98 in males (vs. 67 in the single male holotype of *O. maculosa*), and by chin shields yellow with brownish black mottling (vs. immaculate in *O. maculosa*).

Opisthotropis hungtai sp. nov. differs from *O. haihaensis* by having seven supralabials, the second last one significantly enlarged, narrow and long, significantly wider than high (vs. eight supralabials, the second last one slightly enlarged, slightly wider than high in *O. haihaensis*) (Fig. 5), and MT 16–18 (vs. MT 22–24 in *O. haihaensis*).

Description of holotype. Body cylindrical, slender, round to oval in cross section; TL 501.2 mm (SVL 401.6 mm, TaL 99.6 mm); tail thin and pointed, TaL 20% of TL; head small, indistinct from neck; right upper maxilla with 16 subequal teeth or sockets, teeth small, curved, without diastema; rostral nearly flattened, small, slightly less than twice as broad as deep, barely visible from above; two internasals, crescent-shaped, in contact with each other medially behind the rostral, not in contact with loreal, posteriorly in contact with prefrontal; a single prefrontal, in contact with loreal and preocular laterally, with frontal posteriorly, not in contact with supraocular; a single frontal, hexagonal, in contact with supraocular laterally, with two parietals posteriorly; parietals large, in contact with each other medially; nasal directed dorsally, polygonal, in contact with first and second supralabials ventrally, with loreal and prefrontal posteriorly, with internasal dorsally, with rostral anteriorly; nostril horizontally oval, in the upper part of nasal; a short vertical cleft below the nostril and dividing nasal into anterior and posterior parts, pointing to middle of upper edge of second supralabial; a single loreal, trapezoid, not entering the orbit, in contact with second and third supralabials laterally; a single supraocular, much longer than wide, obliquely set; a single preocular, higher than wide, in contact with frontal; a single postocular; a single anterior temporal, significantly elongate, in broad contact with the elongated sixth supralabial; a single posterior temporal, pentagonal; supralabials 7/7, the sixth one significantly elongate, the last one much shorter than the adjacent preceding supralabial; fourth and fifth supralabials entering orbit; infralabials 7/7, the first one in contact with its fellow behind the mental; two pairs of chin shields; anterior chin

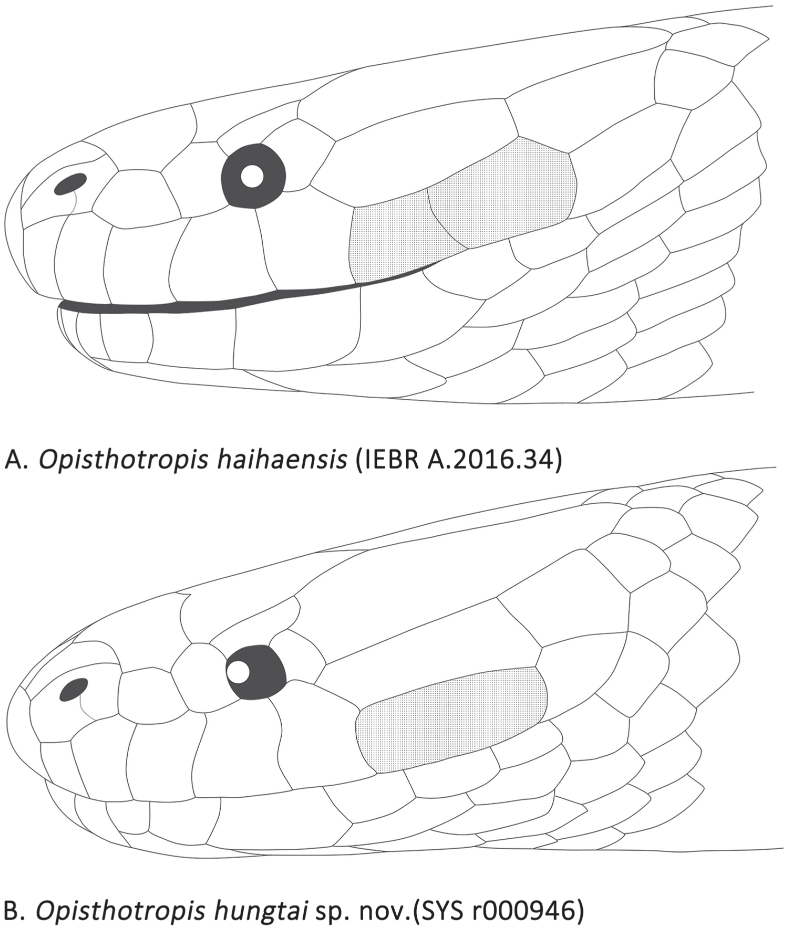

Figure 5. Comparisons of head scalation of *Opisthotropis haihaensis* and *Opisthotropis hungtai* sp. nov. Line illustration by Zhi-Tong Lyu.

