

New species of *Trophoniella* from Shimoda, Japan (Annelida, Flabelligeridae)

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Abstract

Trophoniella hephaistos **sp. n.** was collected from a tank irrigated with seawater pumped directly from Nabeta Bay, Japan. This species is discriminated from other *Trophoniella* by having dorsal tubercles, a tongue-shaped branchial plate, a tunic covered with large sediment grains dorsally and ventrally, having eyes, and anchylosed neurohooks starting from chaetigers 17–20. This is the first record of *Trophoniella* from Japanese waters. Identification keys to species of *Trophoniella* and four gene sequences (*COI*, *16S*, *18S*, *28S*) of this species are provided. Phylogenetic analysis was conducted to clarify phylogenetic position of *Trophoniella* in Flabelligeridae using four genes.

Keywords

Nabeta Bay, Polychaeta, tank, taxonomy

Introduction

Trophoniella Hartman, 1959 belongs to the family Flabelligeridae and currently consists of 25 species and one undescribed species (Salazar-Vallejo 2012b). *Trophoniella* polychaetes live in sediments from shallow water to the deep sea in tropical or subtropical regions (Salazar-Vallejo 2012b). This genus is characterized by having anchylosed neurohooks in the median or posterior chaetigers, bidentate or bifid tips, a thick tunic, a tongue-shaped branchial lobe (except for *Trophoniella enigmatica*), and longitudinal rows of elongated single papillae along the body (Salazar-Vallejo 2012b). *Trophoniella* resembles *Piromis* and *Pycnoderma* in having a thick tunic, often with sediment grains, a tongue-shaped branchial lobe, and multiarticulated notochaetae. However, it is distinct from *Piromis* and *Pycnoderma* by having anchylosed neurohooks in the median or posterior chaetigers (Salazar-Vallejo 2011b).

Nine flabelligerid genera have been recorded from Japanese waters to date, i.e., *Brada*, *Buskiella*, *Daylithos*, *Diplocirrus*, *Flabelligera*, *Pherusa*, *Piromis*, *Semiodera*, and *Stylarioides* (Imajima 1964; Imajima 2006; 2009; Imajima and Hartman 1964; Miura 2014; Salazar-Vallejo 2011a; Salazar-Vallejo 2011b; 2012a, b; 2014; Salazar-Vallejo and Buzhinskaja 2011; Uchida 1992). However, *Trophoniella* was not recorded from Japan in previous studies.

Phylogenetic analyses of Flabelligeridae were conducted several times by using morphological and molecular data sets (Burnette et al. 2005; Osborn and Rouse 2008; 2011; Salazar-Vallejo et al. 2008). A morphological analysis suggested that *Trophoniella* was similar to *Piromis*. However, the molecular data was unable to robustly resolve the phylogenetic position of *Trophoniella*; this is likely an artefact of limited taxon sampling within the genus.

During benthos sampling in an aquarium in the Shimoda Marine Research Center (SMRC), University of Tsukuba, we collected undescribed species of *Trophoniella*. Here, we describe *Trophoniella hephaistos* sp. n. and cytochrome *c* oxidase subunit I (*COXI*), 16S ribosomal RNA (*16S*), 18S ribosomal RNA (*18S*), 28S ribosomal RNA (*28S*) gene sequences to contribute to the DNA barcoding of the Flabelligeridae. A phylogenetic analysis was conducted using four genes to clarify relationships of *Trophoniella* within the family Flabelligeridae. To the best of our knowledge, this is the first report of *Trophoniella* from Japanese waters.

Material and methods

Worms were collected by hand from a tank (MF-5000S, aquaculture system, Japan. 2.4 m in diameter and 1.1 m in depth) installed in the SMRC, University of Tsukuba, Shizuoka (34°40.045'N; 138°56.145'E) (Fig. 1). The tank contained sandy mud and sea water and the worms lived between 0 and 30 cm below the sediment surface. Seawater in the tank was drawn only from Nabeta Bay, directly in front of the SMRC, from a depth of 3 m (location of the head gate: 34°39.950'N; 138°56.283'E). Several samplings



Figure 1. Sampling location of *Trophoniella hephaistos*. Worms were collected from a tank continuously irrigated with seawater pumped directly from Nabeta Bay at a depth of 3 m.

were conducted in Nabeta Bay and other surrounding sites at depths between 2 and 386 m by the first author and members of the SMRC but there was no individual of *Trophoniella* discovered except in the tank. All the specimens were first anesthetized with menthol and then fixed and preserved in 70% ethanol. The anesthesia duration differed among samples. Preserved specimens were observed under stereoscopic MZ 16F (Leica, Germany) and E600 (Nikon, Japan) microscopes. All specimens were deposited in the National Museum of Nature and Science, Tokyo (NSMT), Japan.

Genomic DNA was extracted from a small piece of the epidermal tissue of the holotype (NSMT-Pol-H-601) using the DNeasy Blood & Tissue Kit (Qiagen, USA) following the manufacturer's protocol. Partial cytochrome *c* oxidase subunit I (*COXI*), 16S ribosomal RNA (*16S*), 18S ribosomal RNA (*18S*), 28S ribosomal RNA (*28S*) gene sequences were amplified in the polymerase chain reaction (PCR) with the primer sets of polyLCO (5'-GAYTATWTTCAACAAATCATAAAGATATTGG-3') and polyHCO (5'-TAMACTTCWGGGTGACCAAARAATCA-3') (Carr et al. 2011), 16SarL (CGCCGTTTATCAAAAACAT) and 16SbrH (CCGGTCTGAACTCAGATCACGT) (Palumbi et al. 1991), mitchA (CAACCTGGTTGATCCTGCCAGT) and mitchB (TGATCCTTCCGCAGGTTACCTAC) (Medlin et al. 1988), and LsudiF (ACCCGCTGAATTTAAGCATA) and D3aR (ACGAACGATTTGCACGTCAG)

Table 1. List of flabelligerid, acrocirrid, and cirratulid species included in the phylogenetic analysis, together with accession numbers in GenBank.

Taxon	18S	28S	COI	16S	Collection site	Reference
Flabelligeridae						
<i>Brada villosa</i>	EU791460	EU791462	–	HQ326962	Vattenholmen, Sweden	Osborn and Rouse (2008)
<i>Brada</i> sp.	HQ326967	HQ326968	HQ326970	HQ326963	Central California, USA	Osborn and Rouse (2011)
<i>Buckiella</i> sp.	EU694116	EU694110	EU694128	EU694110	Monterey, California, USA	Osborn and Rouse (2008)
<i>Diplocirrus glaucus</i>	AY708534	DQ790031	–	–	Gullmarsfjorden, Sweden	Struck et al. (2007)
<i>Flabegavierna mundata</i>	HQ326964	–	HQ326969	HQ326958	South Orkney Islands, Antarctica	Osborn and Rouse (2011)
<i>Flabelliderma ockeri</i>	EU694119	–	EU694127	EU694111	La Jolla, California, USA	Osborn and Rouse (2008)
<i>Flabelligera affinis</i>	–	DQ779688	–	DQ779614	Iceland	Rousset et al. (2007)
<i>Flabelligera infundibularis</i>	EU694118	–	EU694131	EU694112	Astoria, Oregon, USA	Osborn and Rouse (2008)
<i>Flabesymbios commensalis</i>	HQ326965	–	–	HQ326959	Malibu, California, USA	Osborn and Rouse (2011)
<i>Pherusa plumosa</i>	AY708528	DQ790056	–	–	Central California, USA	Struck et al. (2007)
<i>Piromis</i> sp.	–	–	–	HQ326961	Santa Monica, California, USA	Osborn and Rouse (2011)
<i>Poecobius meseres</i>	EU694115	EU694123	EU694130	–	Monterey, California, USA	Osborn and Rouse (2011)
<i>Stylarioides</i> sp.	HQ326966	–	HQ326971	HQ326960	Spencer Gulf, South Australia	Osborn and Rouse (2011)
<i>Therochaeta</i> sp.	AY708527	–	–	–	Woods Hole, Massachusetts, USA	Burnette et al. (2005)
<i>Trophoniella hephaistos</i>	LC152761	LC152762	LC136932	LC152760	Shimoda, Shizuoka, Japan	This study
Acrocirridae						
<i>Flabelligera</i> sp.	EU694120	EU694121	EU694126	EU694113	Pacific Antarctic Ridge	Osborn and Rouse (2008)
<i>Suina bombiviridis</i>	GQ422143	GQ422144	FJ944527	FJ944506	Monterey, California	Osborn et al. (2009)
Cirratulidae						
<i>Cirratulus cirratus</i>	DQ779645	DQ779683	–	DQ779609	Iceland	Osborn et al. (2007)
<i>Ctenodrilus serratus</i>	AY340426	AY340388	–	–	Massachusetts, USA	Rousset et al. (2007)

(Lenaers et al. 1989) , respectively. The reaction mixture [0.25 µl TaKaRa Ex Taq (Takara, Japan), 5 µl of 10 × Ex Taq Buffer (Takara, Japan), 4.0 µl dNTP mixture (Takara, Japan), 5 µl of each primer pair (10 µM), 0.75 µl of extracted DNA, and 35 µl of distilled water] was used for amplification. The PCR protocol for *COX1* consisted of an initial denaturation step at 94 °C for 1 min, followed by 35 cycles of 30-s denaturation at 94 °C, 60-s annealing at 50 °C, and 1-min extension at 72 °C, and a final extension at 72 °C for 10 min. The PCR protocols for *16S*, *18S*, *28S* were followed an previous study (Osborn and Rouse 2011). To confirm successful amplification, PCR products were visualized using 1.2 % Agarose S (Nippon Gene, Japan) gel electrophoresis. The DNA sequencing reaction of the PCR products was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA). Direct sequencing was performed using the 3130xl Genetic Analyzer (Applied Biosystems, USA). Sequencing reactions were conducted using the 1-µM primers applied for the PCR amplification. The newly obtained sequences were deposited in the DNA Data Bank of Japan (DDBJ) (accession nos. LC136932, LC152760, LC152761, and LC152762).

Additional sequences of Flabelligeridae, Acrocirridae, Cirratulidae were obtained from GenBank (following Osborn and Rouse (2011)) (Table 1). All sequences were aligned using Mafft ver. 7.205 under the E-INS-i strategy (Katoh and Standley 2013). Alignment-ambiguous positions were removed using trimAL under the gappy strategy (Capella-Gutiérrez et al. 2009). Kakusan recommended a GTR+G evolutionary model for each of the genes (Tanabe 2007), a phylogenetic tree was constructed using maximum likelihood (ML) methods in the program RAxML-VI-HPC (Stamatakis 2006). The robustness of the ML tree was evaluated by 1,000 bootstrap replicates (-f option).

Results

Systematics

Family Flabelligeridae de Saint-Joseph, 1894

Genus *Trophoniella* Hartman, 1959

New Japanese name: Yoroi-habouki-zoku

Trophoniella hephaistos sp. n.

<http://zoobank.org/5A3B2B5C-655E-41CF-B877-31FDFA955E84>

New Japanese name: Shimoda-yoroi-habouki

Figs 2–5

Material examined. Holotype. No. NSMT-Pol-H-601 Incomplete, posterior end absent. Unknown sex, non-reproductive adult, body length 9.0 cm, body width 0.3 cm, 103 chaetigers, 24 September 2015, collected by N. Jimi, tank of the SMRC, sandy mud.

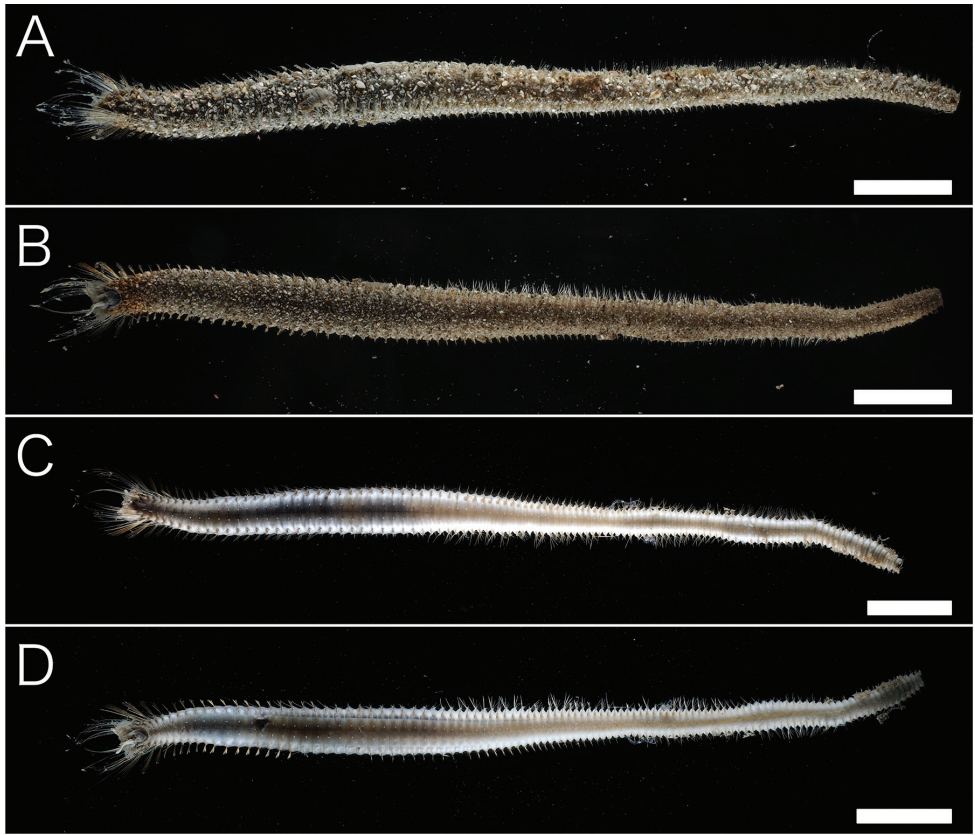


Figure 2. *Trophoniella hephaistos* (holotype: No. NSMT-Pol-H-601). **A** Dorsal view **B** ventral view **C** dorsal view without sediment particles **D** ventral view without sediment particles. Scale bar: 1 cm.

Paratypes. No. NSMT-Pol-P-602. Complete, two specimens. Unknown sex, non-reproductive adult, body length 10.2–11.2 cm, body width 0.4–0.5 cm, 129–141 chaetigers, 24 September 2015, collected by N. Jimi, tank of the SMRC, sandy mud. No. NSMT-Pol-P-603. Incomplete, posterior body absent, nine specimens. Unknown sex, non-reproductive adult, body width 0.4–0.5 cm, 24 September 2015, collected by N. Jimi, tank of the SMRC, sandy mud. No. NSMT-Pol-P-604. Incomplete, posterior body absent, one specimen. Unknown sex, body width 0.3 cm, 26 November 2014, collected by N. Jimi, tank of the SMRC, sandy mud.

Diagnosis. Body covered by large sediment grains dorsally, ventrally, and laterally, without posterior region. Sediment grains not immersed in the tunic. Papillae arise in four rows ventrally and two rows dorsally from first chaetiger to posterior end, longitudinal rows. Tongue-shaped branchial plate. Paired black eyes on center of prostomium. Anchylosed bidentate neurohooks start from chaetiger 17–20, accessory tooth length same as fang.

Description. Body length 10.2–11.2 cm (complete specimens), width 0.3–0.7 cm, 129–141 chaetiger (complete specimens). Body white in ethanol, cylindrical anteriorly

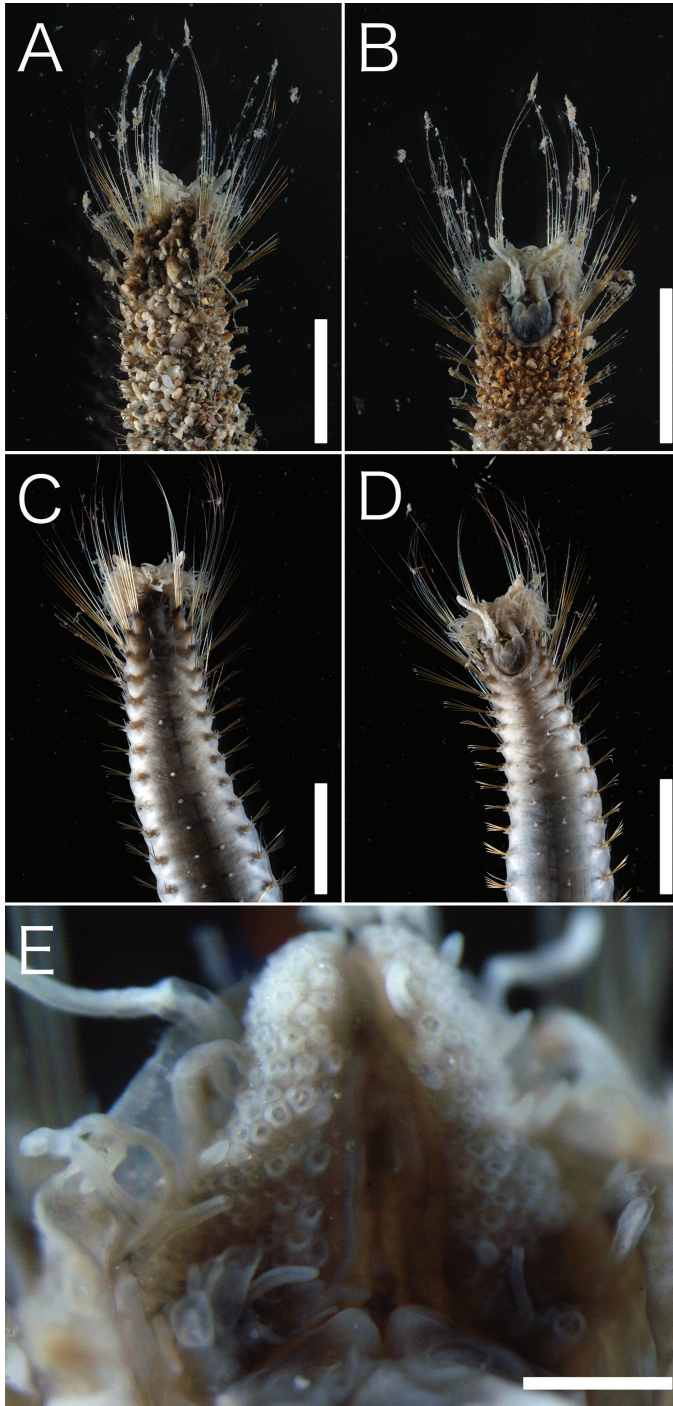


Figure 3. *Trophoniella hephaistos* (holotype: No. NSMT-Pol-H-601). **A** Anterior dorsal view **B** anterior ventral view **C** anterior dorsal view without sediment particles **D** anterior ventral view without sediment particles **E** branchial plate without branchiae and palps. Scale bar: 5 mm (**A, B, C, D**); 0.5 mm (**E**).

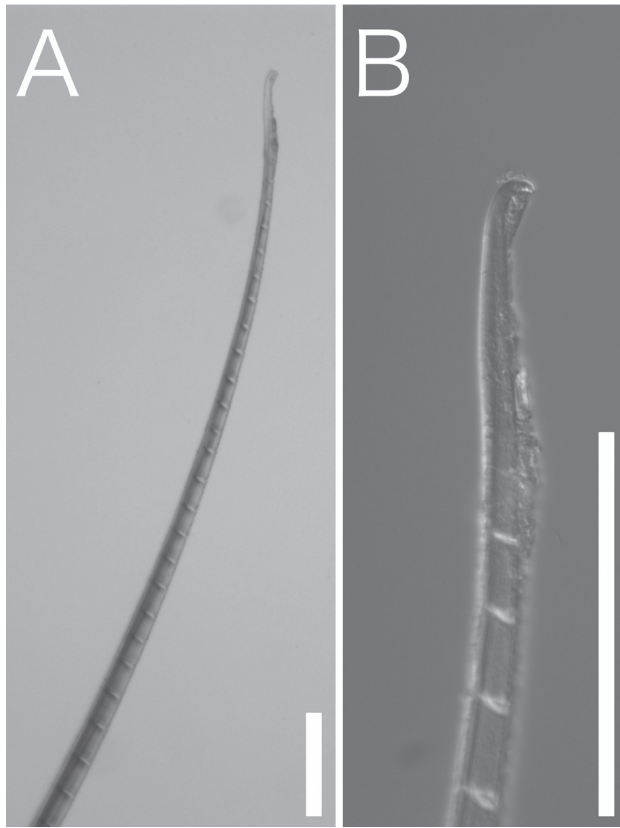


Figure 4. *Trophoniella hephaistos* (holotype: No. NSMT-Pol-H-601). Stereoscopic micrographs of **A** chaetiger 35, notochaeta **B** tip of (**A**). Scale bar: 100 μ m.

and tapering posteriorly (Fig. 2). Tunic thick, papillated, with large sediment grains dorsally, ventrally, and laterally (Figs 2A, B, 3A, B), without posterior end region. Sediment grains with long axes of 70–1000 μ m, contain sand and shell fragments, not immersed in the tunic. Papillae capitate, sparse, arise in four rows ventrally and two rows dorsally from first chaetiger to posterior end, longitudinal rows. Dorsal 1–6 and ventral 1–3 chaetiger's papillae are large. Cephalic cage chaetae approx. 1.5 times longer than body width. Chaetiger 1–5 involved in cephalic cage, chaetiger 1 dorsolateral, and chaetiger 2–3 lateral. Chaetal transition from cephalic cage to body chaetae gradual. Chaetiger 1 has about 9 notochaetae and 7 neurochaetae. Anterior dorsal margin of first chaetiger arise multifid lobe (Fig. 3C). Cephalic hood margin papillated, thin, transparent. Caruncle well developed, reaching the end of the tongue-shape branchial plate. Branchia arise from tongue-shaped branchial plate (Fig. 3E), thin, long (0.5–2 mm), green in live, white in ethanol, over 100 filaments arise from two groups (Fig. 3B, D). One pair palps, green in alive, white in ethanol, cylindrical, grooved, long (2 mm in length) (Fig. 3B, D). Prostomium low-cone, paired black eyes on center. Notochaeta all multiarticulated capillaries with articles, bidentate (Fig. 4A, B). Multiarticulated capil-

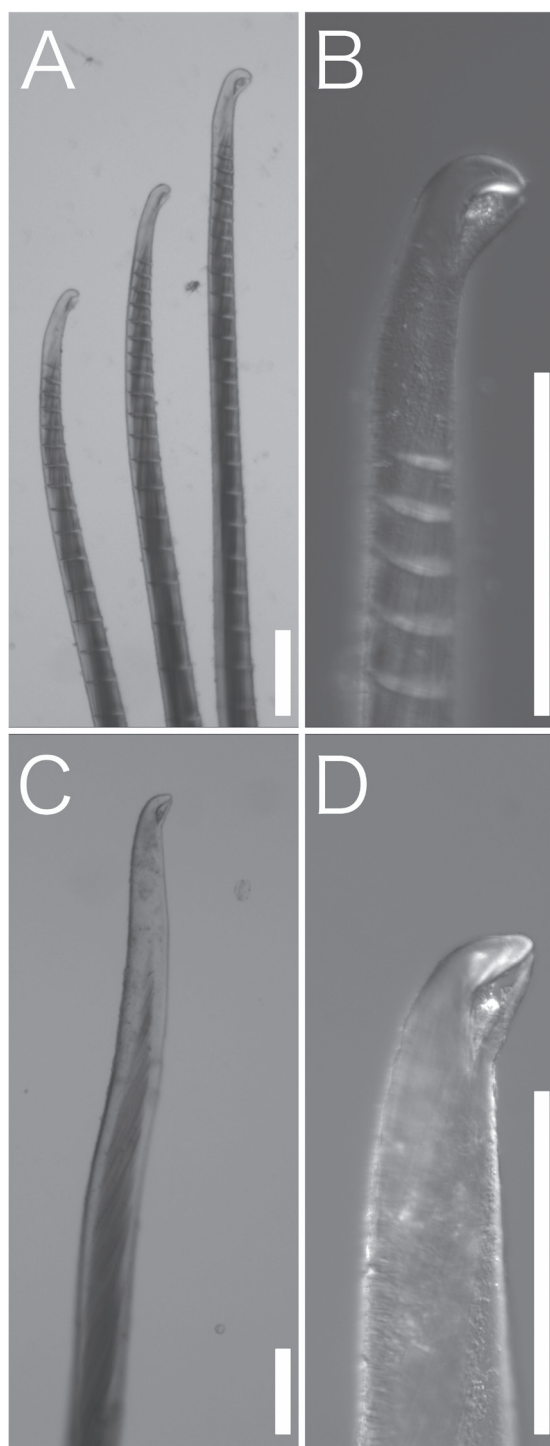


Figure 5. *Trophoniella hephestos* (holotype: No. NSMT-Pol-H-601). Stereoscopic micrographs of **A** chaetiger 16, neurochaeta **B** tip of (**A**) **C** chaetiger 35, neurochaeta **D** tip of (**C**). Scale bar: 100 µm.

lary neurochaeta in chaetiger 1, chaetiger 2–16 bidentate neurohooks (Fig. 5A, B). Anchylosed bidentate neurohooks start from chaetiger 17–20 (Fig. 5C, D), yellow, bidentate. Accessory tooth thin, length same as fang. Parapodia poorly developed, chaetae arise from body wall. Noto- and neuropodia have two prechaetal papillae and three postchaetal papillae. Gonopodial lobe absent. Pygidium simple, no anal cirri.

Etymology. The worm is coated with sediment particles, resembling armor. Hephaistos (Ἡφαίστος) was the name of the ancient Greek god of blacksmiths who forged the armor worn by Achilles. Hephaistos is also spelled Hephaestus. The Japanese name is derived from the type locality (Shimoda), Japanese armor (Yoroi), and flabelligerids in Japanese (Habouki).

Distribution. This new species is currently only known from the tank of the type locality. The seawater in the tank was drawn only from Nabeta Bay from a depth of 3 m directly facing the SMRC. The natural habitat of this species remains unknown. Due to the location of the head gate, *T. hephaistos* could be a shallow-water species. However, several sublittoral (~50–60 m) invertebrates were collected from this tank (Dr. Hiroaki Nakano, pers. comm.). Additional sampling efforts in Nabeta Bay will clarify the natural habitat of this species.

Phylogenetic analysis. The final lengths of the aligned sequences were 669 bp (*COXI*), 485 bp (*16S*), 1893 bp (*18S*), and 910 bp (*28S*). The bootstrap value of 98% in ML analysis strongly supported the monophyly of Flabelligeridae, but internal relationships of Flabelligeridae were not resolved (Fig. 6). The sister group of *Trophoniella* was *Piromis*. The bootstrap value in ML analysis (100%) demonstrated the monophyly of this clade (Fig. 6).

Remarks. *Trophoniella hephaistos* sp. n. resembles *T. enigmatica* Salazar-Vallejo, 2012 and *Trophoniella indica* (Fauvel, 1928) in having dorsal tubercles at the anterior chaetigers, a tunic covered with large sediment grains dorsally and ventrally, and anchylosed neurohooks starting from chaetiger 14 or posterior. However, *T. hephaistos* is discriminated by the presence of anchylosed neurohooks starting from chaetigers 17–20, whereas those of *T. enigmatica* start from chaetiger 40, and of *T. indica* from chaetiger 14. Additionally, *T. enigmatica* does not have a tongue-shaped branchial plate and *T. indica* does not have eyes. Chaetiger number of *T. hephaistos* was more than twice as many as that of *T. indica*. *Trophoniella hephaistos* has dorsal body papillae in two longitudinal rows, whereas *T. enigmatica* in three and *T. indica* in five.

Trophoniella hephaistos also resembles *Trophoniella avicularia* Caullery, 1944 and *Trophoniella harrisae* Salazar-Vallejo, 2012 in having anchylosed neurohooks starting from chaetigers 18–20. *Trophoniella hephaistos* also has dorsal tubercles in the anterior chaetigers, while *T. avicularia* does not. *Trophoniella harrisae* has sediment particles only on its dorsal area, whereas *T. hephaistos* has particles on both its dorsal and ventral areas.

The phylogenetic analysis showed *Trophoniella* to be the closest relative of *Piromis* in Flabelligeridae supported by a high bootstrap value (See Fig. 6). Our findings are consistent with previous morphological studies that indicated a close relationship between *Trophoniella* and *Piromis* based on their shared characters such as tongue-shaped lobe, multiarticulated notochaeta, and thick tunic (Salazar-Vallejo 2011b; Salazar-Vallejo et al. 2008).

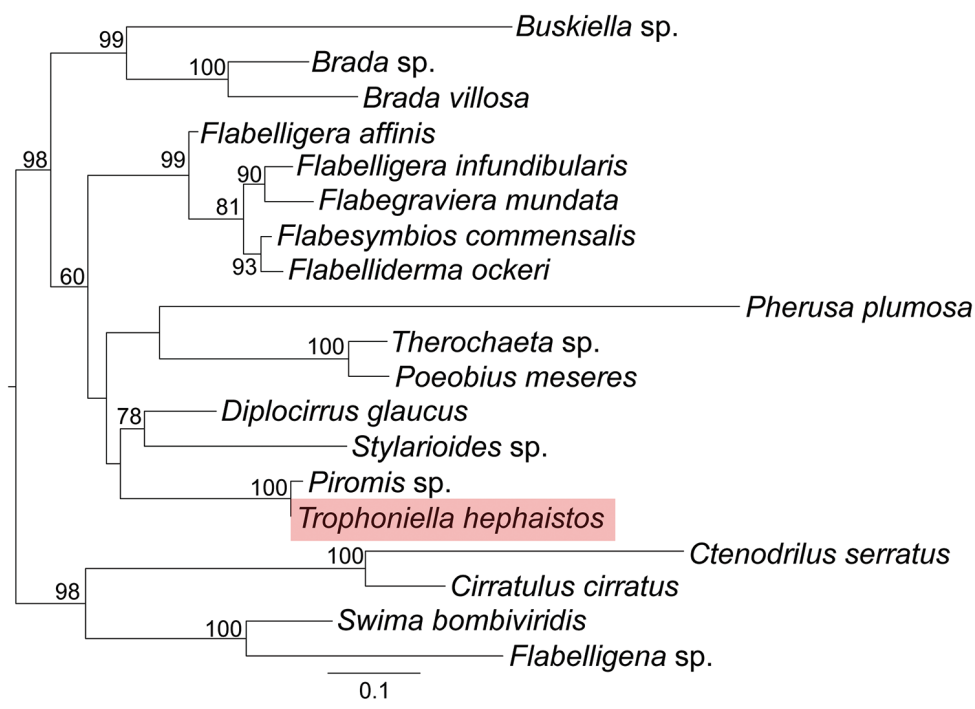


Figure 6. Maximum-likelihood (ML) phylogenetic tree of Flabelligeridae based on *COXI*, *16S*, *18S*, *28S* sequences. *Ctenodrilus serratus*, *Cirratulus cirratus*, *Swima bombiviridis*, *Flabelligena* sp. were used as an outgroup. Nodal support values (bootstrap support value) higher than 50% are indicated on each branch.

Key to species of the genus of *Trophoniella*

The key by Salazar-Vallejo (2012b) is amended with the addition of this new species at couplet 20.

- 19 Anchylosed neurohooks from chaetiger 14; neurohooks with accessory tooth longer than fang, eyes absent..... ***T. indica* (Fauvel, 1928)**
- Anchylosed neurohooks from chaetiger 17, or from posterior chaetigers; neurohooks with accessory tooth about as long as fang, eyes present..... **20**
- 20 Anchylosed neurohooks from chaetiger 17–20; Branchial plate tongue-shaped ***T. hephaistos* sp. n.**
- Anchylosed neurohooks from chaetiger 40; Branchial plate not tongue-shaped ***T. enigmatica* Salazar-Vallejo, 2012**

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A new species of *Websterinereis* from the Gulf of California and redescription of *Websterinereis foli* (Fauvel, 1930) (Annelida, Nereididae)

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Abstract

A new species of *Websterinereis* Pettibone, 1971, *W. pettiboneae* **sp. n.** is described from La Paz Bay, Gulf of California, Mexico. This species is similar to *W. foli* (Fauvel, 1930) in the neuropodial falcigers shape, but can be separated by the tentacular cirri length, notopodial prechaetal lobe shape, and the size of the notopodial dorsal and ventral ligules on posterior parapodia. *Websterinereis foli* is redescription based upon type material. Additional observations on the inter-annual density variation of *W. pettiboneae* **sp. n.** during a four-year study are also provided. A key to all species of *Websterinereis* is included.

Keywords

Mexico, Nereididae, new species, polychaetes, taxonomy

Introduction

The family Nereididae de Blainville, 1818 comprises 44 genera which can be separated by a number of characters associated with the eversible pharynx and parapodial structures. *Eunereis* Malmgren, 1965 and *Websterinereis* Pettibone, 1971 are very similar to

each other because the pharynx in both has papillae on the oral ring, and there are no paragnaths or papillae on the maxillary ring. These genera can be separated because *Eunereis* has notopodial homogomph falcigers whereas *Websterinereis* presents only notopodial homogomph spinigers. *Websterinereis* was established by Pettibone (1971) and includes four previously described species: *W. foli* (Fauvel, 1930) from New Caledonia and the Marshall Islands, Pacific Ocean (Reish 1968), *W. glauca* (Claparède, 1870) from England and along the French Atlantic coast, *W. tridentata* (Webster, 1879) from the east coast of the United States, and *W. punctata* (Wesenberg-Lund, 1949) from the Persian Gulf. Most of the records of *Websterinereis* species are restricted to the type locality; the only species with a wider record is *W. glauca*. These species can be separated into two groups by the presence of anchylosed chaetae, apparently formed by fusion of the blade to the handle. In *W. punctata* anchylosed chaetae are bifid and restricted to the supra-acicular fascicle of median and posterior neuropodia; in the epitokes of *W. glauca* there are one or two dark unidentate anchylosed chaetae in a supra-acicular position on the posterior neuropodia. It is noteworthy that in *W. tridentata* (type species for the genus) and *W. foli* there are no anchylosed chaetae; *W. foli* has falcigers with short blades in comparison with those present in *W. tridentata*, however, a few falcigers of these two species give the appearance of being simple because of blade loss. Of all the described species only *W. glauca* has reduced notopodial prechaetal lobes present as low ridges, while the other species have larger, more developed lobes, at least in the anterior parapodia.

In this contribution a new species of *Websterinereis* is described which had previously been confused with *W. foli* due to the morphological similarity of their compound falcigers. In order to further clarify the taxonomic status of this taxon, a re-description of *W. foli* is provided based on type material. An additional comment on inter-annual density variation, observed during a four-year study, is given for the new species of *Websterinereis*.

Methods

Specimens of the new species were collected during a long-term study of coral reef recuperation following a tanker vessel grounding in San Lorenzo Channel, La Paz Bay, in the south-western Gulf of California, Mexico. In 2001 thirty concrete and rock, artificial-reef structures were deployed on the bottom of the grounding site. Later, live fragments of the coral *Pocillopora* spp. were attached over the artificial reef surfaces. From 2004 to 2009 a seasonal monitoring survey was carried out aimed at evaluating the structural and ecological recovery of the restored site (Balart et al. 2010). It included samplings of rocky benthic infauna in ten of the artificial reef structures as a proxy for benthic reef community recovery. An area of 0.20×0.20 m on a lateral wall in each structure was sampled (0.04 m^2 ; total sampled area by survey 0.4 m^2). This area was fragmented with chisel and hammer and the fragments transferred to polyethylene bags *in situ*. Sorting and taxonomic analysis of formalin-fixed worm material

was performed in the Laboratory of Biosystematics (UANL). All identified specimens were deposited in the Polychaete Collection of the Universidad Autónoma de Nuevo León (UANL). Paratypes were deposited in the Los Angeles County Museum, USA. Terminology of parapodial structures used in this work was taken from the proposed by Bakken and Wilson (2005), elaborated on the basis of previous proposals used by several authors including Hylleberg et al (1986), Hutchings and Reid (1990) and Wilson et al. (2003).

The mean density (individual per m²) of the ten artificial reef structures sampled per survey was used to evaluate the variation in abundance of the new species of *Websterinereis* throughout the study period. Relationships between density data and environmental variables were also analyzed.

Systematic account

Family Nereididae de Blainville, 1818

Genus *Websterinereis* Pettibone, 1971

Websterinereis Pettibone, 1971: 19.

Type species. *Nereis tridentata* Webster, 1879, by original designation.

Diagnosis. Prostomium sub-pyriform to pentagonal, one pair of frontal antennae, a pair of globose biarticulate palps, and two pairs of eyes of different shape. Peristomium with four pairs of short tentacular cirri. Pharynx with pair of jaws. Maxillary ring unarmed, oral ring with papillae on areas VI and VII-VIII. First two parapodia uniramous, remainder biramous. Notopodium represented by dorsal cirri with dorsal and median ligulae, notopodial prechaetal lobe present on anterior parapodia. Neuropodium with superior and inferior lobe forming prechaetal area; postchaetal lobe subulate to triangular, ventral ligule generally subulate. Ventral cirri short. Notochaetae homogomph spinigers; neurochaetae homogomph and heterogomph spinigers and heterogomph falcigers, those in posterior parapodia with short to long blades; ankylosed chaetae may be present. Pygidium with pair of anal cirri.

Websterinereis pettiboneae sp. n.

<http://zoobank.org/B1311381-9CA7-4F61-8217-8D15EB4823A4>

Figs 1, 2

Type material. Holotype (UANL 7845) and 3 Paratypes (LACM-AHF Poly 9104), San Lorenzo Channel, La Paz Bay, Gulf of California, Mexico, Stn 12 (24°23'11.4"N, 110°18'55.5"W), July 2006.

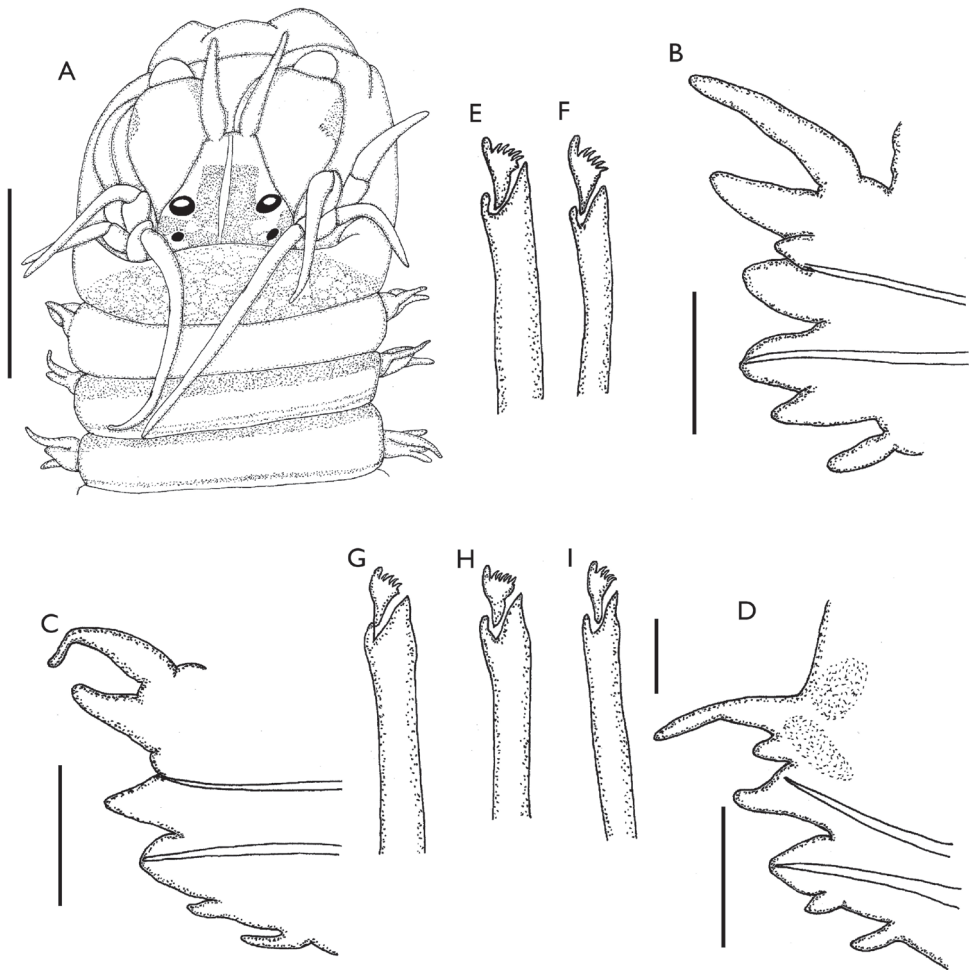


Figure 1. *Websterineris pettiboneae* sp. n. **A** Anterior end, dorsal view **B–D** Parapodia of chaetigers 10, 26 and 42, anterior view **E** Supra-acicular neuropodial heterogomph falciger, chaetiger 10 **F** Infra-acicular neuropodial heterogomph falciger, chaetiger 10 **G** Supra-acicular neuropodial heterogomph falciger, chaetiger 26 **H** Infra-acicular neuropodial heterogomph falciger, chaetiger 26 **I** Supra-acicular neuropodial heterogomph falciger, chaetiger 42. Scale bars: **A** = 0.5 mm; **B–D** = 100 µm; **E–I** = 10 µm.

Additional material. Lorenzo Channel, La Paz Bay, Gulf of California, Mexico, (2 specimens), Stn 28 (24°23'12"N, 110°18'55.1"W), April 2006; (1 specimen), Stn 5 (24°23'12.2"N, 110°18'55.1"W), July 2006; (2 specimens), Stn 27 (24°23'12"N, 110°18'54.9"W), July 2006; (1 specimen), Stn 1 (24°23'12.8"N, 110°18'54.2"W), October 2006; (4 specimens, 2 epitokes), Stn 3 (24°23'12.8"N, 110°18'54.8"W), October 2006; (1 specimen), Stn 5 (24°23'12.2"N, 110°18'55.1"W), October 2006; (12 specimens), Stn 9 (24°23'11.7"N, 110°18'55.4"W), October 2006; (1 epitokous specimen), Stn 12 (24°23'11.4"N, 110°18'55.5"W), October 2006; (1 specimen), Stn 13 (24°23'11.5"N, 110°18'54.8"W), October 2006; (3 specimens),

Stn 3 (24°23'12.8"N, 110°18'54.8"W), 3 October 2007; (3 specimens), Stn 9 (24°23'11.7"N, 110°18'55.4"W), 3 October 2007; (1 specimen), Stn 13 (24°23'11.5"N, 110°18'54.8"W), 3 October 2007.

Description. Holotype complete with restricted blackish pigmentation (Fig. 1A); prostomium with anteriorly truncate, extended dark area, leaving pale mid-dorsal thin band, not reaching anterior prostomial margin; palpophores with some pigmentation over external, subdistal surfaces; tentacular segment with continuous dorsal transverse wide band, reduced to progressively thinner bands along anterior and posterior segmental margins.

Body 12 mm long, 0.8 mm wide including parapodia, with 60 chaetigers. Prostomium subpyriform, longer than wide. Two pairs of black oval eyes in rectangular arrangement, distal pair with larger lens than proximal pair. Antennae tapered, extended beyond tips of palpostyles. Palps and palpostyles globose. One apodous anterior segment, 1.5 times longer than first chaetiger. Tentacular cirri short, tapered, longest reaching chaetiger 3 (Fig. 1A).

Pharynx with brown jaws, each with six teeth. Maxillary ring lacking paragnaths or papillae; oral ring with subconical papillae in area VI, and five globose papillae in line along areas VII–VIII.

Parapodia of first two chaetigers uniramous, remainder biramous. In anterior parapodia notopodia with subulate dorsal ligules, notopodial prechaetal lobes short triangular, and ventral ligules subtriangular, rounded distally; neuropodia with postchaetal lobes distally rounded, superior and inferior lobes not distinct, ventral ligules subulate. Dorsal cirri inserted basally, four times longer than ventral cirri, and 1.4 times than notopodial dorsal ligule (Fig. 1B). Median parapodia with digitiform dorsal ligules, notopodial prechaetal lobes reduced to small ridge; ventral ligules triangular; neuropodial postchaetal lobes subconical, ventral ligules reduced to small subulate protuberance. Dorsal cirri three times longer than ventral cirri (Fig. 1C). Posterior parapodia with dorsal ligules reduced, half as long as those of median parapodia, notopodial prechaetal lobes absent, ventral ligules triangular; neuropodial postchaetal lobes subtriangular, ventral ligules reduced, conical. Dorsal cirri 2.5 times longer than ventral cirri, with red pigmented glandular areas (Fig. 1D).

Anterior parapodia with notochaetae represented by four supra-acicular homogomph spinigers; supra-acicular neurochaetae include two homogomph spinigers and two heterogomph falcigers with thick handle and short triangular blade (Fig. 1E); infra-acicular neurochaetae represented by five heterogomph falcigers (Fig. 1F). Median parapodia with supra-acicular notochaetae represented by two supra-acicular homogomph spinigers; supra-acicular neurochaetae include two homogomph spinigers and one heterogomph falciger with thick handle and short triangular blade (Fig. 1G), infra-acicular neurochaetae represented by four heterogomph falcigers (Fig. 1H). Posterior parapodia with notochaetae represented by two supra-acicular heterogomph spinigers; supra-acicular neurochaetae with a single heterogomph falciger (Fig. 1I); infra-acicular neurochaetae three heterogomph falcigers, similar to supra-acicular falcigers.

Pygidium with terminal anus and two anal cirri.

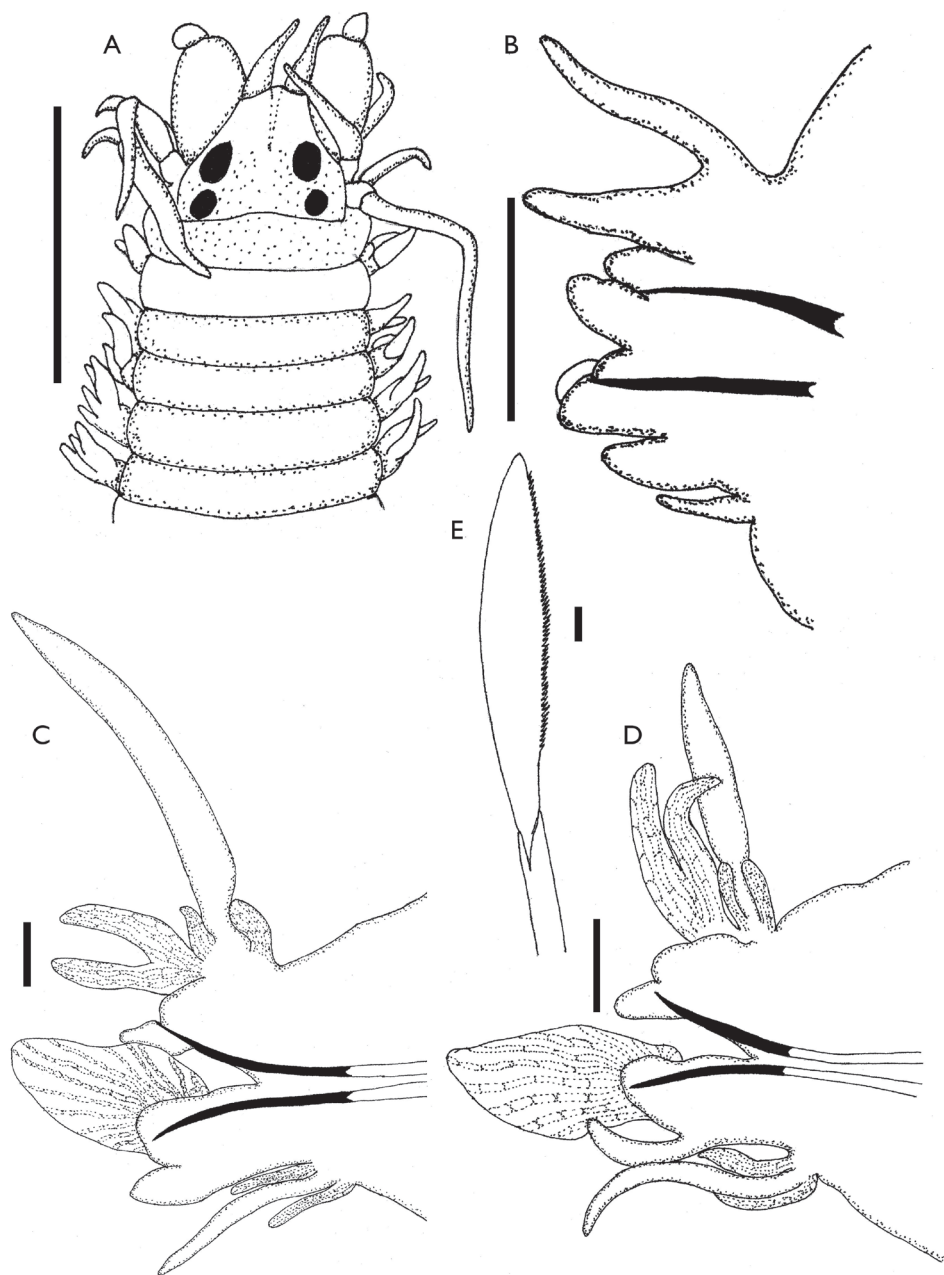


Figure 2. *Websterineris pettiboneae* sp. n. (epitoke). **A** Anterior end, dorsal view **B–D** Parapodia of chaetigers 10, 30 and 43, anterior view **E** Natatory chaeta. Scale bars: **A** = 0.5 mm; **B–D** = 100 μ m; **E** = 10 μ m.

Epitokous female. Best preserved specimen with 64 chaetigers, 9 mm long and 0.5 mm wide (excluding parapodia). Prostomium pentagonal, wider than longer, with frontal median dorsal groove. Antennae minute, shorter than anterior end of

palpi. Two pairs of eyes in trapezoidal arrangement, anterior pair enlarged, oval in shape, posterior pair rounded in shape. Biarticulate palps globose, each with spherical palpostyle. Tentacular ring with four pairs of tentacular cirri, posterodorsal pair extending back to anterior margin of sixth chaetiger (Fig. 2 A). Pharynx equal to non-epitokous specimens.

