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Unravelling the moons: review of the genera *Paratetilla* and *Cinachyrella* in the Indo-Pacific (Demospongiae, Tetractinellida, Tetillidae)

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Abstract

Paratetilla bacca (Selenka, 1867) and *Cinachyrella australiensis* (Carter, 1886) occur in a broad range of marine environments and are allegedly widely distributed species in the Indo-Pacific. We coin the term 'moon sponges' for these species as they are spherical in shape with numerous porocalices resembling the lunar surface. Both species have a complex taxonomic history with high synonymization, in particular by Burton (1934, 1959). An examination of the junior synonyms proposed by Burton (1934, 1959) was conducted to establish the validity of the names. More than 230 specimens from Naturalis Biodiversity Center were reviewed that belong to the genera *Paratetilla* and *Cinachyrella* from marine lakes, coral reefs, and mangroves in Indonesia. The aim of the current study was to untangle the taxonomic history, describe the collection of moon sponges from Indonesia, and develop a key. We extensively reviewed the taxonomic literature as well as holotypes of most of the species synonymized by Burton. The taxonomic history of

Paratetilla spp. and *Cinachyrella australiensis* showed some cases of misinterpreted synonyms, misidentifications, and lack of detailed descriptions for some species. The conclusion of the revision is that there are three valid species of *Paratetilla* (*P. arcifera*, *P. bacca*, and *P. corrugata*) and four valid species of *Cinachyrella* (*C. australiensis*, *C. porosa*, *C. paterifera*, and *C. schulzei*) in Indonesia. This is furthermore corroborated by molecular work from previous studies. *Paratetilla arcifera* Wilson 1925 and *C. porosa* (Lendenfeld, 1888) are resurrected. A full review of taxonomic history is provided as well as a key for identification of moon sponges from Indonesia. All species are sympatric and we expect that there are undescribed species remaining within the Tetillidae from the Indo-Pacific. Our current review provides the framework from which to describe new species in the genera *Paratetilla* and *Cinachyrella* from the Indo-Pacific.

Keywords
anchialine systems, coral reef, mangrove, marine lake, Porifera

Introduction

Moon sponges include two good examples of allegedly widely distributed species in the Indo-Pacific: *Paratetilla bacca* (Selenka, 1867) and *Cinachyrella australiensis* (Carter, 1886). They are conspicuous dwellers of a broad range of marine environments, including coral reefs, rocky shores, and coastal mangroves, as well as landlocked marine systems called marine lakes (e.g. Hooper et al. 2000, de Voogd and Cleary 2008, de Voogd et al. 2009, Becking et al. 2011). We use the term 'moon sponges' as these species are spherical in shape with numerous porocalices resembling the lunar surface and colored various shades of yellow, orange and brown. This common name has now been adopted by different authors (e.g., Szitenberg et al. 2013). Naturalis Biodiversity Center houses hundreds of moon sponges with a great diversity in morphology that were collected in Indonesia from 2006–2011 with the aim to survey the sponge biodiversity.

The genera *Paratetilla* and *Cinachyrella*, belong to the family Tetillidae, suborder Spirophorina, order Tetractinellida, class Demospongiae. As spirophorids, they are characterized by the presence of rugose sigmaspires (van Soest and Hooper 2002). Similar to most tetillids, their globular shape is composed of triaenes and oxeas arranged in a radiate skeleton. Recent revisions of the order and the family have been compiled in the Systema Porifera by van Soest and Hooper (2002) and van Soest and Rützler (2002), respectively. Although 26 nominal genera have been described, only ten valid genera are recognized, which are differentiated by the presence of cortical structures, specialized pore-sieves (porocalices) and composition of the complementary spicules (Rützler 1987, van Soest and Rützler 2002, Carella et al. 2016) (Table 1). The principal types of spicules of this family are: 1. *Megascleres*, oxeas and triaenes (pro-, plagio, ortho, and anatriaenes), and 2. *Microscleres*, microxeas and sigmaspires. Identification at species level is mainly based on the geometry and size range of all spicule types and presence/absence of triaenes (van Soest 1977, Rützler 1987, Rützler and Smith 1992, Lazoski et al. 1999, de Voogd and van Soest 2007, Carella et al. 2016).

The species *P. bacca* and *C. australiensis* share an obscure taxonomic history, including incomplete descriptions, intermingled identifications, and tens of different species synonymized (see synonyms of *C. australiensis* in Burton 1934: 523, and *P. bacca* in Burton 1959: 200). Therefore, we expected that a detailed revision would reveal species lumped together under both taxonomic entities. The aims of this paper are two-fold: (1) to review the taxonomic history of the genus *Paratetilla* and the species *Cinachyrella australiensis*, and (2) to identify and describe the different *Paratetilla* and *Cinachyrella* species from Indonesia in the Naturalis Biodiversity Center collection.

Materials and methods

Taxonomic revision

Literature from 1867 to date was reviewed in order to compile the descriptions of the 11 nominal species for the genus *Paratetilla* Dendy, 1905. The *Cinachyrella* species revision was based on the literature cited by Burton (1934), who lumped together 16 nominal species as synonyms of *Cinachyrella australiensis* (Carter, 1886). The World Porifera Database WPD (van Soest et al. 2018) was used as a valuable guide for consulting the valid species and addressing the literature review. Type material and reference collections deposited at the American Natural History Museum (**AMNH**) in New York, at the Smithsonian Institution National Museum of Natural History (**NMNH**) in Washington D.C., the Natural History Museum (**NHMUK**, formerly **BMNH**) in London, and the Naturalis Biodiversity Center in Leiden (**RMNH**), were examined. The majority of the holotypes were studied for the current research; the ones we did not review were either unavailable or the description of the text was clear and comprehensive.

Sampling

Individuals of *Cinachyrella* spp. and *Paratetilla* spp. were collected by snorkelling and SCUBA diving during expeditions to Bali (2003), Bunaken (Sulawesi, 2006), Pulau Seribu (Java, 2005), Raja Ampat (Papua, 2007), Berau (East Kalimantan, 2008), and Ternate (Moluccas, 2009). Sampling was systematically achieved in marine habitats such as coral reefs and mangroves, and within marine lakes (Raja Ampat and Berau). Specimens were photographed *in situ* and notes made on morphological and ecological features such as color, size, depth, and substrate. A total of 237 specimens were collected and preserved in ethanol 70%; an additional 11 specimens from the Naturalis Biodiversity Center collection from Indonesia and elsewhere were reviewed as well as 20 type specimens. Table 2 provides an overview of sample numbers per species and Suppl. material 1 (Table S1) provides full collection details per sample.

Table 1. Valid genera of Tetillidae Sollas, 1888 and principal characteristics used to distinguish them. (+) present, (-) absent. (AN) Antarctic, (AT) Atlantic, (CA) Caribbean, (IP) Indo-Pacific. Modified from Rützler (1987), van Soest and Rützler (2002), Carella et al. (2016). Number of valid species consulted at the World Porifera Database (van Soest et al. 2018; accessed 04 Jun 2018).

Genus	Cortex (reinforced by)	Porocalices (shape)	Accessory spicules	Valid species	Distribution
Tetilla Schmidt, 1868	–	–	–	54	AT, CA, IP
Craniella Schmidt, 1870	+ (minute smooth oxea)	–	–	42	AN, AT, CA, IP
Cinachyra Sollas, 1886	+ (minute smooth oxea)	+ (flask)	–	3	AN, AT
Paratetilla Dendy, 1905	–	+ (hemi-spherical or narrow)	+ (calthrop-like)	5	IP
Cinachyrella Wilson, 1925	–	+ (hemi-spherical)	–	42	AT, CA, IP
Amphitethya Lendenfeld, 1907	+ (amphiclads)	–	+ (amphiclads)	2	IP
Fangophilina Schmidt, 1880	–	+ (differentiated, narrow)	–	4	AT, CA, IP
Acanthotetilla Burton, 1959	+ (megacanthoxea)	+ (narrow)	+ (megacanthoxea)	7	AT, CA, IP
Antarctotetilla Carella et al., 2016	pseudocortex (oxeas loosely arranged)	–	–	4	AN
Levantiniella Carella et al., 2016	–	+ (small, rounded)	–	1	AN

Table 2. Number of samples reviewed per taxon. The column "Indonesia" refers to all samples recently collected in Indonesia (years 2006–2011), "other material" to older specimens in museum collections from Indonesia or other countries; "types" refer to type specimens of valid species and junior synonyms.

Species	Indonesia	Other material	Types	Total
Paratetilla bacca	38	4	4	46
Paratetilla arcifera	21	4	1	26
Cinachyrella australiensis	117	3	9	129
Cinachyrella porosa	47	–	5	52
Cinachyrella paterifera	14	–	1	15
Total	237	11	20	**268**

Morphology

Radial and superficial histological sections of sponges were hand cut with a surgical blade; tissue sections were dried on a heat-plate more than 1 hour, mounted in Durcupan ACR resin and examined using light microscopy. Spicule preparations were made by dissociation of a fragment of sponge in sodium hypochlorite and consecutive washing steps, three times in distilled water, twice in 70% ethanol, and suspending in 95% ethanol. The dissociated spicules were dropped onto glass microscope slides, dried and mounted in Durcupan for light microscopy. Spicule preparations for Scanning Electron Microscopy (SEM) were made after two extra washing steps with 95% ethanol. Spicule dimensions and character definitions follow Rützler (1987), Rützler and Smith (1992) and van Soest and Rützler (2002). Spicule dimensions are based on 25 measurements for type specimens and for reference material. Data are given as minimum–mean–maximum in the text.

Results and discussion

Systematic descriptions

Order Astrophorida
Family Tetillidae Sollas, 1888
Genus *Paratetilla* Dendy, 1905

The genus *Paratetilla* was established by Dendy (1905) based on the presence of a layer of modified triaenes (calthrops-like). Eleven nominal species have been described with this diagnostic character: *Stelletta bacca* Selenka, 1867, *Tethya merguiensis* Carter, 1883, *Tetilla ternatensis* Kieschnick, 1896, *Tetilla amboinensis* Kieschnick, 1898, *Tetilla violacea* Kieschnick, 1898, *Tetilla rubra* Kieschnick, 1898, *Paratetilla cineriformis* Dendy, 1905, *Paratetilla eccentrica* Row, 1911, *Paratetilla aruensis* Hentschel, 1912, *Paratetilla corrugata* Dendy, 1922, and *Paratetilla lipotriaena* de Laubenfels, 1954. The revision of the taxonomic history of these species reveals that some ambiguous statements have been made (Table 3).

Recent checklists and biodiversity studies in the Indo-Pacific have only recorded *P. bacca*, following Burton's taxonomic decision in 1959 to synonymize all nominal *Paratetilla* species except *P. lipotriaena*. Two exceptions were found in the literature, the review by Desqueyroux-Faundez (1981) of Topsent's material (1897) from Amboina Island, who identified it as *Paratetilla merguiensis*, and the inventory of sponges from South China Sea by Hooper et al. (2000), where *P. arcifera* was listed in addition to *P. bacca*.

Table 3. Historic milestones in the taxonomy of the genus *Paratetilla* Dendy, 1905. Asterisk (*) indicates misidentification of *Cinachyrella* specimens as *Paratetilla*.

Year	Author	Descriptions / Statements
1867	Selenka	Description of *Stelletta bacca*. Selenka's material was collected in Samoa Island and due to the presence of triaenes this species was associated to the family Corticatae (now Astrophorida: Ancorinidae). The description is brief but the sketches included are illustrative, including "Vierstrahler" (=calthrop-like) spicules. Sigma-like spicules are neither mentioned in the description nor drawn in the figures. Currently, type specimen could not be located.
1883	Carter	Description of *Tethya merguiensis*, including sigmaspires, calthrop-like spicules, oxeas and triaenes and their respective measurements and sketches.
1884	Ridley	In his monograph, Ridley kept *Stelletta bacca* in the genus *Stelletta*. The diagnostic characteristic for *Stelletta* for his decision was the absence of bacillar or acerate flesh-spicules. He also noticed that the Samoan *Stelletta* "is probably a *Tethya*, as its stellate agrees with the large stellate of that genus, and its forks are rare and probably foreign to the sponge" (see footnote in Ridley 1884, p. 472).
1887	Vosmaer	Statement about *Stelletta bacca* mentioning that it can hardly belong to *Stelletta* genus without further argumentation.
1888	Sollas	Establishment of Family Tetillidae, type genus *Tetilla* Schmidt, 1868. Sponges in this family have sigmaspires (microscleres) and slender protriaenes (megascleres) as diagnostic characters. In this family Sollas included the species *Craniella (Alcyonium) cranium* Müller (1789), species under the genus *Tethya* by Lamarck (1815) and Gray (1867), and species within the group Tethyina Carter (1875). Carter's material of *Tethya merguiensis* was redescribed and transferred to the genus *Tetilla*, as *Tetilla merguiensis*. *Tethya cranium* var. *australiensis* was redescribed as *Tetilla* (?) *australiensis*. Many other species were also described by Sollas within this family.