shields larger, in contact with each other medially, and in contact with the first four infralabials on both sides; posterior chin shields smaller, in contact with each other; dorsal scales in 15–15–15 rows; dorsal scales of body smooth throughout; dorsal scales of tail weakly keeled; ventrals 170; cloacal plate divided; subcaudals 76, paired.

Coloration of holotype in life. Eye black; scales on dorsal surface of head glossy dark brown with scattered yellow flecking; chin shields yellow with brownish black mottling at each margin; body and tail glossy dark brown with single yellow spot on each scale, yellow spots becoming larger on sides of body; ventrals yellow with brownish black lateral margins and few scattered brown flecks; subcaudals yellow with brownish black anterior and lateral margins.

Coloration of holotype in preservative. Ground color of upper head and body surface dark brown (Fig. 4B), that of venter yellowish-beige. Dorsal scales each with

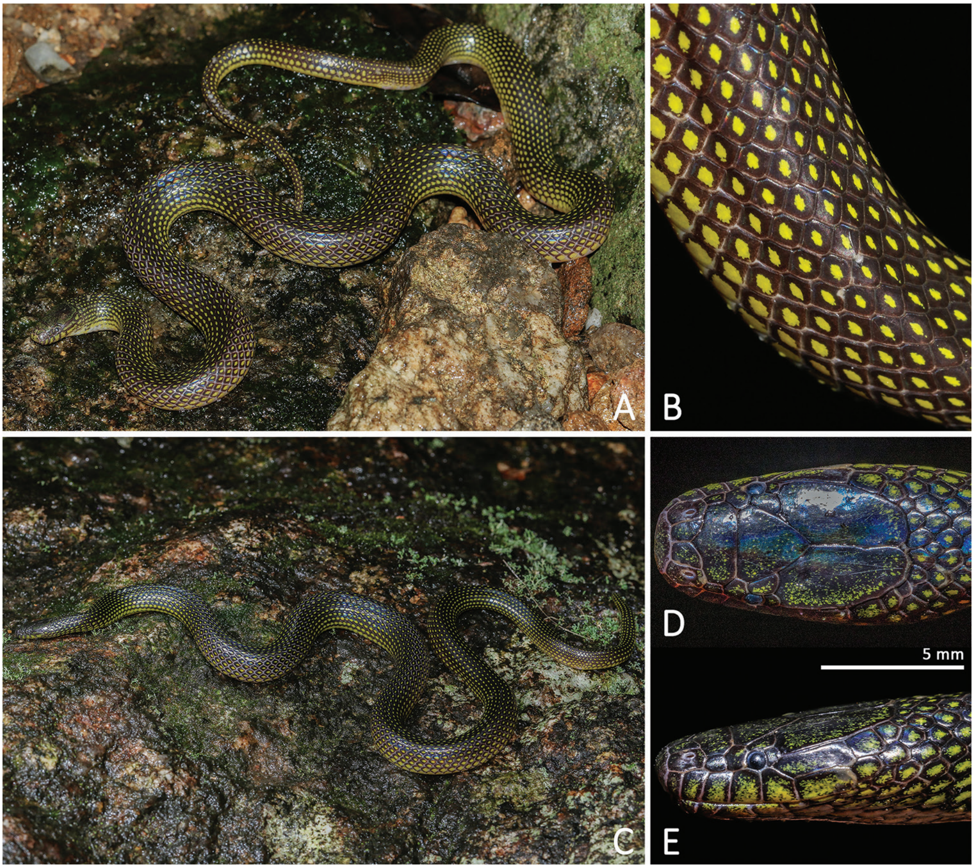

Figure 6. Morphological features of the adult female paratypes of *Opisthotropis hungtai* sp. nov. from Dawuling Forestry Station, Guangdong, China. **A, B** Habitus view and close-up of mid-dorsal body of SYS r001515 **C–E** habitus view and close-up of head scales of SYS r002017. Photos by Jian Wang.

light yellow blotch in the center. Dorsal blotches almost equal in size. Blotches becoming wider towards body sides; largest at outermost dorsal scale row, where the light blotches stretch towards the posterior scale end. Dorsal tail scales likewise with light central blotches. Dorsal head surface in part with indistinct light mottling that becomes more obvious on temporals. All supralabials with a light blotch. Infralabials, chin shields and smaller throat scales anterior to ventrals light yellow with brown mottling/blotches per scale. Belly with few, scattered dark flecks. Outermost edges of light ventrals brown. Ground color of subcaudals light yellow with black anterior and lateral margins.