Body divided into unmodified anterior region and a heteronereidid region; parapodia of first 19 chaetigers similar of those of atokous specimens (Fig. 2B). Parapodia of heteronereidid region moderately compressed. Notopodia formed by dorsal cirrus accompanied by two basal lobes, a small notopodial dorsal ligule, and subulate ventral ligule; with two enlarged postchaetal lobes. Neuropodia with superior and inferior lobes fused, foliose postchaetal lamellae present; neuropodial ventral ligule subtriangular in median parapodia and digitate in posterior parapodia. Ventral cirri long and thin, accompanied by two basal lobes (Fig. 2C–D). Last eleven chaetigers unmodified. Normal chaetae replaced on chaetigers 20 by natatory chaetae with broad, paddle-shaped appendages, inner margin slightly denticulate (Fig. 2E). Anterior parapodia with four homogomph spinigers in notopodial supra-acicular position; neuropodia with three supra-acicular homogomph spinigers and one heterogomph falciger; infra-acicular chaetae five heterogomph falcigers. Median parapodia with two homogomph spinigers and 15–18 natatory chaetae in notopodial supra-acicular position; neuropodial infra-acicular chaetae two homogomph spinigers and two heterogomph falcigers, with 14–15 natatory chaetae. Posterior parapodia with two heterogomph falcigers and 13–14 natatory chaetae in notopodial supra-acicular position; neuropodial infra-acicular chaetae one homogomph spiniger, one heterogomph falciger, and 18–20 natatory chaetae.

Pygidium similar to those of atokous specimens.

Etymology. Specific name is in honor of Marian H. Pettibone for her great work on increasing the knowledge of polychaetes.

Remarks. *Websterinereis pettiboneae* sp. n. resembles *W. foli* in the shape of the compound falcigers, although there is greater variation in the shape of compound falcigers in *W. foli*. These species differ in the following features: *W. pettiboneae* has longer tentacular cirri reaching chaetiger 3, notopodial prechaetal lobes are triangular, and notopodial dorsal and ventral ligule are progressively smaller in posterior parapodia. In *W. foli* the longest tentacular cirri reaches chaetiger one, with a thin, cirriform prechaetal notopodial lobe inserted at the base of the notopodial ventral ligule, and the dorsal and ventral ligule increasing slightly in posterior parapodia.

Distribution. *Websterinereis pettiboneae* sp. n. is known only from Canal de San Lorenzo, La Paz Bay, Gulf of California, Mexico.

Density. The mean density of *W. pettiboneae* sp. n. varied from 2.5 ± 2.5 individuals per m^2 , in May 2005, to a maximum of 587.5 ± 110.8 individuals per m^2 recorded in July 2008 (Fig. 3). In general, densities were higher during the warmer and colder months and the lower densities between them; it suggests two peaks of recruitment for this species in the rocky reefs of southern Gulf of California. However, no significant relationship between temperature or salinity with worm density could be established.

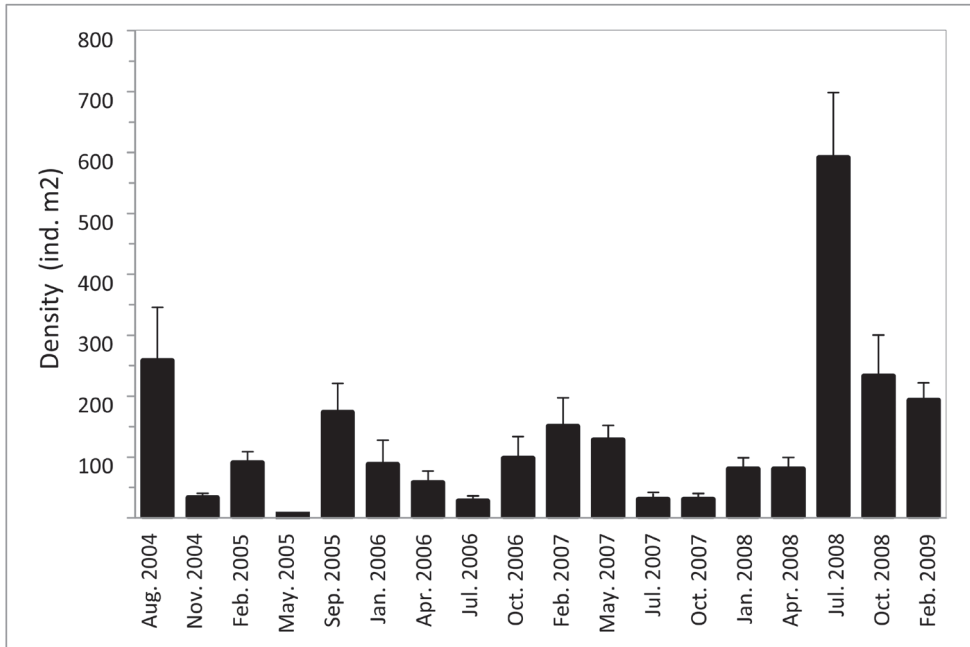


Figure 3. Mean density (individual per m² ± ES) of *Websterinereis pettiboneae* sp. n. in the restored area of the reef at San Lorenzo Channel, Bahía de La Paz, southern Gulf of California.

Websterinereis foli (Fauvel, 1930)

Fig. 4

Leptonereis foli Fauvel, 1930: 529, fig. 3.

Websterinereis foli: Pettibone 1971: 23, figs 10–11; Hutchings and Reid 1990: 91; Pamungkas and Glasby 2015: 19.

Nicon sp. Martens et al. 1995: 17, figs 20–24.

Type material. Holotype of *Leptonereis foli* (MNHN-685), Île des Pins, New Caledonia, 1 Jan. 1928, leg. Mme A. Pruvot-Fol.

Redescription. Holotype incomplete, in two fragments; anterior fragment 15 mm long, 1.1 mm wide including parapodia at chaetiger 10, with 54 chaetigers; medial region fragment 2.5 mm long, 0.7 mm wide including parapodia, with 8 chaetigers.

Pigmentation blackish; prostomium with longitudinal narrow band throughout its length, leaving thin pale mid-dorsal line, pale subtriangular area around the anterior eyes, and pale semicircular area around posterior eyes; palpophores pale; tentacular segment with solid blackish dorsal pigmentation, laterally pale, reduced to wide dorsal longitudinal band on first chaetiger.

Prostomium subpentagonal, longer than wide, with slight depression along anterior half. Two pairs of black eyes, distal ones reniform larger than proximal ones which are rounded and show lenses. Antennae tapered, not reaching tips of palpostyles; palps

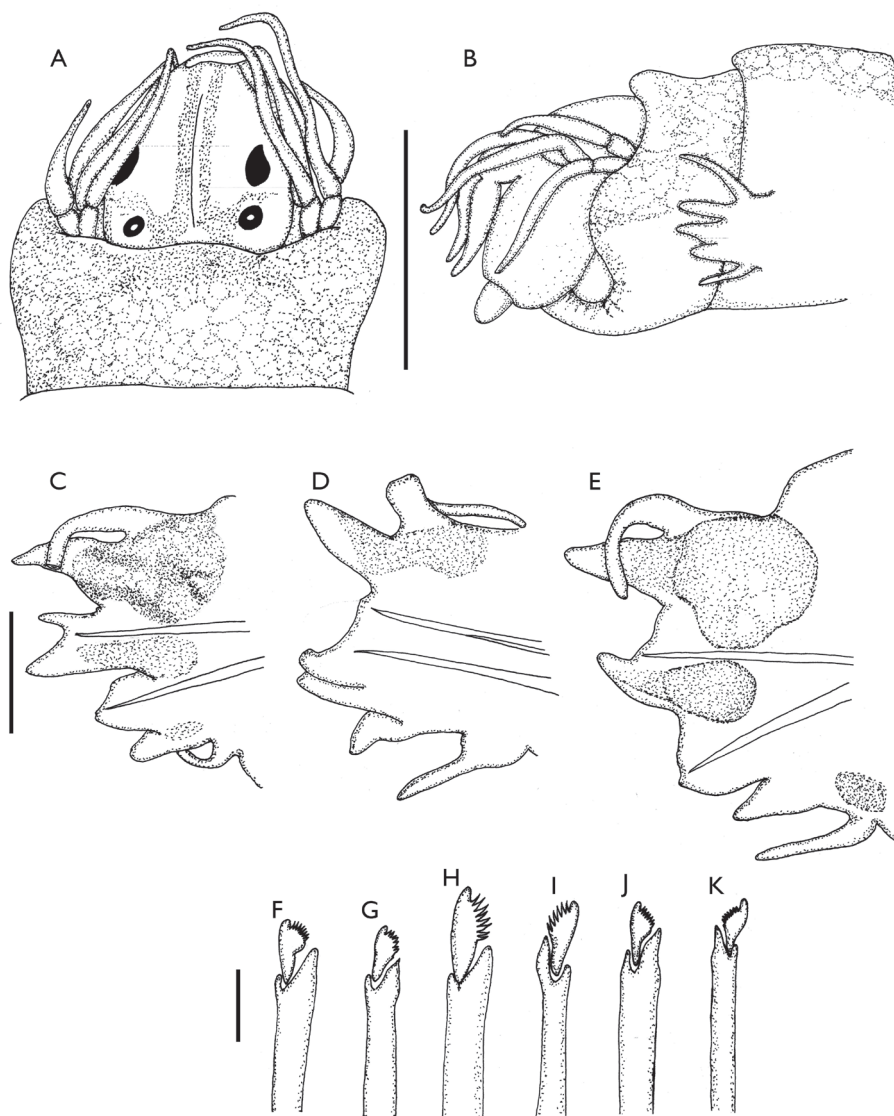


Figure 4. *Websterinereis foli*. Holotype (MNHN-685). **A** Anterior end, dorsal view **B** Anterior end, lateral view **C–E** Parapodia of chaetigers 10 (dorsal cirri incomplete), 20 (dorsal cirrus folded backwards) and 38, anterior view **F** Supra-acicular neuropodial heterogomph falciger, chaetiger 10 **G** Infra-acicular neuropodial heterogomph falciger, chaetiger 10 **H** Supra-acicular neuropodial heterogomph falciger, chaetiger 20 **I** Infra-acicular neuropodial heterogomph falciger, chaetiger 20 **J** Supra-acicular neuropodial heterogomph falciger, chaetiger 38 **K** Infra-acicular neuropodial heterogomph falciger, chaetiger 38. Scale bars: **A–B** = 0.5 mm; **C–E** = 100 μ m; **F–K** = 10 μ m.

globose, palpostyles conical; both antennae and palps directed ventrally as result of an artifact of fixation. One apodous anterior segment, shorter than first chaetiger. Tentacular cirri short, tapered, longest pair reaching chaetiger one (Fig. 4 A–B).

Pharynx with single jaw (left one lost), thin, with seven well-developed teeth. Maxillary ring without paragnaths or papillae; oral ring with triangular papillae on area VI, area V lacking papillae, areas VII–VIII, with seven rounded papillae.

Parapodia of first two chaetigers, uniramous, thereafter biramous. Anterior notopodia with triangular dorsal and ventral ligules, with thin notopodial prechaetal lobe inserted at base of notopodial ventral ligule; neuropodial postchaetal lobes subtriangular, superior and inferior lobes absent, neuropodial ventral ligules subconical. Dorsal cirri inserted basally, longer than ventral cirri. With large glandular area on notopodia, and smaller one on base of neuropodial ventral ligule (Fig. 4C). Median parapodia with subulate dorsal ligules, prechaetal lobes reduced to small rounded protuberances, ventral ligules triangular; neuropodial postchaetal lobes subconical, ventral ligules subtriangular. Dorsal cirri longer than ventrals, both inserted basally. Glandular area present in supra-acicular region (Fig. 4D). Posterior parapodia with triangular dorsal ligules, notopodial prechaetal lobes absent, ventral ligules triangular; neuropodial postchaetal lobes broad, wider than long, ventral ligules subtriangular. Dorsal and ventral cirri subequal (Fig. 4E).

Anterior parapodia with four homogomph spinigers in supra-acicular notochaetae; supra-acicular neurochaetae include three homogomph spinigers and two heterogomph falcigers with thick handle and short triangular blades (Fig. 4F); infra-acicular neurochaetae seven heterogomph falcigers with blades diminishing gradually ventrally (Fig. 4G). Median parapodia with three homogomph spinigers in supra-acicular notochaetae; supra-acicular neurochaetae three homogomph spinigers and two heterogomph falcigers with thick handle and oval blades (Fig. 4H); infra-acicular neurochaetae seven heterogomph falcigers with thin handles and triangular blades (Fig. 4I). Posterior parapodia with five homogomph spinigers in supra-acicular notochaetae; supra-acicular neurochaetae include two homogomph spinigers and one heterogomph falciger (Fig. 4J); infra-acicular neurochaetae six heterogomph falcigers (Fig. 4K). Pygidium unknown.

Remarks. After reviewing the holotype of *W. foli* some differences were noted from the description by Pettibone (1971). In her description of *W. foli* Pettibone combined her observations of the holotype of *Leptonereis foli* Fauvel, 1930 and the holotype and paratypes of *Ceratocephala corallicola* Reish, 1968. This explains why her description begins with the measurements of a specimen that does not match the holotypes of either species, as 20 mm long and up to 112 chaetigers. Since Pettibone (1971) mixed morphological features of these two species originally described from very distant localities we have restricted our redescription of *W. foli* to only the specimen that Fauvel (1930) designated as the holotype.

Distribution. Central Pacific (New Caledonia, Marshall Islands), Australia (Western Australia, New South Wales, South Australia, Lizard Islands), Indonesia.

Key to *Websterinereis* species modified from Pettibone (1971)

- 1 Anterior parapodia with notopodial prechaetal lobes small, inconspicuous; unidentate ankylosed chaetae present in epitokous stage *W. glauca*

–	Anterior parapodia with notopodial prechaetal lobes distinct.....	2
2	Neuropodial falcigers with long blades.....	3
–	Neuropodial falcigers with short blades	4
3	Longest tentacular cirri reach chaetiger 6; notopodial prechaetal lobe present along body; bidentate ankylosed chaetae present on median and posterior parapodia	<i>W. punctata</i>
–	Longest tentacular cirri reach chaetiger 2 (1-4); notopodial prechaetal lobe present only on anterior region; ankylosed chaetae absent.....	<i>W. tridentata</i>
4	Longest tentacular cirri reach chaetiger 1; notopodial prechaetal lobe thin, digitiform; notopodial dorsal and ventral ligules increasing in length slightly on posterior parapodia	<i>W. foli</i>
–	Longest tentacular cirri reach chaetiger 3; notopodial prechaetal lobe triangular; notopodial dorsal and ventral ligule are progressively smaller in posterior parapodia.....	<i>W. pettiboneae</i>

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Revision of Partulidae (Gastropoda, Stylommatophora) of Palau, with description of a new genus for an unusual ground-dwelling species

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Abstract

We describe a new stylommatophoran land snail of the family Partulidae from Palau. The new species has a combination of morphological and ecological characters that do not allow its placement in any existing partulid genus, so we describe a new genus for it. The new genus is characterized by a large (18–23 mm) obese-pupoid shell; smooth protoconch; teleoconch with weak and inconsistent, progressively stronger, striae; last half of body whorl not extending beyond the penultimate whorl; widely expanded and reflexed peristome; relatively long penis, with longitudinal pilasters that fuse apically into a fleshy ridge that divides the main chamber from a small apical chamber; and vas deferens entering and penial-retractor muscle attaching at the apex of the penis. Unlike all other partulids, the new species is strictly associated with rocks in contact with the ground. Comparing the other three Palauan species – currently assigned to *Partula* – to our new genus and to other partulids makes it clear that they require their own genus because their morphology is quite different from that of true *Partula* and from that of all other genera. Hence, we resurrect the name *Palaopartula* Pilsbry for these snails.

Keywords

Land snail, Oceania, new species, Pacific, *Palaopartula*, *Partula*, pulmonate

Introduction

The land-snail fauna of oceanic islands in the Pacific is disharmonic, with about 20 of the nearly 130 terrestrial snail families represented. Except for camaenid and bradybaenid species near the Asian and Australian continental margins (Chiba 2004, Hirano et al. 2014), helicoid families are noticeably lacking on Pacific Islands despite being the most diverse larger-bodied snails in adjacent continental areas. Oceanic islands instead are rich in operculate and smaller-bodied snails, presumably because these are more successful dispersers to far-flung islands (Cowie and Holland 2006). Nearly half of the families on oceanic islands in the Pacific – Assimineidae, Cyclophoridae, Diplommatinidae, Helicinidae, Hydrocenidae, Neocyclotidae, Pupinidae, and Truncatellidae – are operculates, of which there are only about 20 terrestrial families globally. The other families are eupulmonates that include moderate-sized Ellobiidae; moderate- to small-bodied Succineidae, Rhytididae, Charopidae, Endodontidae, Punctidae, Euconulidae, Trochomorphidae, and Zonitidae; and moderate- to small-bodied orthurethrans in the families Achatinellidae, Draparnaudiidae, Partulidae, Vertiginidae, and Amastridae (Cowie et al. 1995, Cowie and Robinson 2003, Rundell 2010). Orthurethrans, once thought to be ancestral stylommatophorans with relict island lineages, like Partulidae and Achatinellidae (Solem, 1990), are now viewed as a derived clade (Wade et al. 2006). More than 50% of all extinctions documented since 1500 are mollusks; nearly 40% of these are terrestrial snails from oceanic islands (Régnier et al. 2009). Whereas the conservation status of most terrestrial vertebrate species has been assessed, only a small fraction of described species of terrestrial mollusks has been evaluated (Régnier et al. 2015a); as a result very few species are listed under protective legislation, even in groups clearly in decline (Régnier et al. 2015b). This lack of attention masks the extinction of many land snail species (Régnier et al. 2009, 2015a). Non-marine mollusks also suffer from poor sampling. Basic survey data for terrestrial mollusks are lacking for many Pacific Ocean islands, and many species face extinction before they are ever discovered (Richling and Bouchet 2013).

Palau harbors an estimated 200 species of land snails, of which only 78 have been described (Rundell 2010, Yamazaki et al. 2013). Ninety-five percent of the fauna discovered to date is endemic to these islands (Rundell 2010), and future discoveries are likely to prove so too. As currently known, the fauna comprises approximately 70% operculates and 30% eupulmonates, but of the 34 eupulmonates reported from Palau, five are alien (Rundell 2005). Among the 29 native eupulmonates, Helicarionoidea comprises the largest number of species, with 13; most of the others are tiny species of the families Achatinellidae, Charopidae, Endodontidae, and Succineidae. The helicarionoids, along with three partulids and one ellobiid (*Pythia scarabaeus* Linnaeus), include the only moderately large eupulmonates known from Palau. Hence, the land snails of Palau are, at the familial level, only a subset of the already disharmonic snail fauna that characterizes Pacific oceanic islands more generally.

During a visit in 1998, one of us (FK) discovered an unusual stylommatophoran snail of moderate size that was not readily assignable to any genus known from the

country. Subsequently, we discovered that the species had been collected previously by others and that specimens were already lodged at the Florida Museum of Natural History. In trying to identify these specimens we confirmed that they were morphologically distinct from any known Pacific-island species. Herein we provide evidence for their familial assignment to Partulidae and describe a new genus and species for these specimens. In comparing this snail to its closest relatives it became obvious that Palauan snails currently assigned to *Partula* in fact do not accord well morphologically with that genus. Furthermore, they have been found to comprise a separate clade of partulids evolutionarily independent of lineages that are properly assigned to *Partula* (Lee et al. 2014). To facilitate comparisons with our new genus, we first resurrect *Palaopartula* Pilsbry for the three known species of Palauan partulids. We then describe our new genus and species.

Materials and methods

We hand-collected specimens, drowned them overnight, and preserved them in 75% ethanol. We dissected pallial organs, genitalia, and buccal masses from specimens under 75% ethanol using a dissecting microscope, and we isolated radulae from buccal masses using a 3% sodium hypochlorite solution. We imaged radulae and jaws using a Field Emission-SEM, photographed genital anatomy, and drew pallial organs with the aid of a drawing tube. We used Helcion Focus software for photo stacking. We counted whorls from the suture of the first whorl to the body whorl (Fig. 1A), and fractions of a whorl were determined with the aid of a cardboard circle divided into ten equal parts of 36°. We measured shells to 0.1 mm. Width is the greatest width of the shell perpendicular to the shell axis, and height is the greatest distance between the apex and the base of the aperture parallel to the shell axis (Fig. 1B). We include the expanded lip in both measures. Aperture width is the greatest distance from the columellar edge to the distal edge of the aperture, including the expanded lip. Aperture height is measured from the suture to the base of the expanded lip, parallel to the shell axis (Fig. 1B). We express measurements as means, ranges, and standard deviations. Specimens are deposited at the Florida Museum of Natural History (UF). We also studied material from Academy of Natural Sciences, Philadelphia (ANSP) and from the Fred Kraus collection (FK), see Appendix 1. Higher-level systematics follows Bouchet and Rocroi (2005).

We isolated genomic DNA from 1 cubic mm of foot tissue of the new taxon using a solution of 10% Chelex beads (Bio-Rad Laboratories) in sterile water heated to 65 °C for 4 hours. DNases and other protein contaminants were digested using Proteinase K. We amplified a 655-bp nucleotide fragment of cytochrome oxidase I (COI) with GoTaq DNA Polymerase (Promega, Madison, WI) using the primer pairs LCO1490/HCO2198 (Folmer et al. 1994) and were able to sequence 540 bp of that. Sequencing was performed in both directions at University of Florida, Interdisciplinary Center for Biotechnology Research, using their standard procedures. The sequence is deposited

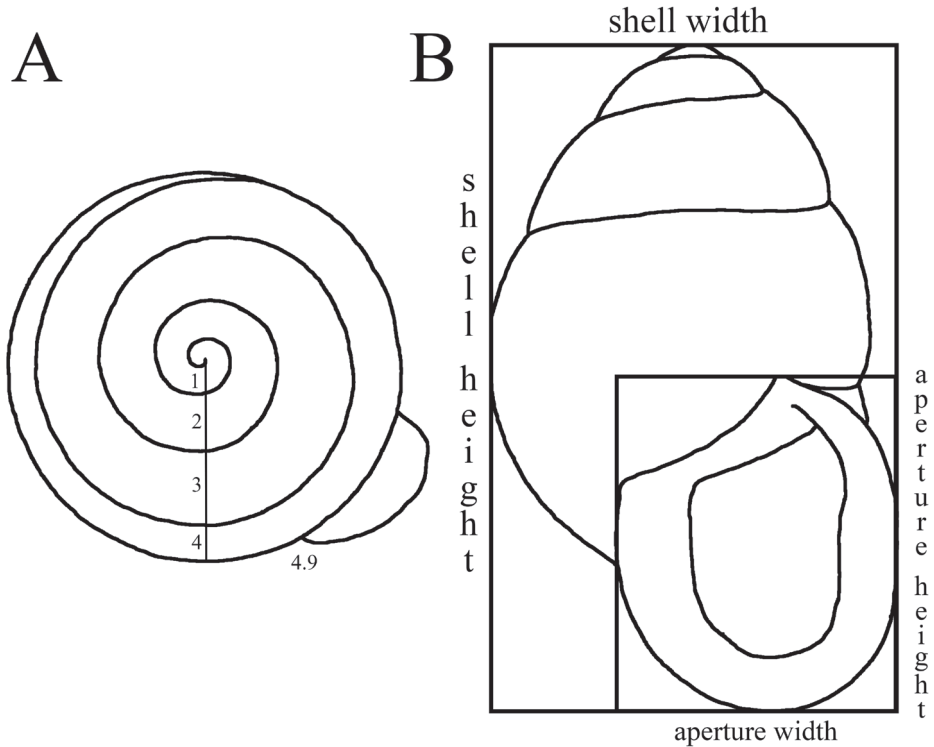


Figure 1. Shell measurements: **A** Whorl count **B** Shell width, shell height, aperture width, aperture height.

in GenBank under accession number KX685957. Comparative COI sequences were provided by the authors of Lee et al. (2014). We conducted a phylogenetic analysis of our taxon versus other partulids using Bayesian analysis in MrBayes (Ronquist and Huelsenbeck 2003) as implemented in Geneious version 6.1.7 (<http://www.geneious.com>, Kearse et al. 2012). The GTR + I + G model of evolution was selected using jModelTest 2.0 (Darriba et al. 2012). We ran the analysis for 10,000,000 generations running four chains: one cold and three heated to a temperature coefficient of 0.2. Trees were sampled every 10,000 cycles after a burn-in period of 100,000 generations. We present our analysis unrooted because other orthurethran outgroups available to us for rooting are distantly related to partulids, we could not obtain a stable root using them, and they are likely uninformative due to their long branch lengths.

Familial assignment to Partulidae

The familial placement of this new, unusual stylommatophoran species is not immediately obvious based on shell characters. The shell resembles some Camaenidae and Bradybaenidae, but these are precluded because the new species lacks a head wart,

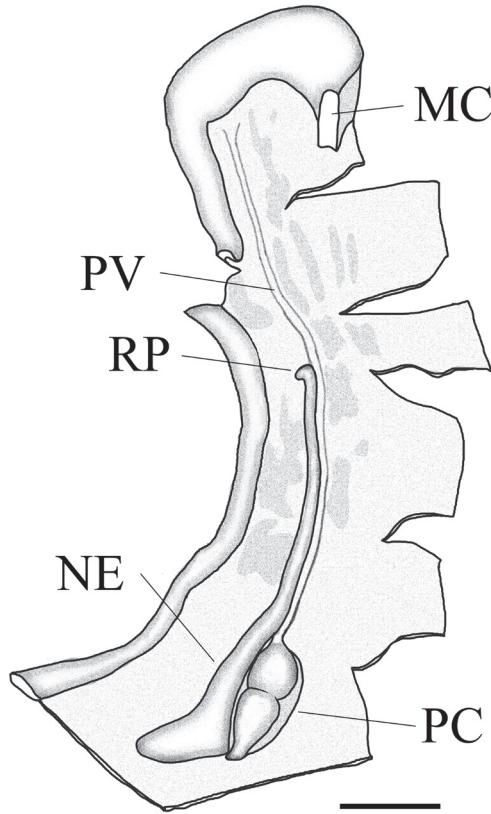


Figure 2. Pallial organs of *Sphendone insolita* sp. n., paratype, UF 248690. MC = mantle collar; NE = nephridium; PC = pericardium; PV = pulmonary vein; and RP = renal pore. Scale bar: 5 mm.

which is present in many camaenids (Scott 1998), and the pallial complex is orthurethran (Fig. 2) instead of sigmurethran, as in both Bradybaenidae and Camaenidae. Of the orthurethran families, the large pupoid shell with greatly expanded lip (Fig. 3A–C) is most closely approached by the Achatinellidae, Draparnaudiidae, Partulidae, and Enidae. The shells are much larger (18–23 mm) and lack the apertural lamellae of the pupilloid families. The radula has three tooth types (Fig. 3G–I) and differs from that of the Achatinellidae, which has only a single tooth type, considered marginal by Cooke and Kondo (1960). The pallial organs (Fig. 2) are not pseudosigmurethran, as in the Cerastidae (Solem 1964; Budha et al. 2012). The shell does not have a columellar lamella, like the Amastridae and many Cochlicopidae. The widely expanded lip is unlike the simple or thinly reflected or thickened lips of the Achatinellidae, Amastridae, Cerastidae, and Cochlicopidae but is typical of some Enidae and the partuloid families Partulidae and Draparnaudiidae. The Enidae and Draparnaudiidae differ by having penial accessories (Tillier and Mordan 1995, Schileyko 1998) that are absent in this species. Among stylommatophorans found in the Pacific region that are >10 mm in

maximum dimension, all morphological features examined by us are consistent only with the Partulidae. For these reasons we assign this new genus and species to that family. Biogeographically, this is reasonable inasmuch as the family is already known from Palau and adjacent areas, whereas several of these other orthurethran families are not. Further, a BLAST comparison of a 540-bp fragment of CO1 recovered from the new species (UF 271885) confirmed the sequence was most similar to sequences of other partulid species in GenBank (see below).

Notes on terminology of genital anatomy in Partulidae

The penis in *Samoana*, *Palaopartula* and *Partula* is divided into two chambers: a main chamber and an apical chamber that are usually defined by a constriction between them and by different sculpture. Pilsbry and Cooke (1934) considered the apical chamber in *Samoana* to be an epiphallus, which is a specialization of the vas deferens, whereas they referred to the distal or apical chamber in *Partula* and *Palaopartula* as a specialization of the penis. However, they also suggested that the epiphallus in *Samoana* and the distal chamber of the penis in *Partula* may be homologous structures, and they urged further research to determine function and settle on a fixed terminology for these structures in various partulid genera (Pilsbry and Cooke 1934). Schileyko (1999) referred to the apical chamber in *Partula* and *Palaopartula* as a flagellum, which is a specialization of the epiphallus, and this conflicts with Pilsbry and Cooke's interpretation of this structure as a specialization of the penis. Schileyko's interpretation suggests that the apical chamber (epiphallus) of *Samoana*, *Partula* and *Palaopartula* are homologous. Although we agree that these structures are likely to be homologous, we prefer to use the term "apical chamber" rather than "epiphallar chamber" for this structure because it does not imply knowledge of its function or origin. We employ the terminology of Pilsbry and Cooke (1934) for the apical chamber in *Samoana* and Schileyko (1999) for the apical chamber in *Partula* and *Palaopartula* in Figure 6 to aid comparisons.

Systematic descriptions

Family Partulidae Pilsbry, 1900

Genus *Palaopartula* Pilsbry, 1909

Palaopartula Pilsbry, 1909, in Pilsbry 1909–1910, pages 166, 306.

Palaeopartula Richardson, 1990, page 6 [incorrect subsequent spelling].

Palaopartula Schileyko, 1999, page 271, figure 327.

Type species. *Partula thetis* Semper, 1865; by original designation.

Content. *Partula calypso*, *Partula leucothoe*, and *Partula thetis*, all Semper 1865.

Distribution. Known only from Palau.

Diagnosis. Shell large, elongate, with a tall, relatively flat-sided and acutely pointed spire (Fig. 4). Protoconch small, early teleoconch whorls descend rapidly, remaining tightly coiled and narrow. Aperture elongate, with a greatly expanded peristome, its palatal and parietal sides nearly parallel, palatal edge with a slight central thickening, base rounded, parietal edge joining high on the body whorl. Umbilicus very deep and not covered by the parietal callus. Penis long and narrow, divided nearly equally between a main chamber with strong pilasters running its length that are crossed by weaker pilasters and an apical chamber with narrow pilasters or pustules (Kondo 1955, figs 118–123).

Comparisons with other genera. *Palaopartula* has historically been grouped with *Partula*. It differs from *Partula*, *Eua*, and *Samoana* in having a relatively large and more elongate shell with a high and rapidly descending spire (Fig. 5B–D). In contrast, *Partula* (Fig. 5G–H), *Eua* (Fig. 5E), and *Samoana* (Fig. 5F) have relatively blunt apices, with rounded whorls that expand relatively rapidly and descend slowly. The height/width ratio range of the three *Palaopartula* species is 2.0–2.3, versus 1.5–1.9 for the *Partula*, *Eua* and *Samoana* species listed in Appendix 1. The early teleoconch whorls of *Palaopartula* are variable in sculpture: *P. calypso* (Fig. 5B) and *P. leucothoe* (Fig. 5C) have pitted spiral striae like most *Partula* and *Samoana*, although the spiral striae are much weaker; *P. thetis* (Fig. 5D) is unlike any other partulid in being sculptured with raised axial and spiral sculpture that join to form nodules. The peristome of *Palaopartula* species is more widely reflected than in any other genus of Partulidae, and the parietal edge attaches to the shell higher on the body whorl and does not obstruct the umbilicus, making the umbilicus look particularly deep. *Palaopartula* differs from *Eua* in having a long thin penis (Fig. 6D), unlike the short broad penis of *Eua* (Fig. 6A). Internally the penis of *Palaopartula* is divided into two chambers, a main penial chamber and an apical chamber, each with 5–15 longitudinal pilasters; this contrasts with *Eua*, which has only one chamber with one large fleshy pilaster (Kondo 1955). The vas deferens of *Palaopartula* joins the apical chamber laterally rather than joining the penial chamber apically, as in *Eua*. The penial and apical chambers of *Palaopartula* are similar in width and length and both contain 5–15 longitudinal pilasters, whereas the penial chamber of *Samoana* is short and bulbous with only two large pilasters that fuse to form a V (Fig. 6B), and the apical chamber is long and narrow and contains 5–10 longitudinal rows of nodules. *Palaopartula* has an unbranched penial retractor muscle that attaches apically as opposed to the retractor muscle of *Samoana* which also has a secondary branch that attaches to the penial chamber (Fig. 6B). *Palaopartula* differs from *Partula* in having a narrow and usually tapering penis, whereas *Partula* has a more variable penis that is usually apically inflated and strongly curved (Kondo 1955). In *Palaopartula*, the pilasters in both chambers fuse to form a ridge between the chambers, unlike *Partula*, which has pilasters that do not fuse to form a ridge between the two chambers (Fig. 6E). The vas deferens of *Palaopartula* remains narrow for its entire length whereas the vas deferens of *Partula* broadens before entering the apical chamber. Molecular data also do not support placement of *Palaopartula* within *Partula*

(Lee et al. 2014) but link it instead with *Samoana*, from which it differs radically in shell and genital morphology. Accordingly, we here resurrect *Palaopartula*.

Remarks. This genus is isolated to the west of all previously named partulid genera (Fig. 7). The species are arboreal, with *P. thetis* typically being found in *Pandanus* leaf axils (FK, pers. obs.). Judging by genetic distances, *Palaopartula* is distantly related to *Partula* but clusters more closely to the other partulid genera (Fig. 8), although we are unable to polarize this network to determine directionality of evolution.

Genus *Sphendone* gen. n.

<http://zoobank.org/FBC28415-B5A9-4549-B4CC-27D0F7B9850B>

Type species. *Sphendone insolita* sp. n.

Content. One species, *Sphendone insolita* sp. n.

Diagnosis. Shell obese-pupoid (Fig. 3B), protoconch sculptured with growth lines, strongest near the apical suture (Fig. 5A); spiral sculpture absent or consisting of very weak and inconsistent striae. Wavy spiral striae become progressively stronger and clearer on the penultimate and body whorls. The final half of the body whorl does not extend beyond the penultimate whorl (Fig. 3A–B). Peristome widely expanded and reflexed, palatal and parietal margins nearly parallel, base evenly rounded. Palatal margin with slight central thickening; parietal margin attaching to body whorl at level of umbilicus. Penis relatively long and narrow, sculptured with approximately 10 longitudinal pilasters that coalesce to form a ridge between the penis and a very short and thin-walled apical chamber with about 10 thin and widely spaced pilasters. The vas deferens and penial-retractor muscle enter at the penis apex. Oviduct usually contains only one (sometimes two) eggs or embryos.

Comparisons with other genera. The shells of *Eua*, *Samoana*, *Palaopartula*, and *Partula* are not pupoid in shape; they are attenuated apically. The protoconch of the new species lacks strong spiral striae or pitting, unlike the strong striae of *Eua*, or the pitted striae of *Palaopartula*, *Partula*, and *Samoana*. *Sphendone* is similar only to *Eua* in the apical insertion of the vas deferens into the penis, unlike the lateral insertion into the apical chamber in *Samoana*, *Palaopartula*, and *Partula* (Figure 6). However, *Sphendone* shares an elongate, two-chambered penis with *Samoana*, *Palaopartula*, and *Partula* that is distinctly different from the short, broad penis with a single chamber found in *Eua*. The apical chamber of *Sphendone* is very short, unlike *Samoana*, *Palaopartula*, and *Partula*, which have large apical chambers (Fig. 6). The interior of the penis in *Sphendone* is sculptured with approximately ten longitudinal pilasters, unlike the single fleshy pilaster of *Eua* or the two large pilasters in the main chamber of the penis of *Samoana* (Kondo 1955). The pilasters of the main and apical chambers coalesce, forming a ridge between the two chambers similar to that seen in *Palaopartula* and unlike that in *Samoana* and *Partula*. The penial-retractor muscle enters apically and does not branch, whereas *Samoana* has a retractor muscle with a secondary branch that attaches to the penial chamber.

Remarks. A comparison of a partial COI sequence (540 bp) of *Sphendone* (UF 271885) with sequences from all other partulid genera (655 bp) shows the new genus is well differentiated from other partulid genera (Fig. 8) although we are unable to determine its sister-taxon relationships from an unrooted network.

Etymology. *Sphendone* is a feminine Greek noun for a sling missile and is used here in reference to the unique bullet shape of the shell among partulids. The accent is on the first syllable.

Distribution. Known only from Palau.

***Sphendone insolita* sp. n.**

<http://zoobank.org/2CC94994-C317-4CDA-A815-D07C1084FD8C>

Figs 2–3

Holotype. UF 425857, 7.2600°N, 134.4493°W, collected along trail to German Lighthouse, Ngeruktabel (Uruktafel) Island, Palau, F. Kraus, 24 August 1998.

Paratypes (n = 76). Palau: Ngeruktabel (Uruktafel) Island: along trail to German Lighthouse, 7.2600°N, 134.4493°W, F. Kraus, 24 August 1998 (UF 271885, 8 alcohol preserved, UF 271886, 16 dry shells); at ruins of Japanese artillery battery, 150 meters, F. G. Thompson, 23 October 1985 (UF 248690, 16 alcohol preserved; UF 248689, 31 dry shells); along mossy wall downhill of compound ruins, J. Starmer, 21 August 1999 (UF 332693, 6 dry shells).

Other material examined. Palau: Eil Malk (Mecherchar) Island: southeastern peninsula, from hermit crab, F. G. Thompson, 22 October 1985 (UF 249044, 1 dry shell).

Diagnosis. Large, obese-pupoid shell approximately 18–23 mm in height and 13–15 mm in width, with 4.5–5.1 whorls. Body whorl descends below the penultimate whorl. Protoconch sculptured with growth lines, strongest near the sutures; spiral sculpture lacking or, less commonly, comprising faint and irregular striae. Wavy spiral striae are progressively stronger and more regular on penultimate and body whorls but never become regular and strong. Peristome widely expanded and reflexed, palatal and parietal margins nearly parallel, base evenly rounded. Palatal margin with slight central thickening; parietal margin attaching to the body whorl at umbilicus. Penis long, with apical insertion of the vas deferens and retractor muscle. Approximately ten longitudinal pilasters coalesce to form a ridge that defines a small apical chamber below the insertion of the vas deferens.

Description of holotype. Shell obese-pupoid, height 22.2 mm, width 14.0 mm, with 4.9 whorls (Fig. 3A–C). Whorls moderately inflated, with impressed sutures. Apex somewhat bluntly rounded (Fig. 5A). Protoconch and teleoconch whorls sculptured with strong growth lines, especially near the sutures; there are also irregularly expressed, weak and wavy spiral striae that become progressively stronger in later whorls. Last whorl descending underneath the penultimate whorl. Aperture elongate, sides nearly straight and parallel. Outer edge of peristome curving slightly inward at middle, base evenly rounded. Aperture height 12.1 mm, width 9.3 mm. Interior of aperture

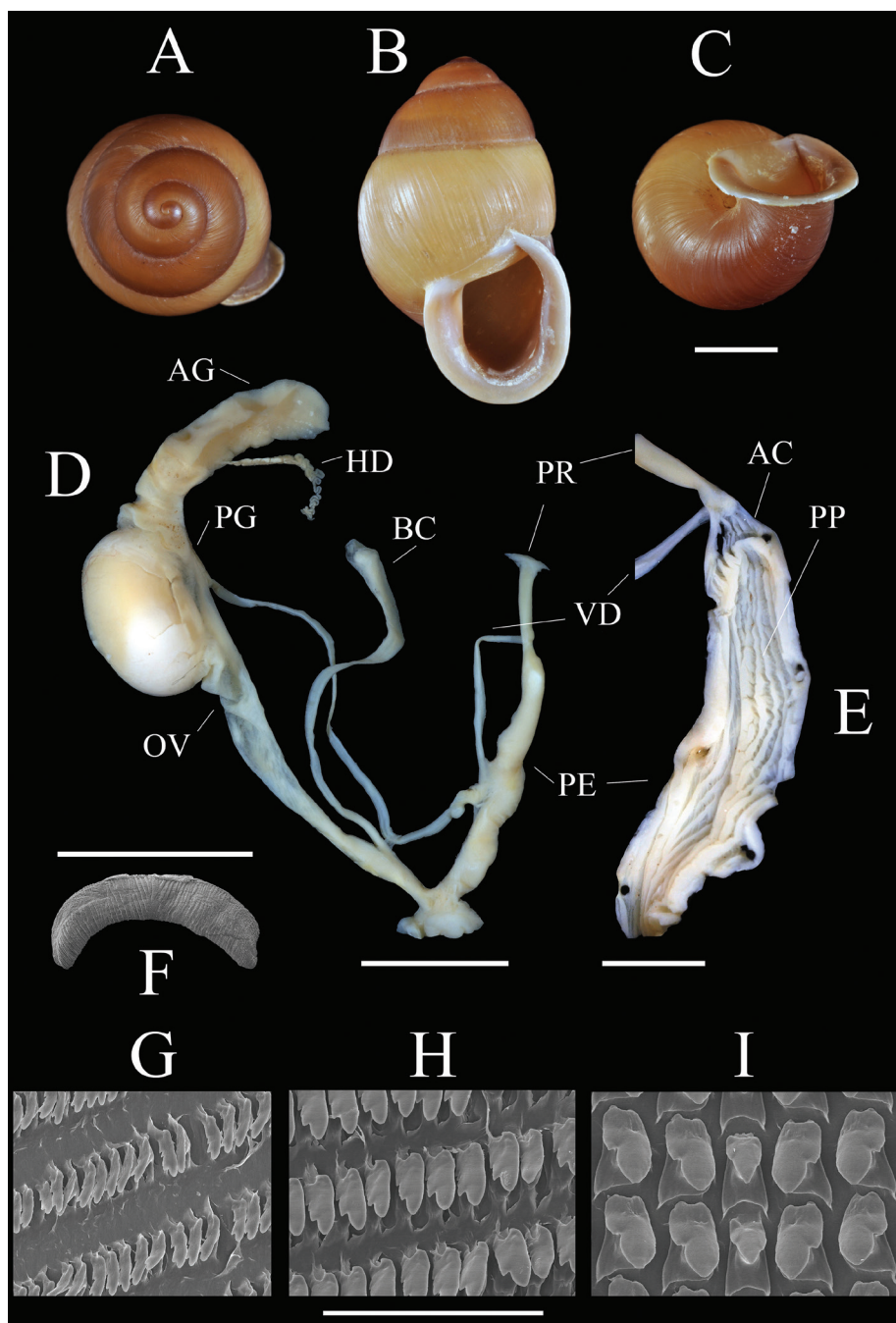


Figure 3. *Sphendone insolita* sp. n.: **A–C** Shell, holotype, UF 425857 **D** Genitalia, paratype, UF 248690 **E** Penial sculpture, paratype, UF 248690 **F** Jaw, paratype, UF 248690 **G–I** Radula, holotype UF 425857. AC = apical chamber; AG = albumen gland; BC = bursa copulatrix; HD = hermaphroditic duct; OV = free oviduct; PE = penis; PG = prostate gland; PP = penial pilasters; PR = penial retractor muscle; and VD = vas deferens. Scale bar: 5 mm (**A–C, D**); 2 mm (**E**); 1 mm (**F**); 100 μ m (**G–I**).

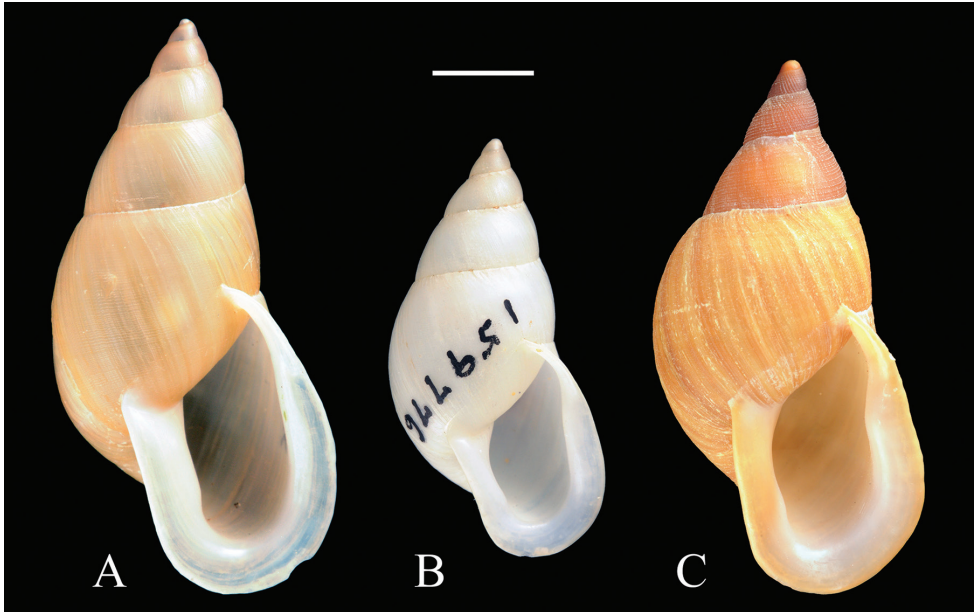


Figure 4. Shells of *Palaopartula*: **A** *Palaopartula calypso*, ANSP 191976 **B** *P. leucothoe*, ANSP 294471 **C** *P. thetis*, FK 2840. Scale bar: 5 mm.

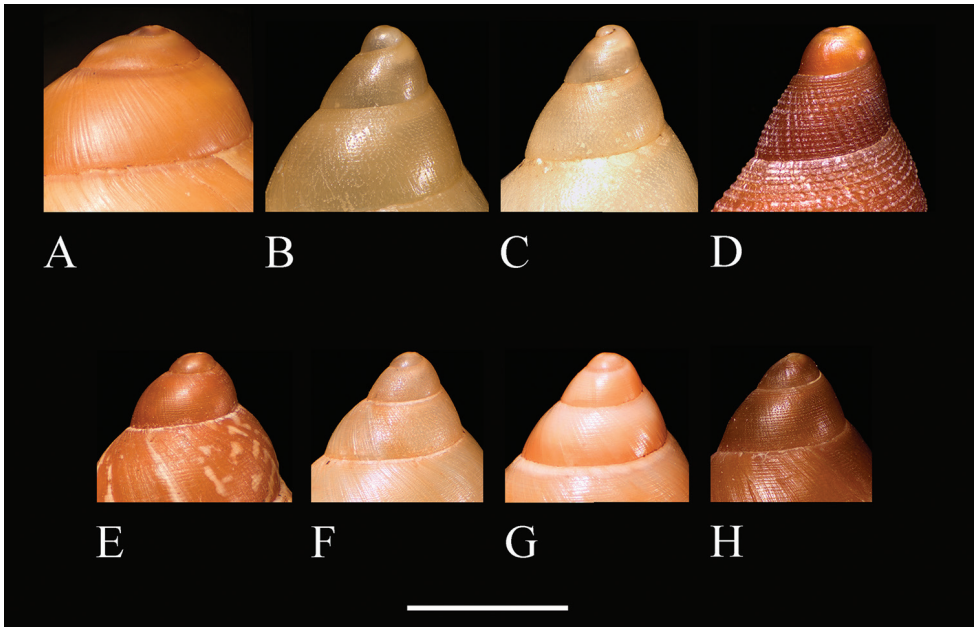


Figure 5. Apical sculpture of partulid genera: **A** *Sphendone insolita* sp. n., holotype, UF 425857 **B** *Palaopartula calypso*, ANSP 191976 **C** *Palaopartula leucothoe*, ANSP 294471 **D** *Palaopartula thetis*, FK 2840 **E** *Eua zebrina* (Gould, 1847), UF 158688 **F** *Samoana strigata* (Reeve, 1850), UF 192725 **G** *Partula gibba* Ferussac, 1821, UF 195878 **H** *Partula varia* Broderip, 1832, UF 158682. Scale bar: 5 mm except 2.5 mm for *Palaopartula* species.

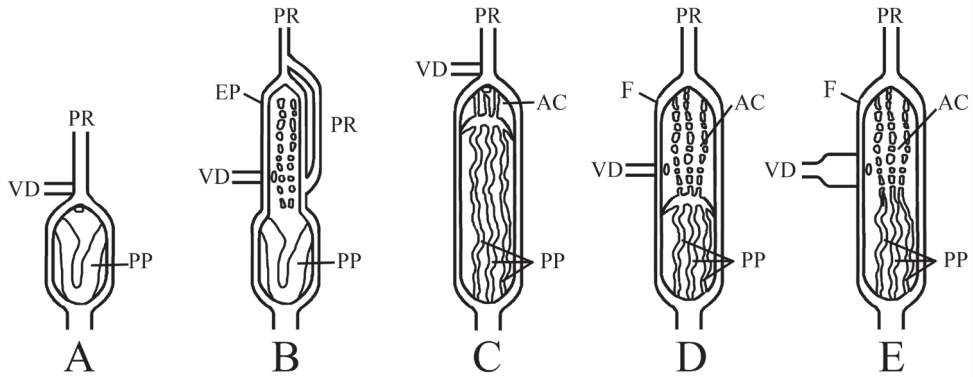


Figure 6. Schematic summary of penial anatomy of partulid genera, from Kondo (1955) and Schileyko (1999): **A** *Eua* **B** *Samoana* **C** *Sphendone* **D** *Palaopartula* **E** *Partula*. AC = apical chamber; EP = epiphallus; F = flagellum; PP = penial pilasters; PR = penial retractor muscle; and VD = vas deferens.

brown. Peristome nearly complete, broadly expanded and reflexed, thickened, brown towards the aperture, fading to brown-white and reflexed abaperturally. Parietal callus thin in the middle and much thickened at the inner and outer insertions of the lip. Shell color medium brown, with a poorly defined paler band below the suture on early whorls that widens on subsequent whorls. Penultimate whorl pale brown to straw yellow-brown except for a poorly defined and narrow darker-brown band below the suture. Body whorl darkens, the second half entirely darker brown.