Year	Author	Descriptions / Statements
1896*	Kieschnick	Description of *Tetilla ternatensis* based on material from Ternate Island (Indonesia); he mentioned "Vierstrahler" (=calthrops).
1897	Lindgren	*Tethya merguiensis* Carter, 1873 as junior synonym to *Stelletta bacca*, based on a comment by Sollas (1888, p. 205) of his monograph: "*Stelletta bacca*, Selenka, which Vosmaer correctly excludes from *Stelletta*, while Ridley includes it, is as mounted preparations show, identical with *Tetilla merguiensis*, Carter". However, neither Ridley (1884) nor Vosmaer (1887) supported their inclusion or exclusion of the species with any description of the Selenka specimen, but apparently, they were based merely on the published description. It is remarkable that Sollas in the same monograph (1888) identified the Challenger specimens as *Tetilla merguiensis*, including for the first time this genus and species under the family Tetillidae due to the characteristic sigmaspires.
1898*	Lindgren	Redescription of *Tetilla bacca*, with *Tetilla merguiensis* as junior synonym, including material of Torres Straits (North Australia), two localities at Java (Indonesia) and Carter's specimens from Mergui Archipelago. Size range for each station is shown for oxeas and triaenes, arguing that larger spicules are found to the west while smaller sizes to the east. Redescription of *Tetilla ternatensis* based on Java material. It is remarkable that he mentioned the presence of numerous microxeas (240 × 4 µm) and sigmaspires 24 µm.
1898	Kieschnick	Description of *Tetilla amboinensis*, *Tetilla violacea* and *Tetilla rubra* from Amboina Island, all of them with "Vierstrahler" (=calthrop-like) spicules. *T. amboinensis* and *T. violacea* with calthrops in a layer below the surface of the sponge; while the former is characterized by smaller number of triaenes and bundles of oxeas up to the surface of the sponge, the latter by very abundant triaenes, bundles of oxeas projected over the surface of the sponge, and a typical violet color. *T. rubra* separated from the other two by its brick-red color and with calthrops mainly on the basal part of the sponge.
1900	Kieschnick	Extensive description of the same three new species.
1900*	Thiele	Redescription of *Tetilla ternatensis* Kieschnick, 1896. Thiele drew attention on the misidentification of *T. ternatensis* by Lindgren (1898), clarifying that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886). Moreover, Thiele proposed that *T. ternatensis*, as well as Kieschnick's species *T. amboinensis*, *T. violacea* and *T. rubra*, should be junior synonyms of *T. bacca* arguing that *T. bacca* shows a large morphological variability.
1900*	Kirkpatrick	Extension of the geographical range of *T. bacca* and *T. ternatensis* to Christmas Island. *T. bacca* specimens were described with identical spicules to Lindgren's (1898) material from Java. *T. ternatensis* also similar to Lindgren's (1898) material of *T. ternatensis.*
1903*	Lendenfeld	Designation of a new species *Tetilla lindgreni* based on Lindgren's specimens (1898) from Java and Kirkpatrick's specimens (1900) from Christmas islands, both identified as *T. ternatensis* without calthrops and with small microxeas. Thus, Lendenfeld concluded that those specimens belong to a new species (*T. lindgreni*) because they did not show calthrops as in the original description of Kieschnick (1896). Junior synonyms for *Tetilla bacca*, including the material of Selenka, Carter, Sollas, and Kirkpatrick. *T. ternatensis* and *T. violacea* described by Kieschnick and recorded by Thiele (1900) were also included as junior synonyms of *T. bacca*. *Tetilla amboinensis* Kieschnick (1898) was transferred to genus *Cinachyra* and *T. rubra* was established as its junior synonym.
1905	Dendy	The genus *Paratetilla* was erected within the family Tetillidae, based on the presence of calthrop-like spicules. Thus, *Tetilla bacca* is transferred to *Paratetilla* genus, including their junior synonyms *T. merguiensis,* as well as the three Kieschnick's species *T. ternatensis*, *T. amboinensis* and *T. violacea* based on Thiele's annotation (1903). Description of *Paratetilla cineriformis* based on material from Gulf of Manaar (Sri Lanka). Although the spicules shown by *P. cineriformis* resembled *T. merguiensis*, Dendy (1905) argues that the general aspect of the sponge was quite different as porocalices have no specific arrangement and the layer of calthrops was more irregular than in Carter's species.
1907	Lendenfeld	The genus *Amphytethya* was created based on its characteristic amphitriaenes. Many other species under the genus *Cinachyra*, *Fangophilina* and *Tetilla* were described.
1911	Row	Description of *Paratetilla eccentrica* from the Red Sea. Cortical triaenes (= calthrop-like) with high modifications, in some cases even becoming into "walking-sticks".
1912	Hentschel	Description of *Paratetilla aruensis* from Aru- and Kei- Islands (Indonesia), with characteristic amphitriaenes. Relocation of the genus *Amphitethya* Lendenfeld, 1907 as a junior synonym of *Paratetilla*.

Year	Author	Descriptions / Statements
1922	Dendy	All nominal species with calthrop-like spicules were synonymized to *Paratetilla bacca*, except for *P. aruensis* Hentschel, 1912. Two varieties were identified: *P. bacca* var. *violacea* based on *T. violacea* characteristics, and the new variety *P. bacca* var. *corrugata* from Diego Garcia in the Indian Ocean.
1925	Wilson	Description of *Paratetilla arcifera* from Philippines. Wilson recognized as valid four additional species: *P. bacca* (Selenka, 1867), *P. amboinensis* (Kieschnick, 1898), *P. cineriformis* (Dendy, 1905) and *P. eccentrica* (Row, 1911). However, he also commented that *P. bacca* is a comprehensive variable species, as previously proposed by Thiele (1903) and later established by Dendy (1922). Establishment of *Cinachyrella* genus. Validation of the genus *Amphitethya* Lendenfeld, 1907.
1954	de Laubenfels	Description of *Paratetilla lipotriaena* from Micronesia (West-Central Pacific), characterized by variable calthrop-like spicules and the absence of triaenes, and relatively similar to *P. eccentrica* Row, 1911.
1959	Burton	All nominal species described within the genus *Paratetilla* were included as synonyms of *P. bacca*, except for *P. lipotriaena*.
1987	Rützler	Review of Family Tetillidae, including seven genera (all except for *Fangophilina*). Nomination of *Paratetilla cineriformis* as type species of genus *Paratetilla*.
1994	Hooper and Wiedenmayer	Review of all *Paratetilla bacca* synonyms based on Burton (1959) taxonomic decision.
2002	van Soest and Rützler	Review of the eight genera included within family Tetillidae. Although *Paratetilla* characters were a combination of two descriptions, a paragraph in the discussion included the size differences between both Selenka's and Carter's material (*Stelletta bacca* and *Tethya merguiensis*, respectively). The origin of calthrop-like spicules was also discussed as probably modified plagiotriaenes resembling some *Cinachyrella* species, arguing the possibility of the inclusion of the widespread species *Paratetilla bacca* within *Cinachyrella* genus.
2008	van Soest and Beglinger	Redescription of *Paratetilla corrugata* based on material from the Gulf of Oman, and giving validity to the variety *P. bacca* var. *corrugata* by Dendy (1922). The presence of trichodragmata is characteristic of this species.
2018	van Soest et al. (WPD)	Junior synonyms for *Paratetilla bacca* (Selenka, 1867): *Tetilla bacca* (Selenka, 1867), *Stelletta bacca bacca* Selenka, 1867, *Tethya merguiensis* Carter, 1883, *Stelletta bacca* Selenka, 1887, *Tetilla violacea* Kieschnick, 1896, *Tetilla ternatensis* Kieschnick, 1896, *Tetilla rubra* Kieschnick, 1898, *Paratetilla cineriformis* Dendy, 1905, *Paratetilla eccentrica* Row, 1911, *Paratetilla arcifera* Wilson, 1925. Other accepted *Paratetilla* species in WPD: *Paratetilla amboinensis* (Kieschnick, 1898), *Paratetilla aruensis* Hentschel, 1912, *Paratetilla corrugata* Dendy, 1922, *Paratetilla lipotriaena* de Laubenfels, 1954.
2018	This study	*Paratetilla* species from Indonesia: *Paratetilla bacca* (Selenka, 1867), *Paratetilla arcifera* Wilson, 1925, and *Paratetilla corrugata* Dendy, 1922 (not observed in our Indonesian material), *Paratetilla aruensis* Hentschel, 1912 with amphitriaenes, it is suggested to be transferred to *Amphitethya*.

***Paratetilla bacca* (Selenka, 1867)**

Figs 1, 2

Stelletta bacca Selenka, 1867: 569, pl. xxxv, figs 14, 15 (type not found, material from type locality seen).

Tethya merguiensis Carter, 1883: 366, pl. xv, figs 6–8; Carter, 1887: 80 (type seen).

Tetilla merguiensis; Sollas, 1888: 14; Topsent, 1897: 441, pl. xviii, fig. 4–5, pl. xxi figs 34.

Tetilla ternatensis Kieschnick, 1896: 527. Thiele, 1900: 39, pl. ii, fig 13; Not *Tetilla ternatensis* Lindgren, 1898: 329 pl. 17, fig. 14; pl. 19, Fig. 25 a-e, a', b'.

Tetilla bacca; Lindgren, 1897: 485; Lindgren, 1898: 328; Thiele, 1900: 39, pl. ii, fig 13; Kirkpatrick, 1900: 132 (material seen); Lendenfeld, 1903: 19.

Tetilla amboinensis Kieschnick, 1898: 10.
Tetilla violacea Kieschnick, 1898: 15.
Tetilla rubra Kieschnick, 1898: 18.
Paratetilla cineriformis Dendy, 1905: 97, pl. iii, fig. 7 (type seen).
Paratetilla eccentrica Row, 1911: 306, pl. xxxv, fig. 1, pI. xxxvi, fig. 8 (type seen).
Cinachyra amboinensis; Hentschel, 1912: 331.
Paratetilla bacca; Dendy, 1922: 21 (material seen).
Paratetilla bacca var. *violacea*; Dendy, 1922: 22, pl. 1, fig. 6 (material seen).
Paratetilla lipotriaena de Laubenfels, 1954: 244, text figure no. 168 (type seen).

Material examined. Neotype ZMA.POR.13029, Tutuila Island, American Samoa. Holotype of first junior synonym *Tethya merguiensis* Carter, 1883 (?) NHMUK 1894.11.16.17, Mergui Archipelago, Myanmar. Holotype NHMUK 1954.2.23.106 Gulf of Manaar, Sri Lanka (as *Paratetilla cineriformis* Dendy, 1905). NHMUK unreg. type, Crossland Collection, Red Sea (as *Paratetilla eccentrica* Row, 1911). NHMUK 1898.12.20.19, Flying Cove Fish, Christmas Islands (as *Tetilla bacca=Paratetilla merguiensis* Kirkpatrick, 1900). NHMUK 1921.11.7.10, Sealark Sponges, Indian Ocean (as *Paratetilla bacca* var. *violacea*). Holotype USNM 23049, East part of Lagoon, Ponape, Caroline Islands, 1 Aug 1949 (as *Paratetilla lipotriaena* de Laubenfels, 1954). **INDONESIA**. Bali, *Bali reef,* RMNH.POR.1732; East Kalimantan, *Berau reef,* RMNH.POR.11281, RMNH.POR.11282, RMNH.POR.11283; *Kakaban Lake,* RMNH.POR.11289, RMNH.POR.11290, RMNH.POR.11291, RMNH.POR.11292, *Haji Buang Lake,* RMNH.POR.11284, RMNH.POR.11287, RMNH.POR.11288, RMNH.POR.11285, RMNH.POR.11286, RMNH.POR.3515. Sulawesi, *Bunaken reef,* RMNH.POR.3100, RMNH.POR.3106, RMNH.POR.3115; *Bunaken mangrove,* RMNH.POR.2819; *Spermonde Archipelago,* ZMA.POR.13221. Ternate, *Ternate reef,* RMNH.POR.5344, RMNH.POR.5467. West Papua, *Wallace Lake,* RMNH.POR.11293, RMNH.POR.11294, RMNH.POR.11295; *Outside Wallace Lake,* RMNH.POR.11296, RMNH.POR.11297, RMNH.POR.11298; *Ctenophore Lake,* RMNH.POR.11302; *Gam Mangrove,* RMNH.POR.11299, RMNH.POR.11300, RMNH.POR.11301; *Outside Ctenophore Lake,* RMNH.POR.11303; *Big Caulerpa Lake,* RMNH.POR.11304; *Gam Island,* RMNH.POR.11305, RMNH.POR.11306, RMNH.POR.11307.

Other material: East Kalimantan, *Makassar Straits,* ZMA.POR.1735, Siboga Expedition, St. 81. Singapore, RMNH.POR.2506, RMNH.POR.2512. Western Indian Ocean, ZMA.POR.20673.

Description. ***External morphology.*** Globular sponges, size between 1 and 5 cm in diameter. Surface hispid due to the projecting spicules, covered by numerous porocalices (Figure 1A, B). Porocalices are bowl-shape, with oval to circular apertures, up to 5 mm in diameter and 7 mm deep, numerous, scattered uniformly over the surface of the sponge; in preserved material, some porocalices are closed and only a narrow aperture is visible giving to the sponge a rough appearance. External color generally brown when alive, which turns dark brown in ethanol, choanosome light brown, and

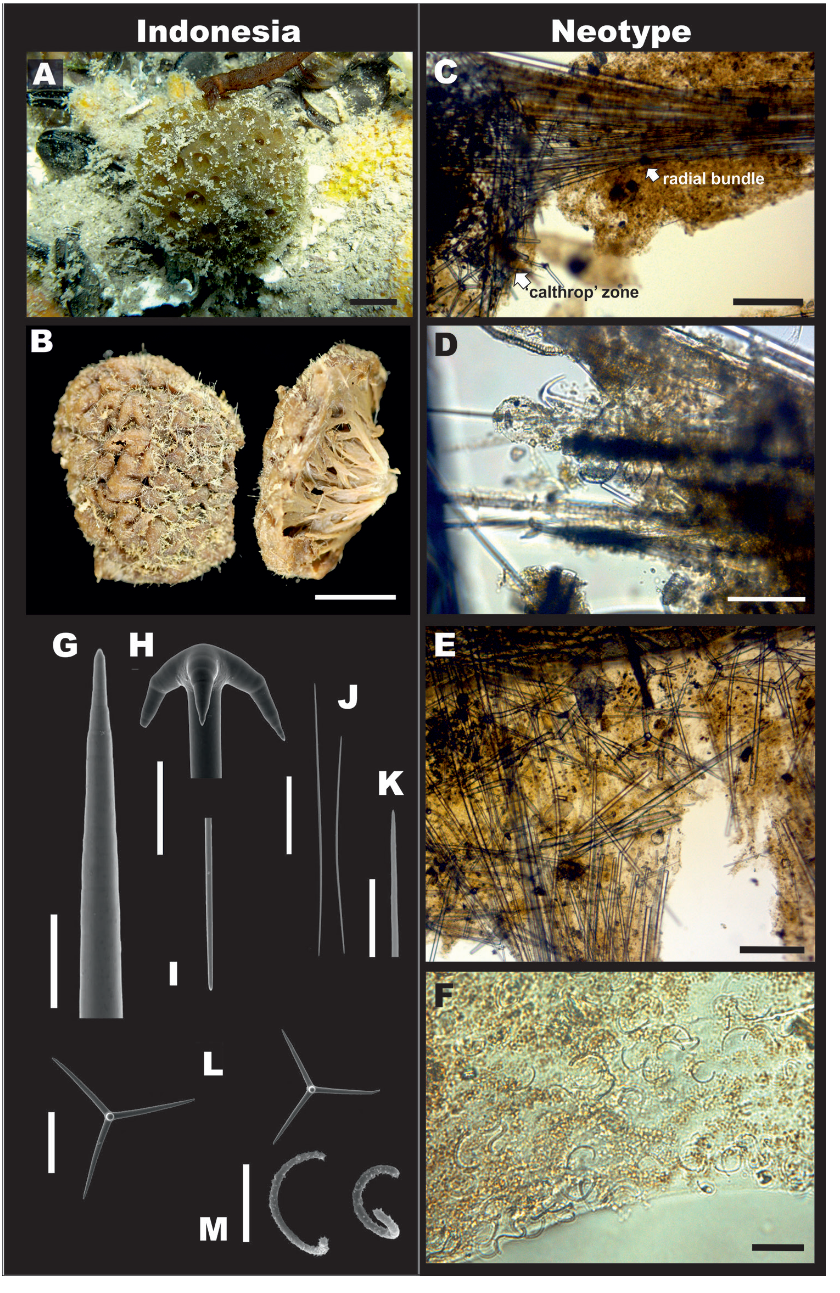

Figure 1. *Paratetilla bacca*. **A,B, G-M** RMNH.POR.11292, Kakaban Lake, Indonesia (left side). **C–F** neotype material of *Paratetilla bacca*, ZMA.POR.13029, Tutuila Island, American Samoa (right side). **A** *in situ* photograph **B** preserved specimen showing the porocalices (scale bar 1 cm) **C** skeleton showing oxeas, calthrops and triaenes **D** skeleton, showing anatriaenes, protriaenes and oxeas **E** skeleton showing detail of the 'calthrop' zone **F** sigmaspires **G** oxea, detail **H, I** anatriaene, cladus and rhabd end, **J** thin microxea, **K** thin microxea, detail **L** calthrops **M** sigmaspires. Scale bars: 200 µm (**A–C**); 40 µm (**D, G–I**); 200 µm (**E**); 20 µm (**F**); 50 µm (**J**); 10 µm (**K, M**); 100 µm (**L**).