Variations. Measurements, body proportions and scale counts are listed in Table 3. All paratype specimens are very similar to the holotype in appearance (Fig. 6) except: more maxillary teeth, ventrals and subcaudals, and relatively longer tail length in specimens KFBG 2002.01, SYS r001515, 2017 from Dawuling Forestry Station and SYS r000538 from Mt. Wuhuang; in the three female specimens from the same locality (Heishiding Nature Reserve) as the holotype, there are 17 maxillary teeth (vs. 16 maxillary teeth) and fewer subcaudals, 56 (broken tail) in SYS r000720, 69 in SYS r001350, 70 in SYS r001525 (vs. 76 in the male holotype).

Distribution and habits. *Opisthotropis hungtai* sp. nov. is currently known from Heishiding Nature Reserve (ca 300 m a.s.l.) and Dawuling Forestry Station (ca 900 m a.s.l.) in western Guangdong, and Mt. Wuhuang (ca 500 m a.s.l.) in southeastern Guangxi.

The specimen from Mt. Wuhuang was collected in a rocky stream. Besides, specimens from Heishiding Nature Reserve were found in pelitic gutterways along the dirt path, and specimens from Dawuling Forestry Station were collected in a pelitic stream. The collection sites were all surrounded by well-preserved, dense deciduous forest.

Discussion

As a representative snake group of the Oriental Realm, the mountain Keelback genus *Opisthotropis* receives more attention for its important role as an environmental indicator. Mountain Keelbacks are generally adapted to rocky forest streams (Wang et al. 2017a, b). However, species delimitations in this genus are still poorly resolved. The true diversity of *Opisthotropis* was underestimated, which is fatal for appropriate conservation of these habitat specialists. According to the integrative taxonomic approach, i.e., combining detailed morphological and molecular analyses, used in this study, the record of *O. maculosa* should be removed from the Chinese herpetofauna. So far, the true *O. maculosa* is restricted to northern Thailand, with only a single individual recorded. *Opisthotropis haihaensis* occurs in the mountain regions along the China-Vietnam border with only two female specimens recorded up to now, and *O. hungtai* is known only from the hilly regions between Guangxi and Guangdong of southern China. Extended surveys are urgently needed over the broad region from southern China to northern Thailand to investigate the distribution and the population status of these three species. Due to their beautiful color patterns, the snakes are in high demand in the animal trade market (Ziegler et al. 2019), and they must be evaluated for inclusion in one of the conservation categories in the IUCN Red List of Threatened Species.

The discovery of *Opisthotropis hungtai* sp. nov. brings the total number of species of *Opisthotropis* to 24. Nevertheless, with regard to recent phylogenetic results (Ren et al. 2017; Wang et al. 2017; Ziegler et al. 2019; this study), the relationships of clades within this genus still remain largely unresolved. As the mitochondrial CYTB gene is unable to generate significant support values, further work employing multilocus nuclear-gene and matrilineal mtDNA genealogy is recommended to decipher this puzzle. In addition, the similar appearance of *O. maculosa*, *O. haihaensis* and *O. hungtai*, together with their distant genetic divergence, indicates cryptic speciation in the genus *Opisthotropis*. The non-monophyletic relationships between *O. maculosa* and the clade composed of *O. hungtai* and *O. haihaensis* in our phylogenetic tree indicate that identical or similar phenotypes have evolved independently.

Key to the species included in *Opisthotropis maculosa* sensu lato

1	Prefrontal touching supraocular	***O. maculosa***
–	Prefrontal not touching supraocular	**2**
2	Supralabials eight, the second last one significantly enlarged; maxillary teeth 22–24	***O. haihaensis***
–	Supralabials seven, the second last one slightly enlarged; maxillary teeth 16–18	***O. hungtai***

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