Variation. Measurements of 56 adult shells: height 18.3–22.7 mm, mean 21.1 ± 0.8 mm; width 12.9–14.9 mm, mean 14.0 ± 0.4 mm; whorls 4.5–5.1, mean 4.9 ± 0.1 . Aperture height 10.5–12.1 mm, mean 11.3 ± 0.4 mm. Aperture width 8.4–9.8 mm, mean 9.2 ± 0.3 mm. Most shells are similar to the holotype in coloration, but three of 79 shells are uniformly white. These white-shelled individuals have normal surface sculpture and are not worn. Nor are they albino, as evidenced by their normal mantle pigmentation. Most shells are dextral, but two of 79 are sinistral.

Pallial system (2 specimens). Nephridium nearly 2/3 length of pallial cavity, broad at base, tapering anteriorly, and sharply turned at renal orifice (Fig. 2). Pericardium approximately 1/3 length of nephridium. Pulmonary vein long and unbranched, ending near mantle collar. Mantle lacks any other obvious venation.

Radula (2 specimens). Central tooth two-thirds height of lateral teeth, trigonal, with poorly defined ectocones (Fig. 3I, central row). First lateral teeth bicuspid, ectocone 1/3–1/2 height of broad mesocone, which narrows abruptly at the tip (Fig. 3I, flanking central row). First ten lateral teeth similar in size and shape. Next five rapidly becoming narrower and beginning to develop multiple ectocones (Fig. 3H). Next 80 teeth narrow, slowly grading into marginals, width approximately one-quarter height, with two to several ectocones (Fig. 3G).

Jaw (1 specimen). Crescent-shaped, thin, stegognathous, composed of many narrow flat plaits that converge towards middle of cutting edge, which is not raised and does not bear a central cusp (Fig. 3F).

Reproductive system (10 specimens). Prostate gland short, extending only a short distance beyond albumen gland (Fig. 3D). Vas deferens weakly attached by fibers above penial-oviduct juncture, attached strongly to penis at its mid-point and again to penial-retractor muscle just above insertion on apex of penis; entering penis apically. Penis relatively long, cylindrical, divided into two chambers; the main chamber sculptured with numerous longitudinal pilasters crossed perpendicularly by weaker pilasters; the apical chamber sculptured with relatively weak pilasters. Pilasters fuse at the junction of the two chambers, forming a ridge below the insertion of the vas deferens (Fig. 3E). Atrium very short. Vagina short. Bursa copulatrix receptical oblong, tapering gently and imperceptibly to its duct. Single large egg 6.4–6.6 mm, mean 6.5 ± 0.1 mm ($n = 6$), with hard calcareous shell (Fig. 3D) found in six of ten dissections, one of these also had an embryo; another embryo found in an individual without an egg. Hermaphroditic duct narrow and highly convoluted.

Comparisons with other species. The new species differs from other partulids as stated for the genus.

Etymology. The trivial name is a feminine Latin adjective meaning unusual, in recognition of both the unusual shell shape and ecological habits for a partulid.

Distribution. Known only from southeasternmost Ngeruktabel (Uruktafel) and nearby Mecherchar (Eil Malk) Islands, Palau, Caroline Islands (Figs 7, 9). These two islands are separated by shallow waters and were connected in the past few thousand years, as the maximum depth between the two islands is only 25 m (Defense Mapping Agency 1996). Because all the hundreds of islands within the central fringing reef of Palau comprised a single island during the last glaciation event (Colin 2009), the species may be more widely distributed among other of the Rock Islands than is currently apparent.

Ecological notes. Live individuals of the new species were collected only from beneath rocks, between soil and the overlying rock, or deep in rock piles. Dead shells were also found on the soil surface and in leaf litter among stones. The site is well-developed limestone rainforest (Fig. 10) that was partially cleared during WWII but is now difficult to distinguish from undisturbed forest (Crombie and Pregill 1999).

Discussion

Palau comprises more than 700 small islands at the western end of the Pacific Ocean, totaling 490 km² of land and extending over 700 km, although the majority of islands lie within a single fringing reef approximately 130 km in length. These islands are situated some 800 km east of the Philippines and 850 km north of New Guinea and form the westernmost component of the Caroline Islands. They lie along the southern end of the Kyushu-Palau Ridge, a relict intra-oceanic volcanic-arc system the evolution of which ended 15–25 MYA (Yan and Shi 2011). Clockwise rotation of the Philippine Sea Plate brought the ridge to lie along the boundary of the Caroline Plate (Hall et al. 1995; Hawkins and Ishizuka 2009), and subsequent uplift left the islands as the only subaerial

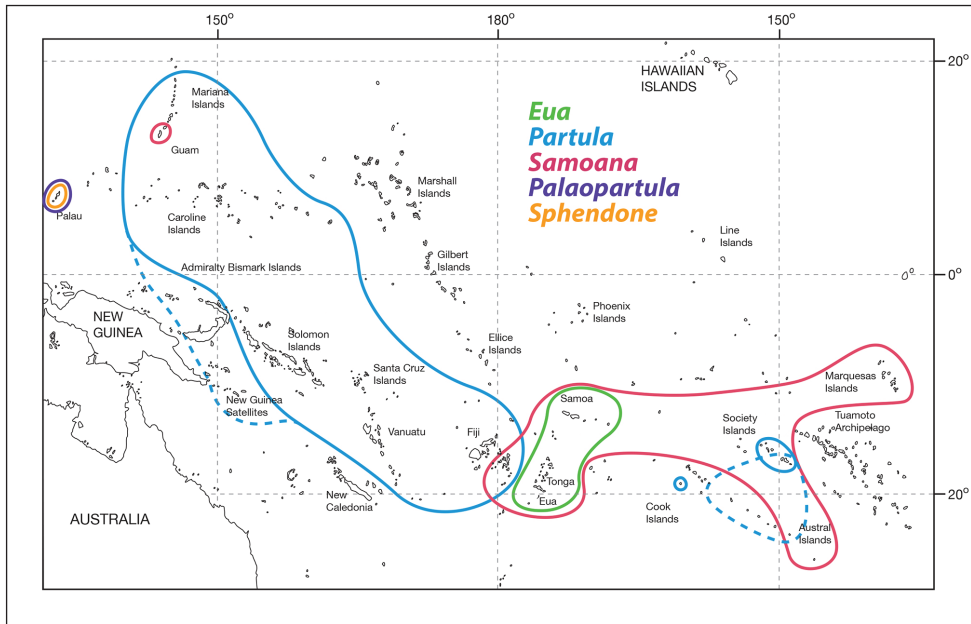


Figure 7. Geographic ranges of the five partulid genera. Map modified from Lee et al. (2014).

portion of the Kyushu-Palau Ridge (Neall and Trewick 2008). The islands consist of oceanic volcanics, many of which are capped with uplifted reef limestone (Hawkins and Ishizuka 2009), indicating prior submergence. During the last glaciation event, when sea levels were 120 m lower than today, all the hundreds of islands within the central fringing reef comprised a single island (Colin 2009). The islands of Palau have never been connected to any continental landmass (Hall et al. 1995; Hawkins and Ishizuka 2009), and their biotic colonization, like that of all oceanic islands, necessarily involved over-water dispersal (Cowie and Holland 2006). The broad distribution of Partulidae across the vast expanse of oceanic Pacific islands makes clear their exceptional dispersal abilities, so their presence among the largest native land snails of Palau is unsurprising.

Partulidae comprises more than 120 currently recognized species (Kondo 1955, 1968, Cowie 1992) endemic to the western and south-central Pacific from the Mariana Islands and Palau east to the Austral and Marquesas Islands (Fig. 7). The family is particularly diverse in the Society Islands, where they are among the largest and best-studied land snails (Crampton 1916, 1932, Murray and Clarke 1980, Cowie 1992, Lee et al. 2014). However, many species have declined or are extinct as a result of the loss of native lowland forest and human introduction of alien species, especially predators like *Euglandina rosea*, released in disastrous and unsuccessful biocontrol efforts (Murray et al. 1988). These losses have prompted zoo and lab-rearing efforts (Pearce-Kelly et al. 1997) followed by reintroduction to enclosures to prevent additional extinctions (Coote et al. 2004), and back into natural habitats in the wild (Coote et al. 2016). Relative to the species of *Palaopartula*, which appear to be generally rare (O’Foighil and

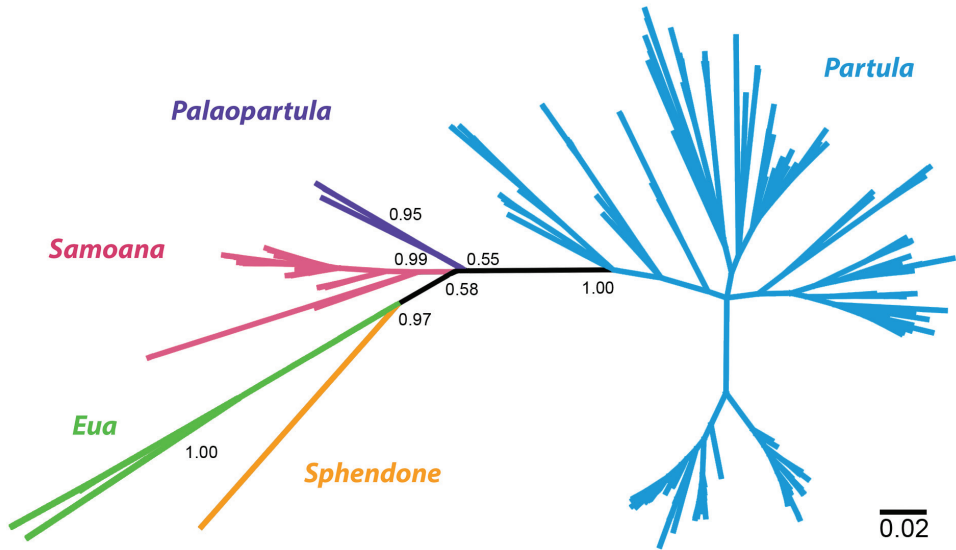


Figure 8. An unrooted network of partial COI sequences (540 bp for *Sphendone*, 655 bp for the other species) of Partulidae constructed using MrBayes as implemented in Geneious version 6.1.7. Node labels are posterior probabilities. The scale bar is equal to 2% sequence divergence.

Rundell 2012a, b, c), we found *Sphendone insolita* to be relatively common. Invasive rodents have been suggested as one agent for decline of *Palaopartula* species (O’Foighil and Rundell 2012a, b, c), and it may be that the fossorial habits of *S. insolita* confer some degree of protection from those predators and allow for its larger numbers.

All known partulids, like many other Central Pacific taxa, including Microcystinae and some Achatinellidae, are ovoviviparous. Although ovoviviparous species may have an advantage colonizing islands (Tompa 1984) they often have low fecundity (Baur 1994). *Partula suturalis* reared under laboratory conditions average 353 days to reach adult shell size and an additional 192 days before producing their first offspring. Afterwards, a single offspring is born approximately every 22 days (Murray and Clarke 1966). Partulids produce fewer than 90 offspring during their approximately 5 year life-span, far fewer than other snails with similar life-spans (Cowie 1992). The oviducts of most adult *Partula* simultaneously contain both eggs and embryos. Gravid individuals of ten species inhabiting Moorea averaged 1.37 eggs and 1.13 embryos (Crampton 1932), and four species from the Mariana Islands averaged 1.94 eggs and 1.20 embryos (Crampton 1925). Seven gravid individuals of *Sphendone insolita* averaged only 0.85 eggs and 0.28 embryos, and their eggs are particularly large, averaging 6.5 mm in greatest width, or nearly 0.29 of the total shell height. This is relatively larger than *Partula solitaria*, which was noted for having particularly large eggs at 3.5 mm, or 0.22 of shell height (Crampton 1932). The relatively small number of large eggs and embryos in *Sphendone insolita* suggests this species reproduces relatively slowly compared even to other partulid species. Low reproductive rate is likely to make the new species

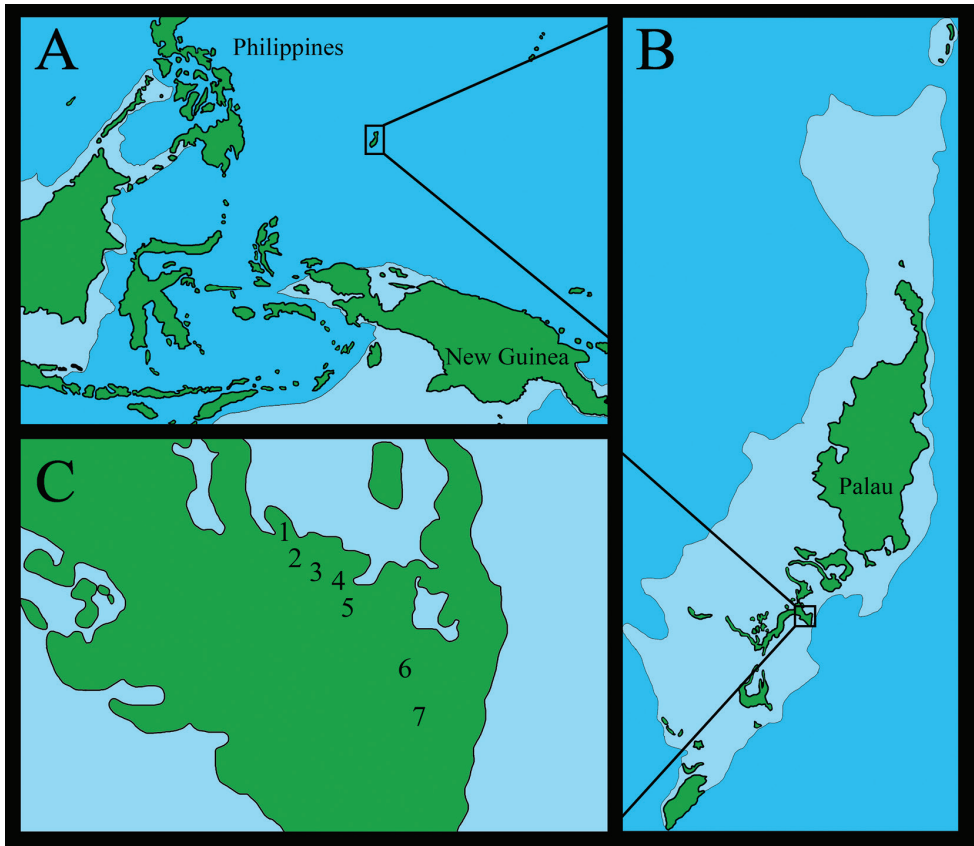


Figure 9. A–C GPS stations on Ngeruktabel Island, Palau, demarcating the trail to the German lighthouse, along which the type series of *Sphendone insolita* was collected.

particularly vulnerable to population suppression from introduced predators or habitat disturbance. In fact, *Partula* species on Tahiti that were rare but had the largest instantaneous clutch sizes (Crampton 1916) persist, whereas their more common congeners with smaller instantaneous clutch sizes have not (Bick et al. 2015).

Sphendone insolita is relatively common where found but may have specific habitat requirements that give it a limited and/or discontinuous distribution within Palau. Nearly all partulids are arboreal; however, a few species live on the ground in leaf litter – such as *P. compressa* and *P. crassilabris* – or in leaf litter and under stones – like *P. producta* (Pilsbry 1910). The new species is the only one associated with deep rock and boulder talus or found in crevices under and between rocks on the ground but not in surrounding leaf litter. Until further surveys better delimit this species' range, populations should be considered spatially restricted, making this species potentially vulnerable to habitat modification such as deforestation or limestone mining. The habitat specificity, small range, and apparently slow rate of reproduction of this species should make this a species of special concern to land managers.

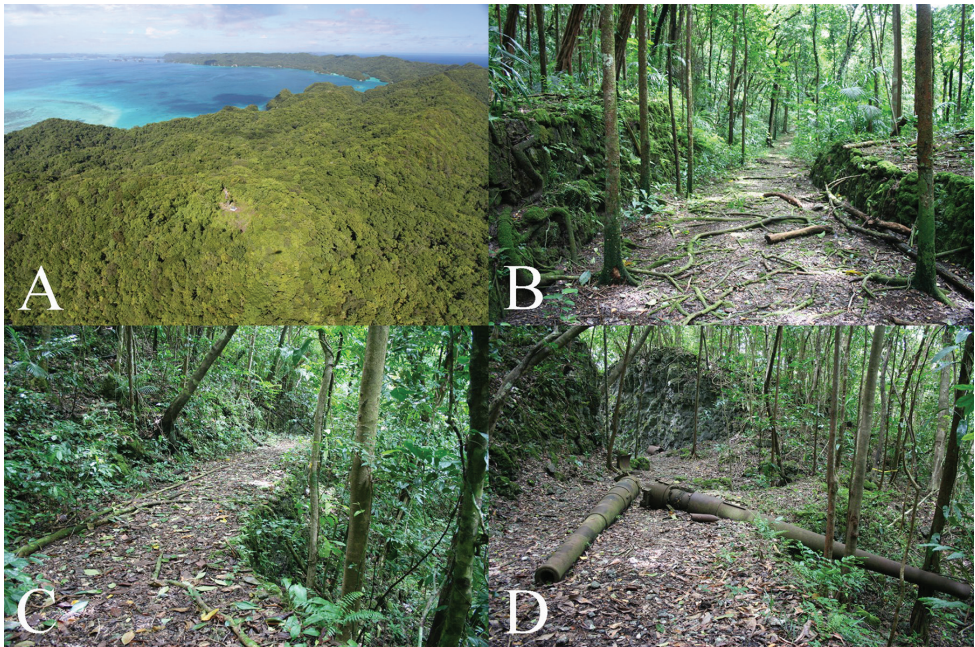


Figure 10. Photos of forested habitat at the type locality of *Sphendone insolita* on eastern Ngeruktabel Island. **A** Aerial view of the area, looking toward the southwest, showing the German lighthouse at the highest point **B–D** Forested trail along which the type series of *S. insolita* was collected.

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Appendix I

Specimens examined

- Eua expansa* (Pease 1872): Samoa: Savaii Island, near Salailua, L. Price, November 1965 (UF 485789, 3 shells).
- Eua zebrina* (Gould 1846): American Samoa: Tutuila Island (UF 158688, 22 shells), C. M. Dumbauld, March 1941 (UF 29715, 3 shells).
- Palaopartula calypso* Semper 1865: Palau: Babeldaob Island, Oikull, 7.4122°N, 134.5833°E, F. G. Thompson, 17 October 1985 (UF 248936, 1 shell); Koror Island, small ridge, 7.3444°N, 134.5001°E, F. G. Thompson, 13 October 1985 (UF 248833, 2 shells); South Babelthaup Island, D. Thaanum (ANSP 191976, 18 shells).
- Palaopartula leucothoe* Semper 1865: Palau (ANSP 294471, 5 shells).
- Palaopartula thetis* Semper 1865: Palau: Ngermalk Island, 7.3351°N, 134.4583°E, F. G. Thompson, 10 October 1985 (UF 248593, 1 shell); Ngeruktabel Island: along trail to German Lighthouse, 7.2600°N, 134.4493°W, F. Kraus, 24 August 1998 (FK 2840, 4 shells); at ruins of Japanese artillery battery, F. G. Thompson, 23 October 1985 (UF 248688, 3 shells); northeast side of island, T. M. Iliffe, 11 February 1985 (UF 265851, 5 shells); South Babelthaup Island, D. Thaanum (ANSP 191960, 13 shells); Ulong Islands: west island, northwest shore, R. I. Crombie, 16 January 1995 (UF 252891, 9 shells).
- Partula affinis* Pease 1868: French Polynesia: Society Islands: Tahiti Island, Faarumai, W. H. Pease (UF 192743, 30 shells).
- Partula arguta* Pease 1864: French Polynesia: Society Islands: Huahine Island, A. Garrett (UF 111866, 6 shells).
- Partula auriculata* Broderip 1832: French Polynesia: Society Islands: Raiatea Island, A. Garrett (UF 490635, 27 shells); W. J. Clench (UF 192745, 29 shells).
- Partula caledonica* Pfeiffer 1862: Vanuatu: Efate, Teouma Bay, along coast road, L. Price, 23 November 1972 (UF 484595, 4 shells).
- Partula callifera* Pfeiffer 1857: French Polynesia: Society Islands: Raiatea Island, A. Garrett (UF 490681, 1 shell).
- Partula carteriensis* (Quoy & Gaimard 1832): Papua New Guinea: New Ireland Province: St. Matthias Island, W. J. Eyerdam (UF 185667, 5 shells).
- Partula citrina* Pease 1866: French Polynesia: Society Islands: Raiatea Island, A. Garrett (UF 111915, 4 shells).
- Partula crassilabris* Pease 1866: French Polynesia: Society Islands: Raiatea Island, W. J. Clench (UF 192733, 34 shells).
- Partula dentifera* Pfeiffer 1853: French Polynesia: Society Islands: Raiatea Island, W. J. Clench (UF 111914, 8 shells).
- Partula faba* Martyn 1784: French Polynesia: Society Islands: Raiatea Island, A. Garrett (UF 490636, 15 shells).

- Partula flexuosa* Hartman 1885: Solomon Islands: New Georgia Islands, Gizo Island (UF 410366, 1 shell).
- Partula formosa* Garrett 1884: French Polynesia: Society Islands: Raiatea Island, Fatimu (UF 111935, 11 shells).
- Partula fusca* Pease 1866: French Polynesia: Society Islands: Raiatea Island, western Vaioara Valley (UF 111942, 7 shells).
- Partula garretti* Pease 1864: French Polynesia: Society Islands: Raiatea Island: W. H. Pease (UF 111963, 4 shells); (UF 158657, 18 shells).
- Partula gibba* Ferussac 1821: Mariana Islands: Guam Island, W. H. Eshnaur (UF 195878, 7 shells).
- Partula guamensis* Pfeiffer 1846: Federated States of Micronesia: Pohnpei Island, W. H. Pease (UF 192739, 6 shells).
- Partula hebe* Pfeiffer 1846: French Polynesia: Society Islands: Raiatea Island: W. H. Pease (UF 195879, 19 shells); Apoa Valley (UF 111996, 15 shells).
- Partula hyalina* Broderip 1832: French Polynesia: Society Islands: Tahiti Island, A. Garrett (UF 112002, 6 shells).
- Partula imperforata* Pfeiffer 1877: French Polynesia: Society Islands (UF 112013, 4 shells).
- Partula lugubris* Pease 1864: French Polynesia: Society Islands: Tahiti Island, H. J. Armstrong (UF 192734, 18 shells).
- Partula lutea* Lesson 1831: French Polynesia: Society Islands: Bora Bora Island, W. H. Pease (UF 192737, 31 shells).
- Partula macgillivrayi* Pfeiffer 1855: Vanuatu (UF 112033, 6 shells).
- Partula micans* Pfeiffer 1853: Papua New Guinea, P. Dautzenberg (UF 112035, 15 shells).
- Partula mooreana* Hartman 1880: French Polynesia: Society Islands: Moorea Island, A. Garrett (UF 112037, 8 shells).
- Partula navigatoria* Pfeiffer 1850: French Polynesia: Society Islands: Raiatea Island, Western Vaioara Valley (UF 112039, 8 shells).
- Partula otaheitana* (Bruguiere 1789): French Polynesia: Society Islands: Tahiti Island, Faarumai Paune, W. H. Pease (UF 112056, 6 shells).
- Partula planilabra* Pease 1864: French Polynesia: Society Islands: Tahaa Island, A. Garrett (UF 112067, 9 shells).
- Partula radiata* Garrett 1884: French Polynesia: Society Islands: Raiatea Island, A. Garrett (UF 112070, 6 shells).
- Partula radiolata* Pfeiffer 1846: Mariana Islands: Guam Island, N side of Route 7, 5.0 mi E of Route 6, F. Kraus, 17 May 1995 (UF 281058, 20 shells).
- Partula rosea* Broderip 1832: French Polynesia: Society Islands: Huahine Island, A. Garrett (UF 112096, 4 shells).
- Partula rustica* Pease 1866: French Polynesia: Society Islands: Raiatea Island, W. J. Clench (UF 192740, 37 shells).
- Partula similis* Hartman 1886: Papua New Guinea: Milne Bay Province: Woodlark Island, Guasopa, 9.2241°S, 152.9439°E, J. Slapcinsky, 23 January 2003 (UF 328339, 50 shells).

- Partula suturalis* Pfeiffer 1855: French Polynesia: Society Islands: Moorea Island, A. Garrett (UF 490638, 7 shells).
- Partula taeniata* Mörch 1850: French Polynesia: Society Islands: Moorea Island, A. Garrett (UF 112134, 4 shells).
- Partula thalia* Garrett 1884: French Polynesia: Society Islands: Raiatea Island, W. J. Clench (UF 158680, 16 shells).
- Partula turneri* Pfeiffer 1860: Vanuatu: Anatom Island (UF 112150, 4 shells).
- Partula umbilicata* Pease 1866: Samoa: Upolu Island (UF 192724, 18 shells).
- Partula varia* Broderip 1832: French Polynesia: Society Islands: Huahine Island, T. Dranga (UF 158682, 21 shells).
- Samoana abbreviata* (Mousson 1869): American Samoa: Tutuila Island: T. Dranga (UF 192741, 14 shells); (UF 158646, 8 shells).
- Samoana conica* (Gould 1846): Samoa: Upolu Island, H. J. Armstrong (UF 192732, 14 shells).
- Samoana fragilis* (Ferussac 1821): Northern Mariana Islands: Rota Island, Water Cave, S. Bauman, 2 April 1996 (UF 481329, 1 shell).
- Samoana ganymedes* (Pfeiffer 1846): French Polynesia: Marquesas Islands (UF 195874, 2 shells).
- Samoana inflata* (Reeve 1842): French Polynesia: Marquesas Islands, A. Garrett (UF 490663, 3 shells).
- Samoana strigata* (Reeve 1850): French Polynesia: Marquesas Islands: Nuku Hiva Island, W. H. Pease (UF 192725, 26 shells).

***Sinocoelotes* gen. n., a new genus of the subfamily Coelotinae (Araneae, Agelenidae) from Southeast Asia**

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Abstract

A new genus of the spider subfamily Coelotinae, *Sinocoelotes* **gen. n.**, with nine new species, is described from Yunnan and Sichuan Provinces in southern China. The new species are: *Sinocoelotes cangshanensis* **sp. n.** (♀), *S. hehuaensis* **sp. n.** (♂♀), *S. luoshuiensis* **sp. n.** (♀), *S. mangbangensis* **sp. n.** (♀) from Yunnan; *S. kangdingensis* **sp. n.** (♀), *S. ludingensis* **sp. n.** (♂♀), *S. mahuanggouensis* **sp. n.** (♀), *S. muliensis* **sp. n.** (♀), and *S. yanyuanensis* **sp. n.** (♂) from Sichuan. In addition, six *Coelotes* species are transferred to the new genus: *Sinocoelotes acicularis* (Wang, Griswold & Ubick, 2009), **comb. n.** (♂♀), *S. forficatus* (Liu & Li, 2010), **comb. n.** (♂♀), *S. guangxian* (Zhang, Yang, Zhu & Song, 2003), **comb. n.** (♂♀), *S. pseudoterrestris* (Schenkel, 1963), **comb. n.** (♂♀), *S. pseudoyunnanensis* (Wang, Griswold & Ubick, 2009), **comb. n.** (♂♀) and *S. thailandensis* (Dankittipakul & Wang, 2003), **comb. n.** (♂♀). DNA barcodes of all the species were documented for future use.

Keywords

Taxonomy, description, diagnosis, morphology, new combination, China

Introduction

Coelotine spiders are common in the Northern Hemisphere. So far, a total of 662 valid species belonging to 25 genera (Wang 2002, Chen et al. 2015a, Chen et al. 2015b, Jiang and Chen 2015, Chen et al. 2016, Zhao and Li 2016) are known in the Holarctic and Southeast Asia. Twenty-two genera of Coelotinae are known from

Asia. Among them, 18 genera including 294 species are reported from China (the most species-rich region) (Li and Lin 2016). Coelotinae from China are partly revised (Ovtchinnikov 1999, Wang 2002, Wang 2003, Chen et al. 2015a, Chen et al. 2015b, Chen et al. 2016); however, some genera and species remain poorly studied. The most species-rich genus remaining *Coelotes* Blackwall, 1841, seems to be polyphyletic.

The genus *Coelotes* was described by Blackwall (1841) for *Clubiona saxatilis* Blackwall, 1833, which was later synonymized with *Drassus atropos* Walckenaer, 1830. In the recent years, the genus was mainly revised by Ovtchinnikov (1999, 2000) and Wang (2002). They described 12 new genera and subgenera: *Asiacoelotes* Wang, 2002 (now considered to be a junior synonym of *Iwogumoa*), *Bifidocoelotes* Wang, 2002, *Brignoliolus* (subgenus) Ovtchinnikov, 1999, *Eurocoelotes* Wang, 2002 (now considered to be a junior synonym of *Inermocoelotes*), *Femoracoelotes* Wang, 2002, *Himalcoelotes* Wang, 2002, *Inermocoelotes* Ovtchinnikov, 1999, *Leptocoelotes* Wang, 2002, *Platocoelotes* Wang, 2002, *Spiricoelotes* Wang, 2002, *Tegeocoelotes* Ovtchinnikov, 1999, and *Urocoras* Ovtchinnikov, 1999. Currently, 184 species are included in *Coelotes* (World Spider Catalog 2016), but the genus still remains polymorphic; for example, the epigynal teeth are present in *C. atropos* (Walckenaer, 1830), but absent in *C. ningmingensis* Peng, Yan, Liu & Kim 1998; the epigynal hoods are present in *C. septus* Wang, Yin, Peng & Xie 1990, but absent in *C. terrestris* (Wider, 1834). In general, *Coelotes* is an extremely heterogeneous genus. To improve the systematic composition of *Coelotes*, further work needs to be done.

In this paper, a new genus of coelotine spiders, *Sinocoelotes* gen. n. and nine new species from China are described, and six new combinations are suggested.

Material and methods

Specimens were examined with a LEICA M205C stereomicroscope. Images were captured with an Olympus C7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus SZX12 dissecting microscope. Epigynes and male palps were examined after dissection from the spiders' bodies. Epigyne was cleared by boiling it in 10% KOH solution before take photos of the vulva.

All measurements were obtained using a LEICA M205C stereomicroscope and are given in millimeters. Leg measurements are shown as: Total length (femur, patella + tibia, metatarsus, tarsus). Only structures (palp and legs) of the left body side were described and measured. The terminology used in the text and the figure legends follows Wang (2002). Abbreviations used in this paper and in the figure legends: A = epigynal atrium; ALE = anterior lateral eye; AME = anterior median eye; AME-ALE = distance between AME and ALE; AME-AME = distance between AME and AME; ALE-PLE = distance between ALE and PLE; C = conductor; CD = copulatory duct; CDA = dorsal conductor apophysis; CF = cymbial furrow; E = embolus; EB = embolic base; ET = epigynal teeth; FD = fertilization duct; LTA = retrolateral tibial apophysis; MA = median apophysis; PA = patellar apophysis; PLE = posterior lateral eye; PME = posterior median eye; PME-PLE = distance between PME and PLE; PME-PME = distance between PME and PME; RTA = retro-ventral tibial apophysis; S = spermatheca;

Table 1. Voucher specimen information.

Species	GenBank accession number	Sequence length	Collection localities
<i>S. acicularis</i> (Wang et al., 2009)	KX555516	630bp	Lushui County, Yunnan Province, China
<i>S. cangshanensis</i> sp. n.	KX555514	630bp	Hehua Village, Xiaguan Town, Yunnan Province, China
<i>S. forficatus</i> (Liu & Li, 2010)	KX555512	630bp	Menglun Town, Mengla County, Yunnan Province, China
<i>S. guangxian</i> (Zhang et al., 2003)	KX555515	630bp	Xiaguan Town, Yunnan Province, China
<i>S. hehuaensis</i> sp. n.	KX555513	630bp	Hehua Village, Xiaguan Town, Yunnan Province, China
<i>S. kangdingensis</i> sp. n.	KX555510	630bp	Kangding County, Sichuan Province, China
<i>S. ludingensis</i> sp. n.	KX555509	627bp	Luding County, Sichuan Province, China
<i>S. luoshuiensis</i> sp. n.	KX555517	630bp	Jiangdong Village, Gudong Town, Yunnan Province, China
<i>S. mahuanggouensis</i> sp. n.	KX555508	630bp	Baoxing County, Sichuan Province, China
<i>S. mangbangensis</i> sp. n.	KX555511	630bp	Changlinggan Village, Tengchong County, Yunnan Province, China
<i>S. muliensis</i> sp. n.	KX555520	630bp	Muli County, Sichuan Province, China
<i>S. pseudoterrestris</i> (Schenkel, 1963)	KX555518	627bp	Xishan Forest Park, Yunnan Province, China
<i>S. pseudoyunnanensis</i> (Wang et al., 2009)	KX555519	630bp	Pianma Town, Lushui County, Yunnan Province, China
<i>S. thailandensis</i> (Dankittipakul & Wang, 2003)	KX555507	630bp	Jeep tract, Mae Cham District, Chiangmai Province, Thailand
<i>S. yanyuanensis</i> sp. n.	KX555506	630bp	Yanyuan County, Sichuan Province, China

SA = anterior part of spermatheca; SH = spermathecal head; SP = posterior part of spermatheca; ST = subtegulum; T = tegulum.

Abbreviations used for museums and other institutions: CAS = California Academy of Sciences, San Francisco, USA; HNU = Hunan Normal University, Changsha, China; IZCAS = Institute of Zoology, Chinese Academy of Sciences, Beijing, China; MHBV = Museum of Hebei University, Baoding, China; MHNG = Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHP = Muséum National d'Histoire Naturelle, Paris, France.

DNA barcodes were obtained for future use. A partial fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified and sequenced for 15 species (all nine new species and six species, for which we introduced new combinations) using Primers: LCO1490-oono (5'-CWACAAAYCATARRGATATTGG-3') (Folmer et al. 1994) and HCO2198-zz (5'-TAAACTTCCAGGTGACCAAAAAATCA-3') (Zhao and Li 2016). For additional information on extraction, amplification and sequencing procedures, see Zhao et al. (2013). All sequences were analyzed using BLAST and are deposited in GenBank. The accession numbers are provided in Table 1.

All of the specimens (including molecular vouchers) are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing, China.

Systematics

Family Agelenidae C.L. Koch, 1837

Subfamily Coelotinae F.O.P.-Cambridge, 1893

Genus *Sinocoelotes* Zhao & Li, gen. n.

<http://zoobank.org/1AD20278-53C5-40CE-90A8-A888588CE81D>

Type species. *Sinocoelotes hebuaensis* sp. n.

Etymology. The generic name is derived from its similarity to *Coelotes* and the Latin adjective Sino- for “Chinese” referring to the main distribution region of the genus. The gender is masculine.

Diagnosis. *Sinocoelotes* gen. n. is similar to *Coelotes*. Males of new genus can be distinguished from those of *Coelotes* by the longer and slenderer conductor (about 1/2 length of cymbium, while in *Coelotes* the conductor is broad, less than 1/4 length of cymbium in length, and with blunt tip, see Fig. 1), the shorter and truncated patellar apophysis with a blackened apex, while in *Coelotes* the patellar apophysis is longer than patella, and usually with a ventral part extending longer than dorsal part (see Fig. 1), the short LTA (less than 1/6 length of RTA) (cf. Figs 7A–C and 1A–C). Females of *Sinocoelotes* gen. n. can be distinguished from those of *Coelotes* by the longer copulatory ducts, about 1/2 length of vulva (while in *Coelotes* they are very short or even absent, Fig. 2A–B), the shorter spermathecae (about 1/2 length of epigyne), which can be divided into two parts: anterior part and posterior part (while *Coelotes* has spermathecae subequal to the length of epigyne, and usually S-shaped), and by the oval or finger-like spermathecal heads (while in *Coelotes* spermathecal heads are short, rounded and situated at the anterior part of epigyne) (cf. Figs 8A–B and 2A–B).

Description. Small to medium-sized, with a total length of 5–14 mm, the body brown to dark brown. Carapace narrowed in ocular area, sparsely covered with black setae, and thoracic region with longitudinal fovea and radial groove; sternum usually heart-shaped. Abdomen brown to dark brown, heavily covered with short setae; dorsum with many black irregular patches and five grey chevron-like markings, the antero-median part with one cardiac pattern, and posterior part with dark maculation. Chelicerae with 3 promarginal and 3 or 4 retromarginal teeth. Male palp with one patellar apophysis and two tibial apophyses (RTA and LTA), the patellar apophysis broad and long, its apex blackened and truncated; RTA long and broad, extending beyond distal margin of tibia, subequal to the length of tibia, and with blunt tip; LTA short; cymbium crescent-shaped, the tip long, about 1/3 length of cymbium; cymbial furrow short, less than 1/4 of the cymbium; tegulum slender, and visible part very small; conductor slender, tapered, and its apex not close to the tegulum; median apophysis present, spoon-like; dorsal conductor apophysis well developed. Epigyne with large atrium (occupying about 1/4 of epigynal plate square); epigynal teeth pre-

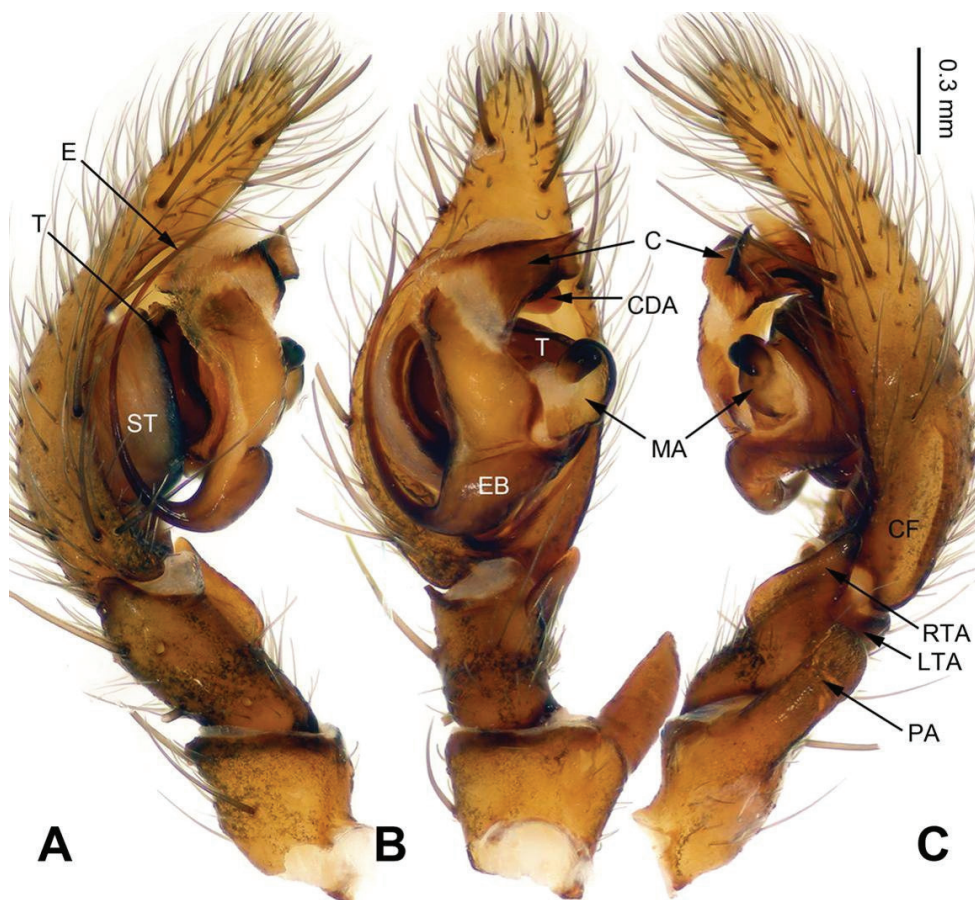


Figure 1. Male palp of *Coelotes pickardi tirolensis*, from Italy. **A** Prolateral **B** Ventral **C** Retrolateral. Scale bar: equal for **A**, **B** and **C**.

sent, long or short, located medially in comparison to epigynal plate height or antero-medially; spermathecae usually long and convoluted, subdivided in 2 parts: anterior and posterior; anterior part of spermathecae broad, posterior part thinner and strongly convoluted, anterior part usually larger than posterior part; spermathecal heads located at the border between anterior part of spermathecae and copulatory ducts; copulatory ducts broad, arc-shaped, situated anteriorly, connected to each other at basal part, and separated about its length at terminal part.

Comments. In addition to morphological study, we analyzed the relationships of coelotine spiders based on molecular data (8 genes, ~ 6.5 kb) on 18 genera and 286 coelotine species. The molecular analyses (in progress) support *Sinocoelotes* gen. n. as monophyletic.

Distribution. So far the genus is known only from China and Thailand (Fig. 21).

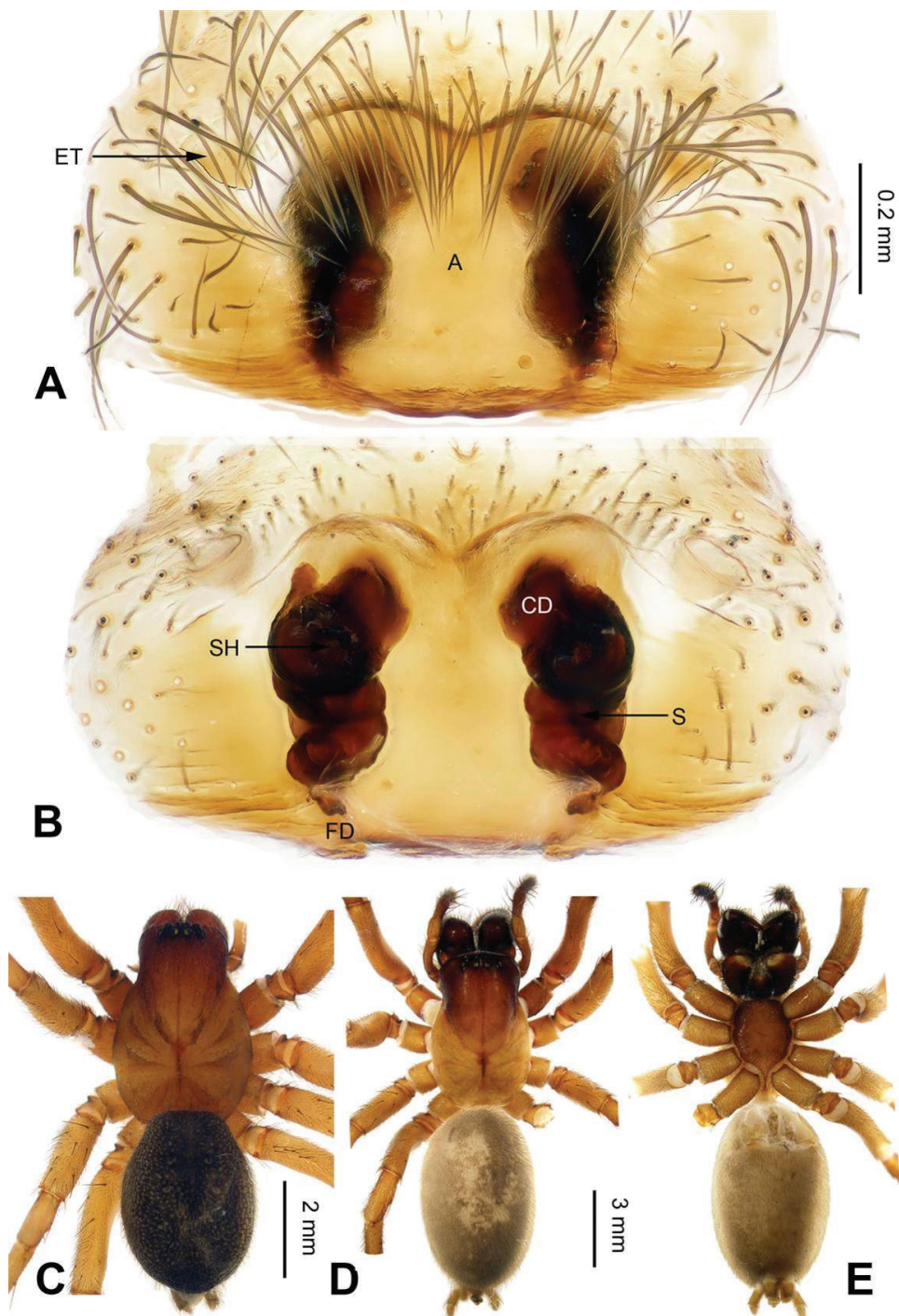


Figure 2. Epigyne and habitus of *Coelotes pickardi tirolensis*, from Italy. **A** Epigyne, ventral **B** Vulva, dorsal **C** Male habitus, dorsal **D** Female habitus, dorsal **E** Female habitus, ventral. Scale bars: equal for **A** and **B**; equal for **D** and **E**.

***Sinocoelotes acicularis* (Wang, Griswold & Ubick, 2009), comb. n.**

Figs 3, 21

Coelotes acicularis Wang et al. 2009: 4, figs 1–9 (♂♀, from Baoshan, Yunnan, China, in HNU and CAS, not examined).

Material examined. 1♀: China: Yunnan Province: Nujiang Lisu Autonomous Prefecture: Lushui County, road from Liuku to Pianma Town, N26°00'09", E98°39'33", 2422 m, 7.XII.2013, Y. Li and J. Liu.

Diagnosis. The female is similar to *S. hehuaensis* sp. n., but can be easily distinguished from it by the longer epigynal teeth (three times longer than in *S. hehuaensis* sp. n.), the different shape of atrium (anterior part much broader than posterior part in this species, but inverted U-shaped in *S. hehuaensis* sp. n.), and the broader and membranous copulatory ducts (which are slender and sclerotized in *S. hehuaensis* sp. n.) (cf. Figs 3A–B and 8A–B).

Description. Described by Wang et al. (2009).

Comments. The species shares a combination of somatic morphology characters with *S. hehuaensis* sp. n., and therefore we transfer it to *Sinocoelotes* gen. n. The molecular analysis supports this transfer.

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes cangshanensis* Zhao & Li, sp. n.**

<http://zoobank.org/0E3AEB72-937A-4AF6-8238-2AFF88E18C3F>

Figs 4, 21

Type material. Holotype ♀: China: Yunnan Province: Dali Bai Autonomous Prefecture: Xiaguan Town, Hehua Village, Cangshan Mountain, Baolinjing valley, N25°36'27", E100°11'18", 2307 m, 20.XI.2013, Y. Li and J. Liu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female can be easily distinguished from other *Sinocoelotes* gen. n. species by the long and broad epigynal teeth (subequal to the atrial length), the broad anterior part of spermathecae (occupying 1/4 of epigyne plate square, and about five times of the posterior part of spermathecae in this species, but occupying less than 1/5 epigyne plate square in other species), anterior part of spermathecae touching each other (only part of SA touching each other in *S. hehuaensis* sp. n. and *S. mangbangensis* sp. n.; part of SP touching each other in *S. luoshuiensis* sp. n. and *S. pseudoterrestris* comb. n.; separated from each other in other species), and the short, laterally located spermathecal heads (laterally located but long in *S. acicularis* comb. n., *S. kangdingensis* sp. n. and *S. mahuanggouensis* sp. n.; medially located in other species) (Fig. 4A–B).

Description. Female. Total length 9.82. Carapace 4.50 long, 3.04 wide. Abdomen 5.32 long, 3.76 wide. Eye sizes and interdistances: AME 0.16, ALE 0.22, PME 0.18, PLE 0.21; AME-AME 0.08, AME-ALE 0.04, PME-PME 0.13, PME-PLE

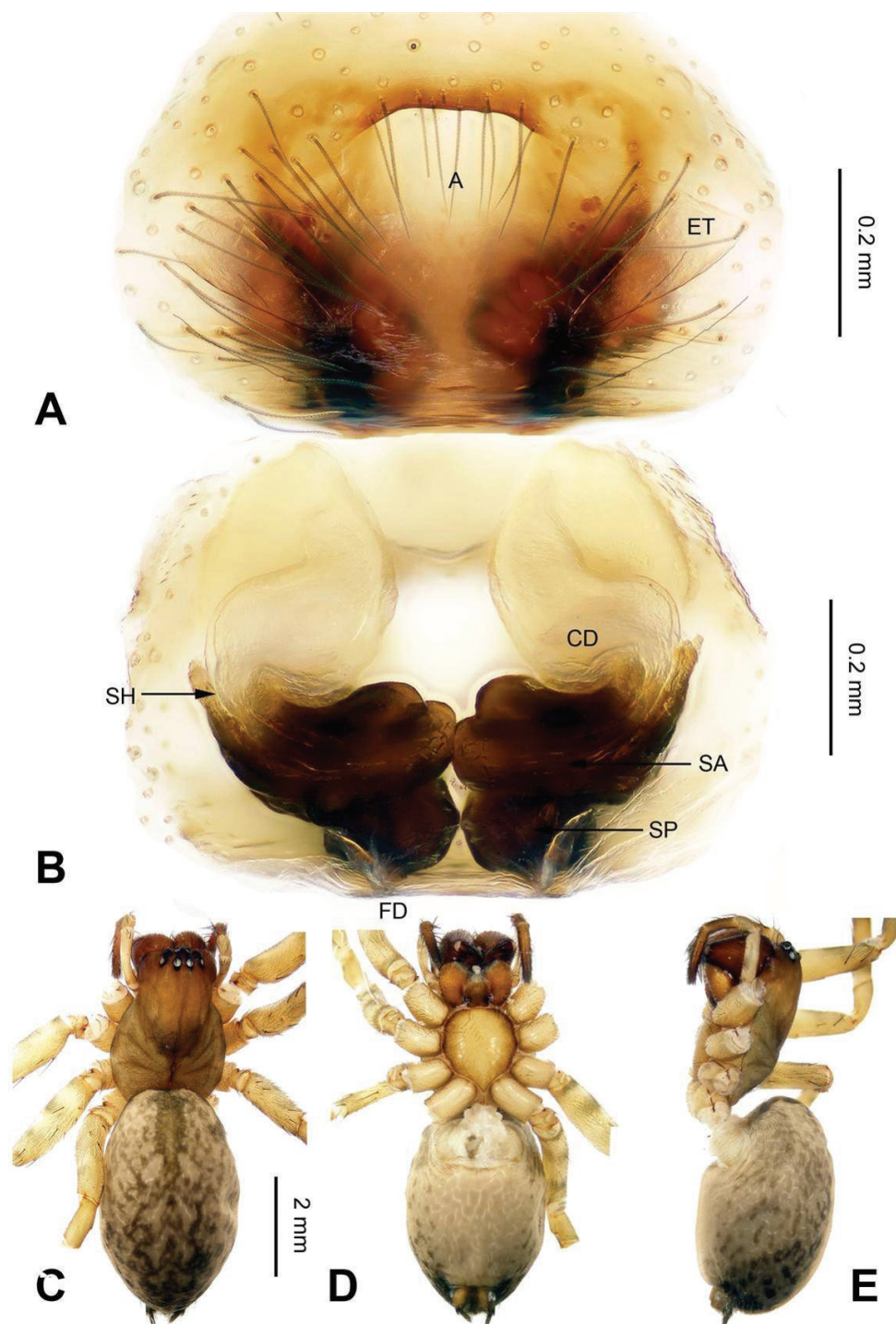


Figure 3. Epigyne and habitus of *Sinocoelotes acicularis*. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **C**, **D** and **E**.