has a 'dried out' appearance (Figure 1B). Numerous small dark brown granules in the tissue (Figure 1E, F). Consistency compact.

Skeleton. No cortex. Choanosomal skeleton composed by bundles of oxeas and triaenes radiating from a central core, ⅕–⅓ of the diameter of the sponge.

Megascleres. The material from Indonesia and the type of *P. merguiensis* have oxeas 850–3085.3–4500 µm × 5–41.5–65 µm (Table 4, Figure 1E, D, G). Anatriaenes always present, very abundant, cladi stout, slightly flattened, 20–62.6–100 µm × 12.5–48.3–75 µm, long rhabd up to 6000 × 20 µm, tapering to dimensions much less than 1µm (Figure 1H, I). Protriaenes scarce in some specimens and absent in the type specimen; when present, they exhibit two different shapes, the first one with stouter and smaller cladi, the second one with thinner and larger cladi (27.5–53.9–100 µm × 37.5–107.4–200 µm × 2.5–6.5–12.5 µm), rhabd up to 5850 × 15 µm, tapering to dimensions of < 1 µm. Calthrop-like short shafted triaenes, three types are distinguished with a wide range of sizes, from which measurements are shown as a general summary (Table 4). In the first type, four rays can be recognized (Figure 1L), three of them large, up to 400–600 µm, and a short one up to 100 µm long, usually pointing down to the centre of the body; the second one with three rays, almost the same length up to 400 µm; and the third one with three rays as well, two of them in an angle of 180° and the other one perpendicular, 50–100 µm. The calthrops are located immediately below the surface, constituting more or less a homogeneous layer.

Microscleres. Thin microxeas are common, 105–241.6–380 µm, 'hair-like'. Sigmaspires, 10–14.1–25 µm, C-S shape (Figure 1F, M).

Ecology. Inhabiting all studied environments in Indonesia, including coral reefs, mangroves, and marine lakes. Specimens more common in mangroves and marine lakes, and shallow reef flats where they are usually found on dead coral skeletons or coral rubble, typically ranging in depth from 0–5m. No specimens collected from deeper coral reefs in Indonesia.

Distribution. *Paratetilla bacca* has a wide distribution in Indonesia, including Berau, Bunaken, Raja Ampat, Ternate, and Java. Previous Indonesian records are from Spermonde Archipelago (Becking et al. 2006), Berau (de Voogd et al. 2009), and Raja Ampat (Becking 2008). In addition, this species has also been reported from Seychelles Islands (Thomas 1973), Southwest Madagascar (Vacelet et al. 1976), Zanzibar (Pulitzer-Finali 1993), Thailand (Putchakarn 2007), Singapore (Lim et al. 2008), Philippines (Longakit et al. 2005) (Figure 2).

Remarks. We did not succeed in locating the holotype of *Paratetilla bacca*, despite concerted effort. At this time, we assume that the type is no longer available. The description by Selenka of the type specimen does not mention the occurrence of any type of sigmaspires. It is a matter of speculation whether Lindgren (1897) actually examined Selenka's material to propose Carter's species *Paratetilla merguensis* as a junior synonym to *Paratetilla bacca*, or whether he based his conclusion merely on the literature. It is possible that sigmaspires may have been overlooked by Selenka in his original description and drawings, yet the arrangement of the megascleres in the skeleton shows a clear similarity with Carter's species *P. merguensis* (Suppl. material 2, Figure S1). In contrast to Selenka's description, Carter (1883) included a complete and detailed account of *P. merguiensis*, which was verified through examination of two slides deposited in the NHM collection (NHMUK 1894.11.16–17); few oxeas are complete in these slides (most broken), therefore limited variation of this character was observed. For most of spicule types enough measurements were possible. Although we did not succeed finding Selenka's type, we did examine one specimen and its associated slide preparation from Samoa identified as *P. bacca* (ZMA.POR.13029), which has all the characteristic spicules, including sigmaspires, that are present in our specimens from Indonesia (Figure 1C-F). This material is designated here with the status of neotype following the rules of the International Code of Zoological Nomenclature, article 75. Therefore, we conclude that *P. bacca* is a valid species, and subsequent species should be designed as junior synonyms. In all of our *Paratetilla* samples, we have furthermore not encountered one specimen without sigmaspires. Here, we show the measurements of the holotype of *P. merguiensis*, as well as specimens from different localities in Indonesia (Table 4). Although there is a large variation in spicules sizes among the different localities, there was also great intra-specific variation and we did not find any reason to declare the validity of any junior synonym included in this revision. In general, populations from marine lakes (Kakaban and Haji Buang) exhibit smaller spicules in comparison with their reefal counterparts at the same localities (Table 4). This variation could be a response to different environmental conditions within the marine lakes (Becking et al. 2011), or a consequence of genetic selection after isolation of these populations about 8000–10000 years ago (Dawson and Hamner 2005, Becking et al. 2013, Becking et al. 2016), or a synergistic effect between environmental and genetic factors.

According to the WPD (van Soest et al. 2018), other four valid *Paratetilla* species are *P. amboinensis* (Kieschnick, 1898), *P. lipotriaena* de Laubenfels, 1954, *P. corrugata* Dendy, 1922 and *P. aruensis* Hentschel, 1912. Based on the description of *P. amboinensis* (Kieschnick, 1898), the shape and skeleton features exhibited by this species fit within the current diagnosis of *P. bacca*, therefore we recommend that these two species should be synonymized. The species *P. lipotriaena* was erected by de Laubenfels based on the absence of triaenes. Our examination of the type specimen (USNM 23049) revealed the presence of triaenes and the same characters as *P. bacca*, therefore we have synonymized this species with *P. bacca.* On the other hand, *P. bacca* can be distinguished from *P. corrugata* Dendy, 1922, because of the abundant trichodragmata exhibited by the latter species. Consequently, *P. corrugata* can still be considered a valid species. Finally, the status of *P. aruensis* Hentschel, 1912 within this genus should be reconsidered. After examination of two slides available at the NHMUK, no calthrops were found, only the typical amphitriaenes originally described for this species. Amphitriaenes make this species more similar to the genus *Amphitethya* instead of *Paratetilla*. Further examination of specimens would corroborate our preliminary conclusion.

In a molecular phylogenetic study, which was based in part on specimens that we review in the current study (see Suppl. material 1, Table S1 for corresponding GenBank numbers), Schuster et al. (2017) distinguishes *P. bacca* as a monophyletic clade in the Tetillidae. Due to the wide distribution of this species and large intraspecific

Table 4. Spicule measurements of six specimens of *Paratetilla bacca* and five specimens of *P. arcifera* from different regions (n = 10 per spicule type and dimension with minimum-**mean**-maximum). Asterisk (*) indicate that rhabds of spicules were broken and no measurement was possible.

Measurements		*Paratetilla bacca*						*Paratetilla arcifera*				
		NHMUK94. 11.16.17/16	**RMNH. POR.11292**	**RMNH. POR.11287**	**RMNH. POR.11281**	**RMNH. POR.11301**	**RMNH. POR.5344**	**USNM21278 (Holotype)**	**RMNH. POR.11266**	**RMNH. POR.11273**	**RMNH. POR.11310**	**RMNH. POR.3114**
Locality		Mergui Archi-pelago	Kakaban Lake	Haji Buang Lake	Berau	Raja Ampat	Ternate	Philippines	Berau	Berau	Ternate	Manado
Habitat		Reef	Marine Lake	Marine Lake	Reef	Mangrove	Reef	Reef	Reef	Reef	Reef	Reef
Oxeas	Length	3114.36–**3114.6**–3115	850–**2340.8**–3150	1000–2922–3850	2520–**3324.6**–3850	3100–3270–3500	1250–3540–4500	1650–2435–3125	1650–3093–4500	1600–3041–4175	840–1996–3100	3100–3600–4000
	Width	40.8–**42.5**–51	5–**29.9**–40	12.5–36–50	30–**48.8**–60	30–42–55	25–49.6–65	20–39.5–65	25–42.2–55	20–33.7–50	10–25.4–50	27.5–43–52.5
Anatriaenes	Rhabd length	*	3000–**3677.8**–4600	3900–4741.7–5300	4250–**5057.1**–6000	*	*	*	*	*	*	*
	Rhabd width	15–**16**–20	5–**12.9**–20	12.5–**14.8**–17.5	7.5–**10.7**–15	7.5–11.3–15	5–7.5–10	*	*	*	5–5.7–7.5	5–6.3–7.5
	Cladi total	20–**27.9**–40	37.5–**58.7**–75	80–**91.5**–100	40–73.6–90	60–74.5–80	22.5–49.5–75	40–68–80	60–65.6–80	22.5–39.8–60	40–48.2–50	50–65–75
	Cladi length	40.8–**52**–71.4	25–**44.4**–65	50–**63.9**–75	20–40.5–50	40–57.3–75	12.5–31.8–50	25–39.4–45	30–38.7–47.5	10–21.3–30	15–20.9–25	35–40.6–50
	Cladi width	10–**12**–15	7.5–**12.1**–20	7.5–**10.9**–15	7.5–10.7–15	7.5–9.5–10	5–7-7.5	5–8.2–10	5–6.6–10	2.5–5-7.5	5–5-5	5–6.3–7.5
Protriaenes	Rhabd length	*	3900–**3900**–3900	3000–**4434.6**–5850	3100–3800–4500	*	*	*	*	*	*	*
	Rhabd width	*	7.5–**10**–12.5	10–**13.3**–17.5	5–8.6–15	2.5–4.8–5	5–5-5	*	*	*	*	5–6-7.5
	Cladi total	*	27.5–**46.9**–70	40–**70.7**–100	50–67.9–100	30–54–70	30–30–30	*	30–38.3–40	40–40–40	*	30–42.8–50
	Cladi length	*	47.5–**84.4**–100	85–**140.5**–185	110–141.4–200	50–133–170	37.5–37.5–37.5	*	50–61.7–70	75–75–75	*	25–40.3–60
	Cladi width	*	5–**7.5**–10	7.5–**9.5**–12.5	5–7.9–10	2.5–2.5–2.5	5–5-5	*	2.5–5.4–7.5	5–5-5	*	2.5–4.3–5
Calthrops	C1	42.5–**168.1**–255	110–**266**–475	270–**369.8**–510	140–296.7–360	220–301–350	250–375.7–600	320–362.5–430	150–253.9–375	110–154–220	150–192.5–250	120–179–220
	C2	22.5–**92.9**–183.6	90–**225**–325	220–**346.4**–460	140–281–350	210–284–350	240–291.4–350	230–287.5–320	75–239.4–390	90–134.4–160	70–125–230	90–129–200
	C3	20–**106**–234.6	40–**203.7**–325	50–**292.5**–400	25–218.7–345	180–254–310	200–272.9–350	120–195–300	140–245.5–355	60–110–150	50–93.3–160	90–129–200
	Width	3.5–**12.2**–20.4	7.5–**18.3**–35	15–**31.7**–45	10–18.3–27.5	10–14.5–17.5	17.5–20.4–25	15–18.8–22.5	10–18.3–25	10–12.5–15	10–13.8–17.5	12.5–15–20
Microxea		173.4–**195.3**–224.4	105–**136.2**–212.5	170–**213.6**–250	250–316.8–385	210–264–300	250–323.6–380	180–308.4–380	270–323.2–400	200–342–500	340–370–410	250–367–450
Sigmaspires		12.5–**14.4**–17.5	10–**13**–17.5	12.5–**15.4**–25	12.5–14.2–17.5	12.5–13.8–15	12.5–14–17.5	7.5–12.5–17.5	12.5–15.4–17.5	15–16.3–20	12.5–15.3–17.5	12.5–14–17.5

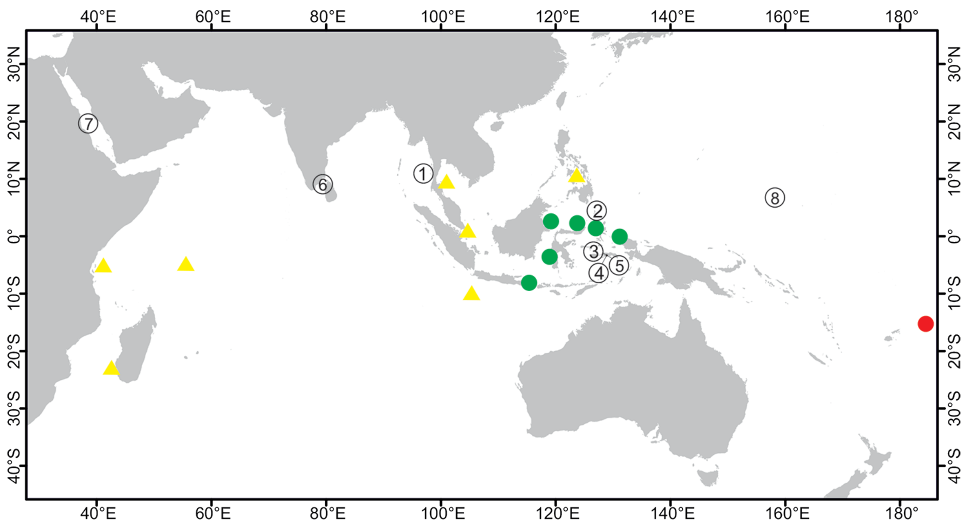

Figure 2. Distribution of *Paratetilla bacca*. Red dot: type locality, *Stelletta bacca* Selenka, 1867, American Samoa. Green dots: Indonesian localities where the species was collected recently. Yellow triangles: Records from localities outside Indonesia, Zanzibar, Southwest Madagascar, Seychelles, Thailand, Singapore, Christmas Island, and Philippines. Circled numbers: type localities of synonymized species, **1** *Tethya merguiensis* Carter, 1873, Mergui Archipelago **2** *Tetilla ternatensis* Kieschnick, 1896, Ternate Island **3** *Tetilla amboinensis* Kieschnick, 1898, Ambon Island **4** *Tetilla violacea* Kieschnick, 1898, Ambon Island **5** *Tetilla rubra* Kieschnick, 1898, Ambon Island **6** *Paratetilla cineriformis* Dendy, 1905, Gulf of Manaar, Sri Lanka. **7** *Paratetilla eccentrica* Row, 1911, Tella Tella Kabira, Red Sea **8** *Paratetilla lipotriaena* de Laubenfels, 1954, Matalanim, Eastern Pohnpei, Micronesia.

morphological variability we recommend further molecular studies, particularly of *P. bacca* from its type locality (American Samoa). This would allow a more detailed description of the genetic variation of *P. bacca* and verify our initial taxonomic proposal based on morphology.

Paratetilla arcifera Wilson, 1925

Figs 3, 4, 5

Paratetilla arcifera Wilson, 1925: 380; plate 40, fig. 2; plate 48, fig. 6 (type seen).

Material examined. Holotype USNM 21278, Albatross Stn. 5400, Malapascua Island, Cebu, Philippines, 46 m, 16 Mar 1909. **INDONESIA**. East Kalimantan, *Berau reef*, RMNH.POR.11131, RMNH.POR.11265, RMNH.POR.11266, RMNH.POR.11269, RMNH.POR.11267, RMNH.POR.11268, RMNH.POR.11270, RMNH.POR.11271, RMNH.POR.11272, RMNH.POR.11273. Bali, RMNH.POR.1870. Java, *Thousand Islands,* RMNH.POR. 2076. Sulawesi, *Bunaken,* RMNH.

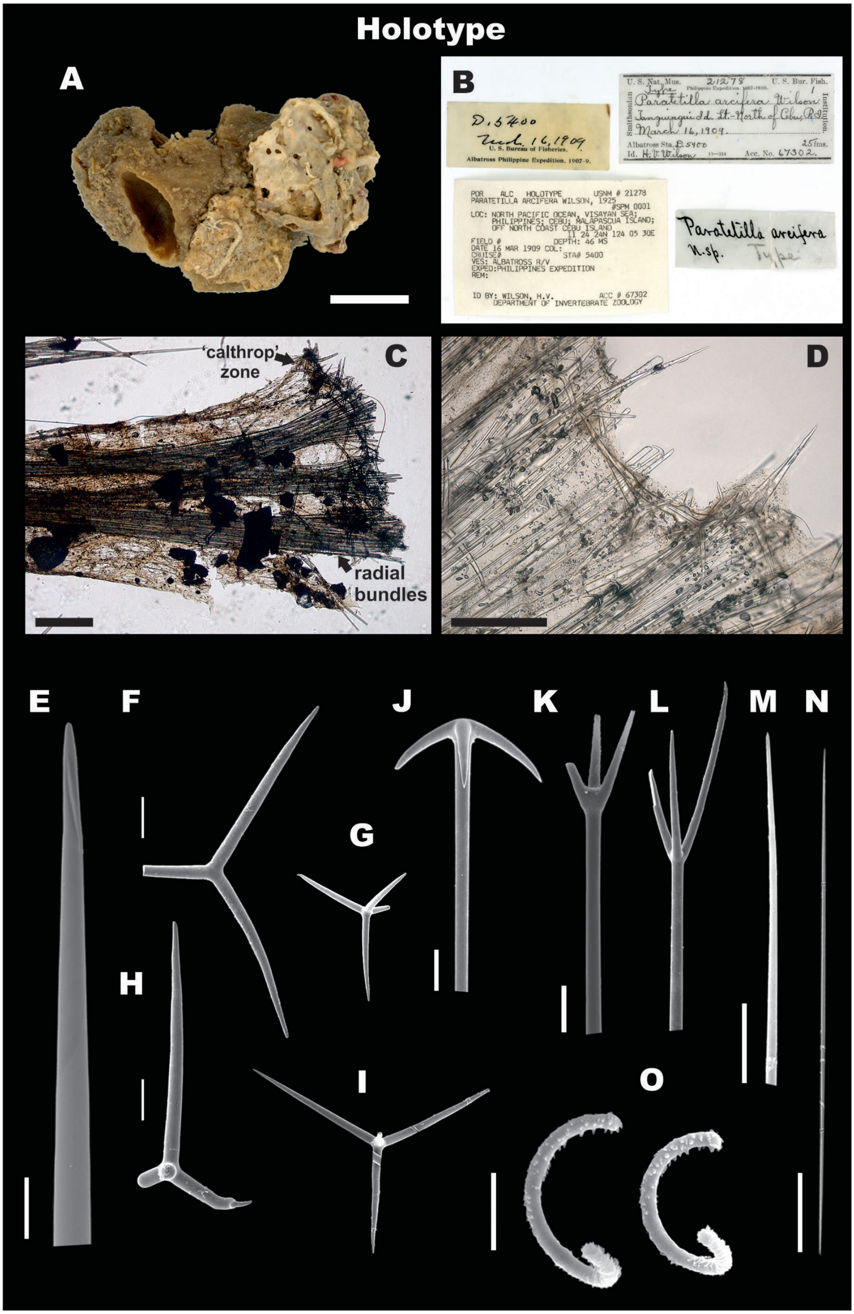

Figure 3. *Paratetilla arcifera*. Holotype USNM 21278, Malapascua Island, Cebu, Philippines **A** preserved specimen showing large porocalices **B** Labels of holotype **C** skeleton, showing calthrops and radial bundles **D** skeleton, showing oxeas, calthrops, and anatriaenes **E** oxea, end detail **F-I** different calthrop shapes and sizes **J** anatriaene **K, L** protriaene, different types **M** thin microxea, detail **N** thin microxea, full length **O** sigmaspires. Scale bars: 1 cm (**A**); 500 µm (**C, D**); 100 µm (**E**); 50 µm (**F–I, N**); 20 µm (**J**); 40 µm (**K, L**); 5 µm (**M, O**).

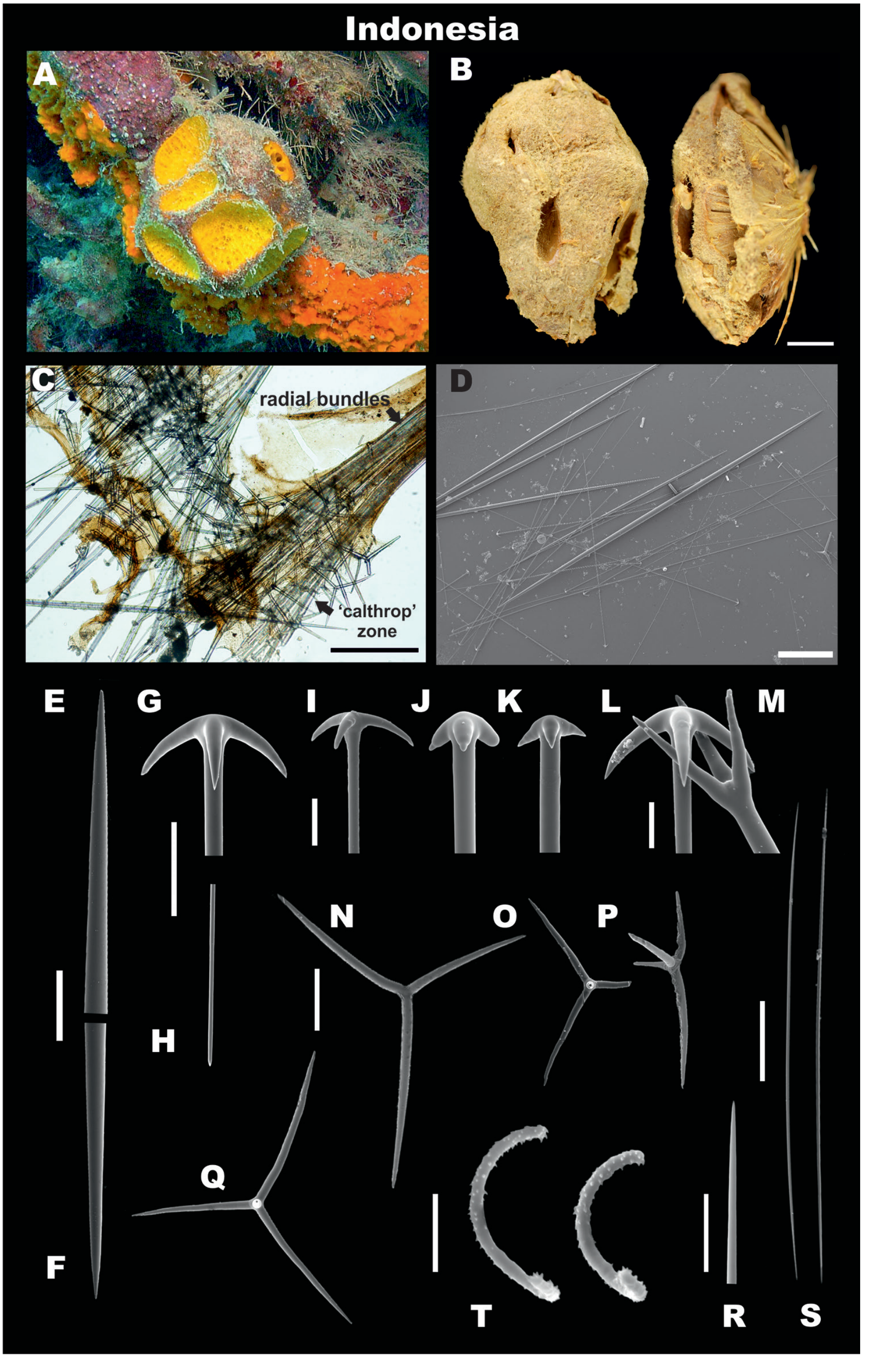

Figure 4. *Paratetilla arcifera* from Indonesia RMNH.POR.11266. **A** in situ photograph. **B** preserved specimen showing the porocalices (scale bar 1 cm) **C** skeleton **D** spicules **E, F** oxea, end detail **G, H** natriaene, cladus. and rhabd end **I-L** anatriaene, different types **M** Protriaene **N-Q** different calthrops **R** thin microxea, detail **S** thin microxeas, full length **T** sigmaspires. Scale bars: 1 cm (**B**), 500 µm (**C, D**), 100 µm **E, F**); 40 µm (**G, H**); 20 µm (**I–M**); 200 µm (**N–Q**); 5 µm (**R, T**); 50 µm (**S**).

POR.3114; *Manado* RMNH.POR.3114. Ternate, *Ternate reef, RMNH.POR.*11310. West Papua, *Kerupiar Island reef,* RMNH.POR.11280; *Outside Ctenophore Lake,* RMNH.POR.11275; *Gam Island,* RMNH.POR.11277, RMNH.POR.11278, RMNH.POR.11279, RMNH.POR.11274, RMNH.POR.11276. **TAIWAN**. *Reef,* RMNH.POR.3196, RMNH.POR.3206, RMNH.POR.3225, RMNH.POR.3236.

Description. External morphology. Globular sponges, size from 3 to 6 cm in diameter (Figs 3A, 4A). Surface hispid due to the projecting spicules, covered by numerous porocalices. Porocalices are bowl-shape, with oval apertures, up to 10 × 5 mm and 6 mm deep, few, mainly on the top surface of the sponge; in preserved material, most porocalices remained open (Figs 3A, 4A). Color generally bright orange when alive, which turns darker or even brown in ethanol. No granules in choanosome. Fleshy consistency.

Skeleton. No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core, and spaced between each other, giving a softer consistency (Figs 3C, D, 4C).

Megascleres. Holotype and Indonesian specimen size ranges are summarized in Table 4. Holotype: Oxeas 1650–2435–4500 µm × 20–36.8–65 µm; anatriaenes very abundant (Figure 3J), rhabds generally broken, up to 6000 × 10 µm, apparently tapering to dimensions of < 1 µm, cladi thin, slightly flattened, 40–68–80 µm × 25–39.4–45 µm × 5–8.2–10 µm; few protriaenes (Figure 3K,L), thinner and small cladi (40–65–80 µm × 60–85–110 µm), rhabds mostly broken, up to 5000 × 15 µm, tapering to dimensions of < 1 µm; two types of calthrop-like short shafted triaenes, one type with four rays of which three are short (150–300 µm) and one is large (400 µm) (Figure 3H), the other type has three rays of almost equal length up to 400 µm (Figure 3 F-G, I); calthrops are abundant in some specimens, but can be in very low numbers till almost absent in some others, they are located immediately below the surface, constituting a thin layer that can be missed in some spicule preparations.

Microscleres. Thin microxeas are common, 180–308.4–380 µm, 'hair-like' (Figs 3M, N, 4R, S). Sigmaspires, 7.5–12.5–17.5 µm, C-S shape (Figs 3O, 4T).