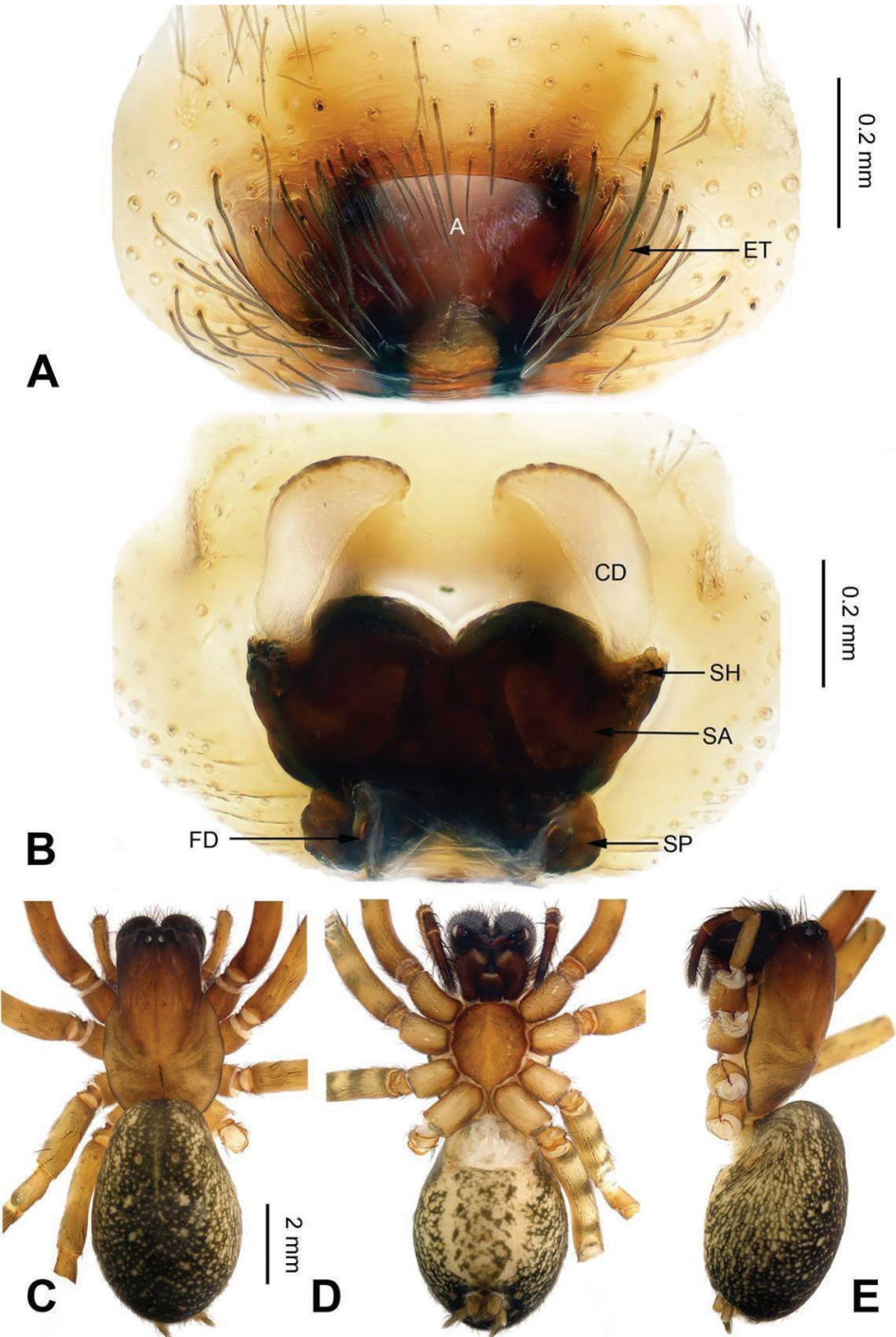


Figure 4. Epigyne and habitus of *Sinocoelotes cangshanensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **C**, **D** and **E**.

0.22. Leg measurements: I 11.50 (3.35, 3.45, 2.75, 1.95); II 12.24 (3.20, 4.16, 3.12, 1.76); III 10.84 (2.88 3.28, 2.88, 1.80); IV 14.57 (3.92, 4.10, 4.23, 2.32). Chelicerae with four retromarginal teeth. Epigyne: atrium small, occupying 1/6 of epigynal plate square, narrowing at the middle part; teeth long, broad, located anteriorly, close to atrial anterior margin, and their length subequal to atrial length, width subequal to atrium width; spermathecae contiguous with each other, anterior part of spermathecae broad; posterior part of spermathecae about four times thinner than the anterior part; spermathecal heads small, located laterally; copulatory openings hidden in anterior part of atrium; copulatory ducts membranous, anterior parts separated from each other by 0.3 length, posterior part separated by approximately 1.5 times length, copulatory duct first goes anteriorly, and then posteriorly (Fig. 4A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes forficatus* (Liu & Li, 2010), comb. n.**

Figs 5, 21

Coelotes forficatus Liu and Li 2010: 2, figs 1A–B, 2A–C, 3A–B, 4A–B, 5A–C (♂ holotype and ♂♀ paratypes from Xishuangbanna, Yunnan, China, in IZCAS, not examined).

Material examined. 1♀: China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County, Menglun Town, Xishuangbanna Nature Reserve, N21°37'55", E101°12'25", 665 m, 3.VII.2013, Q. Zhao and Z. Chen.

Diagnosis. The female is similar to *S. behuaensis* sp. n., but can be easily distinguished from it by the longer and slenderer epigynal teeth (twice as long as in *S. behuaensis* sp. n.), the broader, shorter and laterally originating spermathecal heads (twice as long as *S. forficatus* and medially originating in *S. behuaensis* sp. n.), and the slenderer, longer and inverted U-shaped copulatory ducts (cf. Figs 5A–B and 8A–B).

Comments. The species shares a combination of somatic morphology characters with *S. behuaensis* sp. n., and therefore we assigned it to *Sinocoelotes* gen. n. The molecular analysis supports this transfer.

Description. Described by Liu and Li (2010).

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes guangxian* (Zhang, Yang, Zhu & Song, 2003), comb. n.**

Figs 6, 21

Coelotes guangxian Zhang et al. 2003: 79, figs 1–5 (♂ holotype and ♂♀ paratypes from Dali, Yunnan, China, in MHBU, not examined).

Material examined. 1♀: China: Yunnan Province: Dali Bai Autonomous Prefecture: Xiaguan Town, the south shore of Erhai Lake, Tuanshan Park, N25°36'27", E100°14'39", 1992 m, 19.XI.2013, Y. Li and J. Liu.

Diagnosis. The female can be easily distinguished from all other *Sinocoelotes* gen. n. species by the broad atrium, the long, with blunt tip and anteriorly situated epigynal teeth (long, anteriorly situated, but with pointed tip in *S. kangdingensis* sp. n., *S. ludingensis* sp. n. and *S. luoshuiensis* sp. n.; long, with blunt tip, but not anteriorly located in *S. acicularis* comb. n. and *S. cangshanensis* sp. n.; short, less than 1/2 length of *S. guangxian* comb. n. in other species), the short spermathecae (anterior part is smaller than posterior part), and the broad copulatory ducts (occupying 1/2 of epigynal plate) (Fig. 6A–B).

Description. See Zhang et al. (2003).

Comments. The species shares a combination of somatic morphology characters with *S. hehuaensis* sp. n., and therefore was assigned to *Sinocoelotes* gen. n. The molecular analysis supports the transfer.

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes hehuaensis* Zhao & Li, sp. n.**

<http://zoobank.org/D6B4F7D0-1DF0-4944-B82F-1FE872142A38>

Figs 7–8, 21

Type material. **Holotype** ♂: China: Yunnan Province: Dali Bai Autonomous Prefecture: Xiaguan Town, Hehua Village, Cangshan Mountain, Baolinjing Valley, N25°36'27", E100°11'18", 2307 m, 20.XI.2013, Y. Li and J. Liu. **Paratype:** 1♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The male can be easily distinguished from other *Sinocoelotes* gen. n. species by the longer peg-shaped conductor (about 1/2 length of cymbium; less than 1/3 length of cymbium in *S. ludingensis* sp. n., *S. thailandensis*; bended in *S. yanyuanensis* sp. n.), the longer patellar apophysis (subequal to the length of patella in *S. hehuaensis* sp. n., shorter than the length of patella in other species), the larger and subtriangular dorsal conductor apophysis (large, but with blunt tip in *S. thailandensis*; less than 1/3 length and 1/2 width of *S. hehuaensis* in other species) (cf. Figs 7A–C, 10A–C, 18A–C and 20A–C). The female is similar to *S. cangshanensis* sp. n. but can be distinguished from it by the shorter epigynal teeth (less than 1/3 length of the teeth in *S. cangshanensis* sp. n.), the broader copulatory ducts (two times wider than in *S. cangshanensis* sp. n.), and the longer spermathecal heads (twice as long as in *S. cangshanensis* sp. n.) (cf. Figs 8A–B; and 4A–B).

Description. Male. Total length 7.04. Carapace 3.60 long, 2.76 wide. Abdomen 3.44 long, 2.00 wide. Eye sizes and interdistances: AME 0.16, ALE 0.20, PME 0.19, PLE 0.17; AME-AME 0.09, AME-ALE 0.03, PME-PME 0.10, PME-PLE 0.13. Leg

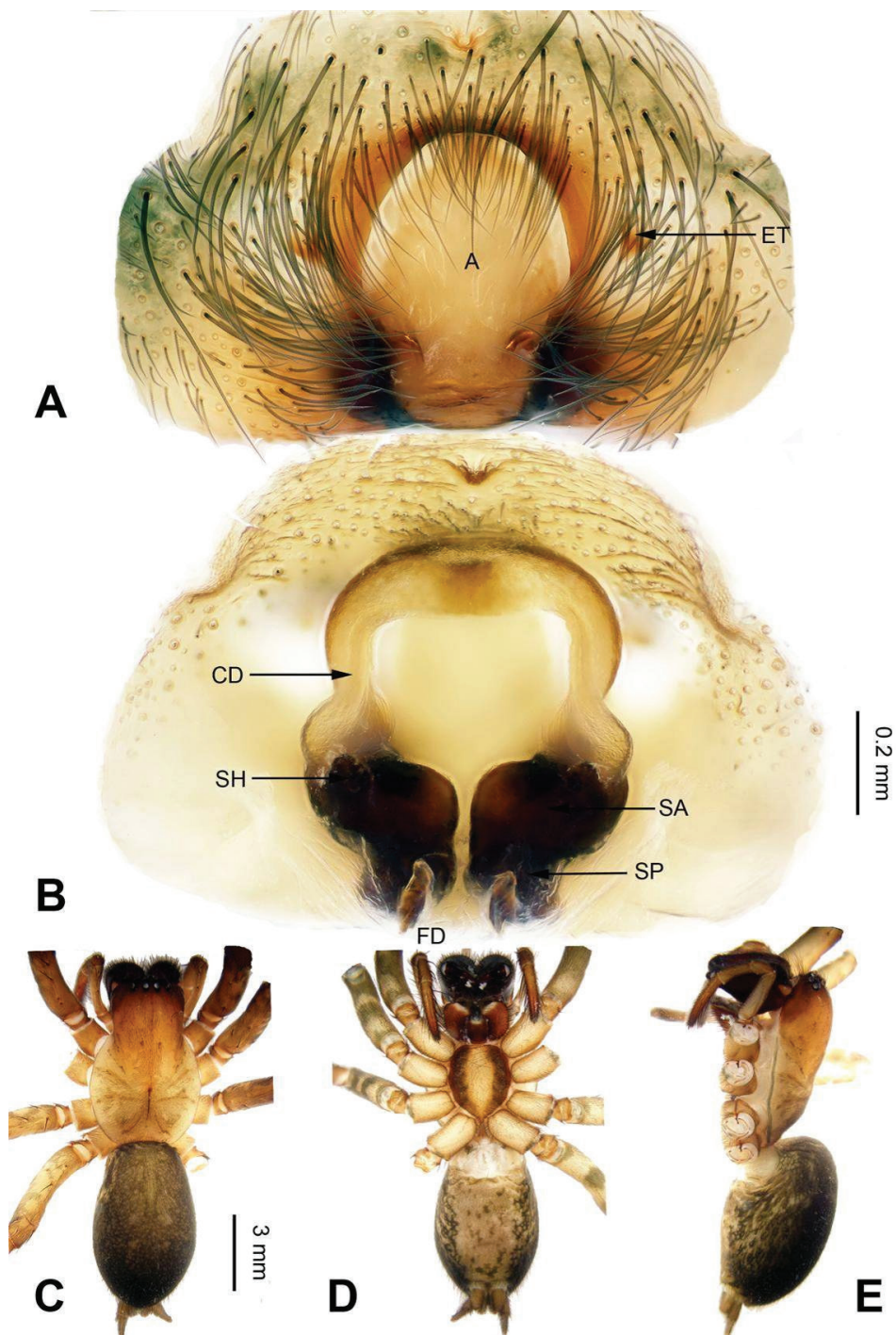


Figure 5. Epigyne and habitus of *Sinocoelotes forficatus*. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

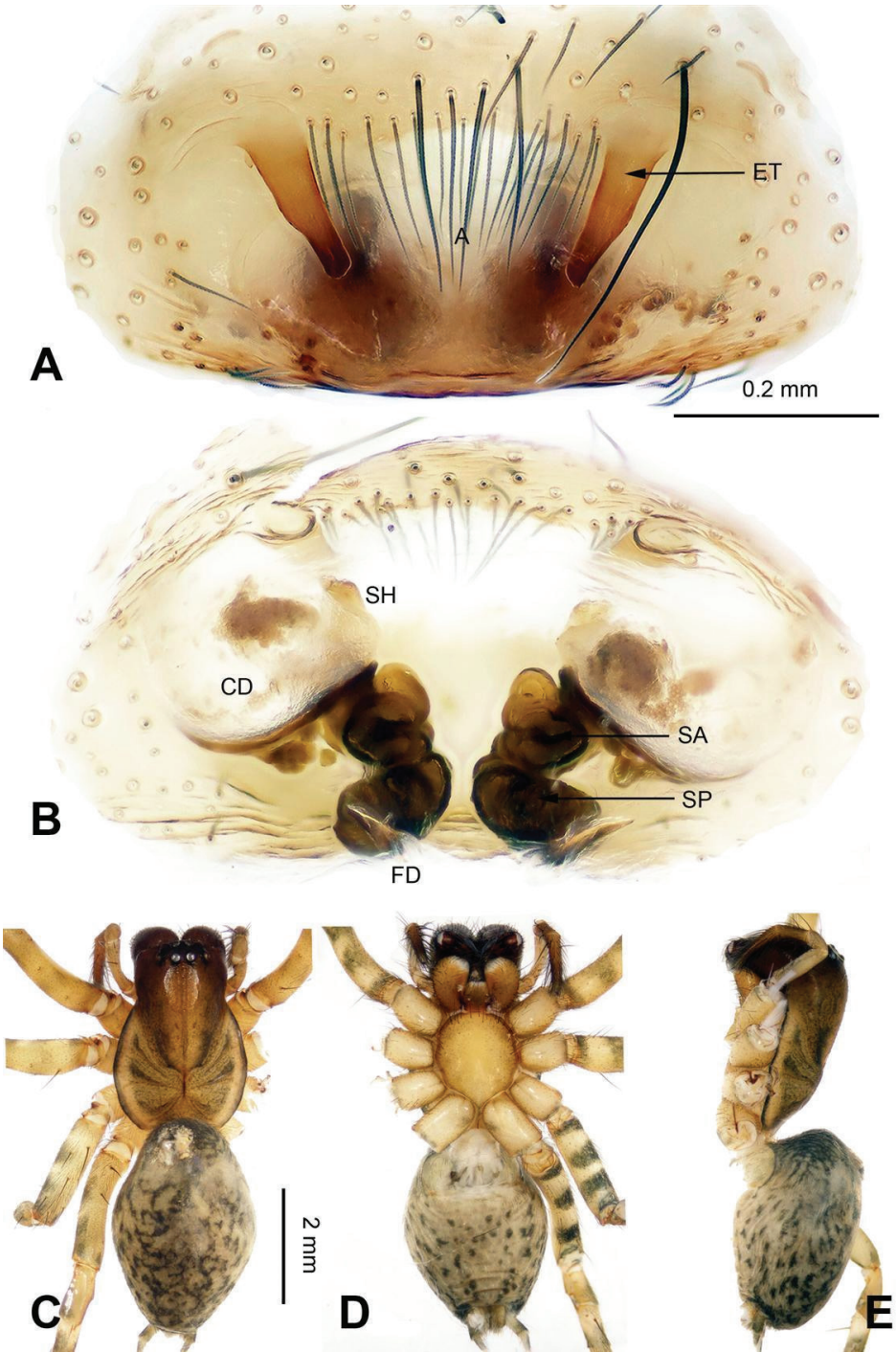


Figure 6. Epigyne and habitus of *Sinocoelotes guangxian*. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

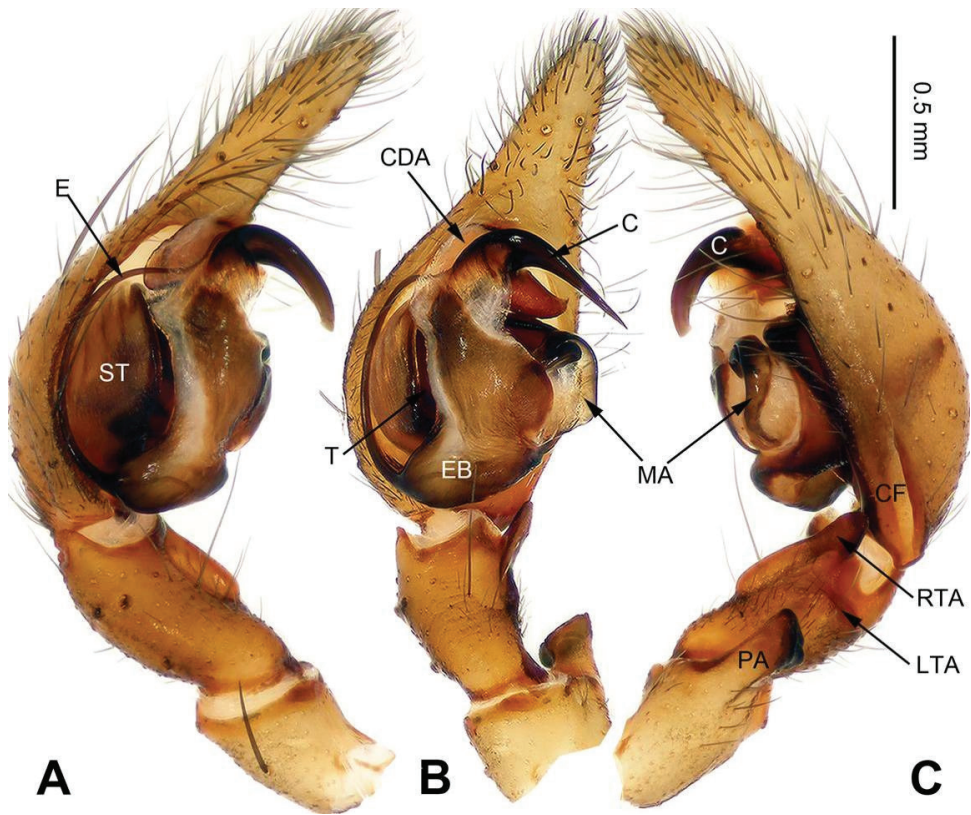


Figure 7. Male palp of *Sinocoelotes behuaensis* sp. n., holotype. **A** Prolateral **B** Ventral **C** Retrolateral. Scale bar: equal for **A**, **B** and **C**.

measurements: I 14.40 (3.92, 4.48, 3.64, 2.36); II 12.60 (3.48, 4.00, 3.20, 1.92); III 11.33 (3.28, 3.40, 3.02, 1.63); IV 15.23 (4.10, 4.50, 4.48, 2.15). Chelicerae with four retromarginal teeth. Palp: patellar apophysis long, subequal to the length of patella; RTA broad, extending beyond the tibia; LTA short, less than 1/5 length of RTA; cymbial furrow short, about 1/6 length of cymbium; conductor long, slender, peg-shaped in ventral view, subequal to 1/2 length of cymbium; dorsal conductor apophysis broad, the visible part (between conductor and tegulum) subtriangular; embolus beginning at seven o'clock position (Fig. 7A–C).

Female. Total length 13.20. Carapace 6.02 long, 4.49 wide. Abdomen 7.18 long, 5.26 wide. Eye sizes and interdistances: AME 0.17, ALE 0.29, PME 0.23, PLE 0.27; AME-AME 0.15, AME-ALE 0.04, PME-PME 0.24, PME-PLE 0.29. Leg measurements: I 16.83 (4.49, 5.76, 4.04, 2.54); II 15.13 (4.36, 5.06, 3.53, 2.18); III 13.99 (3.92, 4.49, 3.52, 2.06); IV 17.69 (4.95, 5.78, 4.68, 2.28). Chelicerae as in male. Epigyne: teeth short, subtriangular, located at posterior 1/2 of epigyne; copulatory ducts broad, long, sclerotized, anterior part connected to each other, and it about half

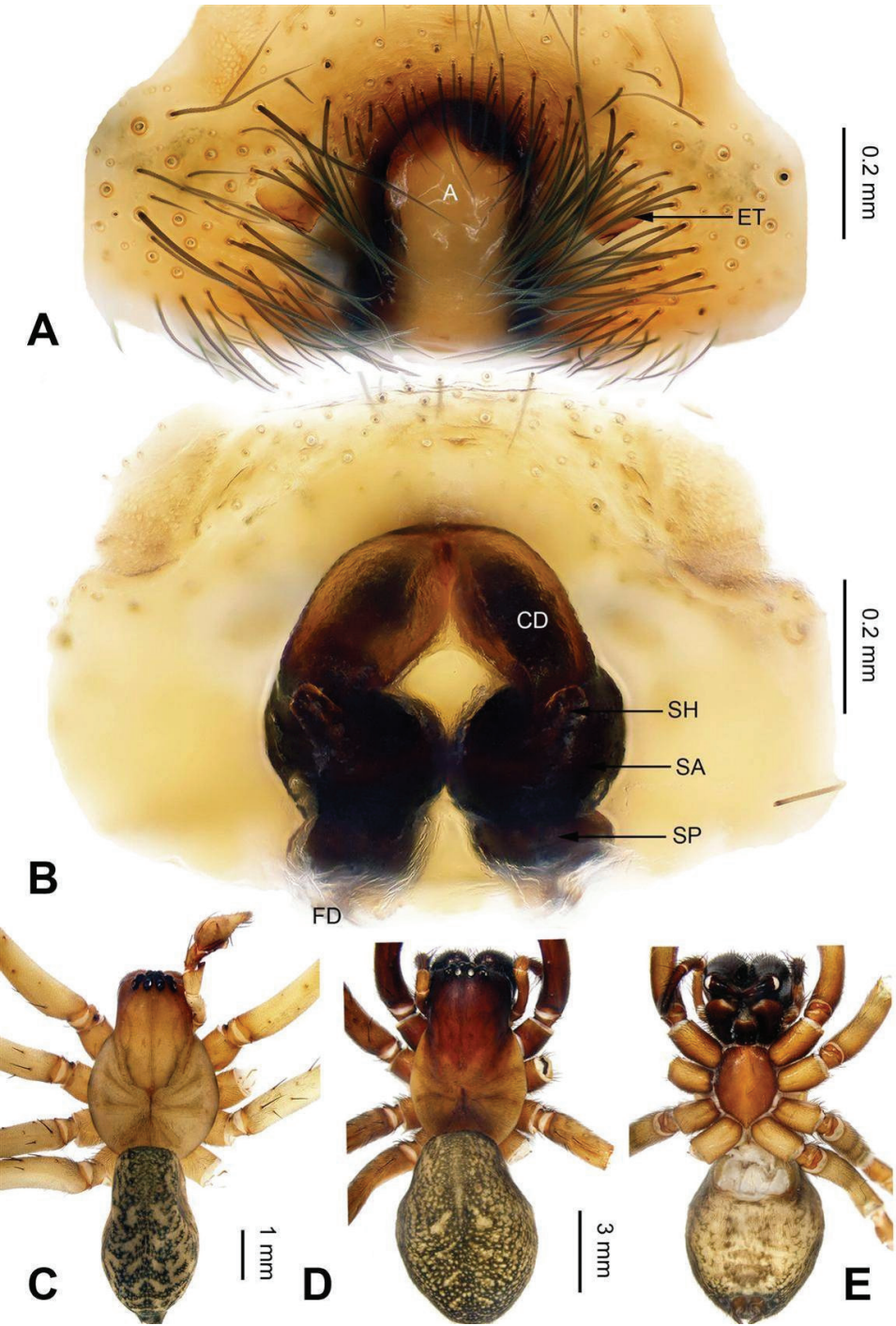


Figure 8. Epigyne and habitus of *Sinocoelotes behuaensis* sp. n., holotype and paratype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Male habitus, dorsal **D** Female habitus, dorsal **E** Female habitus, ventral. Scale bars: equal for **D** and **E**.

of vulval length, almost as wide as spermathecae; spermathecae short and convoluted; anterior part touching each other, posterior part about 1/3 length of anterior part; spermathecal heads long, stick-shaped, twice longer than their width, originating from middle of anterior spermathecae (Fig. 8A–B).

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes kangdingensis* Zhao & Li, sp. n.**

<http://zoobank.org/289D50FA-40AD-469B-B3E8-EEFCE4BBE2F1>

Figs 9, 21

Type material. Holotype ♀: China: Sichuan Province: Garzê Tibetan Autonomous Prefecture: Kangding County, foothills of Paoma Mountain, N30°02'50", E101°58'08", 2900 m, 12.X.2005, X. Zhang and X. Xu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female is similar to that of *S. cangshanensis* sp. n., but can be distinguished from it by the slenderer epigynal teeth (about 1/2 width of *S. cangshanensis* sp. n.), the broader SA, the thinner PA, the ratio between two parts of spermathecae (the PA subequal to the SA in *S. kangdingensis* sp. n., but PA just about 1/4 of the SA in *S. cangshanensis* sp. n.) (cf. Figs 9A–B and 2A–B), the well sclerotized copulatory ducts (Fig. 9A–B).

Description. Female. Total length 8.20. Carapace 3.80 long, 2.65 wide. Abdomen 4.40 long, 2.95 wide. Eye sizes and interdistances: AME 0.14, ALE 0.20, PME 0.15, PLE 0.19; AME-AME 0.10, AME-ALE 0.05, PME-PME 0.11, PME-PL 0.17. Leg measurements: I 9.72 (2.72, 3.28, 2.28, 1.44); II 8.69 (2.50, 2.81, 2.13, 1.25); III 8.06 (2.25, 2.59, 2.07, 1.15); IV 10.76 (2.96, 3.52, 2.96, 1.32). Chelicerae with three retromarginal teeth. Epigyne: atrium small, almost rectangular, posterior part slightly wider than anterior part, about 1/3 width and 1/2 length of epigyne, and it occupying about 1/5 of epigyne plate square; teeth broad, long, subequal to the length of atrium, located anteriorly; spermathecae separated from each other, anterior part by spermathecal width, and posterior part by 1/4 spermathecal width, posterior part subequal to the anterior part; spermathecal heads broad, short, located laterally; copulatory ducts short, slightly sclerotized, semitransparent, terminal parts leading to copulatory opening almost reduced (Fig. 9A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes ludingensis* Zhao & Li, sp. n.**

<http://zoobank.org/A7E9C92C-652C-46B6-B92D-A1054355BB2C>

Figs 10–11, 21

Type material. Holotype ♂: China: Sichuan Province: Garzê Tibetan Autonomous Prefecture: Luding County, the road from Moxi Town to Yajiageng, N29°46'31",

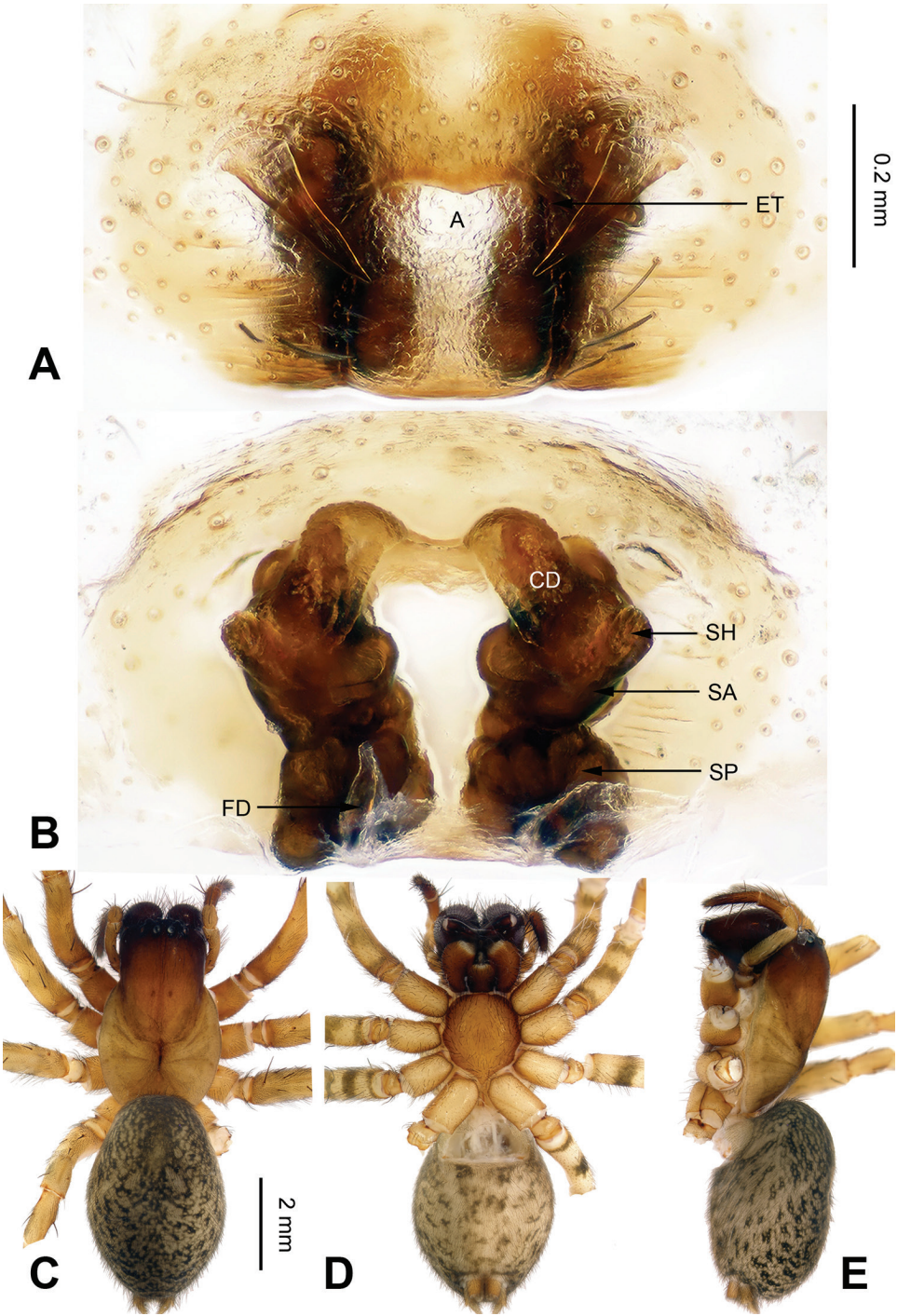


Figure 9. Epigyne and habitus of *Sinocoelotes kangdingensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A, B**; equal for **C, D** and **E**.

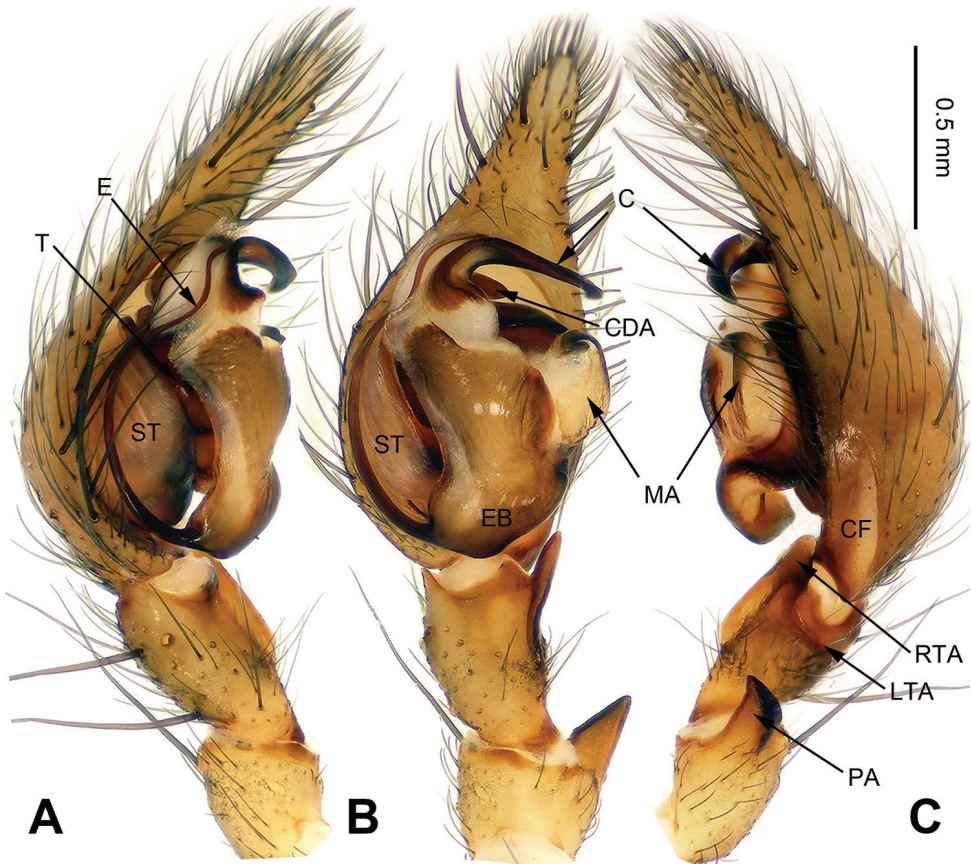


Figure 10. Male palp of *Sinocoelotes ludingensis* sp. n., holotype. **A** Prolateral **B** Ventral **C** Retrolateral. Scale bar: equal for **A**, **B** and **C**.

E102°03'34", 2412 m, 10.X.2005, X. Zhang and X. Xu. **Paratype:** 1♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The male is similar to that of *S. hehuaensis* sp. n., but can be distinguished from it by the slenderer conductor, with the hook-like apex (conductor peg-shaped in *S. hehuaensis* sp. n.), the smaller dorsal conductor apophysis (about 1/2 width and 1/3 length of *S. hehuaensis* sp. n.) (cf. Figs 10A–C and 7A–C). The female is similar to that of *S. kangdingensis* sp. n., but can be distinguished from it by the shape of atrium, anterior part wider than posterior part in *S. ludingensis* sp. n. (anterior part narrower than posterior part in *S. kangdingensis* sp. n.), the broader copulatory ducts, the longer (twice as long as *S. kangdingensis* sp. n.) and medially originating spermathecal heads (laterally originating in *S. kangdingensis* sp. n.) (cf. Figs 11A–B and 9A–B).

Description. Male. Total length 7.12. Carapace 3.40 long, 2.40 wide. Abdomen 3.72 long, 2.20 wide. Eye sizes and interdistances: AME 0.14, ALE 0.20, PME 0.19, PLE

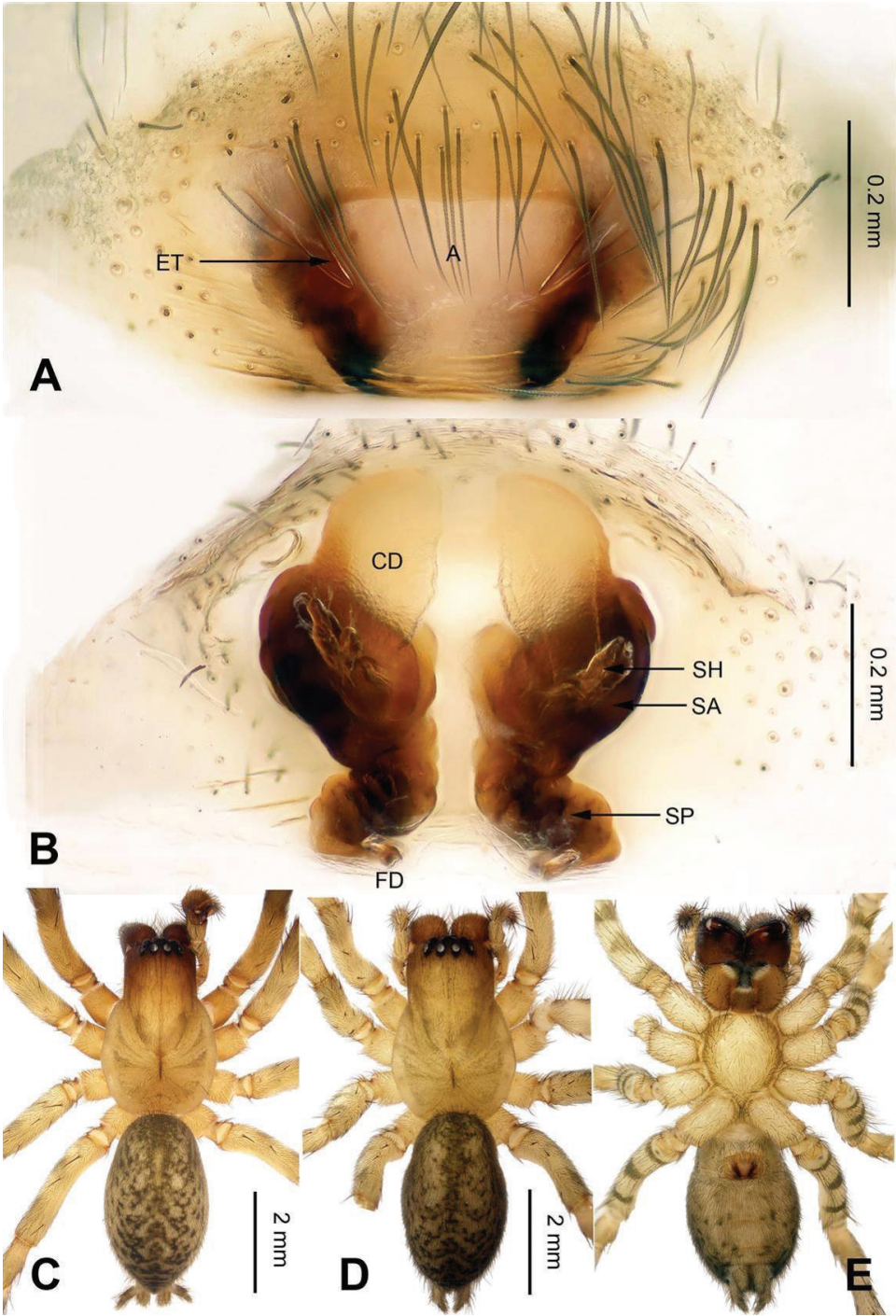


Figure 11. Epigyne and habitus of *Sinocoelotes ludingensis* sp. n., holotype and paratype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Male habitus, dorsal **D** Female habitus, dorsal **E** Female habitus, ventral. Scale bars: equal for **D** and **E**.

0.16; AME-AME 0.09, AME-ALE 0.03, PME-PME 0.09, PME-PLE 0.12. Leg measurements: I 11.04 (3.08, 3.48, 2.80, 1.68); II 9.66 (2.82, 3.13, 2.23, 1.48); III 8.82 (2.60, 2.50, 2.47, 1.25); IV 12.19 (3.36, 3.76, 3.48, 1.59). Chelicerae with four retromarginal teeth. Palp: patellar apophysis short, about 1/2 of patella; RTA broad and long, subequal to the length of tibia; LTA short, less than 1/6 length of RTA; cymbial furrow short, about 1/5 length of cymbium; conductor long, slender, and apex hook-like; median apophysis spoon-like; dorsal conductor apophysis broad, the visible part (between conductor and tegulum) finger-like; embolus beginning at seven o'clock position (Fig. 10A–C).

Female. Total length 6.76. Carapace 3.44 long, 2.36 wide. Abdomen 3.32 long, 2.00 wide. Eye sizes and interdistances: AME 0.14, ALE 0.21, PME 0.14, PLE 0.16; AME-AME 0.09, AME-ALE 0.04, PME-PME 0.13, PME-PLE 0.16. Leg measurements: I 8.90 (2.52, 2.95, 2.08, 1.35); II 7.81 (2.28, 2.50, 1.81, 1.22); III 7.16 (2.03, 2.31, 1.84, 0.98); IV 9.66 (2.69, 3.06, 2.66, 1.25). Chelicerae as in male. Epigyne: atrium, trapezoidal, occupying 1/4 of epigynal plate square, narrowing at the posterior part; teeth long, located anterior-laterally, subequal to the atrial length; copulatory ducts membranous, semitransparent, parallel to each other, wider than basal part of spermathecae; spermathecae separated from each other by spermathecal heads' width, basal part of spermathecae about 1/2 thinner than anterior part; spermathecal heads long, located at mid-anterior of spermathecae (Fig. 11A–B).

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes luoshuiensis* Zhao & Li, sp. n.**

<http://zoobank.org/61671F60-C3D0-4A18-A2EC-3CCFB44B7B06>

Figs 12, 21

Type material. Holotype ♀: China: Yunnan Province: Tengchong County, Gudong Town, Jiangdong Village, Jiangdong Mountain, Luoshui Cave, N24°58'06", E98°52'06", 1881 m, 26.XI.2013, Y. Li and J. Liu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female of the new species has uniquely shaped epigyne and can be easily distinguished from all other *Sinocoelotes* gen. n. species by the broad atrium lacking distinct margins (with distinct anterior and lateral margins in other species), the long and sickle-shaped copulatory ducts, and copulatory ducts span wider than spermathecae, the spermathecal heads short and close to each other (close to each other but five times as long as in *S. luoshuiensis* sp. n. in *S. muliensis* sp. n., and laterally originating in other species) (Fig. 12A–B).

Description. Female. Total length 6.48. Carapace 3.28 long, 2.24 wide. Abdomen 3.20 long, 2.21 wide. Eye sizes and interdistances: AME 0.13, ALE 0.19, PME 0.16, PLE 0.17; AME-AME 0.06, AME-ALE 0.04, PME-PME 0.08, PME-PLE 0.11. Leg measurements: I 9.59 (2.66, 3.15, 2.22, 1.56); II 8.56 (2.47, 2.78, 2.01, 1.30); III 7.72 (2.15, 2.42, 1.98, 1.17); IV 10.37 (2.81, 3.28, 3.82, 1.46). Chelicerae with four retromarginal teeth. Epigyne: atrium large, about 1/3 of epigynal plate square,

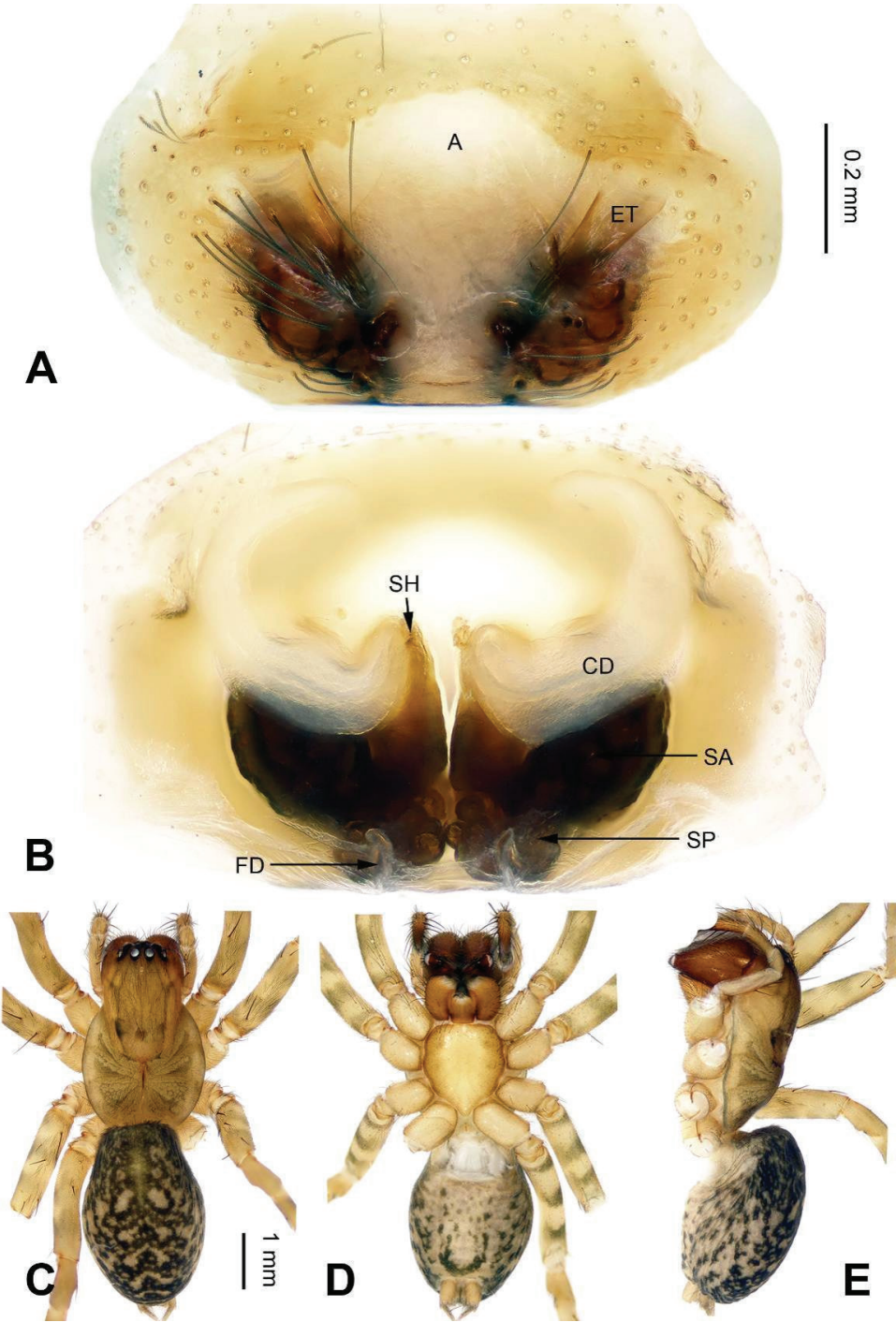


Figure 12. Epigyne and habitus of *Sinocoelotes luoshuiensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

without sharp boundary, narrowing at posterior part; teeth long, about 1/2 length of atrium; spermathecae close to each other, posterior part about 1/5 of posterior part; spermathecal heads long, located mesally, close to each other; copulatory ducts long, hook-like (Fig. 12A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes mahuanggouensis* Zhao & Li, sp. n.**

<http://zoobank.org/5EC7587F-22FA-46E9-85D2-70EDBBFAAEF1>

Figs 13, 21

Type material. Holotype ♀: China: Sichuan Province: Baoxing County, Fengtongzhai Nature Reserve, Mahuang valley, under stones, N30°49'27", E102°44'16", 2440 m, 27.IX.2005, X. Zhang and X. Xu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female can be easily distinguished from other *Sinocoelotes* gen. n. species by the short, wider than long, triangular epigynal teeth, the pear-shaped atrium, the sickle-shaped copulatory ducts, the long and clavate spermathecal heads (Fig. 13A–B).