Ecology. Coral reef habitats at depths from 1- 20/30 m. Absent from marine lakes, mangroves and other localities with higher sedimentation and/or variable salinity.

Distribution. Occur in coral reefs of Berau, Bunaken, Ternate, and Raja Ampat. An additional record from its type locality, Philippines (Wilson, 1925) could be inferred from the literature (see Longakit et al. 2005: Figure 9 as *P. bacca*), and collections from Taiwan (Figure 5).

Remarks. Spicule sizes for most Indonesian specimens vary within the holotype ranges, except for the Ternate population, which exhibits smaller sizes and lack of protriaenes (Table 4). The typical orange color and 'fleshy' soft consistency are easy distinctive characters of this species (Figure 4A). The differences between *P. arcifera* and its congener *P. bacca* lie in the stark orange coloring, the fleshy consistency, the lack of granules, the larger porocalices, and thin microxeas generally longer than in *P. bacca*. *P. arcifera* specimens are typically larger than *P. bacca.* We, furthermore, deem *P. arcifera* a distinct species from *P. bacca,* based on recent molecular phylogenetic analyses that included *P. arcifera* (genbank accession number LT628349) and *P. bacca* (LT628350) specimens reviewed in our current study and support the hypothesis of two species (Schuster et al. 2017).

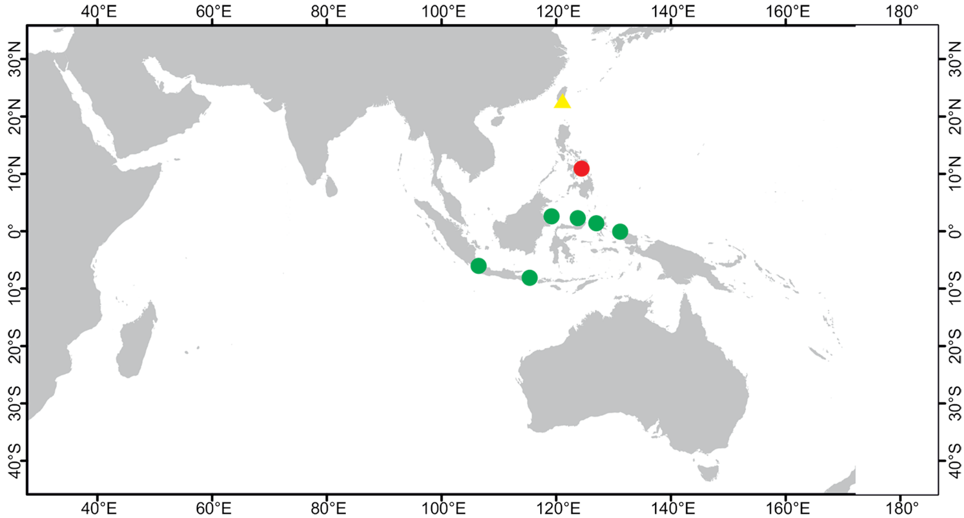

Figure 5. Distribution of *Paratetilla arcifera*. Red dot: type locality, *Paratetilla arcifera* Wilson, 1925, Tanguingui Island, Philippines. Green dots: Indonesian localities where the species was collected recently. Yellow triangle: Records from localities outside Indonesia, Taiwan.

Genus *Cinachyrella* Wilson, 1925

Currently, 42 species are valid within the genus *Cinachyrella* according to the WPD (van Soest et al. 2018), including the homonyms of *C. globulosa* and one additional description of *C. cavernosa* (Lamarck, 1815) sensu Burton (1959). Originally, Wilson (1925) grouped certain species of the genera *Tetilla* and *Cinachyra* under the subgenus *Cinachyrella* based on the presence of porocalices (poriferous pits) and the absence of cortex. Subsequently, a complete review of Caribbean species by Rützler and Smith (1992) included four valid *Cinachyrella* species and it was recently complemented with the description of two new species from Brazilian deep waters (Fernández et al. 2018). The most recent review of the Indo-Pacific species was attempted by Burton (1934). In his monograph, Burton established that 16 nominal species were synonyms of the widespread and variable species *Cinachyrella australiensis* (Carter, 1886) (see Table 5). However, the validity of Burton's conclusion was not accepted by van Soest and Rützler (2002) in the Systema Porifera. Therefore, a further examination of the junior synonyms proposed by Burton (1934) was needed and became one of the principal aims that guide this revision. A general review of the historic events about species descriptions and synonyms is provided in Table 5. Emphasis was given to species described based on Indo-Pacific specimens. Remarks were added to clarify the early confusion introduced by Lindgren (1898) when he identified some *Cinachyrella* specimens as *Tetilla ternatensis* (=*Paratetilla bacca*), although his specimens have conspicuos acanthose microxea and lack of calthrop-like spicules, misleading later descriptions for both genera.

Cinachyrella australiensis has been recorded from a wide geographic area from the Gulf of Oman (van Soest and Beglinger 2008), Thailand (Kritsanapuntu et al. 2001a-b, Putchakarn 2007), Vietnam (Azzini et al. 2007), Singapore (Lim et al. 2008), North

Australia (McDonald et al. 2002), the Great Barrier Reef in Australia (Burton 1934), Southeast Australia (Carter, 1886), and Indonesia (e.g. Becking et al. 2006, de Voogd and Cleary 2008, de Voogd et al. 2009, Becking et al. 2013), inhabiting coastal mangroves, reefs, and marine lakes.

Ecological studies on the morphological plasticity of *C. australiensis* from North Australia (McDonald et al. 2002) and Thailand (Kritsanapuntu et al. 2001) have concluded that this species can adapt to extreme sedimentation and water current regimes through the variation of the body shape and reinforcement of spicules. Although these surveys showed interesting data on the individual sizes, porocalices, silica/organic content, both of them lack robust taxonomic data (type of spicules and their dimensions). It is therefore unclear whether the observed plasticity can be attributed to natural variation within the same species or may possibly be explained by different species inhabiting different habitats.

Table 5. Historic milestones in the taxonomy of *Cinachyrella australiensis* and other *Cinachyrella* species from Indonesia. Asterisk (*) indicates misidentification of *Cinachyrella* specimens as *Paratetilla*.

Year	Author	Descriptions / Statements
1873	Gray	Description of the monotypic genera *Psetalia* and *Labaria*, with the species *P. globulosa* and *L. hemisphaerica*, respectively.
1886	Carter	Description of *Tethya cranium* var. *australiensis* from Port Phillip Heads (South Australia) collected at 36 m depth. This species was characterized by the presence of minutely spined (= acanthose) microxea (210 µm).
1888	Sollas	Establishment of Family Tetillidae. *Tethya cranium* var. *australiensis* was redescribed as *Tetilla* (?) *australiensis*. In addition, Sollas noted that the characteristic microxeas of *T. australiensis* were also present in *T. merguiensis* as well, but were more abundant in *T. australiensis*.
1888	Lendenfeld	Description of genus *Spiretta* within Family Tetillidae, including two new species *S. raphidiophora* and *S. porosa*, from Port Jackson (SE Australia) and Port Denison (NE Australia), respectively. The former with microxea (240 × 2 µm) and the latter without them.
1891	Keller	Description of *Cinachyra schulzei* from the Red Sea and Mozambique, with microxea 250 × 5 µm.
1896*	Kieschnick	Description of *Tetilla ternatensis* based on material from Ternate Island (Indonesia). He mentioned "Vierstrahler" (= calthrops).
1898*	Lindgren	Redescription of *Tetilla ternatensis* based on Java material. It is remarkable that he mentioned the presence of numerous microxea (240 × 4 µm) and sigmaspires 24 µm.
1898	Kieschnick	Description of *Tetilla schulzei* from material of NE Australia to Ambon Island, with microxea (198-220 µm × 4 µm). *T. schulzei* has 'oscula' that we interpret as porocalices. Although Kieschnick entitled *T. schulzei* as new species, it is not clear if he was aware of *Cinachyra schulzei* described by Keller (1891). Three other *Tetilla* species with "Vierstrahler" (= calthrops) spicules were described (see Table 3).
1899	Thiele	Record of *Tetilla australiensis* from Sulawesi (Indonesia). Specimens with acanthose microxea (180-200 µm × 2.5 µm).
1900*	Thiele	With the redescription of *Tetilla ternatensis* Kieschnick, 1896, Thiele noticed the misidentification of *T. ternatensis* by Lindgren (1898) and pointed out that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886).
1900	Kieschnick	Additional record of *Tetilla schulzei* from Ambon Islands, including description of the specimens, with microxea from 198 to 220 µm × 4 µm.
1900*	Kirkpatrick	Extension of geographical range of *T. bacca* and *T. ternatensis* to Christmas Island. *T. bacca* specimens were described with identical spicules to Lindgren's material from Java. *T. ternatensis* also similar to Lindgren's material of *T. ternatensis,* this is having microxeas and missing calthrops.
1902	Sollas	Description of *Cinachyra malaccensis* from Malaysia. Cup-shaped porocalices are described together with different spicules, except for microxea. In the available figures, no microxeas are shown.

Year	Author	Descriptions / Statements
1903*	Thiele	Redescription of *Tetilla ternatensis* Kieschnick, 1898. He drew attention on the misidentification of *T. ternatensis* by Lindgren (1898), clarifying that Lindgren specimens exhibited microxea resembling *Tetilla australiensis* (Carter, 1886).
1903*	Lendenfeld	Designation of a new species *Tetilla lindgreni* based on *T. ternatensis* material described by Lindgren (1898) and Kirkpatrick (1900), excluding the original description of Kieschnick (1896), because the latter one has calthrop-like spicules. Two *Spiretta* species, *S. raphidiophora* and *S. porosa,* transferred to genus *Tetilla*.
1905	Dendy	Monograph on sponges from Sri Lanka. Description of *Tetilla anomala*, showing remarkable siliceous micro-spherules (4 µm) and no microxeas. Description of *Tetilla poculifera* with smooth microxeas (230 × 5 µm). Description of *Tetilla limicola*, pink-color and root tuft; neither porocalices nor microxea are described. The genus *Paratetilla* was established.
1906	Baer	Description of *Tethya armata* from Zanzibar (Africa, Indian Ocean). It is characterized by a dermal cortex formed by microxea (166-296 µm × 1-2 µm).
1907	Lendenfeld	Description of *Cinachyra isis* and *Tethya hebes* from NW Australia, the first one exhibiting smaller microxea (130-160 µm × 2-5.5 µm), and the second one larger rough microxea (= acanthose microxea, 250-275 µm × 4-6 µm). Description of *Cinachyra alba-tridens*, *C. alba-obtusa*, and *C. alba-bidens* species, slightly differentiated by the geometry and abundance of triaenes. He kept the three species because they were collected in three distant localities, Chagos Archipelago, Papua New Guinea, and Tonga Islands, respectively; "alba-group" species do not contain microxeas, and sigmaspires are small (<10 µm).
1911	Row	Description of *Chrotella ibis* from the Red Sea. Species with smooth microxea (150 × 2.1 µm), sharing this character with *Tetilla poculifera*, and *Paratetilla* species *P. merguiensis*, *P. eccentrica* and *P. cineriformis*. In his description, Row clearly differentiated his species from *T. australiensis* due to the latter having acanthose microxea.
1911	Hentschel	Description of *Tetilla cinachyroides* from South Australia. Species with acanthose microxea (112-168 µm × 2.5 µm), sigmaspires (10-12 µm) and spherules (5 µm).
1912	Hentschel	Description of *Cinachyra mertoni* and *Cinachyra nuda* from Aru- and Kei- Islands (Indonesia). Both species contain microxea, the first one smooth 250 µm, whereas in the second one they are acanthose, from 200-280 µm, and no anatriaenes were found. A third species, *Tethya clavigera*, with oscula (similar to porocalices) and no microxea was also described.
1922	Dendy	Description of *Cinachyra vaccinata* and *C. providentiae* from the Indian Ocean. Both of them with microxea (no mention whether acanthose or not), being 200 × 4 µm in the former, and 220 × 5.5 µm in the latter one. *C. vaccinata* characterized by small hair-like protri- and prodiaenes, terminating in an elongated oval swelling tip unique to this species. *C. providentiae* with bottle-shaped porocalices.
1925	Wilson	Establishment of *Cinachyrella* as a subgenus of *Tetilla*, with type species *Tetilla hirsuta* Dendy, 1889. The characters used to distinguish *Cinachyrella* species from the other were special depressions (=porocalices) and no specialization of a cortical zone. Wilson included the following species within *Cinachyrella: Cinachyra malaccensis* Sollas, 1902; *Tetilla limicola* Dendy, 1905; *Tetilla anomala* Dendy, 1905; *Cinachyra isis* Lendenfeld, 1907; *C. hamata* Lendenfeld, 1907; *C. alba-tridens* Lendenfeld, 1907; *C. alba-bidens* Lendenfeld, 1907; *C. alba-obtusa* Lendenfeld, 1907; *C. vertex* Lendenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; *Cinachyra phacoides* Hentschel, 1911; *Tethya clavigera* Hentschel, 1912; *Cinachyra mertoni* Hentschel, 1912; *Cinachyra nuda* Hentschel, 1912; *Cinachyra vaccinata* Dendy, 1922; *Cinachyra providentiae* Dendy, 1922. In addition, *Cinachyrella crustata* and *Cinachyrella paterifera* were described from Philippines. *C. crustata* with distinctive long and stout promonoenes, no microxea. *C. paterifera* with a characteristic cloaca (= large osculum) on top and root-like structure to attach to sediments, microxea (250 × 2 µm) observed in two specimens although almost absent in the third one of the type series, pointing out a high variability in the presence of microxea within the same individual.
1934	Burton	Taxonomic revision of *Cinachyra australiensis*. In his compilation, Burton grouped 16 nominal species described in 32 references and designated them as junior synonyms of the widespread species *C. australiensis*. Three different groups were recognized: the *australiensis*-group characterized by the presence of acanthose microxea; the *schulzei*-group with smooth microxea; and the *porosa*-group without microxea. Description of genus *Raphidotethya*.
1954	de Laubenfels	Identification of *Cinachyra porosa* and *Cinachyra australiensis* from Micronesia (West-Central Pacific).

Year	Author	Descriptions / Statements
1973	Thomas	Records of *Cinachyra cavernosa* (Lamarck, 1815) from the Seychelles Islands, having, microxea (126 × 2 µm) sometimes granulated (= acanthose). Among the junior synonyms of *C. cavernosa*, Thomas included *Tethya cranium var. australiensis* Carter, 1886*, Chrotella australiensis* Burton, 1937, and *Chrotella cavernosa* Burton, 1959. However, in the WPD (van Soest et al. 2018) *C. cavernosa* is still a valid species.
1982	Pulitzer-Finali	Description of *Cinachyra tenuiviolacea* from the Great Barrier Reef (Australia), characterized by a light violet color, small oxeas (up to 2500 µm × 13-25 µm), atrophic anatriaenes, no microxeas, and no protriaenes in the choanosome.
1987	Rützler	Review of Family Tetillidae, including seven genera (all except for *Fangophilina*). Subgenus *Cinachyrella* was elevated to the hierarchy of genus.
1992	Rützler and Smith	Review of four species of *Cinachyrella* for the Caribbean region, mainly described by Uliczka (1929). Geometry and size ranges of all spicule types were shown. According to their descriptions, *Cinachyrella kuekenthali* is the most similar species to *C. australiensis*, since both of them have acanthose microxea.
1994	Hooper and Wiedenmayer	Compilation of *Cinachyra australiensis* synonyms based on Burton (1934) taxonomic decision.
2002	van Soest and Rützler	Review of the eight genera of tetillids, including *Cinachyrella*. *Cinachyra australiensis* was transferred into the genus *Cinachyrella*. The authors considered that all junior synonyms proposed for *C. australiensis* by Burton (1934) should need further taxonomic revision. Moreover, the genera [*Psetalia*] Gray, 1873 (*nomem oblitum*), [*Labaria*] Gray, 1873 (nomen oblitum) and *Raphidotethya* Burton, 1934 were included as synonyms of the genus *Cinachyrella*.
2018	van Soest et al. (WPD)	Accepted synonyms of *Cinachyrella australiensis* (Carter, 1886): *Tethya australiensis* Carter, 1886; *Spiretta porosa* Lendenfeld, 1888; *Cinachyra malaccensis* Sollas, 1902; *Tetilla lindgreni* Lendenfeld, 1903; *Tethya armata* Baer, 1906; *Cinachyra isis* Lendenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; and *Cinachyra providentiae* Dendy, 1922. Valid *Cinachyrella* spp. from the Indo-pacific (excluding species only found in the Red Sea) comprise 6 species
2018	This study	From our detailed examination of Indonesian material and type material, we conclude that in Indonesia there are three species: *Cinachyrella australiensis* (Carter, 1886), *Cinachyrella porosa* (Lendenfeld, 1888), and *Cinachyrella paterifera* Wilson, 1922. Further investigations will reveal if the five species from the *C. schulzei-* group can be synonymized or belong to separate and distinctive species.

***Cinachyrella australiensis* (Carter, 1886)**
Figs 6, 7

Tethya cranium var. *australiensis* Carter, 1886: 127 (holotype seen).
Tetilla? *australiensis*; Sollas, 1888: 43.
Spiretta raphidiophora Lendenfeld, 1888: 43 (type seen).
Tetilla hirsuta Dendy, 1889: 75 (type seen).
Tetilla ternatensis Lindgren, 1898: 329 pl. 17, fig. 14; pl. 19, Fig. 25 a-e, a', b'. Ternate Not *Tetilla ternatensis*; Kieschnick*, 1896: 527.
Tetilla australiensis; Thiele, 1899: 6, pl.1 fig.1; pl. 5, fig.1 a-e. Celebes Sea.
Tetilla ternatensis; Kirkpatrick, 1900: 132 (material seen) Not *Tetilla ternatensis* Kieschnick*, 1896: 527.
Tetilla lindgreni Lendenfeld, 1903: 18.
Tetilla australiensis; Lendenfeld, 1903: 20.
Tethya hebes Lendenfeld, 1907: 98, pl. XVI, figs 19–38. 19`South NW Australia, 91 m depth (syntype seen).
Cinachyra isis Lendenfeld, 1907: 143, pl. XV, figs 54–58, XVI, figs 1–4. Mermaid Strasse (NW Australia) (syntype seen); Dendy, 1922: 16, pl. 10, figs 3a-b.

Tetilla cinachyroides Hentschel, 1911: 281, textfig. 1. NW Australia, Barrow Island.
Cinachyra nuda Hentschel, 1912:333, pl. XIII, fig.2; pl. XVIII fig. 13. Aru Island (type seen).
Cinachyra vaccinata Dendy, 1922: 14, pl. 1, fig. 4; pl. 11, figs 1a-l. Diego Garcia, Chagos Island (type seen).
Cinachyra providentiae Dendy, 1922: 18, pl.1, figs 5–5a; pl. 10, figs2a–f. Providence Island (type seen).
Tetilla (*Cinachyrella*) *hirsuta*; Wilson, 1925: 365, pl. 39, fig.4.
Cinachyra australiensis; Burton, 1934: 523. In part, not *C. australiensis* in porosa-group, nor *C. australiensis* in schulzei-group; de Laubenfels, 1954: 241, text-fig. 166.
Cinachyrella anatriaenilla Fernandez, Kelly, Bell, 2017: 83, figs 2–4.

Material examined. Holotype NHMUK 1886.12.15.367, Port Phillip Heads, Southeast Australia (as *Tethya cranium* var. *australiensis*). Holotype NHMUK 1886.8.27.634, Port Jackson, Sidney, Australia (as *Spiretta raphidiophora* Lendenfeld, 1888). NHMUK unreg. type, Gulf of Manaar, Sri Lanka (as *Tetilla hirsuta* Dendy, 1889). NHMUK 1898.12.20.20 Christmas islands (as *Tetilla ternatensis* Kirkpatrick, 1900). Holotype NHMUK 1908.9.24.19–21, 19°17'S 116°E, Gazelle Exp., Western Australia, (as *Tethya hebes* Lendenfeld, 1907). Syntype NHMUK 1908.9.24.74, Mermaid Strait, NW Australia (as *Cinachyra isis* Lendenfeld, 1907). RMNH unreg. fragment taken from the type (pers. comm. NJ de Voogd) and available in Naturalis collections, Aru Island, Indonesia, as *Cinachyra nuda* Hentschel, 1912. Holotype NHMUK 1921.11.7.6, Diego Garcia, Chagos Islands (as *Cinachyra vaccinata* Dendy, 1922). Holotype NHMUK 1921.11.7.8, Providence Island, Seychelles (as *Cinachyra providentiae* Dendy, 1922). **INDONESIA**. East Kalimantan, *Berau reef,* RMNH.POR.11101, RMNH.POR.11102, RMNH.POR.11103, RMNH.POR.11104, RMNH.POR.11105, RMNH.POR.11106, RMNH.POR.11107, RMNH.POR.11108, RMNH.POR.11109, RMNH.POR.11110, RMNH.POR.11111, RMNH.POR11112, RMNH.POR.11113, RMNH.POR.11114, RMNH.POR.11115, RMNH.POR.11116, RMNH.POR.11117, RMNH.POR.11210, RMNH.POR.11124, RMNH.POR.11125, RMNH.POR.11126, RMNH.POR.11127, RMNH.POR.11128, RMNH.POR.11129, RMNH.POR.11130, RMNH.POR.11118, RMNH.POR.11119, RMNH.POR.11120, RMNH.POR.11121, RMNH.POR.11122, RMNH.POR.11123; RMNH.POR.11132; RMNH.POR.11133, RMNH.POR.11134, RMNH.POR.11135, RMNH.POR.11136; *Pea Bay,* RMNH.POR.11162; *Haji Buang Lake,* RMNH.POR.11137, RMNH.POR.3511, RMNH.POR.3512, RMNH.POR.3513, RMNH.POR.3516, RMNH.POR.3517; *Kakaban Lake,* RMNH.*POR.*11161, RMNH.POR.11138, RMNH.POR.11139, RMNH.POR.11140, RMNH.POR.11141, RMNH.POR.11142, RMNH.POR.11143, RMNH.POR.11144, RMNH.POR.11145, RMNH.POR.11146, RMNH.POR.11147, RMNH.POR.11148, RMNH.POR.11149, RMNH.POR.11150, RMNH.POR.11151, RMNH.POR.11152, RMNH.POR.11153, RMNH.POR.11154, RMNH.POR.11155, RMNH.POR.11156, RMNH.POR.11157, RMNH.POR.11158, RMNH.POR.11159, RMNH.POR.11160. Java, *Thousand*

Islands, RMNH.POR.1969. Ternate, *Ternate reef,* RMNH.POR.11308. Sulawesi, *Bunaken,* RMNH.POR.3108, RMNH.POR.3112, RMNH.POR.3119, RMNH.POR.3122. West Papua, *Sawaundarek Lake,* RMNH.POR.11163, RMNH.POR.11164, RMNH.POR.11165, RMNH.POR.11166, RMNH.POR.11167; *Gam Island, Wallace Lake,* RMNH.POR.11168, RMNH.POR.11169 *Outside Wallace Lake,* RMNH.POR.11170, RMNH.POR.11171, RMNH.POR.11172, RMNH.POR.11173; *Gam Island, Blue Water Mangrove,* RMNH.POR.11174, RMNH.POR.11175, RMNH.POR.11176, RMNH.POR.11177, RMNH.POR.11178, RMNH.POR.11179, RMNH.POR.11180, RMNH.POR.11181, RMNH.POR.11182, RMNH.POR.11183, RMNH.POR.11184, RMNH.POR.11185, RMNH.POR.11186, RMNH.POR.11187, RMNH.POR.11188, RMNH.POR.11189, RMNH.POR.11190, RMNH.POR.11191, RMNH.POR.11192; *Ctenophore Lake,* RMNH.POR.11193, RMNH.POR.11194, RMNH.POR.11195, RMNH.POR.11196, RMNH.POR.11197; *Outside Ctenophore Lake,* RMNH.POR.11198, RMNH.POR.11199, RMNH.POR.11200, RMNH.POR.11201; *Big Caulerpa Lake,* RMNH.POR.11202, RMNH.POR.11203; *Outside Big Caulerpa lake,* RMNH.POR.11204; *Gam Island,* RMNH.POR.11205, RMNH.POR.11206.

Other material: Singapore, RMNH.POR.3520, RMNH.POR.2440, RMNH.POR. 2505.

Other types and material examined (not included as synonyms of *C. australiensis*): NHMUK 1892.8.8.8. Macclesfield Bank, South China Sea *Cinachyra schulzei* (unpublished material). Holotype NHMUK 1908.9.24.75 Red Sea, *Cinachyra trochiformis* Keller, 1891. Holotype NHMUK 1907.2.1.14, Gulf of Manaar, Sri Lanka, *Tetilla poculifera* Dendy, 1905. Holotype NHMUK 1912.2.1.35, Tella Tella Kebira, Red Sea, *Chrotella ibis* Row, 1911. RMNH unreg. fragment taken from the type (pers. comm. NJ de Voogd) available in Naturalis collections, Kei Island, Indonesia, *Cinachyra mertoni* Hentschel, 1912.

Description. External morphology. Globular sponges, size from 4 to 10 cm in diameter (Figure 6A, B). Surface hispid due to the projecting spicules; covered by numerous porocalices. Porocalices are abundant bowl-shape with open oval apertures, up to 10 × 5 mm and 5 mm deep, or bottle-shape, up to 18 × 6.5 mm, with minuscule apertures (2–3 mm diameter), size of porocalices can vary between habitats; a cloaca, defined as a central exhalant cavity (Boury-Esnault and Rützler, 1997), is distinguishable at the top of some specimens (Figure 6A); in preserved material some porocalices are open. Color generally bright yellow when alive, which turns paler or even white in ethanol. In the field, the sponge can appear brownish due to sediment or greenish due to association with algae.

Skeleton. No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core.

Megascleres. Holotype and Indonesian specimens' measurements are shown in Table 6. Holotype, oxeas 3375–4135.5–5500 µm × 15–24.7–37.5 µm (Figure 6D, K); no triaenes were observed in the type specimen; in Carter's description, protriaenes are described (135 µm long) and the absence of anatriaenes was explained as their heads