Description. Female. Total length 11.80. Carapace 5.77 long, 3.97 wide. Abdomen 6.03 long, 3.85 wide. Eye sizes and interdistances: AME 0.26, ALE 0.25, PME 0.21, PLE 0.24; AME-AME 0.11, AME-ALE 0.09, PME-PME 0.23, PME-PLE 0.34. Leg measurements: I 17.56 (4.74, 5.96, 4.17, 2.69); II 15.75 (4.35, 5.19, 3.85, 2.36); III 14.69 (4.05, 4.55, 3.91, 2.18); IV 19.15 (5.13, 6.03, 5.45, 2.54). Chelicerae with three retromarginal teeth. Epigyne: atrium large, occupying 1/3 of epigynal plate square, narrowing posteriorly, pear-shaped; teeth short, wider than long, triangular in shape, located antero-laterally, widely spaced from atrium; spermathecae close to each other, posterior (basal) part subequal to the anterior part; spermathecal heads long, clavate; copulatory ducts long, broad, crescent-shaped (Fig. 13A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes mangbangensis* Zhao & Li, sp. n.**

<http://zoobank.org/44304816-98E9-4CE4-A51E-5AB9D8F1DF37>

Figs 14, 21

Type material. Holotype ♀: China: Yunnan Province: Tengchong County, Mangbang Village, N24°58'07", E98°36'48", 2032 m, 23.VI.2013, Z. Zhao and J. Liu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female is similar to that of *S. hehuaensis* sp. n., but can be distinguished from it by longer epigynal teeth (twice as long as in *S. hehuaensis* sp. n.), the

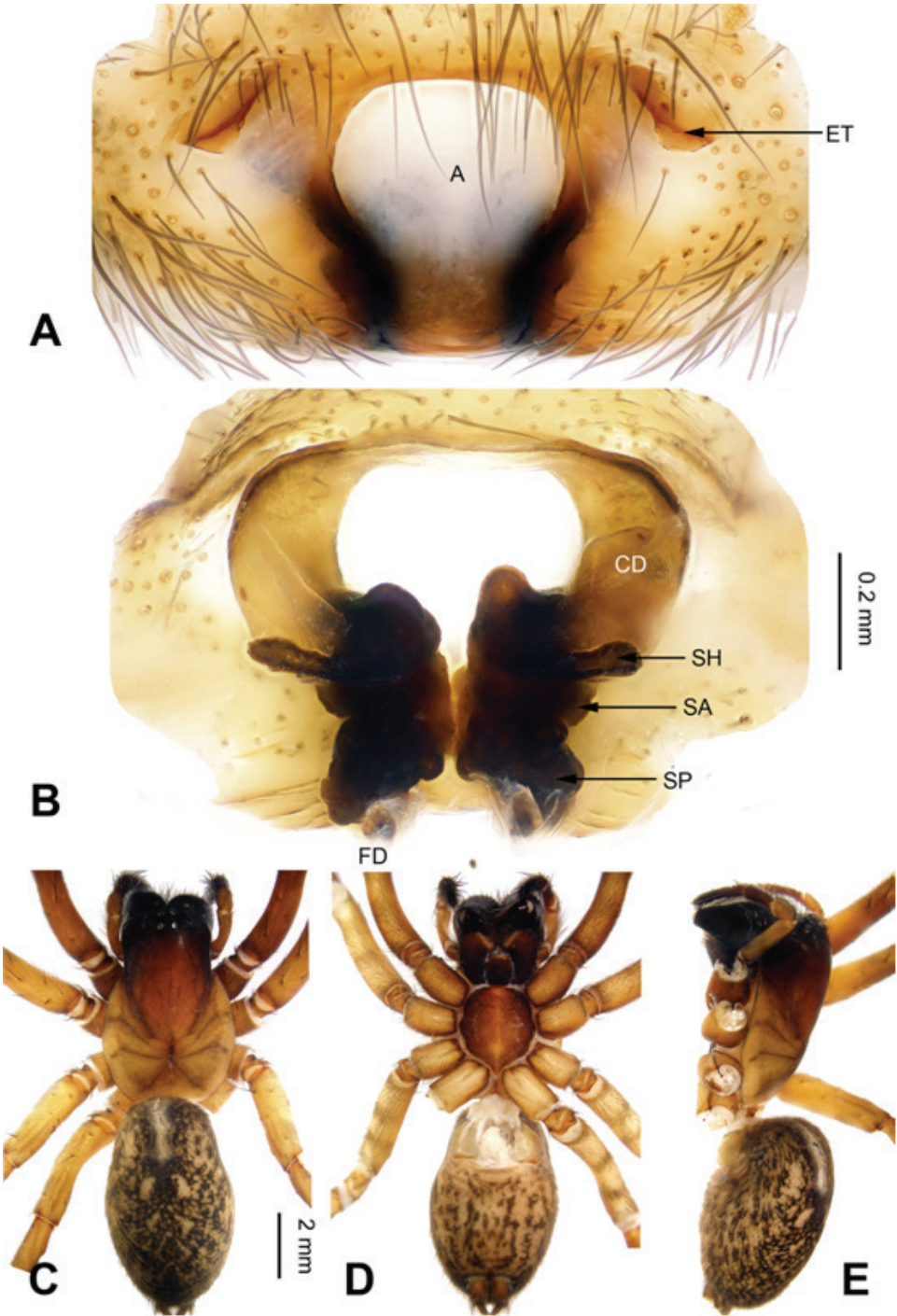


Figure 13. Epigyne and habitus of *Sinocoelotes mahuanggouensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

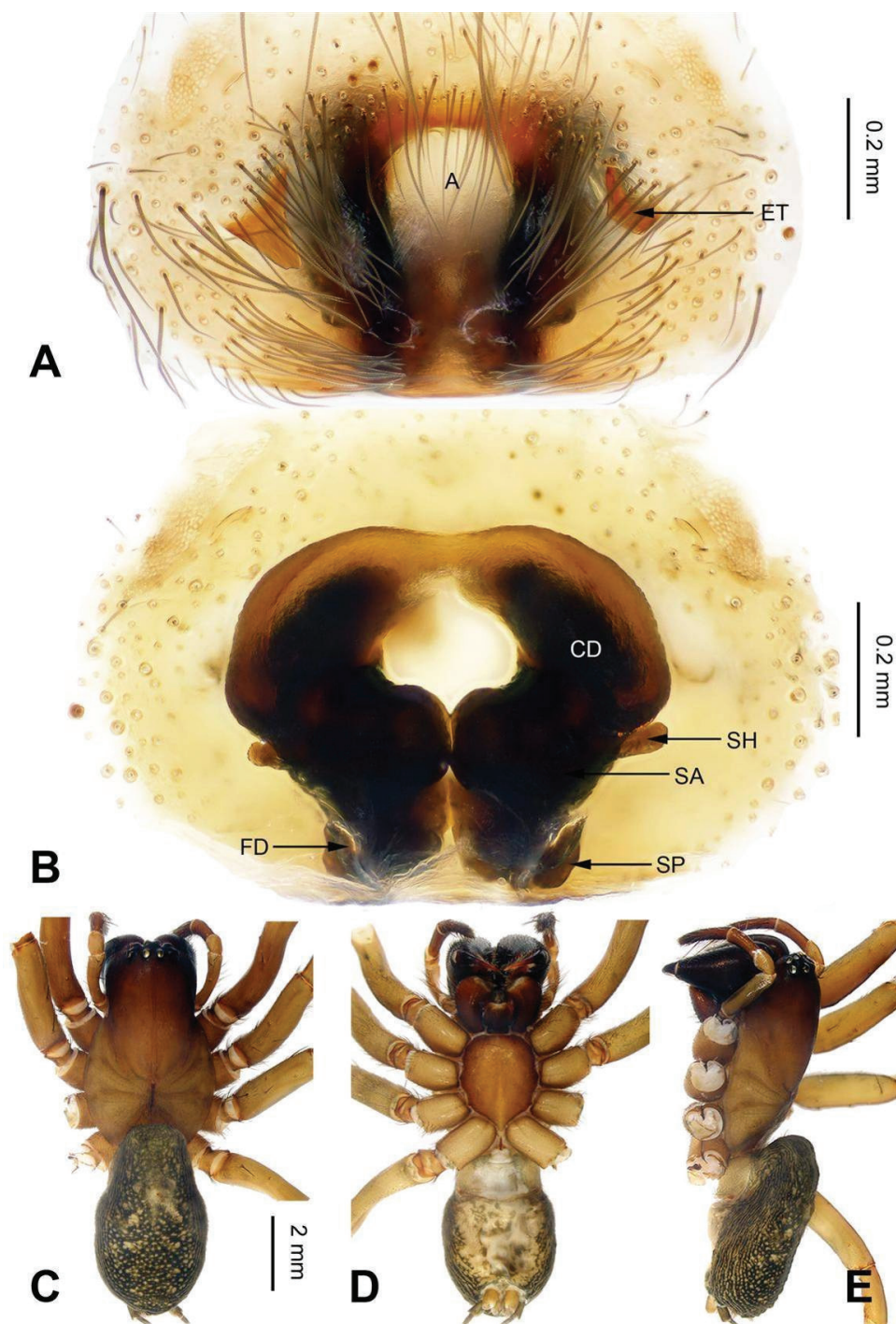


Figure 14. Epigyne and habitus of *Sinocoelotes mangbangensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **C**, **D** and **E**.

broader copulatory ducts, which the posterior part separated from each other further, the slender, laterally and ventrally located spermathecal heads (dorsally situated in *S. hehuaensis* sp. n.) (cf. Figs 14A–B and 8A–B).

Description. Female. Total length 10.12. Carapace 4.94 long, 3.66 wide. Abdomen 5.18 long, 3.10 wide. Eye sizes and interdistances: AME 0.21, ALE 0.29, PME 0.20, PLE 0.24; AME-AME 0.11, AME-ALE 0.05, PME-PME 0.16, PME-PLE 0.28. Leg measurements: I 14.58 (3.96, 4.95, 3.52, 2.15); II 12.81 (3.68, 4.28, 2.97, 1.88); III 11.67 (3.40, 3.72, 2.95, 1.60); IV 13.34 (4.25, 4.98, 4.22, 1.89). Sternum brown (in comparison to previous species) with light median stripe. Chelicerae with four retro-marginal teeth. Epigyne: atrium small, about 1/5 of epigynal plate square, narrowing at posteriorly; teeth subtriangular, as wide as long, located laterally, near to atrial anterior margin, subequal to atrial width (narrowest part); spermathecae not spaced, posterior part thinner than posterior one; spermathecal heads long, finger-like, located laterally; copulatory ducts broad, well sclerotized, and anterior part contiguous (Fig. 14A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes muliensis* Zhao & Li, sp. n.**

<http://zoobank.org/8812B14A-E2BC-4054-B9D4-77BEAA37659C>

Figs 15, 21

Type material. Holotype ♀: China: Sichuan Province: Muli County, N27°54'57", E101°16'20", 2229 m, 13.XI.2013, Y. Li and J. Liu.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female of the new species has uniquely shaped epigyne and can be easily distinguished from all other *Sinocoelotes* gen. n. species by the anteriorly situated atrium (atrium with distinct anterior margin, but lacking distinct posterior margin, and the posterior part broader than anterior part), the teeth broad and located between two atrial lateral margins, the long and strongly twisted spermathecae, closely spaced, the slender, mesally originating spermathecal heads (which are also mesally originating in *S. luoshuiensis* sp. n, but are 1/4 length shorter than those in *S. muliensis* sp. n.; laterally originating in all other species) (Fig. 15A–B).

Description. Female. Total length 5.76. Carapace 2.56 long, 1.72 wide. Abdomen 3.20 long, 1.87 wide. Eye sizes and interdistances: AME 0.09, ALE 0.16, PME 0.12, PLE 0.13; AME-AME 0.07, AME-ALE 0.02, PME-PME 0.08, PME-PLE 0.10. Leg measurements: I: 5.97 (1.73, 2.08, 1.38, 0.78); II: 5.40 (1.62, 1.80, 1.24, 0.74); III: 5.12 (1.50, 1.60, 1.30, 0.72); IV: 7.03 (1.94, 2.31, 1.83, 0.95). Chelicerae with 3 retromarginal teeth. Epigyne: atrium located anteriorly, occupying 1/4 of epigynal plate square, with distinct anterior margin, but lacking distinct posterior margin; teeth broad and long, located on the lateral margins of the atrium; spermathecae narrowly separated from each other, posterior part of spermathecae about 1/4 the anterior part; spermathecal heads slender and long, close to each other; copulatory ducts much thin-

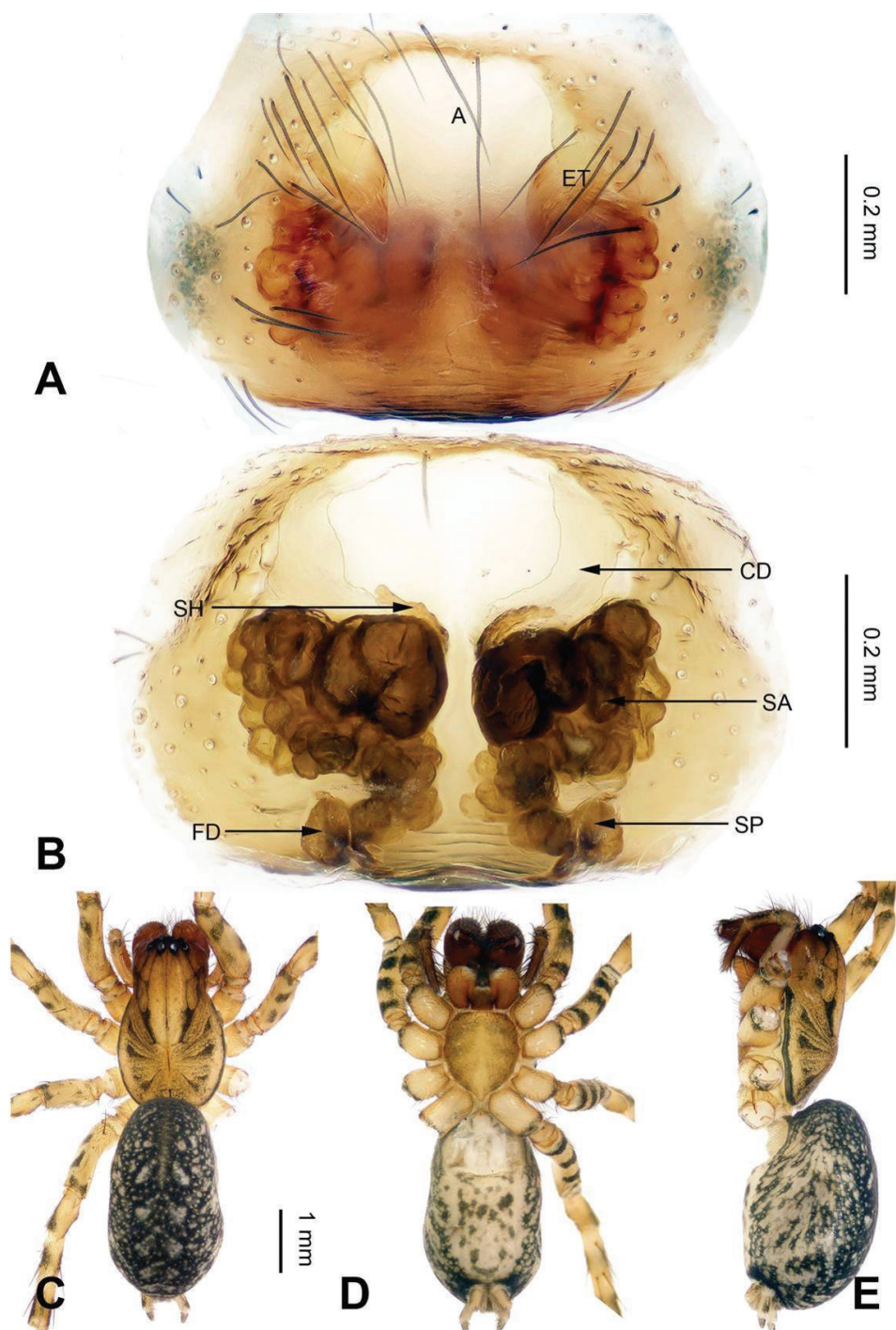


Figure 15. Epigyne and habitus of *Sinocaelotes muliensis* sp. n., holotype. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **C**, **D** and **E**.

ner than anterior part of spermathecae (wider in some species), short (about 1/3 length of epigyne), membranous (Fig. 15A–B).

Male. Unknown.

Distribution. Known only from the type locality (Fig. 21).

***Sinocoelotes pseudoterrestris* (Schenkel, 1963), comb. n.**

Figs 16, 21

Coelotes pseudoterrestris Schenkel 1963: 286, fig. 161 (♀ holotype from Lo Thoei Tong, Yunnan, China, in MNHP, not examined); Song et al. 1999: 378, figs 224N, 224O, 226T, 228B (♂♀, as *C. sacratus*); Wang 2002: 52, figs 127–131 (♂♀); Wang and Jäger 2008: 2279, figs 1–2 (♂).

Material examined. ♀: China: Yunnan Province: Kunming City; Xishan Forest Park, the way to Longmen, in crevices on crags, N24°57'04", E102°38'18", 2437 m, 22.XII.2013, Y. Li and J. Liu.

Diagnosis. The female is similar to that of *S. mangbangensis* sp. n., but can be easily distinguished from it by the longer epigynal teeth (twice as long as in *S. mangbangensis* sp. n.), the smaller posterior part of spermathecae which is about 1/4 of the anterior part (the posterior part is subequal to the anterior part in *S. mangbangensis* sp. n.), the laterally situated spermathecal heads (ventrally situated in *S. mangbangensis* sp. n.), and the membranous copulatory ducts (strongly sclerotized in *S. mangbangensis* sp. n.) (cf. Figs 16A–B and 14 A–B).

Comments. The species shares a combination of somatic morphology characters with *S. hehuaensis* sp. n., and therefore was assigned to *Sinocoelotes* gen. n. The molecular analysis supports the transfer.

Description. Described by Wang (2002).

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes pseudoyunnanensis* (Wang, Griswold & Ubick, 2009), comb. n.**

Figs 17, 21

Coelotes pseudoyunnanensis Wang et al. 2009: 19, figs 88–96 (♂ holotype and ♂♀ paratypes from Nujiang, Yunnan, China, in HNU and CAS, not examined).

Material examined. ♂: China: Yunnan Province: Nujiang Lisu Autonomous Prefecture: Lushui County, Pianma Town, Gaoligong Mountain, N25°58'22", E98°41'02", 3133 m, 8.XII.2013, Y. Li and J. Liu.

Diagnosis. The male has uniquely shaped palps, and can be easily distinguished from all other *Sinocoelotes* gen. n. by the shape of conductor (wave-shaped, broad, and with

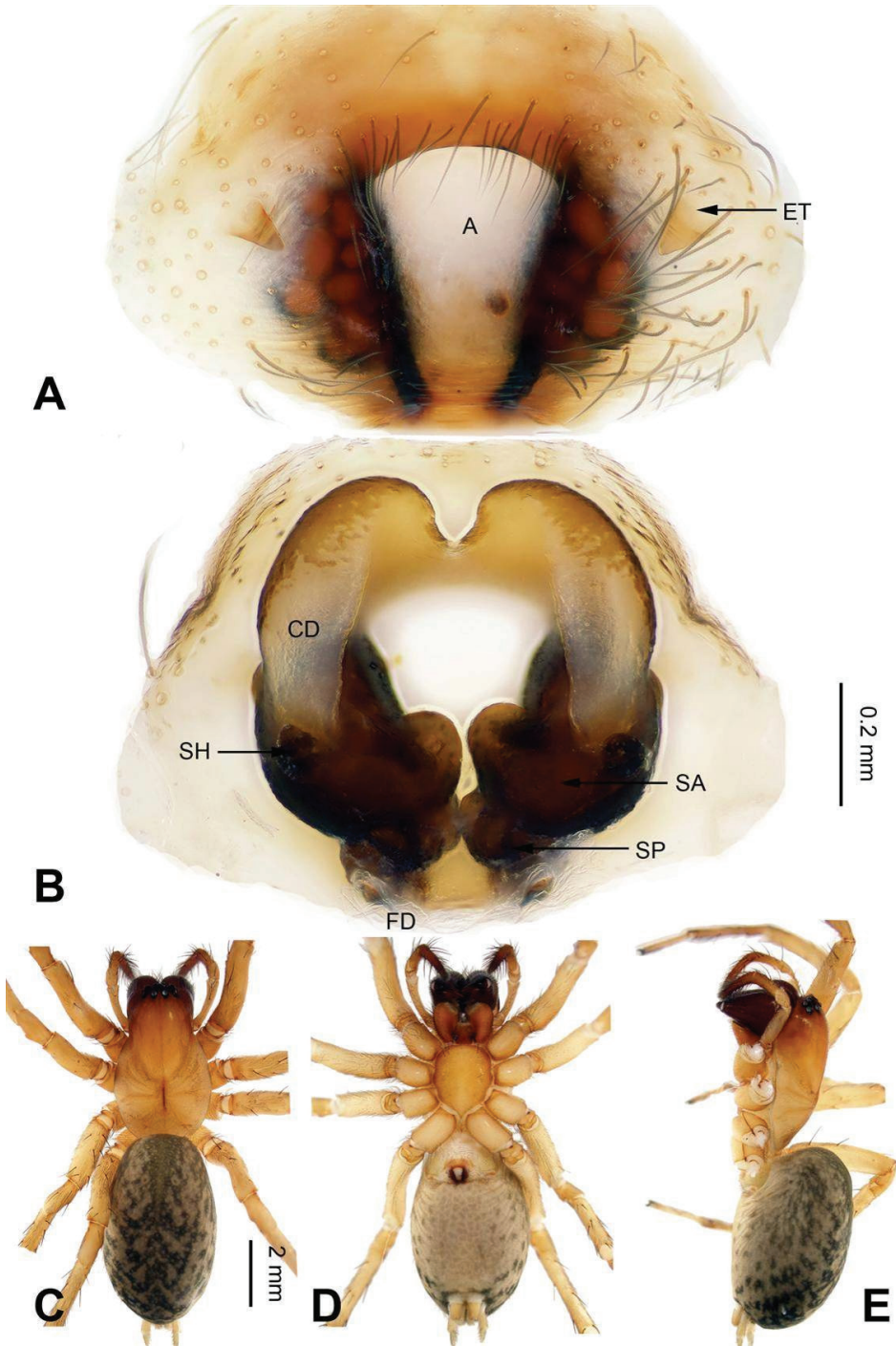


Figure 16. Epigyne and habitus of *Sinocoelotes pseudoterrestris*. **A** Epigyne, ventral **B** Vulva, dorsal **C** Female habitus, dorsal **D** Female habitus, ventral **E** Female habitus, lateral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

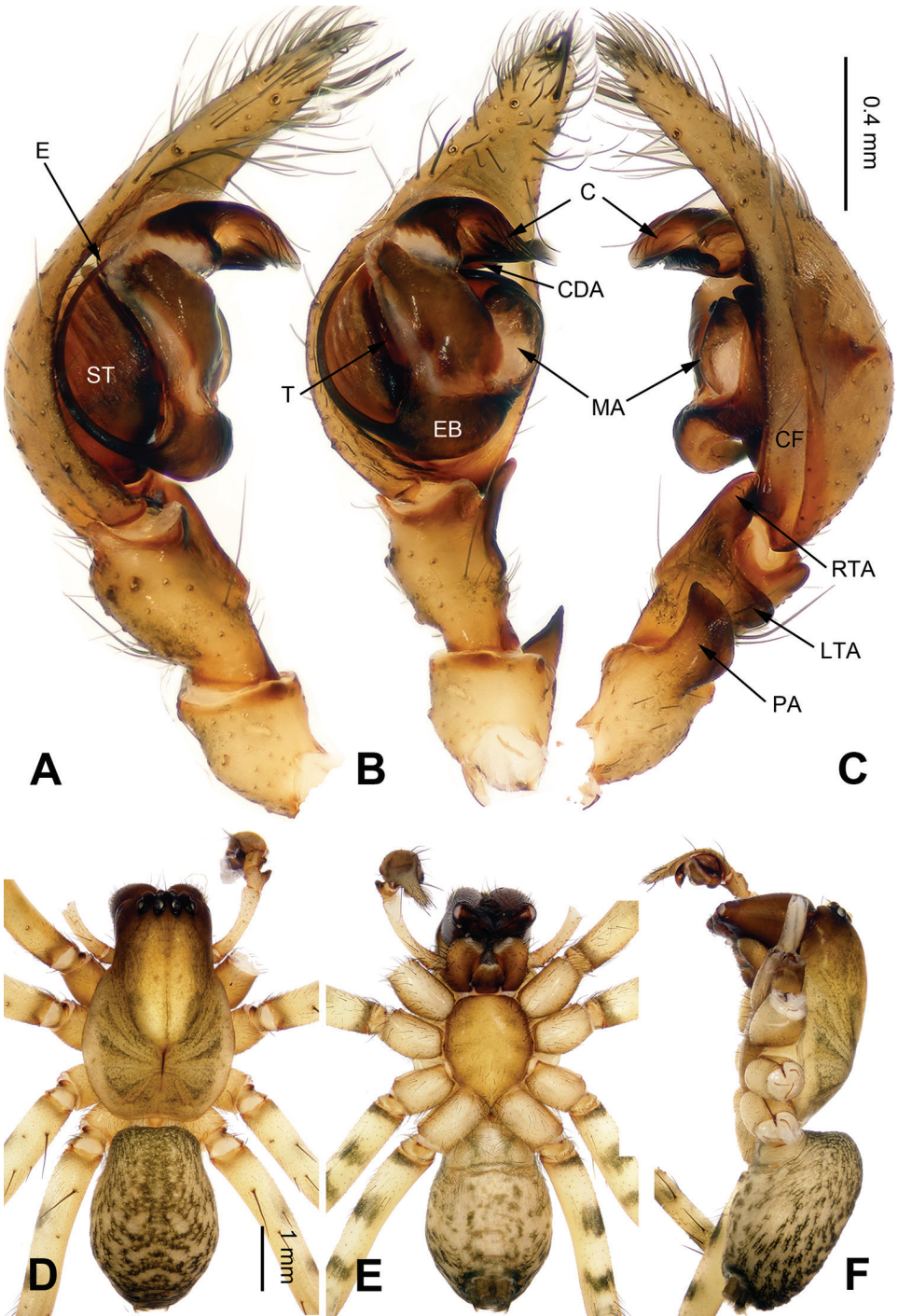


Figure 17. Male palp and habitus of *Sinocoelotes pseudoyunnanensis*. **A** Prolateral **B** Ventral **C** Retrolateral. **D** Habitus, dorsal **E** Habitus, ventral **F** Habitus, lateral. Scale bars: equal for **A**, **B** and **C**; equal for **D**, **E** and **F**.

round-blunt tip in *S. pseudoyunnanensis*, but slenderer and with pointed tip in other species), the longer LTA (about 1/3 length of RTA in *S. pseudoyunnanensis*, less than 1/6 length of RTA in other species), the broader patellar apophysis (the terminal part wider than basal part, and the apex subequal to the width of tibia, the terminal part wider than basal part, but the apex about 1/2 width of tibia in *S. hehuaensis*, the terminal part subequal to, or even slenderer than basal part in other species) (cf. Figs 17A–C and 7A–C, 10A–C, 20A–C).

Description. Described by Wang et al. (2009).

Comments. The species shares a combination of somatic morphology characters with *S. hehuaensis* sp. n. and therefore was assigned to *Sinocoelotes* gen. n. The molecular analysis supports this transfer.

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes thailandensis* (Dankittipakul & Wang, 2003), comb. n.**

Figs 18–19, 21

Coelotes thailandensis Dankittipakul and Wang 2003: 735, figs 24–25 (♂ holotype from Thailand, in MHNG, not examined); Dankittipakul et al. 2005: 7, figs 9–10 (♂♀); Wang et al. 2009: 26, f. 128–142 (♂♀).

Material examined. 1♂2♀: Thailand: Chiangmai Province: Mae Cham District, Jeep tract, N18°31'41", E98°29'58", 1649 m, 14.X.2014, H. Zhao, Y. Li and Z. Chen.

Diagnosis. The species is similar to *S. hehuaensis* sp. n., but male can be easily distinguished by a shorter and broader conductor (about 1/3 length of the conductor in *S. hehuaensis* sp. n.), the broad and wedge-shaped dorsal conductor apophysis (cf. Figs 18A–C and 7A–C). The female can be distinguished from that of *S. hehuaensis* sp. n. by the broad (almost round) atrium, the broader and shorter copulatory ducts, the shorter spermathecal heads (about 1/3 length of the spermathecal heads *S. hehuaensis* sp. n.) (cf. Figs 19A–B and 8A–B).

Description. Described by Wang et al. (2009).

Comments. The species shares a combination of somatic morphology characters with *S. hehuaensis* sp. n., and therefore was assigned to *Sinocoelotes* gen. n. The molecular analysis supports this transfer.

Distribution. China (Yunnan) (Fig. 21).

***Sinocoelotes yanyuanensis* Zhao & Li, sp. n.**

<http://zoobank.org/B8448C52-A2F2-4E93-8F74-7D6A86A41DD2>

Figs 20, 21

Type material. Holotype ♂: China: Sichuan Province: Yanyuan County, foot of Bailing Mountain, in the apple garden, N27°24'03", E101°31'47", 2620 m, 15.XI.2013, Y. Li and J. Liu. **Paratype:** 1 ♂, same data as holotype.

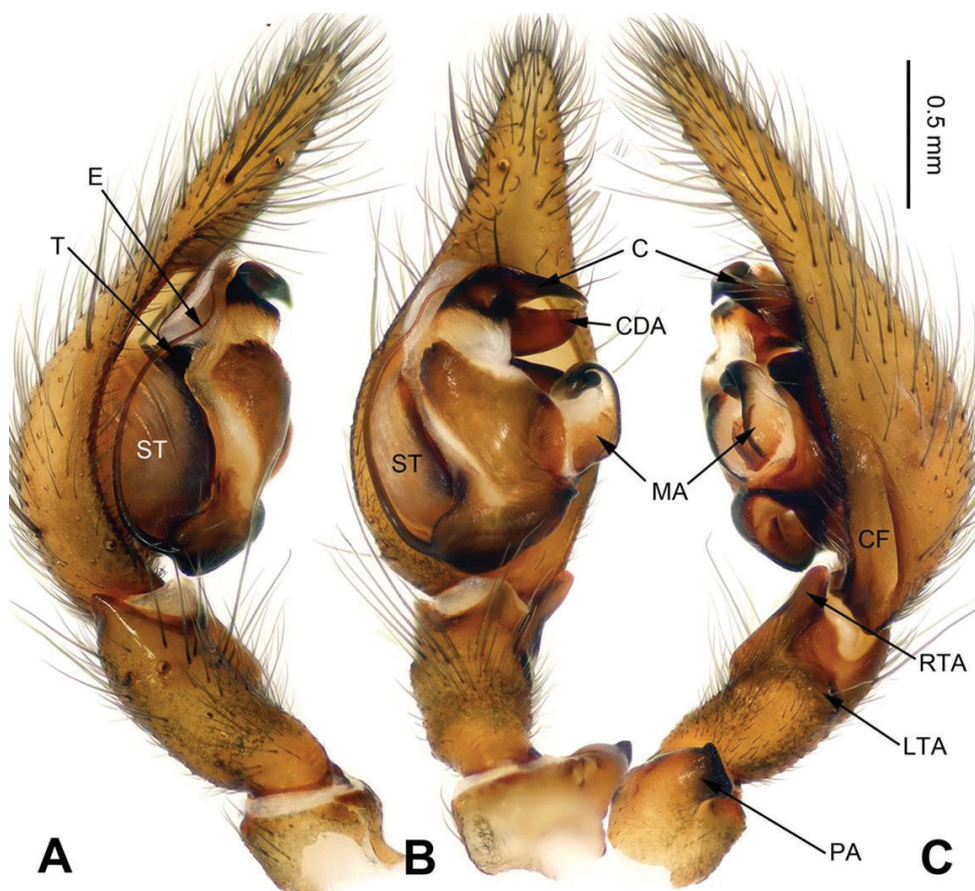


Figure 18. Male palp of *Sinocoelotes thailandensis*. **A** Prolateral **B** Ventral **C** Retrolateral. Scale bar: equal for **A**, **B** and **C**.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The male of the new species has uniquely shaped palps, and can be easily recognized from all other *Sinocoelotes* gen. n. by the clavate patellar apophysis, and the basal part broader than terminal part (bended and 1.5 times as width as *S. janyuanensis* sp. n. in *S. thailandensis*, basal part equal to or even slenderer than terminal part in other species), the broader and bended conductor in ventral view (wave-shaped in *S. pseudoyunnanensis*, straight in other species), short cymbial tip about 1/4 length of cymbium (about 1/3 length of cymbium in other species), the smaller visible part of dorsal conductor apophysis (quite distinct in other species) (cf. Figs 20A–C and 7A–C, 10A–C, 17A–C).

Description. Male (holotype): Total length 8.55. Carapace 4.35 long, 2.91 wide. Abdomen 4.20 long, 2.50 wide. Eye sizes and interdistances: AME 0.13, ALE 0.19, PME 0.16, PLE 0.13; AME-AME 0.08, AME-ALE 0.04, PME-PME 0.11, PME-PLE 0.19. Leg measurements: I 12.43 (3.40, 4.00, 3.08, 1.95); II 10.80 (2.95, 3.45, 2.65,

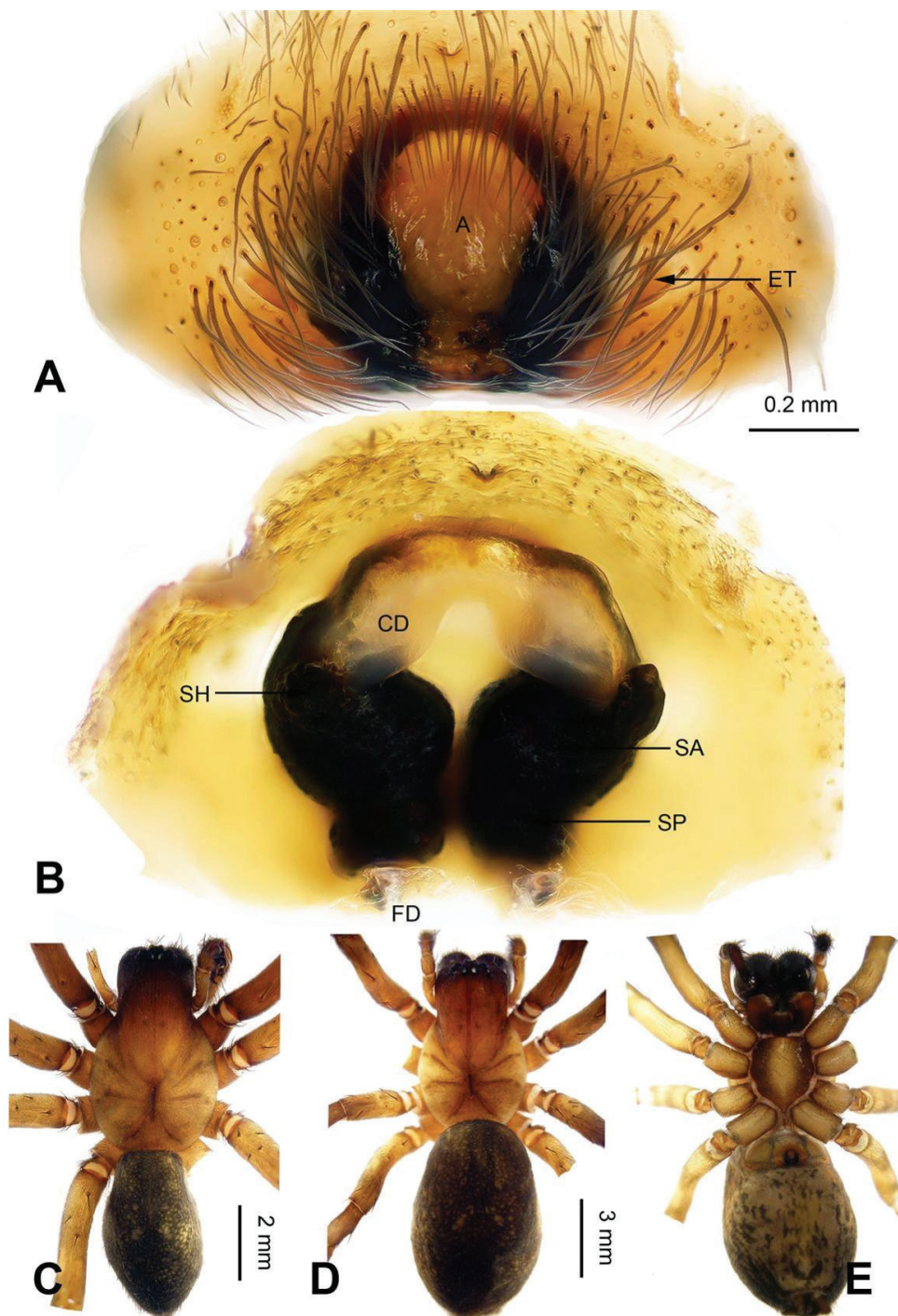


Figure 19. Epigyne and habitus of *Sinocoelotes thailandensis*. **A** Epigyne, ventral **B** Vulva, dorsal **C** Male habitus, dorsal **D** Female habitus, dorsal **E** Female habitus, ventral. Scale bars: equal for **A** and **B**; equal for **C**, **D** and **E**.

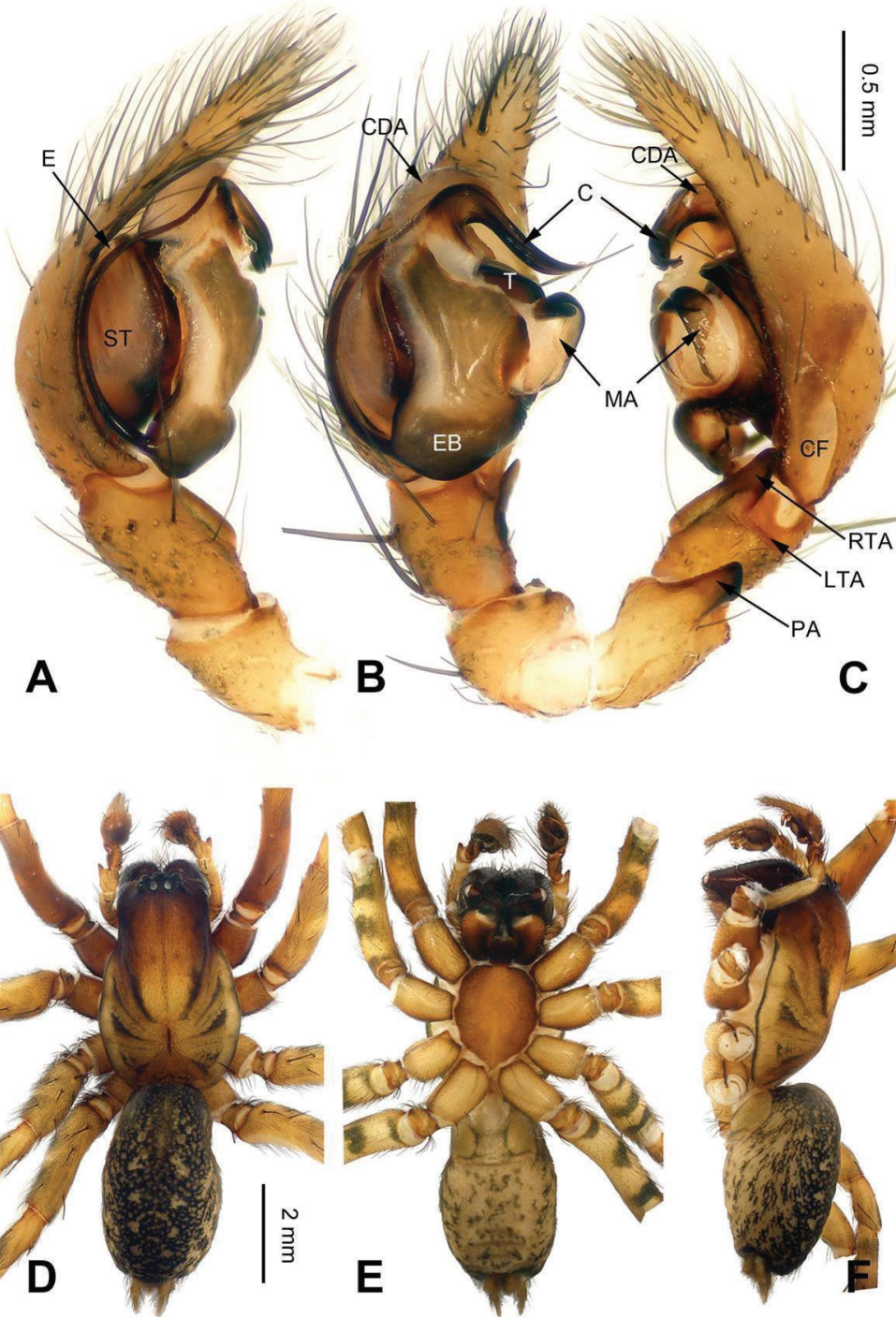


Figure 20. Male palp and habitus of *Sinocoelotes yanyuanensis* sp. n., holotype. **A** Prolateral **B** Ventral **C** Retrolateral. **D** Habitus, dorsal **E** Habitus, ventral **F** Habitus, lateral. Scale bars: equal for **A**, **B** and **C**; equal for **D**, **E** and **F**.

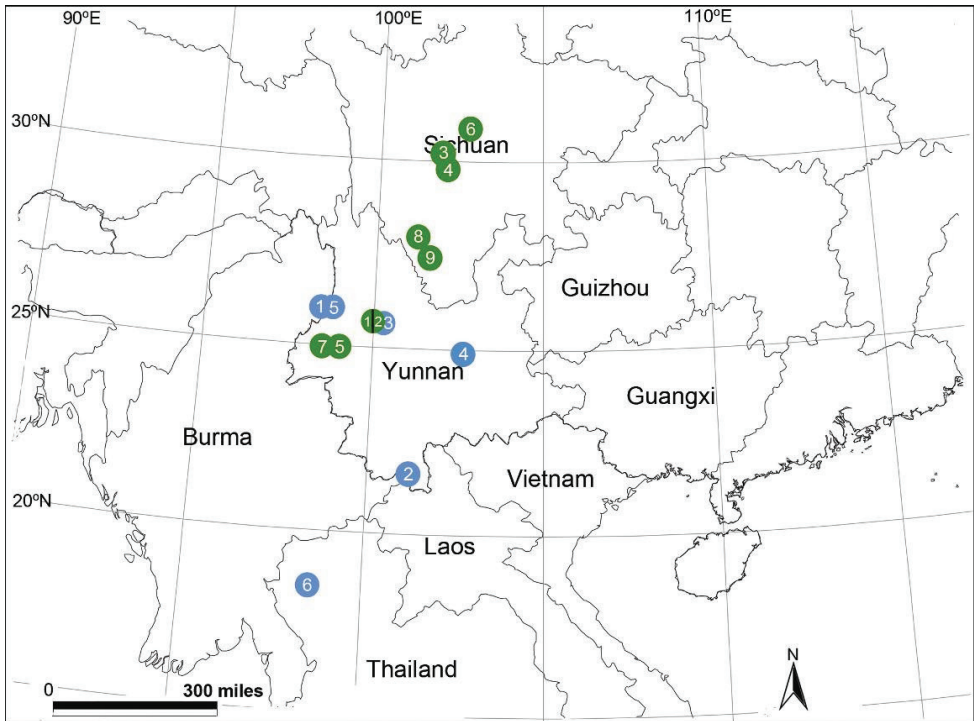


Figure 21. Localities of new (green) and earlier described (blue) species of *Sinocoelotes* gen. n. from China and Thailand. Green: 1 *S. cangshanensis* sp. n. 2 *S. behuaensis* sp. n. 3 *S. kangdingensis* sp. n. 4 *S. ludingensis* sp. n. 5 *S. luoshuiensis* sp. n. 6 *S. mahuanggouensis* sp. n. 7 *S. mangbangensis* sp. n. 8 *S. muliensis* sp. n. 9 *S. yanyuanensis* sp. n. Blue: 1 *S. acicularis* 2 *S. forficatus* 3 *S. guangxian* 4 *S. pseudoterrestris* 5 *S. pseudoyunnanensis* 6 *S. thailandensis*.

1.75); III 10.04 (2.80, 3.16, 2.68, 1.40); IV 13.35 (3.60, 4.25, 3.80, 1.70). Chelicerae with three promarginal and four retromarginal teeth. Palp: patellar apophysis long, subequal to the length of patella, basal part broader than terminal part; LTA short, about 1/6 length of RTA; cymbial furrow short, about 1/4 length of cymbium; conductor broader and long, about 1/3 length of cymbium; dorsal conductor apophysis broad, covered mostly by the tegulum and the base of conductor; embolus beginning at 7 o'clock position (Fig. 20A–C).

Female. Unknown.

Distribution. Known only from the type locality (Fig. 21).

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***Sumakuru*, a deeply-diverging new genus of lyssomanine jumping spiders from Ecuador (Araneae: Salticidae)**

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Abstract

The lyssomanine jumping spider genus *Sumakuru* **gen. n.** is here described for *Sumakuru bigal* **sp. n.**, from the Bigal River Biological Reserve in Ecuador. Known from a single male, the embolus of the palp takes the form of a smoothly arching curve, and appears fully mobile, being connected to the tegulum by a thin sclerite and a twisted hematodocha. Data from four gene regions (28S, 16SND1, CO1, *wingless*) indicate that *Sumakuru* is the sister group to all other sampled lyssomanines, diverging deeply on the stem lineage of the clade of other known lyssomanines. Unlike previous molecular results, the sampled species of *Lyssomanes* Hentz, 1845 are supported as monophyletic, with *Chinoscopus* Simon, 1900 as the sister to *Lyssomanes*.

Keywords

Jumping spider, Lyssomaninae, molecular phylogeny, new genus, new species

Introduction

The distinctive lyssomanine jumping spiders include two described genera, *Lyssomanes* Hentz, 1845 and *Chinoscopus* Simon, 1900, both neotropical (Galiano 1962, 1980; Logunov and Marusik 2003; Maddison 2015). Recent molecular phylogenetic analyses show, as expected, that they form an isolated group (Maddison et al. 2014),

related to the Asemoneinae or Spartaeinae (Su et al. 2007; Maddison et al. 2014). However, these analyses suggest that the living lyssomanine species represent a recent radiation, with relatively short branches separating the sample of 10 diverse species of *Lyssomanes* and one of *Chinoscopus* (Maddison et al. 2014: figs 15–17), which together sit atop a long ancestral branch connecting them to other salticids. This presents a challenge: are there any living lyssomanines yet to be discovered that diverge deeply, breaking up this long branch as *Thrandina* Maddison, 2006 does for the lapsiines, for instance?

A single male of a new species of lyssomanine from the Bigal River Biological Reserve in Ecuador bears a distinctive palp, but it appears to be within the range of morphological diversity in *Lyssomanes* (Galiano 1980, Logunov 2014). Molecular data, however, show it to be remarkably distinct from the other species sampled to date, lying well outside the clade of *Lyssomanes* plus *Chinoscopus*. It is therefore described here as the new genus *Sumakuru*.

Material and methods

The preserved specimen was examined under both dissecting microscopes and a compound microscope with reflected light. Drawings were made with a drawing tube on a Nikon ME600L compound microscope.

Terminology is standard for Araneae. All measurements are given in millimeters. Descriptions of color pattern are based on the alcohol-preserved specimen. Carapace length was measured from the base of the anterior median eyes not including the lenses to the rear margin of the carapace medially; abdomen length to the end of the anal tubercle. The following abbreviations are used: ALE, anterior lateral eyes; PLE, posterior lateral eyes; PME, posterior median eyes (the “small eyes”).

DNA sequences of the genes or gene regions 28S, *wingless*, CO1 and 16SND1 were obtained from the holotype of *Sumakuru bigal* using the protocols of Zhang and Maddison (2013) and Maddison et al. (2014). The first two of these genes are nuclear, the last two mitochondrial. These sequences were added to data from 78 taxa borrowed from the non-salticoid dataset of Maddison et al. (2014), including 10 *Lyssomanes*, 1 *Chinoscopus*, 7 non-salticids, 2 Onomastinae, 5 Asemoneinae, 32 Spartaeinae, 6 Hispaninae, and 15 Salticinae. The Genbank accession numbers of the borrowed data can be obtained from the table Supplementary Material S1 of Maddison et al. (2014), following the voucher identification codes that are here appended to the taxon names in the figures of the phylogeny.

Prior to phylogenetic analysis, multiple sequence alignment was done for 28S and the noncoding portion of 16SND1 with MAFFT (Katoh et al. 2002, 2005) using the LINSI option (--localpair --maxiterate 1000), run via Mesquite (Maddison and Maddison 2015b). Mesquite was used to color the matrix via the option “Highlight Apparently Slightly Misaligned Regions” so as to identify regions that needed correction. Alignment of coding regions was easily done by eye through translation to amino acids.

Maximum likelihood phylogenetic analyses were run using RAxML version 8.2.8 (Stamatakis 2014), run via Mesquite's Zephyr package (Maddison and Maddison 2015a). 100 search replicates were performed to find the maximum likelihood tree, while 1000 bootstrap replicates were done to assess repeatability of the results (1 search replicate per bootstrap replicate). The analyses partitioned the data (see below) and used GTR+G+I for each of the partitions. Analyses were done on the complete dataset of four genes, as well as on two partial datasets, to determine if their results were concordant: the first partial dataset had 28S only, while the second had the other three gene regions (16SND1, CO1, *wingless*).

To choose a partitioning scheme for the RAxML analyses, PartitionFinder 1.1.1 (Lanfear et al. 2012) was given an all-genes matrix with 11 partitions (28S, non-coding region of 16SND1, and first/second/third codon positions for each of ND1, CO1, and *wingless*). Parameters were branchlengths = linked; models = raxml; model_selection = BIC; search = greedy.

Alignments and trees are deposited in the Dryad data repository (<http://dx.doi.org/10.5061/dryad.2g8j2>).