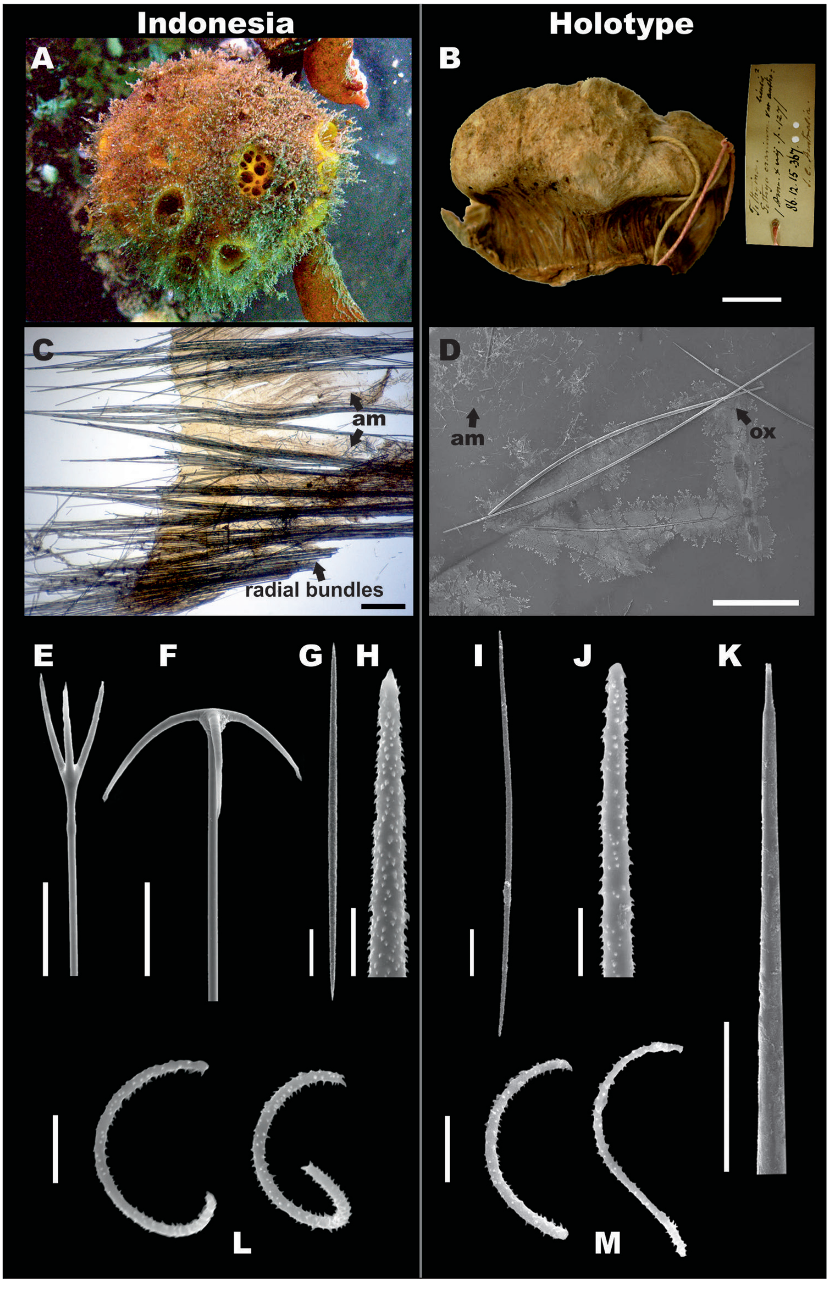

Figure 6. *Cinachyrella australiensis*. **A, C, E-H, L** RMNH.POR.11139, Kakaban lake, Indonesia (left side) **B, D, I-K, M** holotype NHMUK 1886.12.15.367, Port Phillip Heads, Australia (right side) **A** In situ photograph showing porocalices **B** dry specimen, lateral view **C** skeleton showing acanthose microxeas (*am*) and radial bundles with oxeas **D** spicule montage showing acanthose microxeas (*am*), and oxeas (*ox*) **E** protriaene **F** anatriaene **G** Acanthose microxea, full lenght **H** acanthose microxea, detail **I** acanthose microxea, full length **J** acanthose microxea, detail **K** oxea, end detail **L, M** sigmaspires. Scale bars: 1 cm(**B**); 500 µm (**C, D**); 20 µm (**E–G, I**); 5 µm (**H, J, L, M**); 50 µm (**K**).

Table 6. Spicule measurements of eight specimens *Cinachyrella australiensis*, five specimens of *C. anomala*, four specimens of *C. paterifera* from different regions (n = 10 per spicule type and dimension with minimum-**mean**-maximum). Asterisk (*) indicate that rhabd of spicules were broken and no measurement was possible. Double asterisk (**) indicate that a particular spicule type was not observed.

Measurements		***Cinachyrella australiensis***							
		NHMUK86.12.15.367 (Holotype)	**RMNH. POR.11120**	**RMNH. POR.11146**	**RMNH. POR.11123**	**RMNH. POR.11139**	**RMNH. POR.11118**	**RMNH. POR.11308**	**RMNH. POR.11192**
Locality		Port Phillip Heads	Berau	Kakaban	Berau	Kakaban	Berau	Ternate	Raja Ampat
Habitat		Reef?	Reef	Marine Lake	Reef	Marine Lake	Reef	Reef	Mangrove
Oxeas	Length	3375–**4135.5**–5500	1000–**3332**–4500	1375–**2912**–4000	2425–**3822.8**–5500	2250–**3066**–4250	2300–**4315**–5750	1500–**2676**–3800	2000–**2658.3**–3750
	Width	15–**24.7**–37.5	10–**40**–52.5	17.5–**33.9**–55	25–**41.7**–60	17.5–**26.4**–35	37.5–**59.1**–77.5	12.5–**30.3**–60	25–**31.3**–37.5
Anatriaene	Rhabd	**	2750–**3271.9**–3650	2250–**3317.9**–4250	2700–**3083.3**–3300	*	*	*	*
	Rhabd width		5–**6**–7.5	2.5–**5.3**–7.5	4–**4.9**–5	5–**5**–5	5–**5**–5	7.5–**8.4**–10	5–**5.3**–7.5
	Cladi total		50–**63.5**–85	30–**74.2**–100	45–**58**–70	40–**55**–70	60–**81**–100	55–**79.4**–100	70–**83**–100
	Cladi length		40–**49.5**–65	20–**60.4**–80	30–**42.5**–50	35–**45**–60	32.5–**49.5**–57.5	30–**49.1**–67.5	50–**66**–80
	Cladi width		2.5–**4.5**–5	2.5–**3.5**–5	4–**5.6**–10	5–**5**–5	5–**5.1**–6	5–**5.6**–7.5	5–**5**–5
Protriaene	Rhabd length	**	3900–**4550**–5800	3700–**4262.5**–4750	840–**3522.5**–5000	2250–**2375**–2500	**	*	*
	Rhabd width		10–**13.3**–20	12.5–**14.7**–15	10–**12.5**–15	2.5–**5.9**–7.5		7.5–**8.3**–10	2.5–**5**–7.5
	Cladi total		20–**46.9**–70	20–**58.8**–80	40–**60.8**–80	40–**55**–80		45–**50.4**–55	25–**70.5**–100
	Cladi length		35–**66.3**–110	25–**93.8**–170	75–**95.8**–130	50–**79.5**–110		40–**77.9**–120	30–**108**–150
	Cladi width		5–**7.9**–10	10–**11.6**–12.5	10–**10.8**–12.5	2.5–**4.8**–5		5–**5.8**–7.5	2.5–**4.3**–5
Strongyle	Length	**	—	4000–**4000**–4000	2450–**3041.7**–4200			2200–**2650**–2850	
	Width			50–**50**–50	35–**43.3**–60			32.5–**39.4**–50	
Acanthose microxea		117–**166.9**–260	160–**197.3**–230	150–**165**–200	200–**230**–270	150–**183.5**–240	157.5–**189.5**–225	170–**191.4**–225	137.5–**154**–175
Sigmaspires		10–**14.4**–17.5	12.5–**15**–17.5	10–**12.3**–15	12.5–**14.8**–17.5	10–**12**–15	15–**16.5**–20	12.5–**15.7**–20	12.5–**14.8**–17.5

Table 6. Continued.

Measurements		*Cinachyrella porosa*					*Cinachyrella paterifera*			
		NHMUK86.8.27.632–3 (Holotype)	**RMNH. POR.11226**	**RMNH. POR.11244**	**RMNH. POR.11262**	**RMNH. POR.11309**	**USNM21314 (Holotype)**	**RMNH. POR.11207**	**RMNH. POR.11213**	**RMNH. POR.11208**
Locality		Port Denison	Tanah Banban	Teluk Pea	Raja Ampat	Ternate	Philippines	Berau	Raja Ampat	Berau
Habitat		Reef	Marine Lake	Reef	Reef	Reef	Reef	Reef	Reef	Reef
Oxeas	Length	820–**2553.2**–3750	550–**2138.1**–3750	1350–**2702.5**–4000	1250–**2304.2**–3150	1500–**2710**–3500	1400–**3011.5**–4750	2850–**3580.6**–4500	1850–**3060**–5000	800–**2748.2**–4500
	Width	7.5–**29.4**–47.5	5–**28.2**–60	7.5–**29.5**–47.5	12.5–**29.4**–40	7.5–**32.6**–45	10–**34.5**–62.5	30–**46.1**–62.5	12.5–**35.6**–55	5–**34.2**–75
Anatriaene	Rhabd	*	*	*	*	*	*	*	*	4250–**4250**–4250
	Rhabd width	2.5–**5.8**–7.5	10–**12**–15	5–**7.8**–10	5–**5**–5	5–**6.1**–7.5	5–**7.5**–10	5–**6.6**–10	7.5–**8.8**–10	5–**5**–5
	Cladi total	50–**67.6**–100	65–**71**–80	60–**65**–70	50–**62.9**–70	50–**62.5**–75	17.5–**24.2**–30	17.5–**37.5**–75	70–**90**–110	65–**79.3**–110
	Cladi length	30–**42**–60	45–**56**–65	40–**52**–70	40–**51.4**–60	30–**50.4**–62.5	2–**6.5**–10	7.5–**25.7**–80	50–**65**–80	42.5–**58.2**–90
	Cladi width	2.5–**5.6**–7.5	10–**10.5**–12.5	2.5–**6.6**–7.5	2.5–**4.6**–5	5–**5.4**–7.5	5–**5.8**–7.5	5–**6.4**–10	7.5–**7.5**–7.5	2.5–**4.3**–5
Protriaene	Rhabd length	*	*	*	*	*	*	3500–**4210**–5350	*	4300–**4689.3**–5100
	Rhabd width	5–**7.3**–12.5	5–**8.8**–15	2.5–**6.5**–10	2.5–**3.6**–5	2.5–**5**–7.5	10–**10**–10	5–**9.5**–12.5	5–**7.8**–10	10–**15.2**–17.5
	Cladi total	25–**44.4**–65	20–**51.25**–80	40–**59**–80	30–**44.3**–60	50–**53.8**–67.5	30–**32.5**–35	35–**53.9**–75	40–**70**–100	30–**37.3**–60
	Cladi length	35–**73**–110	30–**77.5**–125	60–**100**–160	40–**67.1**–100	50–**78.3**–137.5	22.5–**31.3**–40	20–**74.1**–130	30–**82.5**–140	40–**51.6**–80
	Cladi width	5–**5.1**–7.5	5–**7.5**–15	2.5–**5.5**–10	2.5–**2.5**–2.5	2.5–**4**–5	7.5–**7.5**–7.5	2.5–**6.8**–7.5	5–**6.6**–7.5	10–**11.6**–15
Strongyle	Length	2650–**2650**–2650	**	3350–**3350**–3350	**	**	*	2450–**2800**–3250	2100–**2975**–3700	1800–**1862.5**–1925
	Width	35–**35**–35		45–**45**–45			45–**45**–45	40–**43.1**–50	35–**45.3**–62.5	35–**37.5**–40
Acanthose microxea										
Sigmaspires		5–**8.6**–12.5	7.5–**8.5**–10	5–**8.9**–12.5	5–**8**–10	5–**8**–10	10–**13.2**–17.5	12.5–**15.3**–17.5	12.5–**14.5**–17.5	12.5–**16.2**–20
Protriaene (hair–like)	Rhabd length						*	*	*	550–**698.9**–820
	Width						2.5–**2.5**–2.5	2.5–**2.5**–2.5	2.5–**2.5**–2.5	2–**2.2**–2.5
	Cladi total						7.5–**12.5**–17.5	7.5–**10.9**–17.5	12.5–**13.6**–15	7.5–**11.7**–20
	Cladi length						12–**15.5**–20	17.5–**21.6**–25	12–**14.5**–17.5	10–**14.4**–25
	Cladi width						2.5–**2.5**–2.5	2–**2.1**–2.5	2.5–**2.5**–2.5	1–**1.7**–2.5

broke off when collected; Indonesian specimens have a wide size range of oxea 1000–5500 µm (Figure 6C), abundant anatriaenes (Figure 6F), with rhabd 2250–3224.4–4250 µm × 2.5–5.7–10 µm, cladi thin, mainly with obtuse angles 30–70.6–100 µm × 20–51.7–80 µm × 2.5–4.9–10 µm; protriaenes (Figure 6E), with thin and long cladi (20–57.1–80 µm × 25–86.9–170 µm × 2.5–7.5–12.5 µm), rhabd up to 5800 × 20 µm, tapering to dimensions of < 1 µm; few prodiaenes also observed, having smaller cladi (20–30 µm × 20–30 µm); no calthrop-like triaenes.

Microscleres. Numerous acanthose microxeas, holotype, 117–166.9–260 µm (Figure 6I, J), slightly larger in the Indonesian material 137.5–184.7–270 µm (Figure 6G, H); sigmaspires vary within the same range in both, holotype and Indonesian specimens, 10–14.4–20 µm, C-S shape (Figure 6L, M).

Ecology. *Cinachyrella australiensis* occurs in reefs, mangroves, and marine lakes, ranging in depths from 0 to at least 30 m, possibly deeper. Specimens can be covered by sand and mud; or in symbiosis with algae, resulting in green external color. This species produces 1–2 mm sized buds (Figure 8) and buds are extensively observed in specimens collected from marine lake habitats.

Distribution. *Cinachyrella australiensis* has a wide distribution in Indonesia, including Berau, Bunaken, Raja Ampat, Ternate, and Java. Previous Indonesian records are from Spermonde Archipelago in Sulawesi (de Voogd and Cleary 2005, Becking et al. 2006, de Voogd et al. 2006), North Sulawesi (Calcinai et al. 2017), Berau (de Voogd et al. 2009, Becking et al. 2013), Thousand Islands in Java (de Voogd and Cleary 2008), and Raja Ampat (Becking 2008). In addition, this species has also been found in Gulf of Oman (van Soest and Beglinger 2008), Seychelles Islands (Thomas 1973) Southwest Madagascar (Vacelet et al. 1976), Zanzibar (Pulitzer-Finali 1993), Thailand (Kritsanapuntu et al. 2001a-b, Putchakarn 2007), Singapore (Lim et al. 2008), Vietnam (Azzini et al. 2007), Philippines (Longakit et al. 2005), Northern Territory of Australia (McDonald et al. 2002), and the Great Barrier Reef in Australia (Burton 1934).