Taxonomy

Sumakuru Maddison, gen. n.

<http://zoobank.org/AF495AC9-F56E-44B3-AB88-D1D73AA1089D>

Type species. *Sumakuru bigal* Maddison, sp. n.

Etymology. From the Quechua *sumak*, “great, marvellous” and *uru*, “spider”. The same root *sumak* is the source of the name of the volcano Sumaco, from whose southeastern slopes the type species is known. *Sumakuru* is to be treated as grammatically masculine.

Diagnosis. Delicate, pale, and long legged as in other lyssomanines, but with a distinctive palp in which the smoothly arching embolus is connected to the tegulum by a thin sclerite and twisted hematodocha (Fig. 3 arrow). The carapace is narrow, but higher than in *Chinoscopus*; the male chelicerae are simple and relatively short, not long and diverging as in many species of *Lyssomanes*. While the form of the embolus is unique among known lyssomanines, the other features cited are not fully distinctive, as some *Lyssomanes* have a narrow carapace and short male chelicerae. It is unfortunate that we do not yet have morphological synapomorphies to distinguish each of *Sumakuru*, *Lyssomanes* and *Chinoscopus* from one another. However, the molecular data strongly support the distinction of *Sumakuru* from other lyssomanines, as discussed below. Some specific sites in the alignments submitted to Dryad at which *Sumakuru* is unique are: at site 562 of the 28S alignment, *Sumakuru* has T instead of G or A; site 861 of 28S, A instead of G; site 589 of 16SND1, A instead of T (thus rendering the 10th amino acid of ND1 translated as asparagine instead of either isoleucine or valine). Comments on monophyly are given under “Phylogeny and Discussion”.

***Sumakuru bigal* Maddison, sp. n.**

<http://zoobank.org/29AE8C1D-8C6F-4140-A4D6-1612B0CC1C77>

Figs 1–11

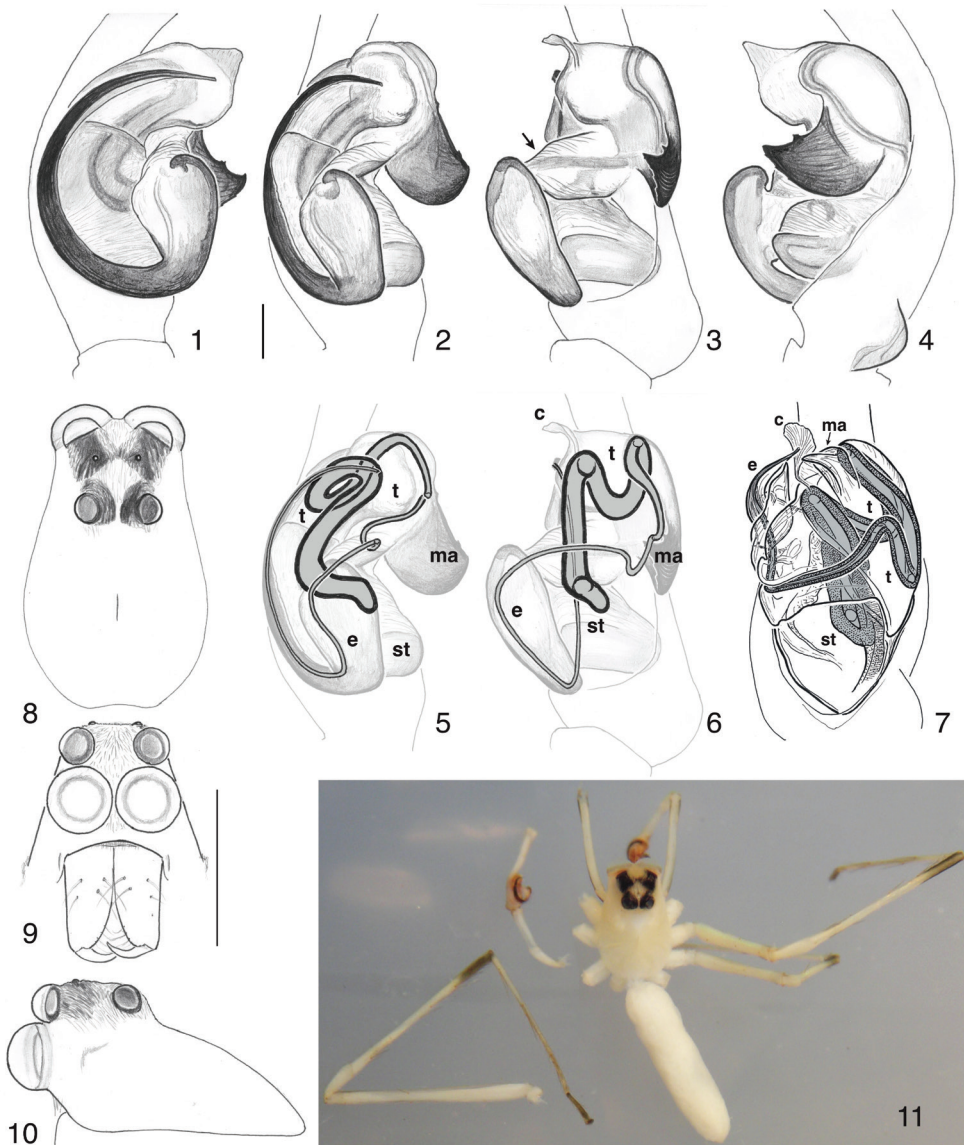
Type material. Holotype: male, ECUADOR: Orellana: Río Bigal Reserve, Mirador Trail. S 0.5282 W 77.4195. 950 m elev. 2–4 November 2010. W & D Maddison, M Vega, M Reyes. WPM#10-043. DNA voucher d448. The specimen pertains to the Museum of Zoology, Pontificia Universidad Católica, Quito, Ecuador (QCAZ), but is currently held in the Spencer Entomological Collection at the Beaty Biodiversity Museum, University of British Columbia (UBC-SEM).

Etymology. Based on the type locality.

Diagnosis. The distinct arching spiral of the embolus (Fig. 1) is unlike any other known lyssomanine, except perhaps *Lyssomanes tarmae* Galiano, 1980, whose embolus is thicker. The carapace is relatively narrow, and the dark markings on the tarsi and ends of the tibiae of legs 2 and 3 are distinctive (Fig. 11).

Notes. The single male was found by beating understory vegetation in a relatively open tropical rainforest along a ridge. It landed injured on the beating sheet, having lost most of its legs. The preserved specimen now has both palpi, but just 3 legs: the second legs on both sides, and the third leg on the right side.

Description. *Male* (holotype, DNA voucher d448). Carapace length 1.7; abdomen length 2.8. Chelicera (Fig. 9): modest in size, vertical. Teeth not examined for fear of breaking this singular specimen, but no large or prominent teeth projecting beyond the endites. Palp (Figs 1–6): segments long, such that femur is as long as the carapace. Tip of cymbium elongate, extending well distal to bulb (Fig. 11). The bulb's basic configuration is much like that of *Lyssomanes viridis* (Walckenaer, 1837) (Fig. 7). The subtegulum is exposed at the proximal side of the bulb, the tegulum occupies the distal retrolateral part of the bulb, and the embolus is on the prolateral side (Figs 5–6). The embolus is connected to the tegulum by a narrow sclerite and twisted hematodocha (arrow in Fig. 3). A diaphanous conductor is terminal (c in Figs 5–6). A broad blade-shaped apophysis, its apparent homolog interpreted as the median apophysis by Galiano (1962 figs 1–2), arises from the retrolateral side of the tegulum (ma in Figs 5–6). The spermophore begins proximally, in the subtegulum, then moves distally into the tegulum (Figs 5–6) then has a loop extending proximally into the tegulum, before coming into the retrolateral side of the tegulum. From there the duct runs through a narrow bridge of sclerite and hematodocha to cross over the face of the bulb to the prolateral embolus (Figs 5–6). The same configuration of the spermophore is seen in *Lyssomanes* (Fig. 7). Legs long, typical for lyssomanines. Carapace (Figs 8–10): narrow, with fovea displaced to the posterior. ALE directly above AME (Fig. 9). Color in alcohol (Fig. 11): pale, almost white, except for black eyes and appendages as noted (Fig. 11). Black pigment on the tarsus and distalmost quarter of the tibia of legs 2 and 3. On the palp is some black pigment on the retrolateral edge of the trochanter and femur, and the distal prolateral edge of the femur. Some pale scales clothe the dark ocular region (Figs 8–10).



Figures 1–11. *Sumakuru bigal* sp. n., holotype, except **7** (*Lyssomanes* for comparison). **1–6** Left palp. **1** Prolateral view **2** Oblique prolateral-ventral view (scale bar 0.1 mm) **3** Ventral view **4** Retrolateral view **5** Oblique prolateral-ventral view showing path of spermophore (as seen by clove oil clearing) and interpretation of parts **6** Same, ventral view **7** Trypsin-cleared left palp of *Lyssomanes viridis*, ventral view, showing path of spermophore **8** Carapace, dorsal view **9** face (scale bar 1.0 mm) **10** Carapace, lateral view **11** Photograph of holotype, with left palp and left second leg separated. Abbreviations: **e** = embolus; **c** = conductor; **ma** = median apophysis; **t** = tegulum; **st** = subtegulum.

Phylogeny and Discussion

Sequences of the holotype of *Sumakuru bigal* were obtained for 28S (GenBank accession number KX578224), 16SND1 (KX578225), CO1 (KX578226) and *wingless* (KX578227). Alignment by MAFFT appeared reasonable except for a few obvious shifts of 3 to 7 nucleotides near the starts or ends of some outgroup sequences, which were corrected by hand (28S *Aelurillus* cf. *ater*, *Cucudeta zabkai*, *Onomastus nigrimaculatus*, *Cocalodes longicornis*; 16SND1 *Afromarengo* sp., *Naphrys pulex*).

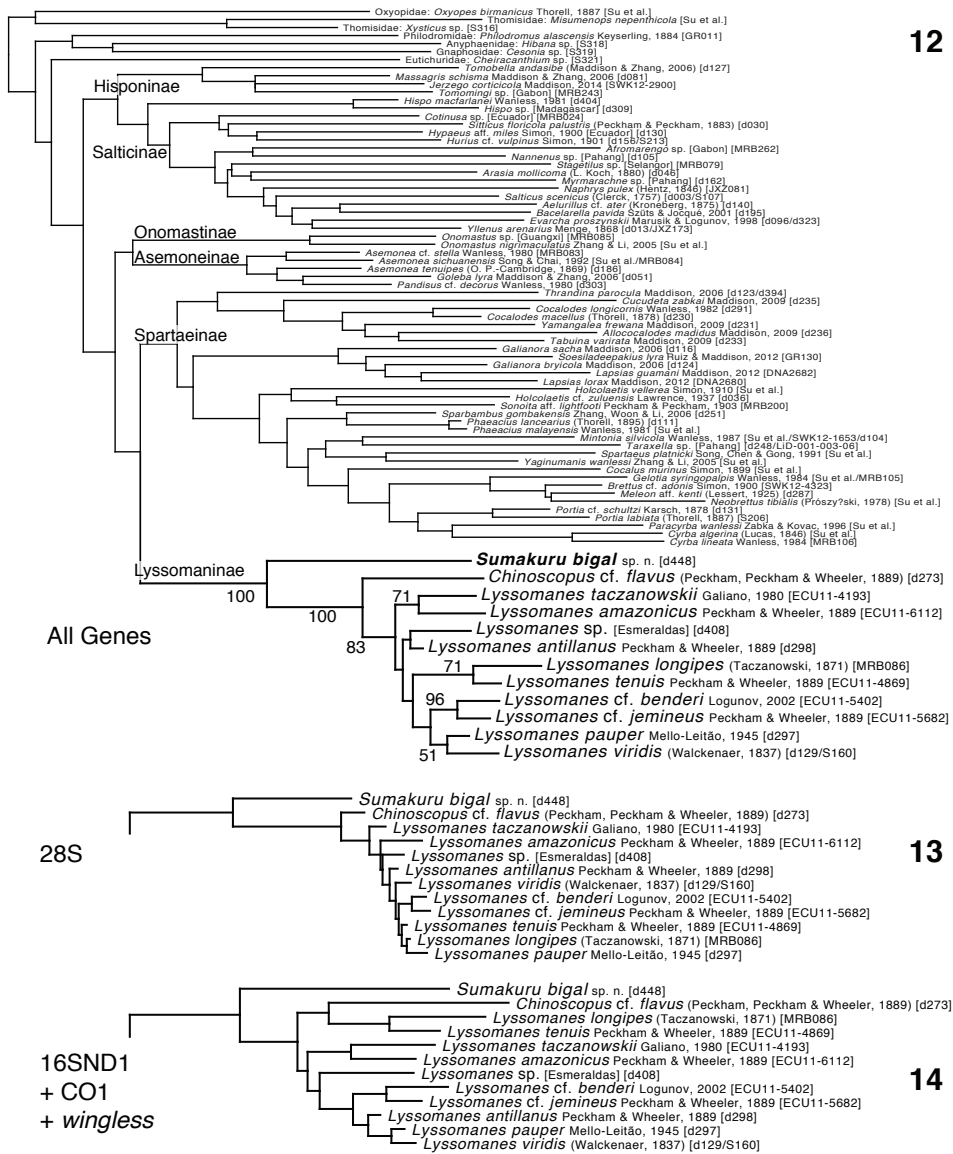
PartitionFinder determined the best partitioning scheme was to keep all partitions separate except to group the noncoding portion of 16SND1 with the first codon position of ND1, and to group first and second codon positions of *wingless*. For all of these GTR+I+G was determined as the best model, except for ND1 second position (GTR+G).

Phylogenetic trees inferred are shown in Figs 12–14. Among the outgroups (i.e. all taxa other than lyssomanines), the All Genes tree in most respects matches that of Maddison et al. (2014), though there are a few differences, including the non-monophyly of hisponines, perhaps because the sample here of non-lyssomanine taxa and genes is reduced compared to theirs.

Sumakuru is placed with strong support as a lyssomanine and as the sister group to *Chinoscopus* + *Lyssomanes*. The monophyly of the Lyssomaninae is supported in 100% of the bootstrap replicates in the All Genes analysis (Fig. 1), and in the separate 28S and 16SND1+CO1+*wingless* analyses (Figs 13, 14). Likewise, the monophyly of *Lyssomanes* + *Chinoscopus* (excluding *Sumakuru*) is supported in the All Genes analysis (100%), 28S analysis, and 16SND1+CO1+*wingless* analysis. Unlike the analyses of Maddison et al. (2014), which embedded *Chinoscopus* within *Lyssomanes*, our All Genes analysis gives reasonable support to the monophyly of *Lyssomanes* (83%).

The molecular phylogeny provides sufficient reason to recognize *Sumakuru* as a distinct genus, given the study's inclusion of the type species of *Lyssomanes* (*L. viridis*) and the close similarity between the species of *Chinoscopus* studied and the type species *C. gracilis* (Taczanowski, 1872). However, the molecular phylogeny does not provide much support for the full monophyly of *Lyssomanes* as currently composed, as we lack molecular data for many species now placed in *Lyssomanes*, and there has been little phylogenetic work using morphology. The delicate body and unusual genitalia of *Chinoscopus* can be interpreted as synapomorphies for that genus, but no such synapomorphies are known for *Lyssomanes* as a whole. Although many excellent figures of male palps of *Lyssomanes* species have been published (e.g. Galiano 1980, Logunov and Marusik 2003, Logunov 2014), the palpi are complex and diverse, and few species have received detailed morphological interpretations. There has therefore been little proposed about phylogenetic relationships within *Lyssomanes*, except for Galiano's (1980) species groups.

That *Lyssomanes* could be monophyletic receives some support from the fact that the ten *Lyssomanes* species in the molecular phylogenetic analysis cover a broad spectrum of the genus, including representatives of Galiano's (1980) *longipes*, *robustus*, *antil-*



Figures 12–14. Maximum likelihood phylogenetic trees from RAXML analyses. Appended to taxon names are the identification codes of voucher specimens used **12** Phylogeny from all 4 genes concatenated; bootstrap percentages shown for lyssomanines only **13** Lyssomanine portion of phylogeny from 28S alone **14** Lyssomanine portion of phylogeny from three gene regions concatenated, 16SND1+CO1+wingless.

lanus, *amazonicus*, *viridis* and *jemieus* species groups. However, the genus includes 90 described species showing great diversity in genitalic morphology (Galiano 1962, 1980, 1984, 1996; Brignoli 1984; Jiménez and Tejas 1993; Logunov 2000, 2002, 2014, 2015; Logunov and Marusik 2003). Nine of Galiano's 15 species groups are not yet rep-

resented in a phylogenetic analysis. Among these other species groups yet to be studied may be other species that belong in *Sumakuru*, or as separate deeply diverging lineages.

Among the *Lyssomanes* species not studied in the molecular phylogeny are some whose similarities to *S. bigal* are likely convergent. For instance, *Lyssomanes spiralis* F.O. Pickard-Cambridge, 1900 also has a spiraled embolus (Galiano 1980: figs 138–199). However, the body is otherwise unlike *Sumakuru*, robust and with long jaws (F.O. Pickard-Cambridge 1900). Its apparent relative *L. cf. jemineus* groups with *Lyssomanes* in the molecular phylogeny (*L. jemineus* and *L. spiralis* were placed by Galiano 1980 in the same species group).

Some species currently placed in *Lyssomanes* stand out as unusual, therefore possibly falling outside of *Lyssomanes*, either as relatives of *Sumakuru bigal*, or as separate deeply-branching lineages. *Lyssomanes tarmae* Galiano, 1980 has a distinctive palp with an arching embolus that resembles that of *Sumakuru bigal*, though more robust. *L. elongatus* Galiano, 1980, known only from the female, has a carapace shape similar to *S. bigal*. Although not obviously similar to *Sumakuru bigal*, the species *Lyssomanes romani* Logunov, 2000 may have a special phylogenetic position, based on the median apophysis which is apparently articulated (Logunov 2000).

Sumakuru appears to have diverged relatively long ago from the lineage leading to *Lyssomanes* and *Chinoscopus*, given the length of the branch below the clade of *Lyssomanes* + *Chinoscopus* (Fig. 12) and the strong bootstrap support for that clade. The lapsiines of South America and the cocalodines of Australasia, both isolated non-salticines concentrated in moist lowland tropical rainforests, similarly have a deeply diverging lineage that has few known species and that exists in higher elevation tropics. In the lapsiines, the phylogenetically isolated lineage is the unusual *Thrandina* with its large PME. In the cocalodines, it is the almost ant-like ground-dwelling *Cucudeta* Maddison, 2009 (though the position of *Depreissia* Lessert, 1942 within the cocalodines is unclear, Maddison et al. 2016). In the lyssomanines, the newly-discovered deeply diverging lineage is *Sumakuru*. These three unusual lineages all live close to the equator (among them, the maximum known latitude is 6°) and at mid to high elevations (all are from 1000 to 2500 m elevation). To find distinctive undiscovered lineages of salticids, it may be especially important to search at 1000–2500 m elevation in equatorial regions.

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A new species of *Falsopodabrus* Pic characterized with geometric morphometrics (Coleoptera, Cantharidae)

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Abstract

A new species of *Falsopodabrus* Pic, 1927 is described, *F. tridentatus* Yang, **sp. n.** (Yunnan, China). Geometric morphometric analyses based on the shapes of pronotum and hind wing and comparisons with two sibling species, *F. himalaicus* Wittmer, 1974 and *F. martensi* (Wittmer, 1979), support the valid status of the new species, also confirmed by the characters of tarsal claws. In addition to *F. himalaicus* and *F. martensi*, *F. kostali* Švihla, 2004 and *F. rolciki* Švihla, 2004 are recorded from China for the first time.

Keywords

China, *Falsopodabrus*, geometric morphometrics, new faunistic record, new species, taxonomy

Introduction

The genus *Falsopodabrus* was proposed by Pic (1927) for *Podabrus refossicollis* Pic, 1907, by monotypic and original designation. In this genus, *F. himalaicus* Wittmer, 1974 and *F. martensi* (Wittmer, 1979) are very similar, and they differ from each other only in the basal teeth of the tarsal claws of the anterior two pairs of legs, which are larger in the former species (Švihla 2004). During this study, another species from

Yunnan, *F. tridentatus* sp. n., was found to share common characteristics with the two described species, and can be differentiated by the presence of basal teeth on all outer tarsal claws. Except for the differences in the claws, it was difficult to distinguish these species only by description or measurements, so Švihla (2004) suggested that additional research would be required to determine whether they are closely related species, subspecies, or merely a single species with variation along a cline.

In order to clarify the species complex of *F. himalaicus*, *F. martensi*, and *F. tridentatus* sp. n., the geometric morphometric technique is introduced in the present study. Geometric morphometrics offer a more comprehensive and effective approach to the study of shape through the multivariate statistical analysis of anatomical landmarks or outline of biological homology (Bookstein 1991; Rohlf and Marcus 1993; Adam et al. 2004). It preserves the information about the relative spatial arrangement of the data through the analysis (Zelditch et al. 2004), making it possible to find and analyze shape variations in the organisms within and between populations (Walker 2000). Moreover, geometric morphometric tools present the advantage of laying results that not only have high statistical power but also have easily visualized results, helping with their interpretation and communication (Rohlf and Marcus 1993; Adam et al. 2004; Zelditch et al. 2004). It has been successfully used to resolve taxonomic uncertainties and in delineating cryptic species of several beetle groups (i.e. Faille et al. 2008; Taravati et al. 2009; Hájek and Fikáček 2010; Xu et al. 2013), especially, it was shown to be a useful tool in discrimination of the cantharid species by analyzing the hind wing shape (Su et al. 2015).

In this article, except the hind wing, the shapes of aedeagus and abdominal sternite VIII of female which are in usual description of cantharid species are analyzed. The pronotum is traditionally measured by the ratio of length and width but fails to capture the geometrical relations between the anatomical points analyzed (Rohlf 1990), so it is also included in the analysis. The subjective of the study is to assess if *F. himalaicus*, *F. martensi*, and *F. tridentatus* sp. n. are separate species or conspecific, by using a geometric morphometric approach.

Material and methods

The material is deposited in the following collections and the primary types were returned to the collections from which they were borrowed or were otherwise deposited in public museums.

CAS	California Academy of Sciences, San Francisco, USA;
IZAS	Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
MHBU	Museum of Hebei University, Baoding, China;
MNHN	Muséum National d'Histoire Naturelle, Paris, France;
NHMB	Naturhistorisches Museum Basel, Switzerland;
NMPC	Narodni muzeum, Praha, Czech Republic.

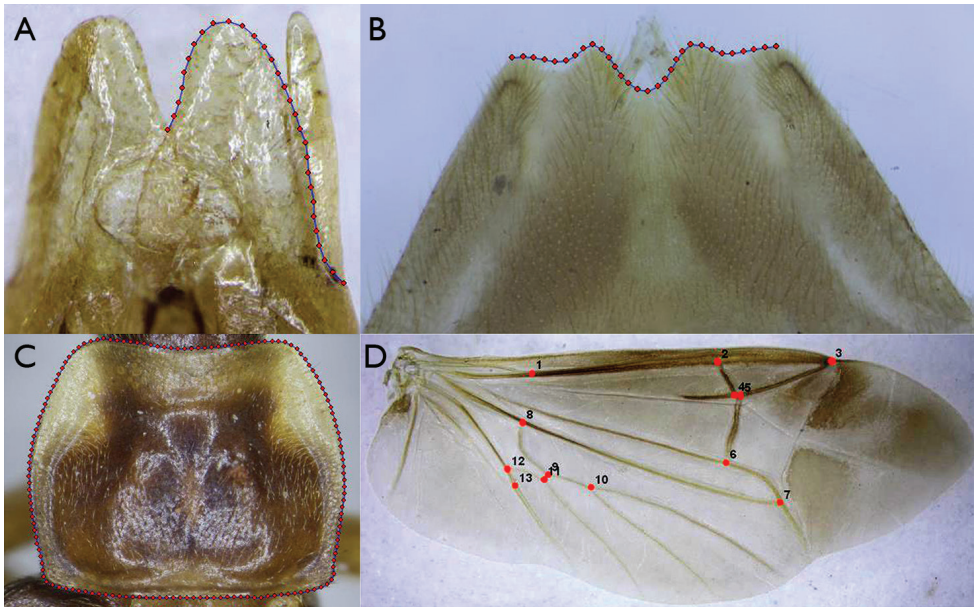


Figure 1. **A** Aedeagus **B** abdominal sternite VIII of female **C** pronotum **D** hind wing showing digitizing landmarks or points around the outline. **A–B** *Falsopodabrus himalaicus* **C–D** *F. tridentatus* sp. n.

Table 1. The number of specimens of each species examined for each character used in the geometric morphometric analyses.

species	aedeagus	female abdominal sternite VIII	pronotum	hind wing
<i>F. himalaicus</i> Wittmer, 1974	9	11	39	28
<i>F. tridentatus</i> sp. n.	12	10	34	20
<i>F. martensi</i> (Wittmer, 1979)	3	9	12	12

The description format and the method used in this study follow that of Okushima and Yang (2013) and Yang et al. (2014). Morphological terminology of female genitalia follows that of Brancucci (1980) and hind wing of Kukalová-Peck and Lawrence (1993).

Four morphological structures were analyzed by the geometric morphometrics, including pronotum, hind wing, aedeagus, and abdominal sternite VIII of female. The numbers of specimens studied for each structure of each species are indicated in the Table 1. All images were taken using a Canon 450D camera mounted on a Nikon SMZ1500 stereomicroscope, and were annotated using the TpsUtil software (Rohlf 2010a). The TpsDig2.16 software (Rohlf 2010b) was used to digitized outlines around the dorsal plate of the paramere of aedeagus (30 semi-landmarks), posterior margin of abdominal sternite VIII of female (30 semi-landmarks) and all margins of pronotum (150 semi-landmarks), and 13 landmarks at vein junctions of the hind wing as that of Su et al. (2015) (Fig. 1).

The shapes of each structure among taxa were analyzed using MorphoJ software (Klingenberg 2011). The relative similarity and discrimination of the three species was analyzed using Canonical Variates Analysis (CVA). CVA is presented using the first two canonical axes. CVA finds shape values that maximize group means relative to variation within groups, by assuming that covariate matrices are identical (Klingenberg 2010). This is an effective method for detecting differences among taxa. The statistical significance of pairwise differences in mean shapes is determined using permutation tests (10 000 replications) with Procrustes and Mahalanobis distances. Both tests are used to assess significance because P -values can differ due to the anisotropy (direction dependency) of shape variation (Klingenberg and Monteiro 2005). The variability in the shape space was assessed using a Principal Component Analysis (PCA). To better visualize the shape variation, we presented the mean configuration of the analyzed structures for each species. The thin plate spline visualization (deformation grids) are used to portray the resulting shape variations. The goal of those morphometrical studies is to investigate the amount and the type of differences between populations. Since all analyses are performed with or without size provided similar results, those presented in this article deal only with shape.

Results

The results provided by the CVs (Fig. 2) of shape differences for aedeagus, abdominal sternite VIII of female, pronotum, and hind wing all showed that *F. martensi*, *F. himalaicus* and *F. tridentatus* sp. n. occupied different areas of each graph respectively. Mahalanobis distances ($P < 0.05$) between the three species were highly significant in all pairwise comparisons, and Procrustes distances ($P < 0.05$) were similar (Tables 2, 3). However, measurements of the aedeagi were insignificantly different between *F. martensi* and *F. himalaicus* (Procrustes distances = 0.0524, $P = 0.115$) or *F. tridentatus* sp. n. (Procrustes distances = 0.0653, $P = 0.1764$), also difference was insignificant for the abdominal sternite VIII of females between *F. tridentatus* sp. n. and *F. martensi* (Procrustes distances = 0.0354, $P = 0.0778$). This suggested that the three species could be successfully delineated by the pronotum and hind wing, but were not fully sorted by the aedeagus and abdominal sternite VIII of female.

To examine the differences of the pronotum and hind wing among *F. himalaicus*, *F. martensi*, and *F. tridentatus* sp. n., the shape variation for these structures are presented by the first two principal components of PCs (Fig. 3). The thin plate spline visualization (Fig. 3A) showed that the pronotum widened in *F. martensi*, while narrowed in *F. tridentatus* sp. n., presenting with anterior and posterior margins curved inwards while lateral margins curved outwards in the former, conversely in the latter species. For the hind wing (Fig. 3B), the radial cell (around by landmarks 2–5) is distinctly lengthened longitudinally in *F. himalaicus*, while shortened in the other two species, of which slightly in *F. tridentatus* sp. n. and distinctly in *F. martensi*; the distances between the vein junctions of RP & MP₁₊₂ (landmark 7) and MP₁₊₂ & MP₃₊₄ (landmark

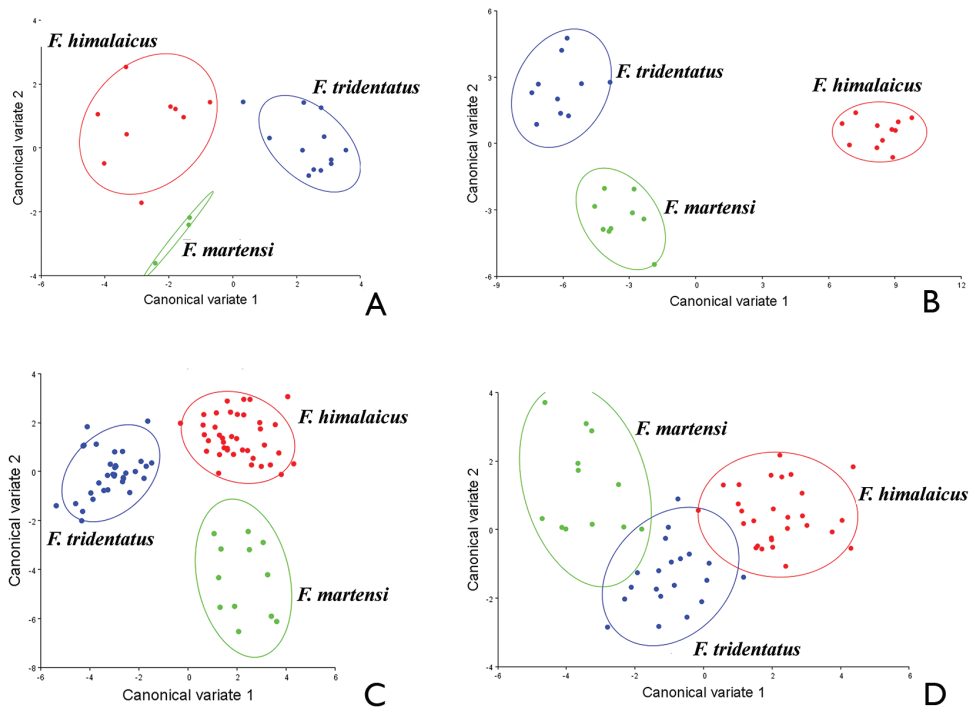


Figure 2. Plots of the first two canonical axes of Canonical Variates Analysis for *Falsopodabrus himalaicus*, *F. tridentatus* sp. n., and *F. martensi*, showing 90% confidence ellipses of population means: **A** aedeagus **B** abdominal sternite VIII of female **C** pronotum **D** hind wing.

Table 2. Difference in shapes of aedeagus (left) and abdominal sternite VIII of female (right) among *F. himalaicus*, *F. tridentatus* sp. n., and *F. martensi*. Mahalanobis and Procrustes distances computed from a canonical variates analysis. *P*-values for the significance of the inter-population distances were computed using permutation tests (10 000 replications).

	<i>F. himalaicus</i>	<i>F. tridentatus</i>	<i>F. martensi</i>	<i>F. himalaicus</i>	<i>F. tridentatus</i>	<i>F. martensi</i>
Mahalanobis distances: <i>P</i> -values (above); distances between population (below)						
<i>F. himalaicus</i>	—	<.0001	0.0168	—	<.0001	<.0001
<i>F. tridentatus</i>	5.0884	—	<.0001	14.5081	—	<.0001
<i>F. martensi</i>	3.6005	5.0217	—	12.3302	6.477	—
Procrustes distances: <i>P</i> -values (above); distances between population (below)						
<i>F. himalaicus</i>	—	0.0024	0.115	—	<.0001	<.0001
<i>F. tridentatus</i>	0.0916	—	0.1764	0.1407	—	0.0778
<i>F. martensi</i>	0.0524	0.0653	—	0.1234	0.0354	—

8) and between CuA₁ & CuA₂ (landmark 11) and CuA & CuA₁₊₂ (landmark 12) both longest in *F. himalaicus*, while shortest in *F. martensi*; the angle formed by RA₃₊₄ & r4 (landmark 5), r4 & RP (landmark 6) and RP & MP₁₊₂ (landmark 7) widened in *F. himalaicus*, while narrowed in *F. martensi*.

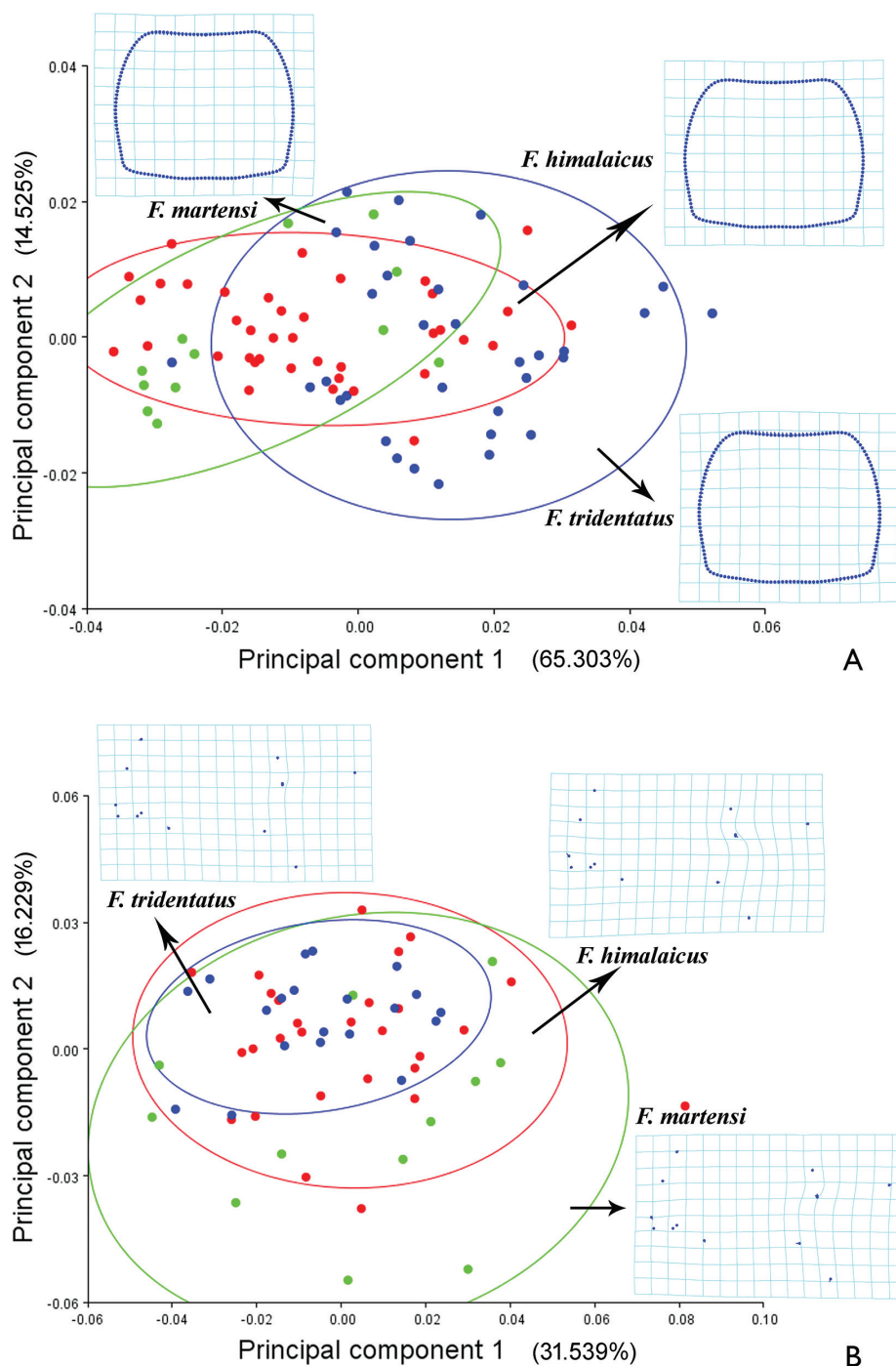


Figure 3. Plots of the first two components of Principal Component Analysis for *Falsopodabrus himalaicus*, *F. tridentatus* sp. n., and *F. martensi*, showing 90% confidence ellipses of population means: **A** pronotum **B** hind wing. The averaged shape of each species is depicted as deformations using thin plate splines.

Table 3. Difference in shapes of pronotum (left) and hind wing (right) among *F. himalaicus*, *F. tridentatus* sp. n., and *F. martensi*. Mahalanobis and Procrustes distances computed from a canonical variates analysis. *P*-values for the significance of the inter-population distances were computed using permutation tests (10 000 replications).

	<i>F. himalaicus</i>	<i>F. tridentatus</i>	<i>F. martensi</i>	<i>F. himalaicus</i>	<i>F. tridentatus</i>	<i>F. martensi</i>
Mahalanobis distances: <i>P</i> -values (above); distances between population (below)						
<i>F. himalaicus</i>	—	<.0001	<.0001	—	<.0001	<.0001
<i>F. tridentatus</i>	5.3921	—	<.0001	3.6132	—	<.0001
<i>F. martensi</i>	5.7685	6.9129	—	5.6757	3.6315	—
Procrustes distances: <i>P</i> -values (above); distances between population (below)						
<i>F. himalaicus</i>	—	<.0001	0.0444	—	0.001	0.0002
<i>F. tridentatus</i>	0.0206	—	<.0001	0.0221	—	0.001
<i>F. martensi</i>	0.0125	0.0300	—	0.0348	0.0303	—

The evidence above, shown by the significant shape differences in pronotum and hind wing, except the characteristic claws, suggest that *F. himalaicus*, *F. martensi*, and *F. tridentatus* sp. n. are separate species.

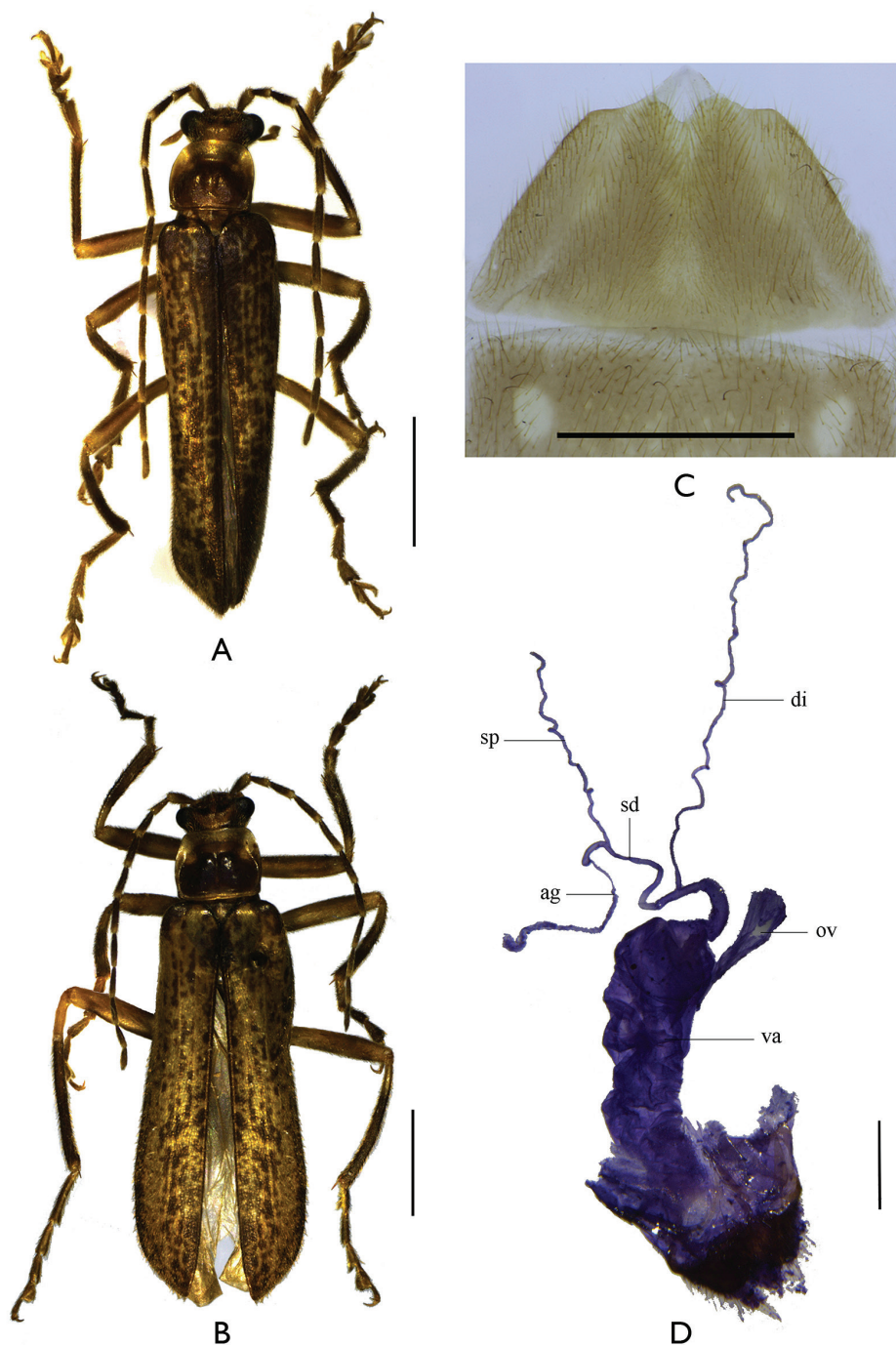
Taxonomy

Falsopodabrus tridentatus Yang, sp. n.

<http://zoobank.org/444B1588-9D1D-4923-B0A2-A003D2A51544>

Figs 4, 5

Type material. Holotype: ♂ (IZAS): China: Yunnan: Gaoligong Shan, Nujiang pref., 16.3 km W Gongshan, 2775m, 27.715°N, 98.502°E, 15.–19.VII.2000, H.-M. Gan, C. Griswold, D. Kavanaugh, H.-B. Liang, D. Ubick, D.-Z. Dong. Paratypes: China: Yunnan: 14♂, 2♀ (CAS): same data to holotype; 1♂, 2♀ (CAS): Gaoligong Shan, Nujiang Prefecture, Nujiang State Nature Reserve, No.12 Bridge Camp area, 16.3 km W of Gongshan, N27.71503° / E98.50244°, 2775m, 15.–19.VII.2000, Stop#00-23, D.H. Kavanaugh, C.E. Griswold, Liang H.-B., D. Ubick & Dong D.-Z. collectors; 1♀ (CAS): Gaoligong Shan, Nujiang Prefecture, Gongshan County, Danzhu He drainage, 13.5 air km SSW of Gongshan, 2700m, N27.63063° / E98.62074°, 30.VI–5.VII.2000, Stop#00-17, D.H. Kavanaugh, C.E. Griswold, Liang H.-B., D. Ubick, & Dong D.-Z. collectors; 1♀ (CAS): Fugong County, Lumadeng Township, Lao Shibali Yakou, 3270m, N27.06429° / E098.75123°, 13.VIII.2005, Stop#DNK-2005-079, D.H. Kavanaugh, H.B. Liang, D.Z. Dong & G. Tang collectors; 1♀ (CAS): Fugong County, Lumadeng Township, Shibali area, 2535m, N27.16536° / E098.78003°, 4.–17.VIII.2005, Stop#DNK-2005-059, D.H. Kavanaugh, H.B. Liang, P. Paquin & D.Z. Dong, collectors; 1♂ (CAS): Fugong County, Lishadi Township, 10km W of Shibali on Shibali Road, 3221m, N27.20055° / E098.71399°, 5.–16.VIII.2005, pitfall traps, Stop#DHK-2005-061, D.H. Kavanaugh, P. Paquin & H.B. Liang collectors; 2♂, 3♀ (IZAS): Gongshan County, Qiqi Reserve, N27.43, E98.34,



Figures 4. *Falsopodabrus tridentatus* sp. n. **A–B** habitus, dorsal view: **A** male **B** female **C** abdominal sternite VIII of female, ventral view **D** female genitalia, lateral view. The abbreviations: ag: accessory gland; di: diverticulum; sd: spermathecal duct; sp: spermatheca; ov: median oviduct; va: vagina. Scale bars **A–B**: 2.0 mm; **C–D**: 1.0 mm.

2000m, 9.VII.2000, Sino-America Exped., Liang H.B; 1♀ (IZAS): Gongshan County, No. 12 Bridge, 2750m, N27.72, E98.60, 15.VII.2000, Sino-America Exped., Liang H.B.; 1♀ (IZAS): same data, 16.VII.2000; 1♂, 2♀ (IZAS): same data, 18.VII.2000.

Distribution. China (Yunnan).

Etymology. The specific name is derived from the Latin *tri* (three) and *dentatus* (tooth), referring to the presence of basal teeth on all outer claws.

Diagnosis. The new species is similar to both *F. himalaicus* and *F. martensi*, but differs from the latter by the presence of basal teeth on all outer claws in both sexes.

Description. Male (Fig. 4A). *Head* black, pale brown on dorsum, each side with a dark brown marking behind antennal socket, mouthparts pale brown, maxillary and labial palpi darkened, apices of mandibles dark brown, antennae black, pale brown at apex of each antennomere, pronotum dark brown, more or less lightened at anterior part of disc, scutellum pale brown, elytra pale brown and mottled with irregular dark brown markings, legs pale brown, darkened at apices of femora and tarsomeres and bases of tibiae and coxae, more or less darkened at outer sides of femora and outer and dorsal sides of tibiae, prosternum pale brown, meso- and metasterna and abdominal ventrites black brown, pale brown at posterior margins of abdominal ventrites and the whole terminal ventrite. Body densely covered with short, recumbent, light yellow pubescence, mixed with slightly long, semi-erect, black brown setae on elytra.

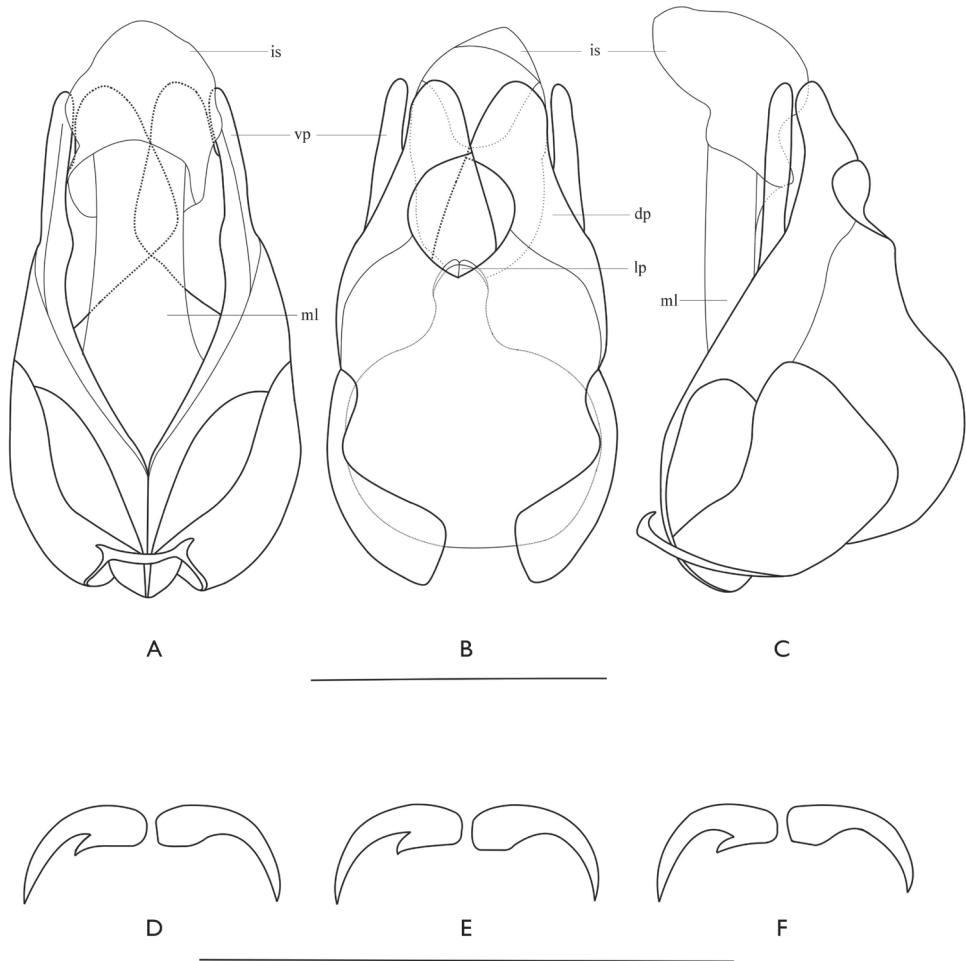
Head with temples obliquely converging posteriorly, dorsum distinctly convex in central part, surface semilustrous, densely and finely punctate; eyes strongly protruding, head width across eyes distinctly wider than anterior margin of pronotum; terminal maxillary palpomeres long-triangular, widest at basal one-third, with apical parts of inner margins arcuate and sharp, acute at apices; antennae extending along basal two-thirds length of elytra, antennomeres II about three times as long as wide at apex, III about one-third longer than II, IV longest, IV–X each with a narrow, smooth, longitudinal impression nearly in middle of outer margin, which longest on V, XI pointed at apex.

Pronotum 1.1 times as wide as long, widest near middle, anterior margin slightly arcuate, lateral margins rounded, posterior margin arcuate and narrowly bordered, anterior angles rounded, posterior angles rectangular, disc convex on posterolateral parts, surface semilustrous, finely and sparsely punctate.

Elytral length about 5.5 times length of pronotum, 3.5 times as long as humeral width, with lateral margins nearly parallel, surface semilustrous, rugose-lacunose and finely punctate.

Legs with all outer tarsal claws each with a basal tooth (Fig. 5D–F).

Aedeagus (Fig. 5A–C): Inflated basally, ventral process of each paramere flattened and nearly straight, with apex rounded, dorsal plate almost as long as ventral process, rounded at apical margin, delaminated into two layers, ventral layer with inner margin largely triangularly protuberant in middle, dorsal layer with inner margin roundly emarginate at basal portion, laterophyse compressed, short and rounded at apex, leaning against each other and situated in middle of dorsal side of median lobe,



Figures 5. Male of *Falsopodabrus tridentatus* sp. n. **A–C** aedeagus (**A** ventral view **B** dorsal view **C** lateral view) **D–F** tarsal claws of left legs, dorsal view (**D** fore leg **E** middle leg **F** hind leg). The abbreviations: dp: dorsal plate of each paramere; is: inner sac of median lobe; lp: laterophyse; ml: median lobe; vp: ventral process of each paramere. Scale bars: 1.0 mm.

inner sac of median lobe swollen and slightly lengthened ventrally, distinctly shorter than tegmen.

Female (Fig. 4B). Like male, except head less convex on dorsum, head width across eyes slightly wider than pronotum, antennae extending only to elytral midlength, antennomeres VI–X without impressions, pronotum 1.2 times wider than long, moderately convex on posterolateral parts of disc, elytra with lateral margins slightly diverging posteriorly, abdominal sternite VIII (Fig. 4C) evenly narrowed posteriorly, posterior margin moderately emarginate in middle and has rounded lobes on either side of middle emargination, nearly straight on lateral portions, present with a membranous triangular lobe behind the middle emargination. Internal reproduc-

tive organs (Fig. 4D): vagina elongate and abruptly extended apically as a thin and long duct; diverticulum and spermathecal duct arising from the end the long duct of vagina; diverticulum long, thin and spiral; spermathecal duct slightly thicker and distinctly shorter than diverticulum; spermatheca thin and spiral, distinctly shorter than diverticulum, basal portion extended into a very short tube, where accessory gland opening; accessory gland nearly as long as spermatheca; median oviduct attached near apex of vagina.

Variation within type series. Body length of the holotype: 9.0 mm, width: 1.7 mm; body length of male paratypes: 8.5–10.0 mm, width: 1.5–2.0 mm; body length of female paratypes: 9.0–11.0 mm, width: 1.7–2.2 mm.

Remarks. Except the difference in the tarsal claws, the new species differs from its sibling species, *F. himalaicus* and *F. martensi*, also by the CVs which could be used for supporting evidence in confirming the species validity. The results of PCs show that the new species with pronotum is slightly narrower than the other two; hind wing with radial cell is least distorted, the distances are between the vein junctions of RP & MP₁₊₂ and MP₁₊₂ & MP₃₊₄ and between CuA₁ & CuA₂ and CuA & CuA₁₊₂ shorter than *F. himalaicus*, while longer than *F. martensi*, the angle formed by RA₃₊₄ & r4, r4 & RP and RP & MP₁₊₂ narrower than *F. himalaicus*, while wider than *F. martensi*.

Falsopodabrus himalaicus Wittmer, 1974

Falsopodabrus himalaicus Wittmer, 1974: 631, fig. 6.

Type material examined. Holotype ♂ (NHMB): “Sikkim 11600' \ Yagtang”, “17.6.1959 \ F. Schmir”, “HOLOTYPUS”, “*Falsopodabrus* \ himalaicus \ Wittm. \ det. W. Wittmer”, “Naturhistorisches \ Museum Basel \ Coll. W. Wittmer”, “CANTHARIDAE \ CANTH00002544”.

Other material examined. China: Xizang: 1♂, 9♀ (MHBU): Mainling, Zhaxiraodeng, 2.VIII.2008, leg. Z.J. Zhou; 1♂, 1♀ (MHBU): Mainling, Oglung, 14.VIII.2008, leg. Z.J. Zhou; 7♂, 7♀ (MHBU): Bomi, 3000 m, 20.VIII.2003, leg. G.D. Ren; 1♀ (MHBU): Bomi, 26.VII.2009, leg. G.D. Ren, Y.B. Ba & Z.J. Zhou; 3♀ (IZAS): Bomi, Yi'ong, 2700 m, 1.IX.1983, leg. Y.H. Han; 1♂, 2♀ (IZAS): Bomi, Yi'ong, 2300 m, 14.VIII.1983, leg. Y.H. Han; 1♂, 4♀ (IZAS): Bomi, Yi'ong, 2300 m, 25.VIII.1983, leg. Y.H. Han; 1♀ (IZAS): Mainling, 2950m, 19.VIII.1974, leg. F.S. Huang.

Distribution. China (new country record: Xizang); India, Bhutan, Nepal (Kopetz, 2009).

Falsopodabrus martensi (Wittmer, 1979)

Stenothemus martensi Wittmer, 1979: 331.

Falsopodabrus martensi: Švihla 2004: 203, fig. 165.

Additional material examined. China: Xizang: 1♂, 2♀ (IZAS): Mêdog, Tiqin, 3400 m, 7.IX.1982, leg. Y.H. Han; 1♂, 3♀ (IZAS): Mêdog, Nage, 3150 m, 22.VIII.1974, leg. F.S. Huang; 1♀ (IZAS): same data, 23.VIII.1974; 1♂, 2♀ (IZAS): Yadong, 2800 m, 23.VII.1960, leg. C.G. Wang; 1♀ (IZAS): Mêdog, 2750 m, 21.VIII.1983, leg. Y.H. Han.

Distribution. China (new country record: Xizang); Nepal, India.

Falsopodabrus kostali Švihla, 2004

Falsopodabrus kostali Švihla, 2004: 204, figs 170–172, 216.

Type material examined. Holotype ♂ (NMPC): “NE India; Meghalaya; 1400m; \ Nokrek N.P.; 3km S Daribokgiri; \ 25°27'N 90°19'E; 26.iv.1999; \ Košťál Z. leg.”, “HOLOTYPUS \ Falsopodabrus \ kostali sp. n. \ V. Švihla det. 2003”.

Other material examined. China: Xizang: 1♂ (IZAS): Xigonghu, 1450 m, 11.V.1983, leg. Y.H. Han; 1♀ (IZAS): Mêdog, Baibung, 850m, 17.V.1983, leg. Y.H. Han.

Distribution. China (new country record: Xizang); India, Myanmar.

Falsopodabrus rolciki Švihla, 2004

Falsopodabrus rolciki Švihla, 2004: 203, figs 167–169, 215.

Type material examined. Holotype ♂ (NMPC): “NE India; Meghalaya; 1999 \ 3km E of Tura; 500–1150m; \ 25°30'N 90°14'E; 1.–8.v. \ J. Rolčík leg.”, “HOLOTYPUS \ Falsopodabrus \ rolciki sp. n. \ V. Švihla det. 2003”.

Other material examined. China: Xizang: 1♂ (NHMB): Tibet, Zayul, 12000ft, Summer 1937, R.I.H. Kaulback; 1♂ (IZAS): Mêdog, Baibung, 850m, 12.VI.1983, leg. Y.H. Han; 1♂ (IZAS): same data, 17.V.1983; 1♀ (IZAS): same data, 18.V.1983; 1♀ (IZAS): Mêdog, Xirang, 1150m, 7.VI.1983; 1♀ (IZAS): Mêdog, Didong, 1000m, 4.VI.1983, leg. Z. Lin; 2♂♂, 2♀♀ (MHBU): Zayü, Xia Zayü, 12.–13.VII.2005, leg. A.M. Shi.

Distribution. China (new country record: Xizang); India, Myanmar.

Falsopodabrus refossicollis (Pic, 1907)

Podabrus refossicollis Pic, 1907: 175.

Stenothemus refossicollis Champion: 126. Synonymized by Wittmer 1974: 62.

Stenothemus championi Pic, 1927: 40 [replacement name for *Stenothemus refossicollis* Champion, 1926, nec Pic 1907].

Podabrus (*Falsopodabrus*) *refossicollis*: Pic 1927: 40.

Falsopodabrus refossicollis: Wittmer 1974: 62.

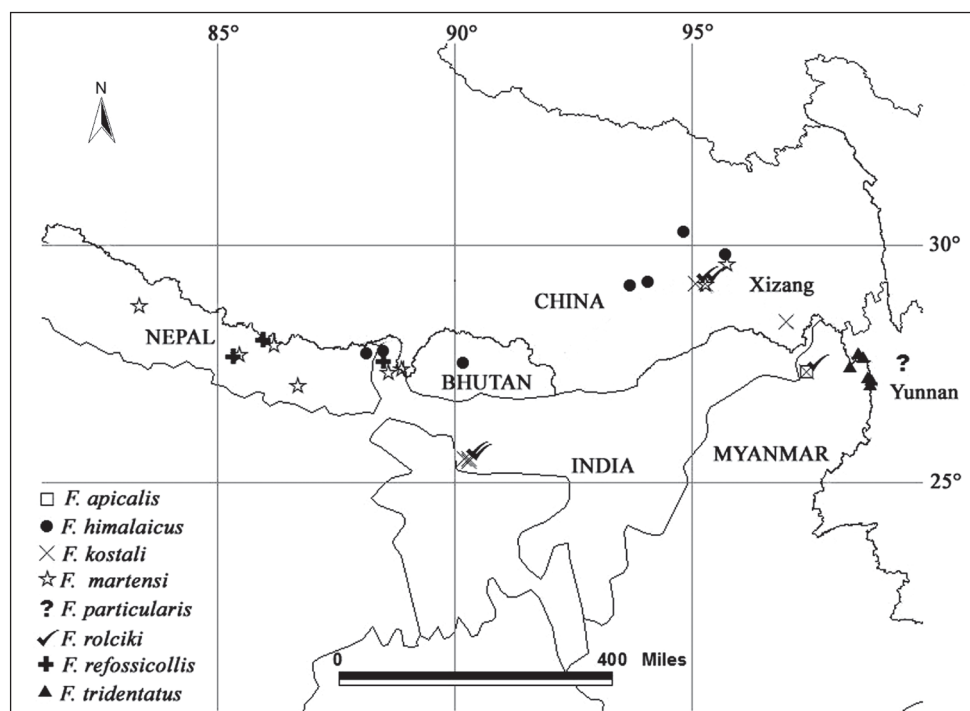


Figure 6. Distribution of *Falsopodabrus*. The location of *F. particularis* (Pic, 1931) lacks specific locality information in Yunnan Province, China.

Type material examined. Holotype ♂ (MNHN): “Kurseong” [India], “Podabrus \ refossicollis Pic“, “Falsopodabrus Pic“, “Falsopodabrus \ refossicollis \ Pic \ det. W. Wittmer”, “TYPE”.

Other material examined. China: Xizang: 1♂ (IZAS): Zham, 2400 m, 4.VII.1975, leg. F.S. Huang; 1♀ (IZAS): Zham, 2200 m, 25.V.1975, leg. Z.Q. Wang; 1♂ (IZAS): Nyalam, Zham, 2200 m, 10.V.1966, leg. S.Y. Wang.

Distribution. China (Xizang); India, Nepal (Okushima 1999).

Discussion

Sibling species are expected to show high morphological similarity. However, some differences in morphology that allow discrimination can be found when morphometric approaches are used (Moraes et al., 2004). In the present study, the species complex of *Falsopodabrus himalaicus*, *F. tridentatus* sp. n., and *F. martensi* were successfully discriminated using CVA performed on the shape variables of pronotum and hind wing, but were not fully delineated by the aedeagus and abdominal sternite VIII of female.

The aedeagus is traditionally the most reliable method to identify the cantharid species, but male genital characters were not sufficient in delimiting the closely related species, as suggested by Barkalov and Ståhls (1997). Similarly, although female abdominal sternite VIII is considered useful in the species descriptions, such as *F. kostali* and *F. rolciki*, it seems to have little diagnostic value in delimitation here.

Surprisingly the shape of the pronotum shows high diagnostic value in delimiting these three sibling species. Also, the hind wing shape is again verified to be a good taxonomic character in discrimination of the cantharid species, as suggested by Su et al. (2015).

Above all, the geometric morphometric results confirm the hypothesis proposed on the basis of tarsal claws morphology, so here we conclude that *F. himalaicus*, *F. tridentatus* sp. n., and *F. martensi* are morphologically similar but separate species. Now *Falsopodabrus* consists of eight species, which are all restricted to the Himalayan area (Fig. 6).

Acknowledgments

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X-ray microscopy reveals endophallic structures in a new species of the ground beetle genus *Trechus* Clairville, 1806 from Baltic amber (Coleoptera, Carabidae, Trechini)

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Abstract

The third fossil species of the genus *Trechus* Clairville, 1806 is described from Baltic amber: *T. exhibitorius* **sp. n.** Details of external and internal morphology were analysed using X-ray micro-computed tomography (micro-CT) and important diagnostic features of the internal male genital sac (endophallus) are described in detail for the first time in a fossil ground beetle. Based on these data, we could assign *T. exhibitorius* **sp. n.** to *Trechus* sensu stricto and this new fossil species seems to represent a basal branch of a lineage comprising species diverse groups of extant *Trechus* mainly distributed in the Caucasus and Anatolia. Thus, our results support previous studies suggesting that *Trechus* is a phylogenetically old lineage already present in the Eocene with numerous species.

Keywords

Eocene, micro-CT, 3-D reconstruction

Introduction

Although the occurrence of ground beetles of the genus *Trechus* Clairville, 1806 in the Eocene Baltic amber was reported already a century ago (Klebs 1910) the first two species were not described at the species level until recently: *T. balticus* Schmidt & Faille, 2015, and *T. eoanophthalmus* Schmidt, Hoffmann & Michalik, 2016. Both species were identified as representatives of *Trechus* sensu auctorum which, based on molecular data, is a non-monophyletic assemblage (see Faille et al. 2010, 2011, 2013). Due to the absence of male genital characters (the type of *T. balticus* is a female; the type of *T. eoanophthalmus* is a male but insufficiently preserved) it was argued that the taxonomic position of both fossil species within *Trechus* sensu lato cannot be assessed with certainty (Schmidt and Faille 2015, Schmidt et al. 2016). However, their striking similarity to extant species of the *Trechus* sensu stricto led the authors to conclude that the fossils are likely to be representatives of the stem lineage of the latter group. If this holds true, the origin of *Trechus* sensu stricto has to be assumed in the Paleogene and thus at least 10–20 Mio years earlier than suggested based on molecular analyses (Faille 2013). Thus, the investigation of fossil *Trechus* material with preserved important character, e.g. male genital characters, would hence be of high value for dating the Trechini phylogeny.

In this paper we describe the third wingless Trechini species from Baltic amber. In contrast to the abovementioned fossils, this amber inclusion represents the first ground beetle fossil with well-preserved male genitalia. We investigated this specimen using light microscopy and X-ray micro-computed tomography (micro-CT) for revealing internal genital characters. We discuss the implications of the observed genital characters especially with regard to its placement within one of the extant *Trechus* lineages.

Material and methods

The specimen was studied and imaged using light microscopy and micro-CT. The methods and technology used were described in detail in a previous work by Schmidt et al. (2016). Micro-CT scans were performed under phase contrast (40 KV, 8 W) using a 4× detector (10 s, 4.15 µm pixel size) and 10× detector (30 s, 1.89 µm pixel size). Additionally, a movie of the volume rendering of the endophallus was obtained using the MovieMaker module in Amira 5.6. The image stacks of the micro-CT scans have been deposited in MorphDBase (www.morphdbase.de/?P_Michalik_20160818-M-8.1; www.morphdbase.de/?P_Michalik_20160818-M-9.1; www.morphdbase.de/?P_Michalik_20160818-M-10.1).

Measurements of the fossil specimen were taken as follows: body size was quantified by the standardized body length, i.e., the sum of: (1) the distance from the apex of the right mandible in closed position to the cervical collar, (2) the median length of the pronotum, (3) the distance from the base of the scutellum along the suture to the apex of the left elytron. The width of the head, of the pronotum, and of the elytra was measured at their widest points. The width of the pronotal apex was measured between the tips of the apical angles, the width of the pronotal base was measured between the tips of the laterobasal angles.

Taxonomy

Trechus exhibitorius sp. n.

<http://zoobank.org/EE059FA2-2249-4132-A112-4C6A48F3FFAD>

Figs 1–16

Holotype. Male in Baltic amber; size of piece approximately $12 \times 5 \times 5$ mm (Fig. 1), with collection label data “GZG.BST.16192 / (alte Nr. G. 645) / Coleoptera: Carabidae / Bembidium / Geologisch-Paläontologisches Institut und Museum / Göttingen” (front side) and “Species „b“ / Nr.2” (back side), in Geoscience Museum, University of Göttingen, Germany (GMG). This amber piece is part of the former Königsberg Collection which is currently preserved at the GMG. This collection includes pieces of Baltic amber collected in the area of the Curonian Spit up until the first half of the 20th century.

Preservation status. The amber piece is markedly darkened, and its surface shows several fine cracks, very probably as a result of its extended exposure to air. The beetle body is partly covered by milky coating and thus its right ventral surface and the mouth parts cannot be investigated by light microscopy (Figs 2, 3). The specimen is slightly shrunken with parts of its exoskeleton, which is thus dissociated from the inclusion wall. The latter represents the negative imprint of the beetle body and could be imaged together with the detached parts of the beetle exoskeleton using micro-CT, e.g., the detached margins of the pronotum (Fig. 4). Parts of the exoskeleton are broken along sutures and impressions, e.g., pronotal median longitudinal impression (Fig. 4), gula, occipital impression, mentum/submentum (if not naturally so), prosternum/proepisternum (Figs 5, 6, 7). The aedeagus is partly moved out off the abdomen and attached in this position by the last abdominal segment; the endophallus with the claw-like apex of the copulatory piece is partly inflated (Fig. 12). At its base, the median lobe is completely disrupted from the sclerites of segment IX (genital ring); latter is lost including parts of the median lobe basal bulb and the left paramere (Fig. 13).

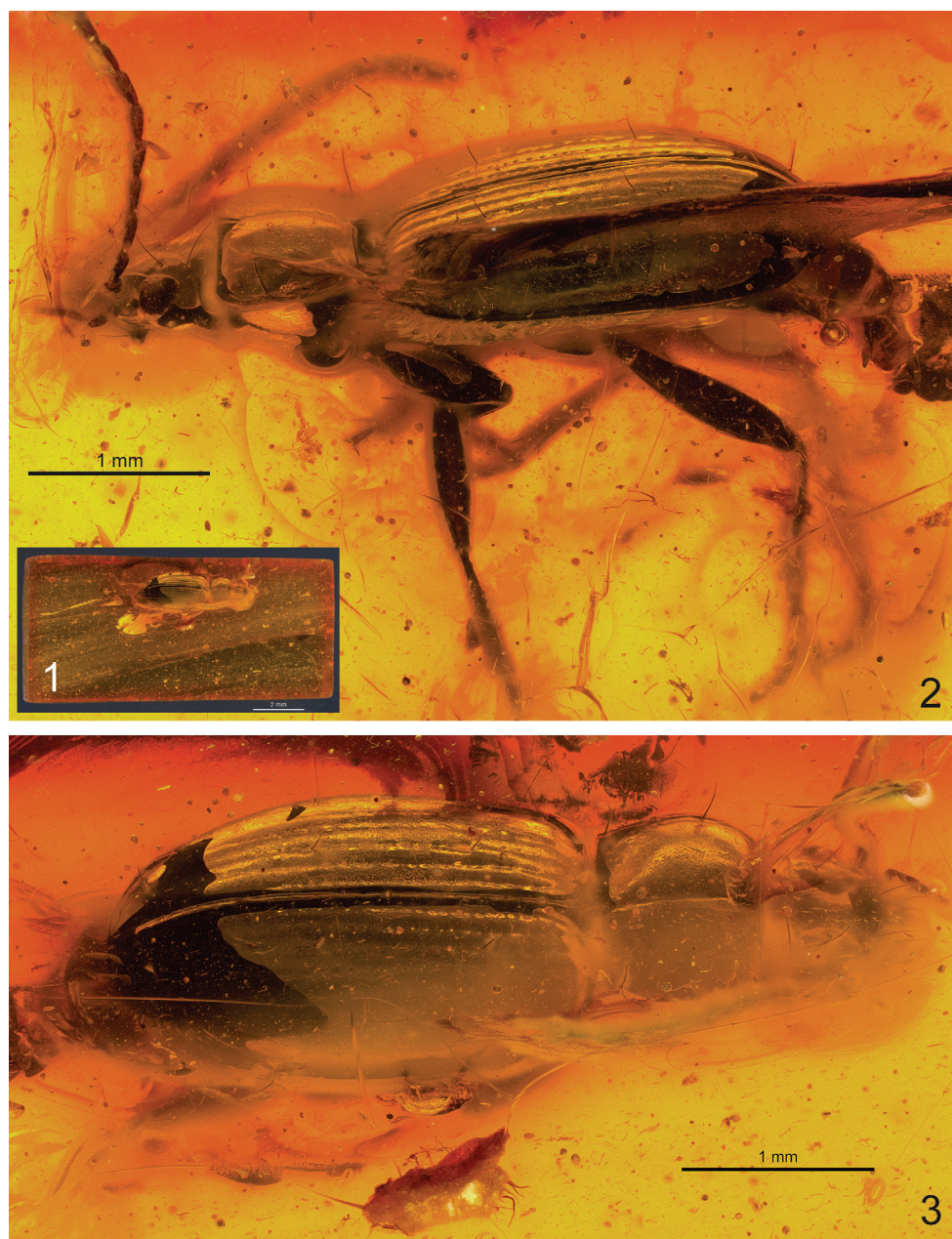
Syninclusions. One Acari specimen (phoretic mite of Parasitidae?) attached on the right elytron of *T. exhibitorius*, stellate hairs, and numerous dirt particles.

Description. Body length: 4.4 mm.

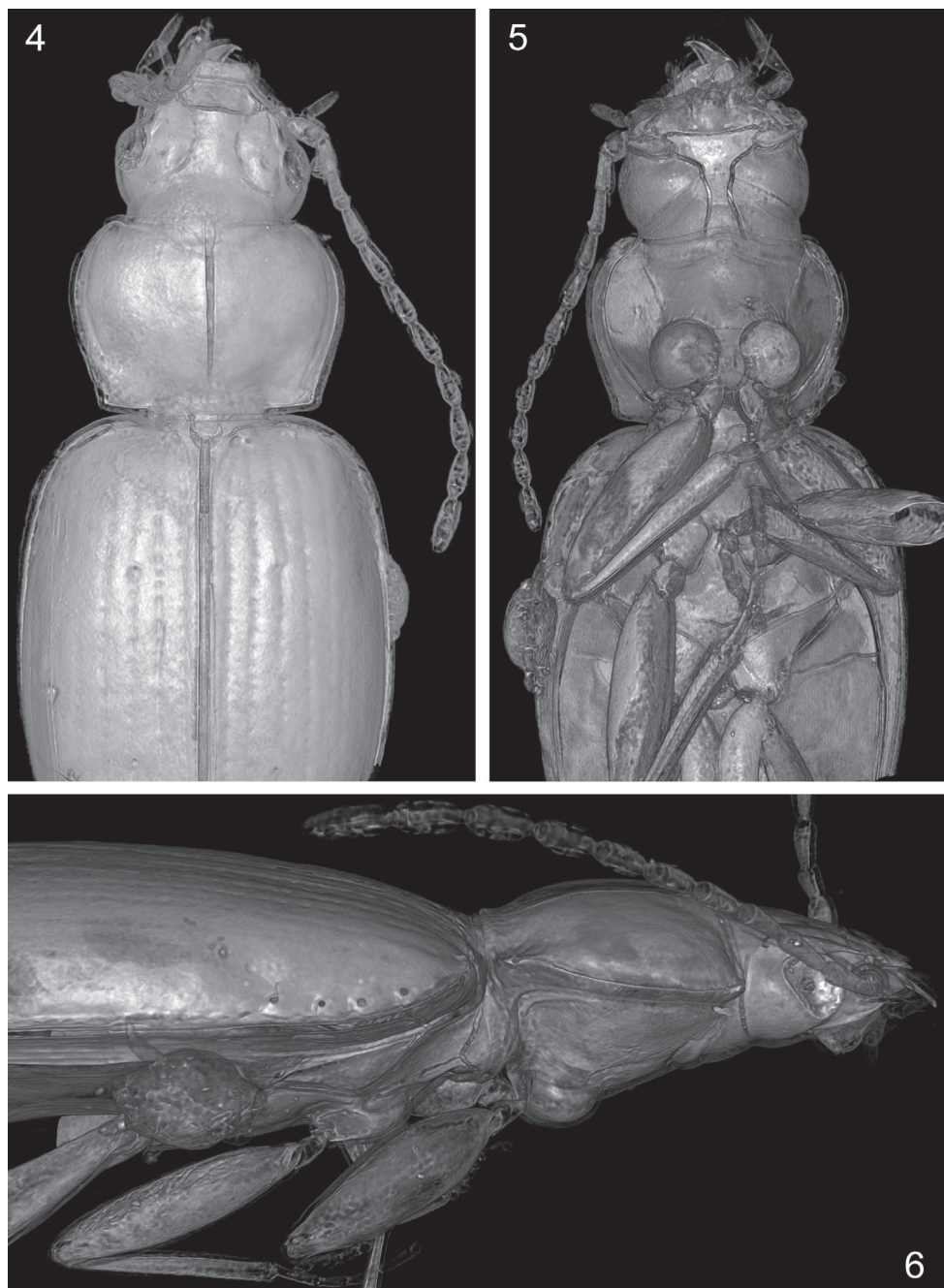
Colour: The whole body surface appears blackish brown, very shiny; variation in colouration of the different parts of the beetle body is not recognizable.

Microsculpture: Surface of head and elytra, disc of pronotum with shallowly engraved slightly transverse meshes, clypeus with slightly engraved almost isodiametric meshes, base and laterobasal furrows of pronotum with moderately engraved almost isodiametric meshes (magnification $\times 100$).

Head: Moderately large and transverse; length 0.94 mm. Mandibles moderately slender, the right one tridentate, with all denticles combined and subequally distributed, but with the apical one much more protruding than the second (Figs 7–9). Labrum with apical margin markedly concave, with three pairs of setae. Clypeus with two pairs of setae in normal position. Shape of apical segments of maxillary and labial palpi as in *Trechus* sensu stricto. Mentum and submentum completely divided by a



Figures 1–3. *Trechus exhibitorius* sp. n., light microscopic images of the holotype. **1** general view of the fossil with contours of the amber piece **2** left lateral aspect **3** dorsal aspect.



Figures 4–6. *Trechus exhibitorius* sp. n., volume rendering of the holotype, anterior portion. **4** dorsal aspect **5** ventral aspect **6** right lateral aspect.

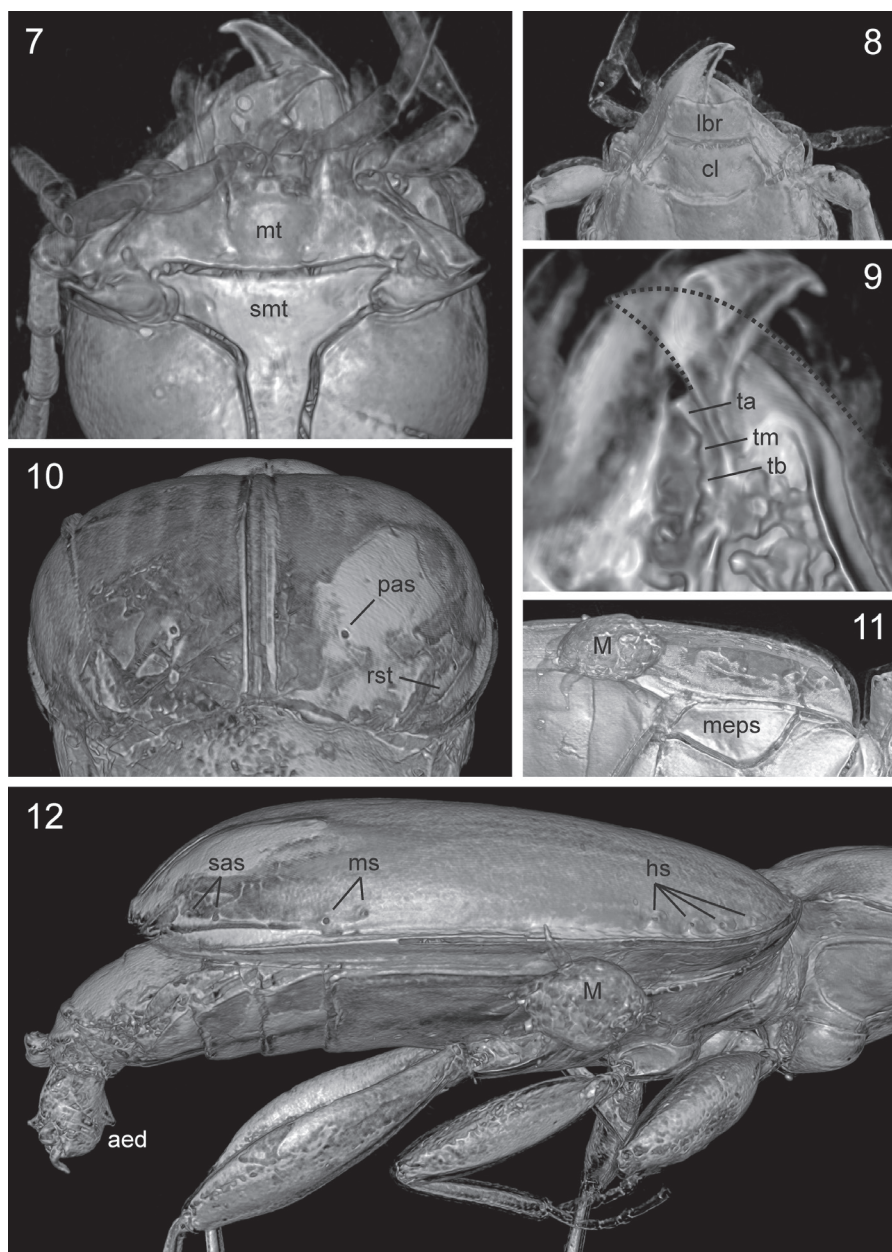
distinct suture (artefact? Fig. 7). Eyes (Fig. 6) rather small, flat; tempora about half as long as eyes, convex, moderately wrinkled to the neck, smooth. Frons and supraorbital area smooth, markedly convex, with supraorbital furrows deep, complete, uniformly bent on disc (Fig. 4); two supraorbital setae present and in normal position for *Trechus*. Antennae moderately slender, with three antennomeres extending beyond the pronotal base; scapus robust, 1.15 times longer and 1.3 times broader than pedicellus, 1.1 times longer than third antennomere; third and fourth antennomeres of the same length.

Prothorax: Pronotum rather large, transverse (width/length = 1.47), length 0.84 mm, 1.53 times broader than head, broadest somewhat before middle, with sides evenly rounded in anterior 2/3 and straight before laterobasal angles; latter small, almost rectangular, not protruded laterally. Basal margin 1.22 times broader than apical margin. Disk markedly convex, smooth. Anterior margin straight in middle, lateroapical angles slightly protruded, rounded. Posterior margin not beaded, slightly convex in middle, markedly incised towards outer quarters, not shifted anteriorly at basolateral angles. Median longitudinal impression distinct, not deepened near base, disappearing near apex; anterior transverse impression very fine, smooth; posterior transverse impression linear, deep on sides, shallower in middle, smooth; laterobasal foveae indistinct, smooth. Lateral groove moderately narrow throughout, very slightly widened towards base, smooth. Both lateral and laterobasal setae present, with the lateral seta located near apical third of pronotum. Proepisternum glabrous, smooth.

Pterothorax: Elytra markedly convex on disc, in dorsal view narrow ovate, length 2.58 mm, length/width = 1.50, widest near their mid-length, moderately wider than pronotum (width of elytra/width of pronotum = 1.30), glabrous beside normal setation. Humeral angles fully rounded, basal groove absent. Parascutellar stria moderately long, parascutellar seta present. Striae finely punctate apart from the apical fifth of elytra; first stria complete, outer striae disappearing near apex; three inner striae deeply impressed with intervals convex, fourth stria finer, fifth stria very fine, sixth and seventh striae absent, eighth stria finely impressed from level of the medial setae of the umbilical series and deeply impressed from level of the preapical group. Each elytron with two discal setae in third stria, and with preapical seta, located in the apical cross of the second and third striae, slightly closer to the suture than to the apical margin of elytra (Fig. 10). Recurrent stria rather short, extending towards the reduced fifth stria anteriorly, hardly bowed, with its front end situated at level of the preapical seta (Fig. 10). Setae of umbilicate humeral series close to the elytral margin, with four setae almost equidistant from each other; setae of the medial group of the umbilicate series far removed from the preapical group (Figs 6, 12). Metepisternum short, glabrous and smooth, with outer margin 1.3 times longer than anterior margin (Fig. 11).

Abdomen: Abdominal sternites V–VII each with one (male) pair of setae near apical margin; surfaces smooth, without hairs or micropunctures.

Legs: Moderately robust, all femora unmodified; protibiae straight and moderately dilated towards apex (structures on protibial surface are not visible using light microscopy due to milky coating, and could not be imaged using micro-CT). Basal two protarsomeres moderately dilated (Fig. 14).



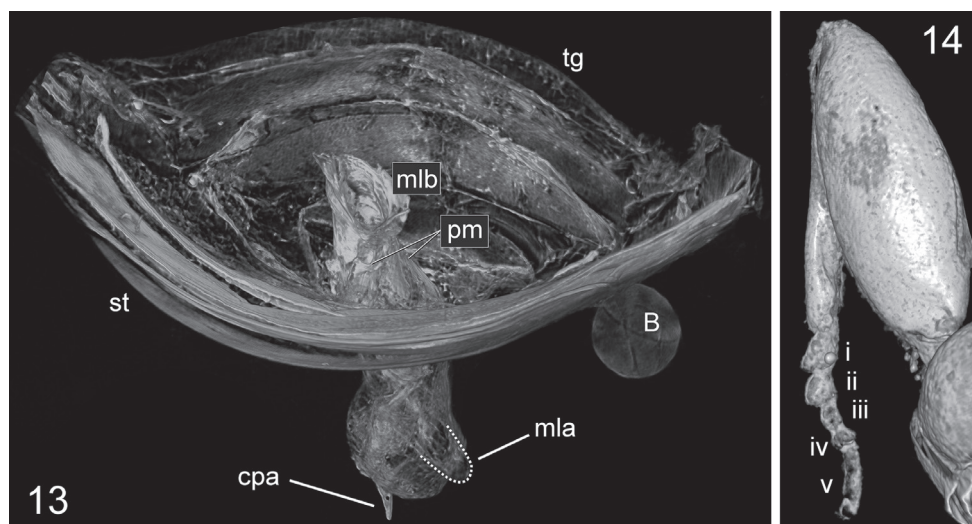
Figures 7–12. *Trechus exhibitorius* sp. n., holotype, volume rendering of selected body parts. **7** head, ventral aspect **8** head, anterior part, dorsal aspect **9** mandibles, view from dorsal (the dorsal surface of the right mandible is cut together with the labrum in order to show the mandibular dentition; the contour of the apical portion of the right mandible is indicated by a dotted line) **10** elytra, caudal aspect **11** elytral epipleuron and left external part of metathorax **12** elytra and abdomen, right lateral aspect. Abbreviations: **aed** = aedeagus; **cl** = clypeus; **hs** = humeral series; **lbr** = labrum; **M** = phoretic mite; **meps** = metepisternum; **ms** = medial series; **mt** = mentum; **pas** = preapical seta; **rst** = recurrent stria; **sas** = subapical series; **smt** = submentum; **ta**, **tb**, **tm** = apical, basal, medial denticle of the right mandible.

Male genitalia (Figs 13, 15, Movie 1): Median lobe in apical half fully closed on dorsal side, in lateral view evenly bent throughout, with basal bulb of average size for *Trechus* (bulb is destroyed on its left side including left paramere missing); apical lamella moderately long, simple, conically tapering. Endophallus armed with two copulatory pieces, one is long rod-shaped and twisted, angularly curved and pointed apically, the other is less distinct, mainly due to its ambiguous distal portion, but with proximal portion semi-circular, very similar in shape and size to that of the first piece.

Derivatio nominis. Species epithet is derived from the Latin term “exhibitorius” = exhibitor. This name was given under the impression that the new species presents itself in a rather vulgar way.

Relationships. Some characters of the pronotal structure, namely the missing laterobasal foveae coupled with rectilinear lateral portions of the basal transverse impression seem to be most useful for correct interpretation of the systematic position of the species in question. These two character states are usually correlated, although in some extant groups, the sublinear basal transverse impression may combine with the moderately impressed laterobasal foveae, the latter being separated from the lateral groove by clearly convex portions of the basal slope of the pronotal disc (e.g. *T. balkaricus* Belousov, 1990 and *T. fuscus* Motschulsky, 1850 with numerous related Caucasian and Turkish species). The boundary between the basal foveae completely missing and barely detectable is rather subjective and is often difficult to be recognized even in extant species. However, the combination of these two characters in the amber species makes a rather reliable basis for further considerations. In this respect, *T. exhibitorius* sp. n. resembles members of the *obtusiusculus* species group from the Balcans, southern Alps and Carpathians (some Caucasian species, such as *T. fischtiensis* Reitter, 1888, seem to be also closely related to this group), the *montanellus* and *liopleurus* species group sensu lato (Belousov, 1987), the former from the Alps, Beskids and Sudetes, the latter from the Caucasus and Turkey. We deliberately neglected the two other groups with a similar structure of the pronotum: the *tingitanus* and *quadristriatus* (including *T. obtusus* Ericson, 1837 and related taxa) species groups since the *tingitanus* group differs drastically by having deeper and strongly punctured exterior elytral striae while the *quadristriatus* group has a clearly convex pronotal basal margin with lateral portions oblique.

In the following, we will discuss our findings with the three remaining species groups. Members of the *obtusiusculus* species group and related Caucasian taxa, all differ readily from *T. exhibitorius* sp. n. in the endophallus armature consisting of a simple, anisotopous, scapus-like plate and therefore do not seem to be directly related to the species in question. The situation becomes much more interesting with regard to the *montanellus* and *liopleurus* groups. Jeannel (1927) considered both groups to be of Asian origin. This assumption seems to be confirmed with the description of *T. mordkovitschi* Shilenkov, 1982 and especially *T. shilenkovi* Belousov & Kabak, 1992, both from Siberia which are very similar to members of these two groups. According to Jeannel (1927) the differences between the *montanellus* and *liopleurus* groups mainly concern the degree of development of the external elytral striae and therefore, the conjunction of the apical recurrent stria with the fifth elytral stria which is clear



Figures 13–14. *Trechus exhibitorius* sp. n., holotype, volume rendering of selected body parts. **13** frontal view inside the abdomen showing the aedeagus which is fixed between the last abdominal segments **14** right front leg with protarsi i–v. Abbreviations: **B** = air bubble; **cpa** = apex of the longer copulatory piece; **mla** = median lobe apex; **mlb** = basal bulb of median lobe; **pm** = parameres; **st** = sternites; **tg** = tergites.

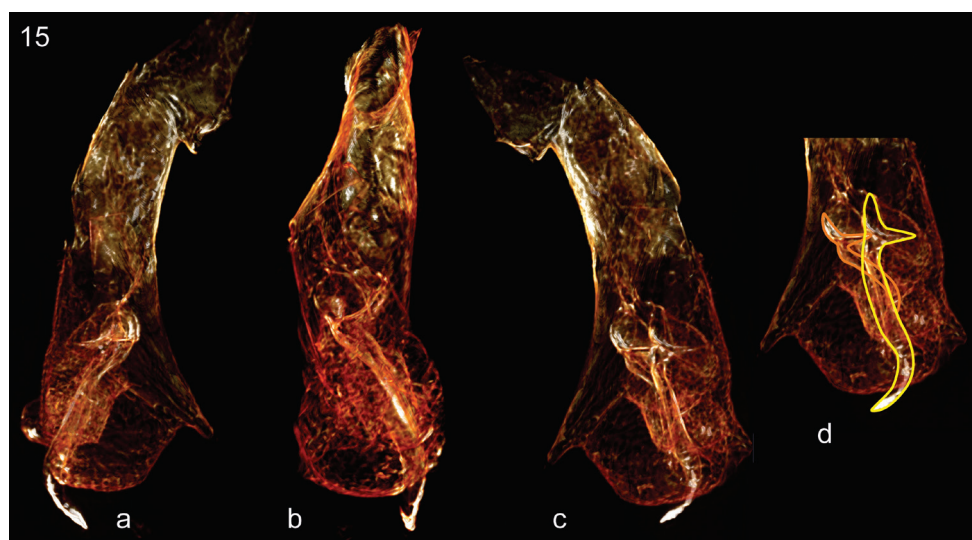


Figure 15. *Trechus exhibitorius* sp. n., holotype, volume rendering of the aedeagal median lobe with endophallus. **a** right lateral aspect **b** dorsal aspect **c** left lateral aspect **d**, same as c, but with contours of the two copulatory pieces indicated by coloured lines.

in members of the *montanellus* species group and indistinct, with the apical striole abruptly interrupted anteriorly and external stria much more reduced, in members of the *liopleurus* species group. Though this observation is correct for many species



Movie 1. *Trechus exhibitorius* sp. n., holotype, volume rendering of the aedeagal median lobe with endophallus.

of the groups under consideration, it is not present in all species. The Caucasian *liopleurus* species group is very heterogeneous and, doubtless, deserves to be split in a number of more natural species subgroups. Within each of these subgroups, we can see similar evolutionary patterns resulting in appearance of large-sized wingless species with parallel-sided habitus, shallow external elytral striae, narrow and parallel internal interspaces and massive pronotum characterized by the basal transverse impression subrectilinear and sharply engraved as well as the basolateral foveae nearly missing. On the other hand, some members of the *liopleurus* group have an ovate habitus, similar to that of members of the *montanellus* group, external elytral striae well-impressed, with clear conjunction of stria 5 with the apical recurrent stria and the pronotum with distinct basolateral foveae and the basal transverse impression which is, though sharply engraved, clearly bent laterally. Among these species, *T. gagrensis* Jeannel, 1927 is especially of high interest, since it is, doubtless, most closely related to *T. liopleurus* Chaudoir, 1850. However, the pronotal structure similar to that of *T. exhibitorius* sp. n. is observed also in some species related to *T. balkaricus* within the *maculicornis* species group as defined by Jeannel (1960) and some species of the *fuscus* (= *bradyceloides*) group (Jeannel 1960; Pawłowski 1979), despite the fact that most of species assigned to these groups have the pronotum with distinct laterobasal foveae and the basal transverse impression rather shallow and clearly bent. To summarize, we can

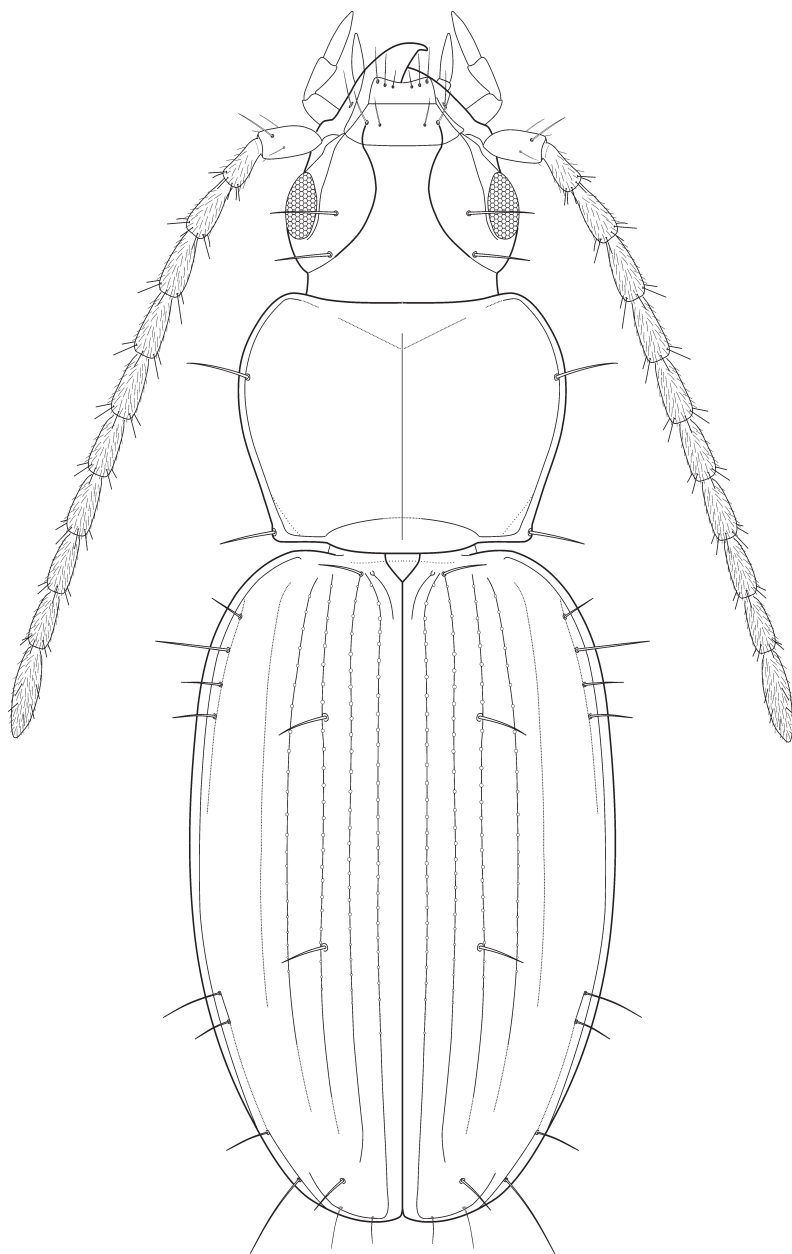


Figure 16. *Trechus exhibitorius* sp. n., reconstruction of the external shape in dorsal view.

infer that the pronotal characters listed above might have evolved independently and might be associated with a similar mode of life; their phylogenetic importance should be cautiously considered.

Fortunately, the fossil in question is the first extinct *Trechus* species with the aedeagus and endophallus armature well preserved. As to the aedeagus shape, its apical portion, slightly attenuated downwards, is very similar to that of both known species of the *montanellus* species group, *T. shilenkovi* from the Altai mountains and members of the *alpigradus* subgroup within the *liopleurus* group, especially *T. arnoldii* Belousov, 1987 from the West Caucasus. The observed structure of the endophallus armature is challenging to interpret, especially bearing in mind that it was fixed half-way inflated. However, we can clearly see one piece which is long and twisted, angularly curved and pointed apically. A large, branch-like and twisted copulatory piece is rather common in the endophallus armature of many *Trechus* species groups. In addition to the *T. sylvicola* K. Daniel & J. Daniel, 1898 from the *montanellus* group listed above, some Turkish species of the *fuscus* group are worth to be mentioned, for example: *T. michaeli* Pawlowski 1978 and *T. ziganensis* Jeanne, 1976. Though both of these species have the pronotum with rather distinct laterobasal foveae and less sharp transverse basal impression, some related species have the pronotum structure quite similar to that of *T. exhibitorius* sp. n. The second piece of the endophallus armature of this species is less distinct, mainly due to its ambiguous distal portion. However, its proximal portion is clearly detectable, semi-circular, and very similar in shape and size to that of the first piece (Fig. 15d). This fact deserves careful consideration. Examination of the inflated endophallus in *Trechus* species shows that in some *Trechus* lineages, including those addressed by this paper, the most primitive structure of the endophallus armature consists of two branch-like similar pieces attached to the proximal end of the endophallus (becoming the distal end when inflated) (unpublished data I.B.). Their basal portions seem to be semi-circular in projection, but are in fact semi-spherical to ensure their firm position on the convex surface of the inflated endophallus (such a condition is typical of members of the *maculicornis* species group). Their evolution resembles a development of the right piece coupled with progressive reduction of the left one. In this case, the basal portion of the left piece becomes either much smaller or is incorporated (at least, topologically) in the basal portion of the right piece. This evolution of the endophallus armature seemed to take place independently in various *Trechus* lineages. If the above interpretation of the endophallus armature in *T. exhibitorius* sp. n. is correct, this species combines a rather primitive structure of the endophallus armature and aedeagus (including an average size of the aedeagus vs. hypertrophied in strongly evolved species) with some specialized external characters commonly found in mesophylous *Trechus*. It should likely be placed near the basal portion of the phylogenetic stem branching into the *montanellus*, *liopleurus*, *fuscus* and, probably, *osmanilis* and *maculicornis* species groups. However, monophyly of the above mentioned species groups needs to be tested using molecular methods.

Differential diagnosis. Two additional *Trechus* fossils were described from the Eocene Baltic amber: *T. balticus* and *T. eoanophthalmus* (Schmidt and Faille 2015, Schmidt et al. 2016). *Trechus exhibitorius* sp. n. is easily distinguished from the blind *T. eoanophthalmus* by the fully developed eyes and the much slender body. *T. balticus* is distinctly smaller (3.6 mm versus 4.4 mm in *T. exhibitorius* sp. n.), has a stouter body

with broader head and shorter elytra, larger and deeper impressed micro-meshes on disc of head and more markedly reduced external elytral striae.

Conclusions

Among the few Carabidae species described from Baltic amber on species level three species are now attributed to the genus *Trechus*. All these species are obligatory wingless characterized by markedly shortened metepisternae and fully rounded humeri, and it can therefore be presumed that these Eocene species lived on the forest floor along mountain slopes, just as it is known for the huge number of wingless trechine beetles today (Schmidt et al. 2016). This conclusion is in contradiction with the assumption of Alekseev and Alekseev (2016) that the amber forest was formed on a plain or slightly hilly area. Moreover, considering the low dispersal ability of the tiny wingless beetles within their mountainous environment, very small distributional areas can be expected for each of the species and therefore the contemporary existence of a large number of closely related allopatric *Trechus* species (Schmidt et al. 2016). This scenario makes the discovery of additional wingless *Trechus* species preserved in Baltic amber highly likely. Thus, trechine beetles gain interest especially with regard to phylogeographic studies including dating of the phylogeny of the respective group (e.g., Faille et al. 2013, 2014, 2015). In this respect the discovery of *T. exhibitorius* sp. n. is a stroke of luck since fossil external and internal characters of the male genitalia could be investigated for the first time and thus, the systematic position of this species within the megadiverse *Trechus* sensu lato can be more certainly assigned than it has been possible for the previously described fossils. In this respect one of the most relevant conclusions based on the finding of *T. exhibitorius* sp. n. is that the *Trechus* clade as verified by Faille et al. (2013) seems at least as old as the Eocene with a minimum age of approx. 35–50 Mya (Standke 2008). Therefore, a distinctly faster molecular clock in *Trechus* compared to other arthropods is highly improbable, as it was estimated by Contreras-Diaz (2007) in a study of *Trechus* endemic to the Canary Islands and subsequently used by Lhose et al. (2011) in an analysis of the quaternary distributional history of *Trechus* from the Alps.

Acknowledgments

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A new species of *Patania* from the Hainan Island, China (Lepidoptera, Crambidae)

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Abstract

Patania clava sp. n. is described from the Diaoluo Mountain of Hainan Island, China. The new species is distinguished from its most similar congener, *P. iopasalis* (Walker, 1859), by the following features: wingspan 33.0–35.0 mm (vs. 21.0–30.0 mm), ventral cilia of the male antenna as long as the diameter of flagellomere (vs. 1/4), the thick finger-like gnathos (vs. the short broad sheet-like), a long thick needle-like cornutus stretching out from (vs. embedded in) a cluster of spicular cornuti near apex. Images of adult and genitalia of the new species are provided.

Keywords

Diaoluo Mountain, Pyraloidea, Spilomelinae, taxonomy

Introduction

The genus *Patania* was established by Moore (1888) based on the type species, *Botys concatenalis* Walker, 1866, from Darjeeling, India. Warren described another new *Patania* species in 1896, *Patania verecunda* (Warren, 1896). Meanwhile, Hampson (1896) regarded *Patania* and *Pleuroptya* Meyrick, 1890 as synonyms of *Sylepta* Hübner, 1823. Hampson's opinion was followed by most researchers (Hampson 1898; Shibuya 1928, 1929; Klima 1939; Bae et al. 2008) except for Rose and Singh (1989) who published a new species of *Patania* separately. Inoue (1980) revalidated *Pleuroptya*, and some new

species, sub-species, and combinations of *Pleuroptya* were recorded since (Yamanaka 1995, 1998; Munroe 1983; Shaffer and Munroe 1989; Leraut 2005). Kirti and Gill (2007) considered *Patania* and *Pleuroptya* congeneric by comparing the morphological characters and male genitalia of their respective type species. The generic name *Pleuroptya* Meyrick, 1890 was suppressed as subjective synonym of *Patania* Moore, 1888 by Kirti and Gill (2007).

Globally, there are approximately 50 described species of *Patania* (Kirti and Gill 2007; Li et al. 2009, Nuss et al. 2003–2015), 28 species being recorded in China (Li et al. 2009; Xu 2015). In this paper, *Patania clava* sp. n., collected from the Diaoluo Mountain, Hainan Island, China, is described as new to science.

Materials and methods

Specimens were collected by 250-W high-pressure mercury lamps. They were hand-collected alive and killed by ethyl acetate. The type specimens of *Patania* species deposited in the Natural History Museum of London (NHM) have been examined by corresponding author. All the type specimens of the new species are deposited in the College of Plant Protection, Southwest University, Chongqing, China (SWUCPP).

The terminology mainly follows Kristensen (2003) and Slamka (2013).

Genitalia preparation followed the procedure of Li and Zheng (1996), using boiling 10% NaOH solutions to digest internal tissues; after careful cleaning and removal of scales and content of coelom, genitalia were examined, compared, and described before being mounted on microscope slides by the first author. The images of the adults were taken with a digital camera (Nikon P7700). The illustrations of the genitalia were prepared with a digital camera Leica DFC 450 attached to a digital microscope Leica M205 A.

Taxonomic account

Patania clava sp. n.

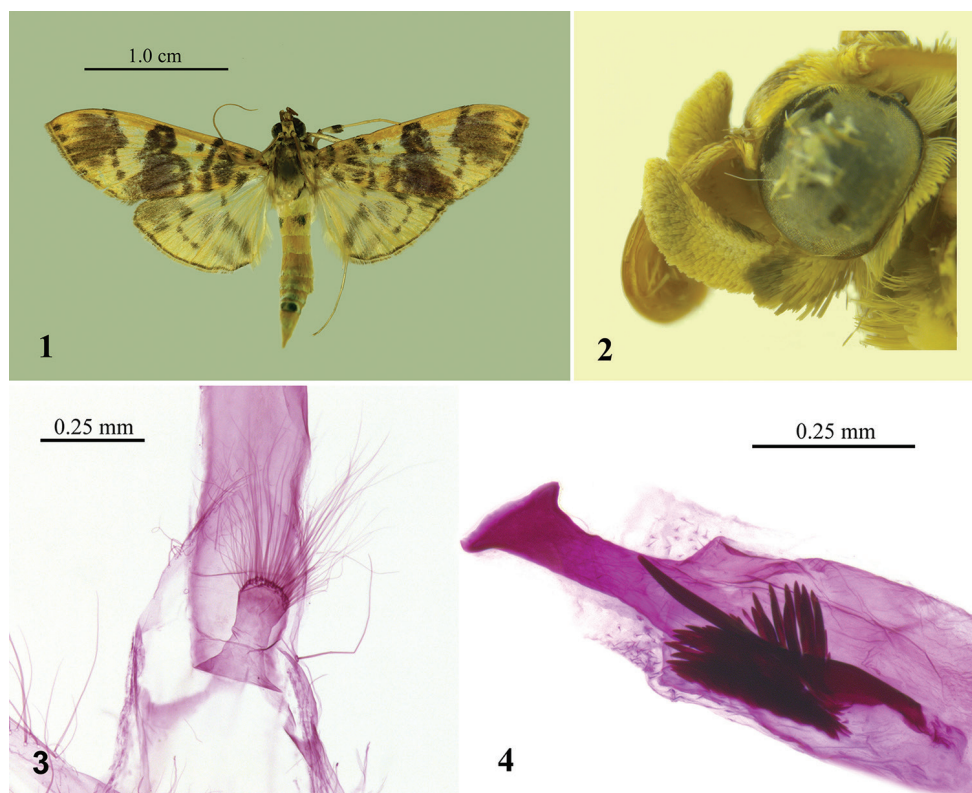
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Figs 1–4, 9–10

Holotype. male, China, Hainan, Mt. Diaoluo, 109.87°E, 18.72°N, 900 m, 23.V.2014, leg. Li-Jun Xu & Dan Xu, pinned, slide number XD15056. Original label: “Hainan, Diaoluo Mountain, vocational village, 900 m, 23.V.2014, Li-jun Xu & Dan Xu”.

Paratype. 1 female, same data as holotype, slide number XD15050.

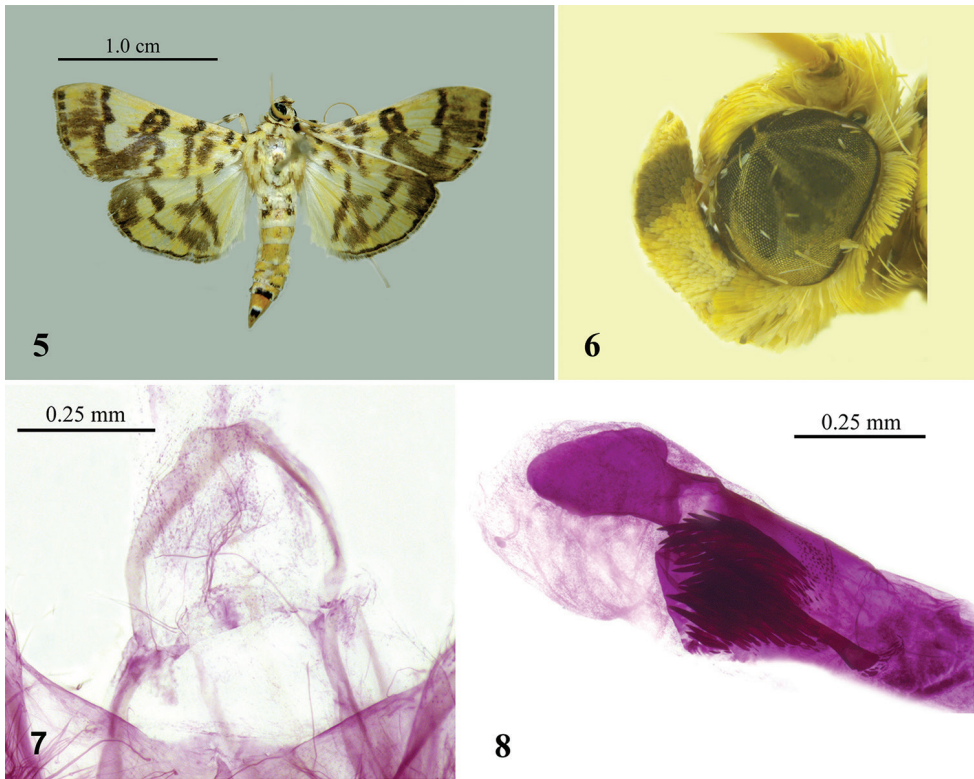
Diagnosis. This species can be distinguished by the wingspan of 33.0–35.0 mm (Fig. 1); the brown patch near base of the labial palpus (Fig. 2), the male antenna with ventral cilia nearly as long as the diameter of flagellomere; in the male genitalia by the thick finger-like gnathos bearing long setae on the apex (Fig. 3), the phallus with a dor-



Figures 1–4. *Patania clava* sp. n., Holotype. **1** Adult **2** Head **3** Gnathos **4** Cornuti.

sally protruding sclerotized structure with a slant nailhead-like apex, and a long thick needle-like cornutus stretching out from a cluster of spicular cornuti near apex (Fig. 4).

Description. Adult (Figs 1–2). Wingspan 33.0–35.0 mm. Body pale yellow. Antenna pale yellow dorsally, orange ventrally. Male antenna with ventral golden cilia nearly as long as the diameter of flagellomere. Labial palpus upturned, pale yellow with a brown patch near base. Maxillary palpus small, pale yellow. Patagium pale yellow, with large fuscous spots. Tegula pale yellow and fuscous. Forewing pale yellow, with fuscous lines, spots and patches; a spot at inner edge near basal line; a large elliptical patch between basal line and antemedial line; orbicular stigma distinct; discoidal stigma reniform, its posterior part overlapping postmedial line partly; a large patch outspread between discoidal stigma and inner margin; postmedial line oblique inward from costa, excurved vertically from M_1 to CuA_2 , with a distinct punctiform pattern between M_2 and CuA_2 , then sharply incurved along CuA_2 as an indistinct line before curving towards the dorsum; a large patch between anterior half of postmedial line and marginal line, marginal line consisting of a line of spots. Hindwing pale yellow; discoidal stigma brown; a brown slant stripe below end of discal cell and a pale brown fuzzy band beyond it; postmedial line oblique inward from costa, excurved vertically from M_1 to CuA_2 , with a distinct punctiform pattern between M_2 and CuA_2 , then sharply

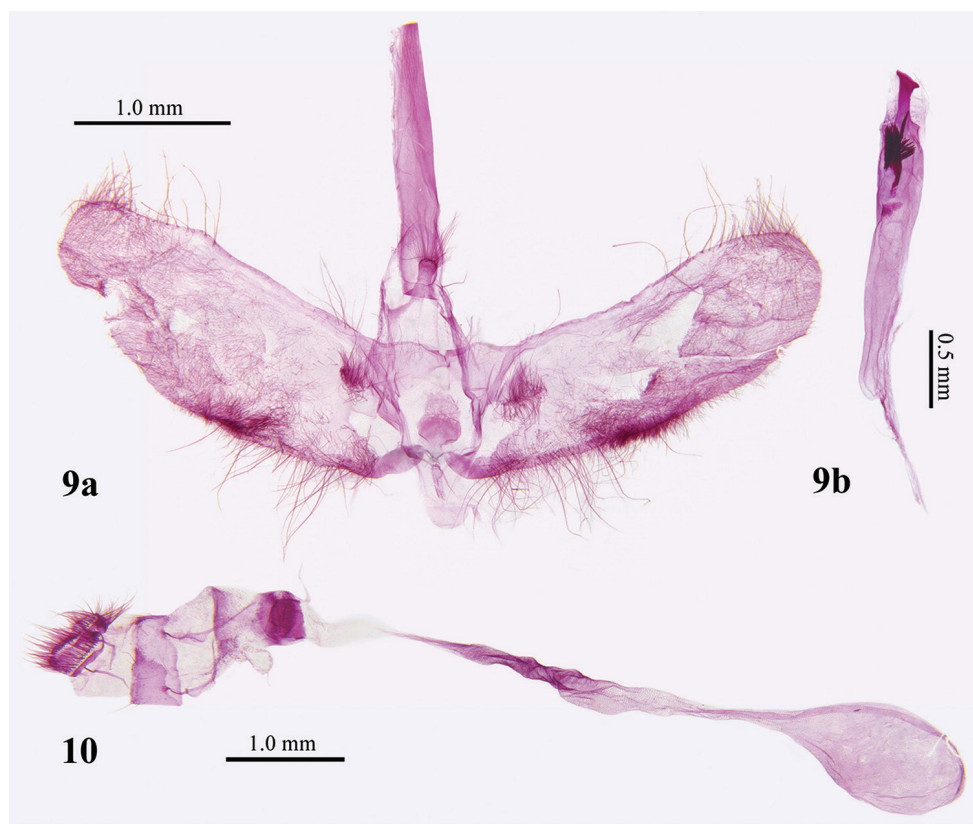


Figures 5–8. *Patania iopasalis* (Walker). **5** Adult **6** Head **7** Gnathos **8** Cornuti. Slide number XLJ14083.

incurved along CuA_2 as an indistinct line before curving towards the dorsum; marginal line fuscous; brown blot near apical angle. Fringes of forewing and hindwing white at base, pale brown terminally. Fore coxa yellow, with two big black spots; femur yellow except for black distal end; tibia pale yellow with distal half black, tibial comb orange. Mid femur white, with a black spot near centre; tibia pale yellow, black distally, a black spot near the base. Hind femur white, with a brown spot near the distal end; tibia white, somewhat pale brown near the base. Abdomen orange dorsally; anterior edge of 2nd segment with two lateral black spots flanking the centre, 7th segment with a big black spot separated slightly at the center; pale yellow ventrally.

Male genitalia. (Figs 3–4, 9). Uncus triangular, blunt on posterior margin. Gnathos thick finger-like, apex circularly widened and dorsally studded with long thin simple setae. Valva ligulate. Fibula near base of valva, flat, triangular, with long dense setae. Transtilla triangular, connected medially, with sparse setae. Saccus oblong, with the anterior apex rounded. Juxta ovate. Phallus cylindrical, with a dorsally protruding sclerotized structure with a slant nailhead-like apex, a long thick needle-like cornutus stretching out from a cluster of spicular cornuti.

Female genitalia. (Fig. 10). Apophysis anterioris about 1.5 times length of apophysis posterioris, triangular extension near base unilaterally. Ductus bursae about



Figures 9–10. Genitalia of *Patania clava* sp. n. **9** Male, Holotype **a** Without phallus **b** Phallus, Holotype **10** Female, paratype.

4 times length of corpus bursae, middle ductus bursae widened, area posterior of widening slightly sclerotized; ductus seminalis originating at posterior end of ductus bursae. Corpus bursae elliptical, without signum. Both ductus bursae and corpus bursae densely studded with tiny granules.

Etymology. The specific name is derived from the Latin *clavus* (nail), in reference to the nail head-like apex of sclerotized structure of the phallus.

Distribution. This species is only known from the Diaoluo Mountain of Hainan Island, China.

Natural history. Unknown except that the moths fly late May and are attracted to light. The habitat in which this species has been collected is located at an altitude of 900 m. The vegetation of the habitat is a blend of shrubs, conifer trees and broad leaved trees.

Remarks. The most similar congener to *P. clava* sp. n. is *Patania iopasalis* (Walker, 1859). However, the wingspan of *P. iopasalis* is smaller with 21.0–30.0 mm (Fig. 5); the labial palpus has no brown patch near the base but a big brown patch near the apex (Fig. 6), the male antenna has ventral cilia about one-fourth the length of the diameter

of flagellomere; in the male genitalia the short broad sheet-like gnathos lacks setae on the apex (Fig. 7), the phallus has an ovate sclerotized structure protruding from apex, and a long thick needle-like cornutus is embedded in a cluster of spicular cornuti (Fig. 8). *Patania clava* sp. n. is also similar to *Patania obfuscalis* (Yamanaka, 1998) in appearance. The latter can, however, be distinguished by its serrated postmedial line of forewing; in the male genitalia by the middle costa slightly inflated and bearing a cluster of setae, the vestigial gnathos, the board-like sclerotized, apically tapering structure protruding from apex, and a short broad thorn-like cornutus near a cluster of spicular cornuti.

The new species is only known from Diaoluo Mountain of Hainan Island at present. *Patania iopasalis* is widely distributed in south Asia, southeast Asia, east Asia, including Hainan Island, China, the Caroline Islands, New Guinea, Australia and Guatemala (Hampson 1896, 1898; Klima 1939; Xu 2015). *Patania obfuscalis* is distributed in Nepal and some areas of China, excluding Hainan Island.

Acknowledgements

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***Prognathodes basabei*, a new species of butterflyfish (Perciformes, Chaetodontidae) from the Hawaiian Archipelago**

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Abstract

A new species of the butterflyfish genus *Prognathodes* is described from specimens collected at a depth of 55–61 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. This species has been observed by mixed-gas divers and from submersibles at depths ranging from 45–187 m throughout the Hawaiian Archipelago, with shallower sightings in the Northwestern Hawaiian Islands and deeper in the Main Hawaiian Islands. It is similar to *P. guezei* (Maugé and Bauchot 1976) from the western Indian Ocean, and at least one other undescribed species of *Prognathodes* from Palau, differing from these species in the number of soft dorsal-fin rays, size of head, and body depth. There are also differences in the life color, and a substantial genetic difference from the Palauan species (d » .08 in mtDNA cytochrome oxidase I).

Keywords

Mesophotic Coral Ecosystem, Closed-Circuit Rebreather, Endemic, Papahānaumokuākea Marine National Monument

Introduction

The genus *Prognathodes* Gill, 1862 (type species *Chelmo pelta* Günther, 1860 = *Chaetodon aculeatus* Poey, 1860) currently includes eleven valid species: seven from the Atlantic, two from the tropical eastern Pacific, and two from the Indian Ocean and western Pacific. Pyle and Chave (1994) first reported the presence of a species of this genus in the Hawaiian Islands at depths of 106–187 m, based on video and observations from research submersibles operated by the Hawaii Undersea Research Laboratory (HURL). They noted its similarity to *P. guezeti* (Mauge and Bauchot 1976), a species then known only from the two type specimens collected at a depth of 80 m off Réunion Island in the western Indian Ocean.

While conducting an exploratory dive using a mixed-gas closed-circuit rebreather off the south shore of O‘ahu (Main Hawaiian Islands) on 17 May 1998, the senior author (RLP) observed (but was unable to collect) a group of three *Prognathodes* near an undercut limestone ledge at a depth of 114 m. Two weeks later (30 May 1998), with the assistance of Peter K. Basabe, RLP collected the first specimen of this species at a depth of 120 m near Kealakekua Bay on the Kona coast of the island of Hawai‘i (TenBruggencate 1998). The following day he collected several more individuals at a depth of 115 m near the site of the observation of 17 May (Allen et al. 1998). All of the collected individuals were brought to the surface alive and maintained in captivity. Unfortunately, when they eventually died, only one was preserved, and it was too badly deteriorated to serve as a type specimen.

In the years that followed, several more individuals of this species were collected from depths of 115–125 m around O‘ahu by mixed-gas rebreather divers. All were maintained in aquaria until their deaths, but none were properly preserved as suitable type specimens. On 27 April 2007, RLP collected two individuals of a similar species of *Prognathodes* at a depth of 116 m at Palau (Republic of Belau), in the western Pacific. Although some color differences between the Palauan and Hawaiian fishes were noted, the authors felt it was necessary to obtain specimens of the Hawaiian population for comparison of morphological and genetic characters before determining whether they are the same species.

In August of 2009, after the establishment of the Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands, the U.S. National Oceanic and Atmospheric Administration (NOAA) began a series of annual surveys of Mesophotic Coral Ecosystems (MCEs) within the Monument using mixed-gas diving technology. During the first of these surveys, the authors collected a group of three individuals of the unidentified *Prognathodes* at a depth of 61 m off the SW side of Pearl and Hermes Atoll. Unfortunately, tissue samples taken from these specimens were misplaced, so it was not possible to make genetic comparisons with the Palauan population.

Finally, in September of 2015, the authors were able to collect three more specimens at the same site off Pearl and Hermes Atoll where the three specimens had been collected in 2009, and obtain additional tissue samples for genetic analyses. Based on

an examination of both morphological and genetic characters of the six Hawaiian specimens, as well as comparisons with the two specimens from Palau and *Prognathodes guezeti*, we can now confirm that the Hawaiian population represents a new species, distinct from both *P. guezeti* and the undescribed Palauan species. We herein describe the Hawaiian population as the new species, *Prognathodes basabei*.

Methods

Specimens were collected with hand nets during deep dives using mixed-gas, closed-circuit rebreathers. Additional observations, videos and images of this species were made from the two *Pisces* submersibles operated by the Hawaii Undersea Research Laboratory (HURL, at the University of Hawai'i), and by mixed-gas rebreather divers in the Main Hawaiian Islands and Northwestern Hawaiian Islands.

Standard length (SL) was measured from the tip of the snout to the caudal-fin base. Total length (TL) was measured from the tip of the snout to the posterior edge of the caudal fin. Head length was measured from the tip of the snout to the posterior-most edge of the fleshy flap near the upper end of the gill opening. Body depth is the greatest depth of body measured as a vertical from the ventral edge of the abdomen to the upper edge of scaled fleshy sheath of the dorsal fin (typically from about fourth or fifth dorsal spine). Width of the body is the maximum width. Snout length is the distance from the tip of the snout to the closest point on the bony orbit. Predorsal length is the distance from the tip of the snout to the angle formed by the scaled fleshy sheath at the insertion point of the first dorsal-fin spine, when erected. Preanal length is the distance from the tip of the snout to angle formed by the scaled fleshy sheath at the insertion point of the first anal-fin spine, when erected. The base of the dorsal fin is measured from the extreme base of the first dorsal-fin spine to the extreme base of the last dorsal-fin soft ray. The base of the anal fin is measured from the extreme base of the first anal-fin spine to the extreme base of the last anal-fin soft ray. Orbit diameter is the maximum diameter of the bony orbit. Interorbital width is the width of the bony interorbital space. Depth of the caudal peduncle is the least depth. Pelvic-fin spine length was measured from the extreme base of the pelvic-fin spine to its distal tip. Pelvic fin length was only measured on specimens with intact filamentous extensions of the first pelvic-fin soft ray, and represents the length of that ray from its extreme base to the distal tip of the filamentous extension. Length of spines and soft rays of dorsal and anal fins were measured from the extreme base to the most distal tip. Caudal fin length was defined as the difference between TL and SL. Pectoral fin length was measured as the longest fin ray, from its extreme base to its distal tip.

The last dorsal- and anal-fin soft rays are branched to the base and were counted as a single ray. Caudal-fin ray counts include small unsegmented and rudimentary rays. Pectoral-fin ray counts include first and last unsegmented rays. Pored lateral-line scale counts include only those scales with pores. Scale-row counts above and below lateral line to origins of dorsal and anal fins (respectively) include small truncate scales at bases

of respective fins. Vertebral counts include the first vertebra fused to the skull, and the last vertebra fused to the hypural plate.

All counts and measurements except vertebrae were made directly from specimens. Measurements were made using dial calipers with ± 0.05 mm precision. Lengths of dorsal- and anal-fin spines and soft rays were made with the aid of a bright light transmitted from behind the fins to reveal the position of their extreme bases. Vertebral counts were made from x-radiographs.

Head length, depth of body, width of body, snout length, predorsal length, preanal length, length of dorsal-fin and anal-fin bases, orbit diameter, interorbital width, caudal peduncle depth, and lengths of fin spines and rays are expressed as percent of SL. Counts and measurements for paratypes, if different from the holotype, are presented in parentheses after the value for the holotype.

The holotype and three paratypes have been deposited at the Bernice Pauahi Bishop Museum fish collection, Honolulu (BPBM), and paratypes have been deposited at the California Academy of Sciences fish collection, San Francisco (CAS), and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Tissue samples were obtained from the holotype and two paratypes (CAS 242132 and USNM 440272). DNA barcodes (cytochrome c oxidase I; COI) were sequenced following the protocol described in Copus et al. (2015). GenBank accession numbers and Barcode of Life Database (BOLD) identifiers for DNA sequences are presented along with museum catalog numbers for type material and non-type specimens.

Taxonomy

Prognathodes basabei Pyle & Kosaki, sp. n.

<http://zoobank.org/A843AA98-2312-4E9E-B1EC-E28B5478085E>

Figs 1–5

Prognathodes sp. 1; Allen et al. 1998:250.

Prognathodes “*basabei*”; Randall 2007:291.

Type locality. Northwestern Hawaiian Islands, Pearl and Hermes Atoll, southwest side, “Prognathodes Point”, 27.7641°N, 175.9859°W.

Holotype. BPBM 41290, female, GenBank KX783257, Barcode of Life PROBA001-16, 93.4 mm SL, Northwestern Hawaiian Islands, Pearl and Hermes Atoll, southwest side, “Prognathodes Point”, 27.7641°N, 175.9859°W, 61 m, 13 September 2015, R. L. Pyle, aboard NOAA ship *Hi‘ialakai* (Cruise: HA-15-05), hand nets, under limestone ledge (ancient seashore). Collected as part of a group of three associated individuals (along with CAS 242132 and USNM 440272).

Paratypes. BPBM 41285, 3 specimens: 97.7–106.3 mm SL, same location, habitat, collector, vessel and collecting method as holotype, 55 m, 17 August 2009, Cruise: HI-09-06; CAS 242132, GenBank KX783255, Barcode of Life PROBA003-16, 102.5



Figure 1. Holotype of *Prognathodes basabei* (BPBM 41290), collected at a depth of 61 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

mm SL, same location, depth, habitat, collector, vessel, cruise and collecting method as holotype, 14 September 2015; USNM 440272, GenBank KX783256, Barcode of Life PROBA002-16, same data as holotype.

Non-type specimen. BPBM 38441, 82 mm SL, Hawaiian Islands, O‘ahu, south shore, 116 m, 31 May 1998, R. L. Pyle, hand nets, along limestone ledge (specimen died in captivity and partially deteriorated).

Diagnosis. A species of *Prognathodes* (*sensu* Smith et al. 2003) distinguished by the following combination of characters: dorsal-fin soft rays 21 or 22; anal-fin soft rays 16 or 17; head 2.63–2.80 in SL; body depth 1.58–1.69 in SL; pelvic-fin spine length 3.63–4.07 in SL; color in life pale yellow dorsally fading to white ventrally (sometimes entirely white) with three black bands with narrow white margins on each side of the body, the first band originating at and including the first dorsal-fin spine, extending diagonally to the eye and continuing horizontally as an orangish brown stripe from the eye to the tip of the snout, the second band originating at and including the fourth to sixth dorsal-fin spines, extending vertically at a slightly posterior angle to the ventral surface of the abdomen just anterior to the anus, tapering slightly and curving slightly posteriorly below the pectoral fin, and the third band originating at and including the last four to five dorsal-fin spines and first four to five dorsal-fin soft rays, extending vertically at a slightly posterior angle to and including the first several anal-fin soft rays, a narrow orange band on the dorso-posterior margin of the operculum, extending ventrally the posterior angle of the operculum, an oblong orange spot with some dark pigmentation on the upper

one-third of the pectoral-fin axis, pelvic fins white on the spine and anterior one-third of fin, and bright orange on the posterior two-thirds of fin, a bright orange submarginal band with narrow white posterior margin extending along the posterior margins of the soft portions of the dorsal and anal fins, and continuing across the caudal peduncle.

Description. Dorsal fin XIII (XII in two paratypes), 21 (22 in one paratype), last soft ray branched to base; anal fin III, 16 (17 in one paratype), last soft ray branched to base; pectoral-fin rays 16 (15 in one paratype); pelvic-fin rays I, 5; principal branched caudal rays 15, upper procurent unbranched caudal rays 4, lower procurent unbranched caudal rays 3; pored lateral-line scales 26 (24–28); scale rows above lateral line to origin of dorsal fin 10 (11 in all but one paratype); scale rows below lateral line to origin of anal fin 24 (21–27); gill rakers on upper limb 6, on lower limb 9 (10 in one paratype); vertebrae 24.

Body deep, the depth 1.58 (1.61–1.69) in SL, and compressed, the width 4.05 (3.80–4.33) in depth; head length 2.63 (2.65–2.80) in SL; snout produced, its length 2.35 (2.19–2.62) in head; orbit diameter 3.59 (3.50–3.83) in head; interorbital slightly convex, the least bony width 4.18 (3.85–4.28) in head; least depth of caudal peduncle 4.33 (4.00–4.33) in head.

Mouth small, the upper jaw 2.77 in head, slightly diagonal, the gape forming an angle of about 20° to the horizontal, the upper jaw slightly protruding; teeth in jaws densely setiform, the longest 7.8 in orbit diameter; nostrils anterior to the eye horizontally in line with the top of the iris, the anterior in a short membranous tube with a well-developed posterior flap, the posterior slightly larger, ovate, with a low fleshy rim. Lower edge of lacrimal smooth; margin of preopercle finely serrate; margins of other opercular bones smooth.

Lateral line forming a broad arc, ending below the base of the third to fifth soft dorsal ray and within the second black band on the body. Scales ctenoid, moderately large on body except for chest and near origins of dorsal and anal fins, where small; head fully scaled except anterior portions of both jaws and around nostrils, the scales on the head small; scales on fleshy sheath surrounding base of dorsal and anal fins moderately large anteriorly and proximally, reducing in size posteriorly and distally; scales on caudal peduncle and covering base of caudal fin small.

Origin of dorsal fin slightly posterior to upper end of gill opening, its base 1.45 (1.43–1.52) in SL; first dorsal-fin spine the shortest, its length 3.09 (2.49–3.68) in head; second dorsal-fin spine 1.27 (1.42–1.98, broken in one paratype) in head; third dorsal-fin spine the longest, its length 0.93 (0.94–1.11, broken in one paratype) in head; fourth dorsal-fin spine nearly as long as the third, its length 1.04 (1.03–1.13, broken in one paratype, deformed in one paratype) in head; fifth dorsal-fin spine shorter, its length 1.20 (1.14–1.23, broken in one paratype) in head; dorsal-fin spines progressively shorter posteriorly, the last 1.80 (1.80–2.06) in head; membranes between anterior dorsal-fin spines deeply incised, progressively less so posteriorly; first dorsal-fin soft ray the longest, approximately the same length as the last dorsal-fin spine, 1.80 (1.70–1.88) in head, dorsal-fin soft rays progressively shorter posteriorly; first anal-fin spine the shortest, its length 2.54 (2.44–3.10) in head; second anal-fin spine the longest, its length 1.31 (1.16–1.31) in head; third anal-fin spine 1.52 (1.39–1.62) in head;



Figure 2. Paratype of *Prognathodes basabei* (BPBM 41285-1), collected at a depth of 55 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

first anal-fin soft ray the longest, its length 1.35 (1.39–1.62) in head, anal-fin soft rays progressively shorter posteriorly; caudal fin slightly convex with a slight concavity at the mid-line, its length 1.79 (1.83–2.00) in head; pectoral fins 1.37 (1.26–1.43) in head; pelvic spine 1.38 (1.36–1.51) in head; first soft ray of pelvic fin with a filamentous extension, its length 1.08 (1.19, broken in all but one paratype) in head.

Color in life as in Figures 1–5. Body pale yellow dorsally fading to white ventrally and on the thorax and lower head (color of body sometimes lacking pale yellow coloration); three prominent black bands on each side of the body with narrow white margins, the first band originating at and including the first dorsal-fin spine, extending diagonally to the eye and continuing horizontally as an orangish brown stripe from the eye to the tip of the snout, the second band originating at and including the fourth to sixth dorsal-fin spines, extending vertically at a slightly posterior angle to the ventral surface of the abdomen just anterior to the anus, tapering slightly and curving slightly posteriorly below the pectoral fin, and the third band originating at and including last four to five dorsal-fin spines and first four to five soft dorsal rays, extending vertically at a slightly posterior angle to and including the first several anal soft rays, the bands becoming dark orangish brown distally on the dorsal fin; a narrow orangish brown stripe extending from the dorsal side of the snout broadening dorsally on the nape to a point just above the interorbital space, becoming darker dorsally; a narrow orange band on the dorso-posterior margin of the operculum, extending ventrally to the posterior angle of the operculum, an oblong orange spot with some dark pigmentation on

the upper one-third of the pectoral-fin axis; pelvic fins white on the spine and anterior one-third of fin, and bright orange on the posterior two-thirds of fin; a bright orange submarginal band with narrow white posterior margin extending along the posterior margins of the soft portions of the dorsal and anal fins and continuing across the caudal peduncle; caudal fin and pectoral fins translucent.

Color in alcohol similar to life color, except body a uniform dull yellow, bands dark brown, and orange areas pale brown.

A single juvenile, about 25 mm SL, was observed by RLP at a depth of 120 m during a dive off Pearl Harbor, O'ahu on 16 August 1998. The general body shape and color pattern were the same as for adults.

Morphometric data for selected characters of type specimens are provided in Table 1.

Distribution. *Prognathodes basabei* has been observed or collected at depths of 45–187 m at several locations throughout the Hawaiian Archipelago, including both the main Hawaiian Islands (Hawai'i, O'ahu, Penguin Banks) and the Northwestern Hawaiian Islands (NWHI; French Frigate Shoals, Lisianski, Pearl and Hermes Atoll, Midway Atoll, Kure Atoll). No observations of this species were made during 61 submersible dives or eight mixed-gas rebreather dives to appropriate depths at Johnston Atoll (Randall et al. 1985; Wagner et al. 2014), nor has any similar fish been observed or collected anywhere in the central or eastern Pacific. Thus, it appears that *P. basabei* is endemic to the Hawaiian Archipelago (although further exploration of MCEs in nearby regions may yet reveal its presence elsewhere). This is consistent with the observation that fish assemblages on deep coral reefs have proportionally more endemic species than on shallow reefs (Pyle 1996, Kane et al. 2014, Kosaki et al. 2016).

Habitat. Pyle and Chave (1994: 92) described the habitat for this species based on videotaped observations from submersibles as follows:

Eighteen (56%) of the observed [fish] were in areas of basalt substrata (e.g., basalt talus, blocky lava, lava tubes and pillows, basalt boulders), 13 (41 %) were in limestone habitats (primarily limestone holes and ledges), and one fish was sighted on a large (2-m diam.) water pipe. Four of the fish were in the vicinity of an unidentified antipatharian coral, three near Cirrhipathes spiralis (Linnaeus), and one near Antipathes dichotoma Pallas.

Subsequent observations of this species by divers and submersible dives, totaling several dozen individuals mostly off O'ahu and various sites within the NWHI, were all found in association with limestone ledges and discontinuities representing ancient shorelines (Figures 3–5). In almost all cases, the fish were found underneath, inside of, or in close proximity to small undercut overhangs or caves, often swimming upside-down in association with the roof of the overhangs and caves. There are no obvious associations with other species, such as antipatharian corals, other corals and sessile invertebrates, or particular fish species; although certain other fish species, such as the anthias *Odontanthias fuscipinnis* (Jenkins, 1901) and the wrasse *Bodianus sanguineus* (Jordan & Evermann, 1903), tend to occupy the same depth and habitat.

Etymology. We take great pleasure in naming this species *basabei*, in honor of Peter K. Basabe, long-time diver, aquarium fish collector and resident of Kona, Hawai'i, both for his role in the collection of the first specimen of this new species in 1998,



Figure 3. *Prognathodes basabei* at a depth of approximately 55 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by G. McFall.

and more generally for his extensive contributions and assistance to many researchers (especially the authors) in the ichthyological community.

Morphological comparisons. *Prognathodes basabei* appears to be most similar in color and morphology to an undescribed *Prognathodes* species collected at a similar depth in Palau. These two species differ from each other in number of dorsal-fin soft rays (21–22 for *basabei*, compared to 17–19 for the Palau species) and anal-fin soft rays (16–17, compared to 15). *P. basabei* also has a smaller head (2.63–2.80 in SL, compared to 2.48–2.49 in SL), deeper body (1.58–1.69 in SL, compared to 1.71–1.76 in SL), and shorter pelvic-fin spine (3.63–4.07 in SL, compared to 4.18–4.46 in SL) than the Palau species. The two species also differ in certain aspects of life color. The anterior edge of the second black band of the Palau species originates at the third dorsal-fin spine, whereas this band originates on the fourth dorsal-fin spine in *P. basabei*. Moreover, both of the dark bands on the Palau species are proportionally broader dorsally, tapering more substantially ventrally than in *P. basabei*. Also, the orangish coloration on the pelvic fins and posterior margin of the soft dorsal and anal fins of the Palau species are much darker and brownish than in *P. basabei*.

P. basabei is also similar in color and morphology to *P. guezei* from the western Indian Ocean. It differs from that species morphologically in number of dorsal-fin soft rays (21–22 for *basabei*, compared to 20 for *guezei*), head size (2.63–2.80 in SL, compared to 2.47–2.48 in SL), body depth (1.58–1.69 in SL, compared to 1.87–1.95 in SL), and shorter pelvic-fin spine (3.63–4.07 in SL, compared to 4.21–4.33 in SL). There are also

Table 1. Morphometric and meristic data for selected characters of type specimens of *Prognathodes basabei*. Values of morphometric data (other than TL and SL) are represented as % of SL.

	Holotype	Paratypes				
Morphometrics	BPBM 41290	BPBM 41285-1	BPBM 41285-2	BPBM 41285-3	CAS 242132	USNM 440272
Sex	Female	Female	Male	Male	Male	Male
Total length (TL) in mm	113.2	125.5	123.1	117.8	122.5	119.6
Standard length (SL) in mm	93.4	106.3	102.2	97.7	102.5	99.8
Head length	38	36	38	38	36	38
Body depth	63	59	60	62	62	62
Body width	16	14	16	14	16	16
Snout length	16	16	17	17	15	14
Predorsal length	48	43	44	42	45	46
Preal length	75	75	77	73	76	77
Base of dorsal fin	69	66	66	68	68	70
Base of anal fin	33	32	31	33	32	30
Orbit diameter	11	9.8	11	9.8	9.9	11
Interorbital Width	9.1	9.1	8.8	9.0	9	10
Caudal Peduncle Depth	8.8	9.0	8.7	8.9	8.5	8.7
Pelvic Spine	28	25	25	26	26.3	25
Pelvic Fin	35	-	-	32	-	-
First Dorsal Spine length	12	12	13	10	14	11
Second Dorsal Spine length	30	25	broken	27	18	23
Third Dorsal Spine length	41	38	broken	39	38	34
Fourth Dorsal Spine length	37	35	damaged	37	broken	33
Fifth Dorsal Spine length	32	32	31	31	broken	31
Last Dorsal Spine length	21	19	21	21	17	18
Longest Dorsal Ray length	21	21	22	21	21	20
First Anal Spine length	15	13	12	13	15	13
Second Anal Spine length	29	29	30	29	31	29
Third Anal Spine length	25	26	23	26	24	26
Longest anal ray length	28	26	24	26	23	23
Caudal fin length	21	18	20	21	20	20
Pectoral fin length	28	25	27	27	28	27
Meristics						
Dorsal Spines	XIII	XIII	XII	XII	XIII	XIII
Dorsal rays	21	21	22	21	21	21
Anal Spines	3	3	3	3	3	3
Anal Rays	16	16	17	16	16	16
Pectoral Rays	16	15	16	16	16	16
Caudal Rays	22	22	22	22	22	22
Pored lateral line scales	26	28	25	24	24	27
Dorsal scale rows	10	10	11	11	11	11
Ventral scale rows	24	27	21	23	24	25
Gill rakers	6+9	6+9	6+9	6+10	13	13

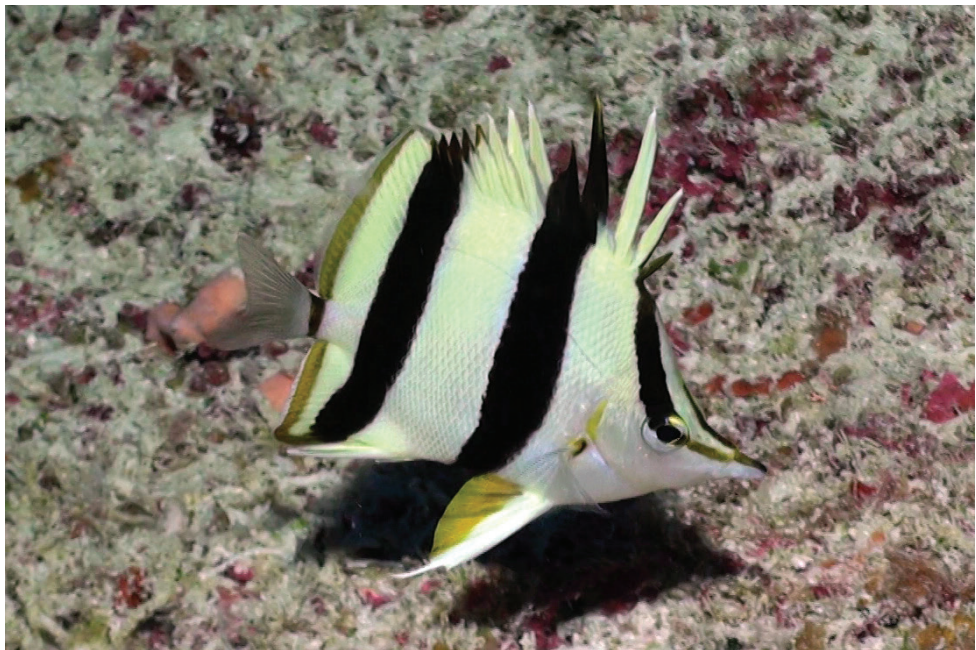


Figure 4. *Prognathodes basabei* at a depth of 90 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.



Figure 5. A group of three *Prognathodes basabei* at a depth of 90 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

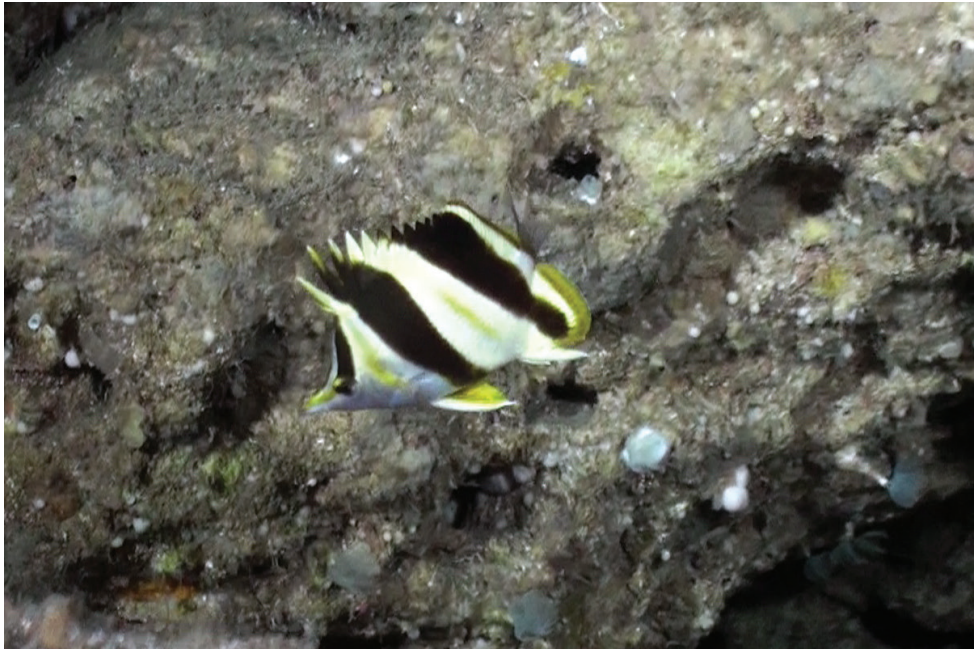


Figure 6. *Prognathodes guezei* at a depth of 117 m off Sodwana Bay, South Africa. Photo by R. L. Pyle.

several differences in life color between the two species. In particular, *P. guezei* (Figure 6) has more pronounced and discrete yellow bars on the body between the black bands, compared with more diffuse and paler yellow in *P. basabei*. As with the Palau species, the anterior edge of the second black band of the *P. guezei* originates at the third dorsal-fin spine, whereas this band originates on the fourth dorsal-fin spine in *P. basabei*, and the two black bands on the body of *P. guezei* taper even more substantially than they do in the Palau species, with the dorsal end of the posterior band in *P. guezei* covering the last five dorsal-fin spines, compared with the last four dorsal-fin spines on *P. basabei*. Also, the orangish coloration on the pelvic fins and posterior margin of the soft dorsal and anal fins of *P. guezei* are much paler and yellowish than in *P. basabei*.

Genetic comparisons. Genetic comparisons provide another compelling justification for regarding *P. basabei* as distinct from the Palau species. The vertebrate mtDNA barcode (cytochrome oxidase I) sequences obtained from the holotype and two paratypes of *P. basabei*, compared to specimens of *Prognathodes* sp. collected in Palau, reveal 8% uncorrected sequence divergence. This is consistent with species-level divergences in other fish taxa (Johns and Avise 1998, Bellwood et al. 2004, Fessler and Westneat 2007, Randall and Rocha 2009, Rocha 2004, Rocha et al. 2008). The accepted mtDNA clock rate of approximately 2% per million years in fishes (Bowen et al. 2001, Reece et al. 2010) indicates divergence between these species on the order of 4 million years.

No tissue samples or DNA sequences have been reported for *P. guezei*, but given the geographic distributions of *P. guezei* in the western Indian Ocean, the Palau species, and *P. basabei*, we anticipate that the genetic divergence between *P. basabei* and *P. guezei* will prove to be even deeper than that between *P. basabei* and the Palau species.

Discussion. *Prognathodes basabei* is an example of the conspicuous new fish species that have been discovered on deep coral reefs over the past two decades, mostly involving the use of modern mixed-gas closed-circuit rebreather diving technology (Pyle 1996, 2000). There has been increased attention focused on mesophotic coral ecosystems (MCEs), coral-reef habitat at depths of approximately 30–150 m in tropical regions worldwide (Hinderstein et al. 2010, Baker et al. 2016).

One particularly unusual characteristic of this species is the tendency for it to be found in groups of three individuals. Although Pyle and Chave (1994) reported that most videotaped observations from submersibles involved apparent pairs or solitary individuals, in most cases these observations were incidental to the research focus on the submersible dives, so no concerted effort was made to determine the total number of individuals at each sighting. Every observation of adults of this species by the authors during mixed-gas dives in both the main Hawaiian Islands and NWHI (nearly two dozen instances), as well as observations by RLP during several submersible dives off south O‘ahu in 2011, involved groups of three individuals; the only exception was the solitary juvenile observed by RLP in 1998. Only two individuals of the Palau species were observed together, and none of the approximately ten individuals of *P. guezeti* observed by RLP at depths of 115–120 m off Sodwana Bay in 2011 were found in a group of three. Butterflyfishes (Chaetodontidae) in general are known to display a variety of social and mating systems, including monogamous pairs, harems, and schools (Reese 1975, Yabuta and Berumen 2013). Territoriality and the distribution of food resources are important determinants of these social systems (Hourigan 1988, Pratchett et al. 2013). Groups of three individuals as a primary social grouping have not been noted in other chaetodontid species. The six type specimens of *P. basabei* were found as two groups of three individuals. In both cases, the groupings included a single female and two males. More samples are necessary to determine whether such associations represent loose social groupings, territorial behavior, a mating system, or coincidence.

Another interesting aspect of this new species is the strikingly similar color pattern it shares with both the Palau species, and with *P. guezeti*, in contrast to the deep genetic divergence that exists between the Hawaiian and Palauan specimens. It will be interesting to compare the genetics of *P. guezeti* once tissue samples can be obtained, and as previously noted, we expect the genetic divergence to be similarly deep. A more thorough analysis and discussion of genetic comparisons between *P. basabei* and the Palauan species will be included in the forthcoming description of the latter species.

Prognathodes basabei is the twelfth recognized member of the genus, a group generally inhabiting deeper habitats than most other chaetodontid species. Nalbant (1995) suggested that the group may have an antitropical distribution, which would apply to *P. basabei* in Hawai‘i and *P. guezeti* in the southwest Indian Ocean, but less so in light of the undescribed species in Palau. One potential explanation for such disjunct distributions is that these are relics of a once more widely distributed genus (paleoendemics; Bellwood and Meyer 2009). Another, perhaps more likely explanation is that the dearth of mesophotic exploration across the tropical central and western Pacific and Indian Oceans has left significant gaps in our understanding of *Prognathodes* distribution, and that additional populations and species await discovery.

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