Remarks. In the type description of *C. australiensis* Carter (1886), the author did not observe anatriaenes as it can be interpreted from his statement: "I saw no anchors (smaller tetractinellids with recurved arms); but as their heads when exposed are generally broken off (for they catch in everything that they touch), it does not follow that they do not form part of the spiculation, particularly as they are present in most of the other species that I have been described (sic)". We examined the holotype kept at the Natural History Museum (NHMUK 1886.12.15.367) and found neither anatriaenes nor protriaenes. In addition, most of the oxeas were broken in the type specimen. Within all the examined material there is a high variability in the presence or absence of triaenes without a distinct geographic pattern. This variation may be related to where the sponge was cut, as it seems that triaenes are particularly abundant around the porocalices compared to other parts of the sponge. These fragile spicules are also easily broken off. We still assign our specimens to the species *C. australiensis* due to the characteristic presence of acanthose microscleres. It is furthermore one of the most common names used in the literature since its description and without further evidence we do not want to cause more confusion. Further examination of *Cinachyrella* specimens from Australia, in particular from the type locality of *C. australiensis*, will

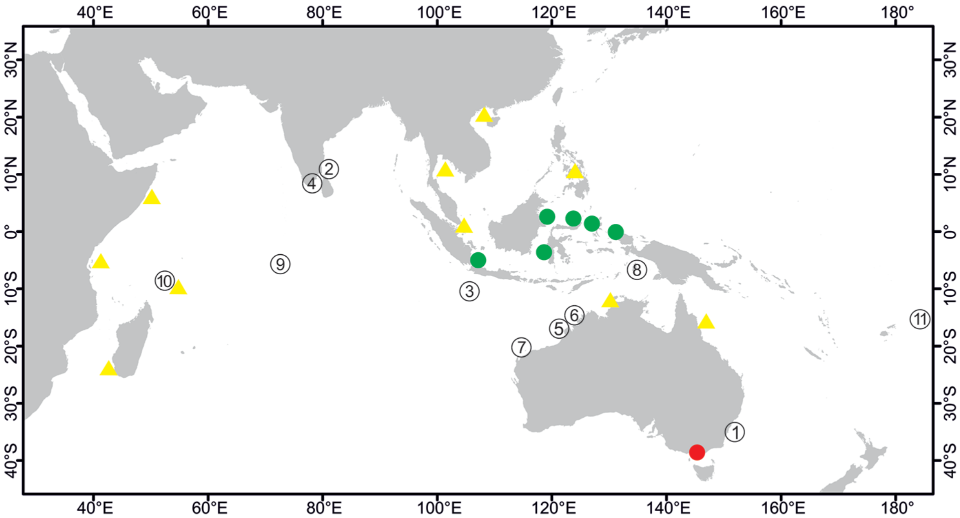

Figure 7. Distribution of *Cinachyrella australiensis*. Red dot: type locality, *Tethya cranium* var. *australiensis* Carter, 1886, Port Phillip Heads, Southeast Australia. Green dots: Indonesian localities where the species was collected recently. Yellow triangles: Non-Indonesian localities, Seychelles Islands, Southwest Madagascar, Zanzibar, Thailand, Singapore, Vietnam, Philippines, Northern Territory of Australia, and the Great Barrier Reef in Australia. Circled numbers: type localities of synonymized species **1** *Spiretta raphidiophora* Lendenfeld, 1888, Port Jackson, Sidney, Australia **2** *Tetilla hirsuta* Dendy, 1889, Gulf of Manaar, Sri Lanka **3** *Tetilla lindgreni* Lendenfeld, 1903, Christmas Island **4** *Tetilla poculifera* Dendy, 1905, Gulf of Manaar, Sri Lanka **5** *Tethya hebes*, 1907, at 19° South on the NW coast of Australia **6** *Cinachyra isis* Lendenfeld, 1907, Mermaid Strait, NW Australia **7** *Tetilla cinachyroides* Hentschel, 1911, Barrow Island, NW Australia **8** *Cinachyra nuda* Hentschel, 1912, Aru Island, Indonesia **9** *Cinachyra vaccinata* Dendy, 1922, Diego Garcia, Chagos Islands **10** *Cinachyra providentiae* Dendy, 1922, Providence Island, Seychelles **11** *Cinachyrella anatriaenilla* Fernandez, Kelly, Bell, 2017, American Samoa.

shed more light in this situation. It is quite possible that after a review of specimens from Southern Australia, it will be evident that the Indonesian specimens that we assign to *C. australiensis* should in fact be assigned to another species. In that case one of the junior synonyms should be used, e.g. *C. raphidiophora* or *C. hirsuta.*

Although our focus was on Indonesian species, it was unavoidable to attempt, for the first time after Burton's review (1934), check the status of his large list of junior synonyms, because some of them were described or later found in Indonesian localities. We gathered as many type specimens as possible, most of them repositories of the NHMUK (London) and NMNH (Washington DC). The main criteria we used to suggest a species as junior synonym of *C. australiensis* were the presence of acanthose microxea and that the mega- and micro-scleres have the same size range of the species. Therefore, here we include as junior synonyms the following species from Burton's list: *Spiretta raphidiophora* Lendenfeld, 1888; *Tetilla hirsuta* Dendy, 1889; *Cinachyra isis* Lenfenfeld, 1907; *Tetilla cinachyroides* Hentschel, 1911; *Cinachyra nuda* Hentschel, 1912; *Cinachyra vaccinata* Dendy, 1922; *Cinachyra providentiae* Dendy, 1922. They all fulfill the *C. australiensis* description.

Here we provide further remarks on the following species, in chronologic order:

Tetilla lindgreni Lendenfeld, 1903 was described as a new species to separate it from *T. ternatensis* Kieschnick, 1896, as *T. ternatensis*is is a *Paratetilla* based on the presence of calthrop-like spicules. Lendenfeld noticed that both, Lindgren's (1898) and subsequently Kirkpatrick's (1900) material, lack such calthrop-like spicules, and instead, they have acanthose microxea similar to other *Tetilla* specimens described in his monograph (Lendenfeld 1903). From that material, we checked Kirkpatrick's specimens and suggest that *T. lindgreni* is a junior synonym of *C. australiensis*.

Tethya hebes Lendenfeld, 1907 has acanthose microxea and it has most of *C. australiensis* characters, yet it was excluded from Lendenfeld's Cinachyrinae-group (with porocalices) because he did not observe porocalices. The type specimens of *T. hebes* examined at the NHM (NHMUK 1908.9.24.66) are two small fragments, about 1.2 × 1 cm, and it is not possible to observe neither discard the presence of porocalices. Apart from that, the general skeletal arrangement and spicule configuration suggest that *T. hebes* fulfil all other morphological characteristics of *C. australiensis*. Therefore, we suggest that *T. hebes* is a junior synonym of *C. australiensis*.

We exclude from *C. australiensis* some junior synonyms that are part of the *schulzei*-group species proposed by Burton (1934). These species have smooth microxea and include Keller's (1891) species from the Red Sea, *Cinachyra schulzei* and *Cinachyra trochiformis*. The taxonomic case of *C. schulzei* becomes more complicated as Kieschnick (1898, 1900) described a new species named *Tetilla schulzei* from material collected in Amboine islands of Indonesia with porocalices and spicules diagnostic of *Cinachyrella*, including microxea. However, Kieschnick did not mention any observation whether or not the microxea of *T. schulzei* have acanthose surface. The set of characters of *Cinachyra schulzei* Keller, 1891 and *Tetilla schulzei* Kieschnick, 1898 correspond to *Cinachyrella*. However, we consider that both species should be treated as homonyms because they were described under two different genera, from different and distant localities and we were not able to find their type material to verify if they could be synonymized. Other species within the *schulzei*-group are *Cinachyra mertoni* Hentschel, 1912 from Kei island in Indonesia; *Tetilla poculifera* Dendy, 1905 from Sri Lanka; and *Chrotella ibis* Row, 1911 from the Red Sea. Special attention and a further revision is proposed for the *schulzei*-group of species, as we did not observe any specimen of the genus *Cinachyrella* with smooth microxea within the Indonesian material examined in this study. It is important to mention that thin smooth microxea were observed in both *Paratetilla* species, *P. bacca* and *P. arcifera*, but they also have calthrops as a diagnostic character of the genus.

We also exclude from *C. australiensis* two of the junior synonyms still present in the WPD (van Soest et al. 2018). First, *Tethya armata* Baer, 1906, because it is clear from the description that this species has a proteinous cortex reinforced by microxeas, resembling other *Craniella* species. Second, we exclude the junior synonym *Cinachyra malaccensis* Sollas, 1902, as the description does not mention the presence of microxea, therefore we suggest to synonymise it with *C. porosa*.

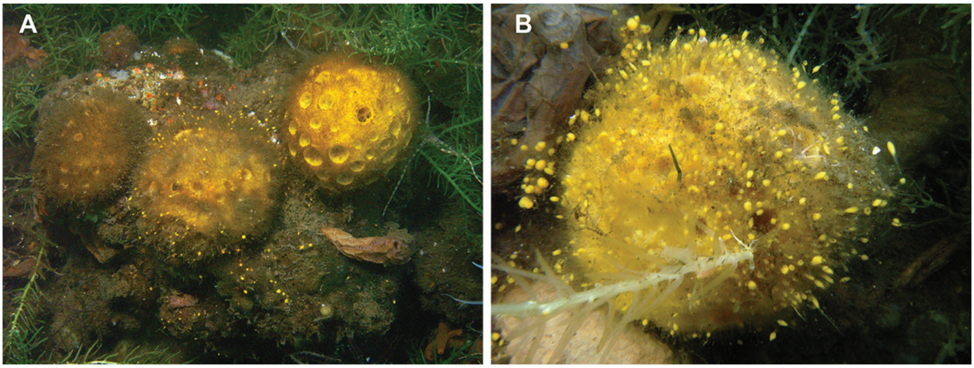

Figure 8. Budding and sediment capture of *Cinachyrella* species **A** Three individuals of *C. porosa* in Haji Buang lake, East Kalimantan, Indonesia, showing distribution of buds beyond the individuals and sediment capture **B** Close up of *C. porosa* with detail of buds. Each individual is approximately 4 cm in diameter.

In our view, the recently erected species of *Cinachyrella anatriaenilla* is junior synonym of *C. australiensis,* because the oxea and the microscleres fall within the size range of the type species of *C. australiensis* as well as the specimens we have included in this review. The authors distinguish their species from *C. australiensis* on the basis of having only one category of oxeas versus two categories in *C. anatriaenilla*. However, we do not recognize size classes in oxea in any of the *Cinachyrella* specimens and types, but rather a continuos range in size (1000–5500 µm for *C. australiensis*). The oxea of *C. anatriaenilla* fall within the size range of the type specimen of *C. australiensis* as well as the other reviewed material of *C. australiensis*. In addition, the authors based their statements on the revision of the type specimen of *C. kuekenthali*, which is from the west Atlantic, but they did not review the type specimen of *C. australiensis* nor any of the other species with acanthose microxea from the Indo-Pacific.

Recent molecular studies (Szitenberg et al. 2013, Schuster et al. 2017) show that *Cinachyrella* is a polyphyletic genus. It is beyond the scope of the current study to review the taxonomic status of the genus *Cinachyrella*. Within *C. australiensis* there are different genotypes (Schuster et al. 2017) that possibly represent morphologically cryptic species. Among the high morphological variation observed within our Indonesian specimens, some trends could be highlighted among the different populations. For instance, specimens from reefs of Berau were generally larger (up to 8 cm in diameter) and their porocalices had a bottle-shape with a small aperture (1 to 4 mm) and the cavity was often occupied by a shrimp. Although these characteristics resemble *C. providentiae*, the latter is one of the junior synonyms that we propose for *C. australiensis* based on spicule dimensions and forms. Specimens from Raja Ampat generally had smaller acanthose microxeas (Table 6), while in some specimens collected in marine lakes few abnormal spicules were observed. Yet, in all cases we could not detect consistent, quantifiable morphological differences.

Cinachyrella porosa **(Lendenfeld, 1888)**
Figs 9, 10

Spiretta porosa Lendenfeld, 1888: 43 (type seen).
Cinachyra malaccensis Sollas, 1902: 219, pl. XIV, fig. 2; pl. XV, fig. 5. Malacca Strait.
Tetilla porosa; Lendenfeld, 1903: 22.
Tetilla anomala Dendy, 1905: 91, pl. III, fig.5 (type seen).
Cinachyra albatridens Lendenfeld, 1907: 149, pl. XV, figs 7–9 (type seen).
Cinachyra albaobtusa Lendenfeld, 1907: 154, pl. XVI, figs 45–52 (type seen).
Cinachyra albabidens Lendenfeld, 1907: 151, pl. XVI, figs 39–44 (type seen).
Tethya clavigera Hentschel, 1912: 327, pl. XVI, fig.1, pl. XVIII, fig. 10 In Aru Island, Beach Ngaiboor Trangan.
Cinachyra anomala; Dendy, 1922: 20, pl. 1, fig. 3 (material seen).
Cinachyra porosa; de Laubenfels, 1954: 240, pl. XI, fig. b (material seen).

Material examined. Holotype NHMUK 1886.8.29.632-633, Port Denison, Australia (as *Spiretta porosa*). NHMUK 1907.2.1.12, Chilaw, Sri Lanka (as *Tetilla anomala*). NHMUK 1908.2.9.40-42, Diego Garcia, Chagos Archipelago (as *Cinachyra albatridens*). NHMUK 1908.9.24.72, Anachoreten (=Keniet) Islands, Papua New Guinea (as *Cinachyra albaobtusa*). NHMUK 1908.9.24.71, Tonga Islands (as *Cinachyra albabidens*). **INDONESIA**, East Kalimantan, *Berau reef,* RMNH.POR.11228 [LT628324]; *Pea Bay,* RMNH.POR.11242, RMNH.POR.11243, RMNH.POR.11244 [JX177888]; *Bamban Lake,* RMNH.POR.11222, RMNH.POR.11223, RMNH.POR.11224, RMNH.POR.11225 [LT628327], RMNH.POR.11226; RMNH.POR.11226; *Bandong Lake,* RMNH.POR.11227; *Haji Buang Lake,* RMNH.POR.11236, RMNH.POR.11237, RMNH.POR.11238, RMNH.POR.11239, RMNH.POR.11240 [LT628325], RMNH.POR.11230, RMNH.POR.11231, RMNH.POR.11232 [LT628326], RMNH.POR.11233, RMNH.POR.11234, RMNH.POR.11235, RMNH.POR. 3514; *Kakaban Lake,* RMNH.POR.11241. Java, *Thousand Islands,* RMNH.POR.1998, RMNH.POR.2108. Sulawesi, *Bunaken,* RMNH.POR.3105. Ternate, *Ternate reef,* RMNH.POR.11309. West Papua, *Sawaundarek Lake,* RMNH.POR.11245 [JX177884], RMNH.POR.11246 [LT628323], RMNH.POR.11247, RMNH.POR.11248; *Ctenophore Lake,* RMNH.POR.11249, RMNH.POR.11250, RMNH.POR.11251, RMNH.POR.11251, RMNH.POR.11252, RMNH.POR.11253, RMNH.POR.11254, RMNH.POR.11255, RMNH.POR.11256, RMNH.POR.11257, RMNH.POR.11258, RMNH.POR.11259; *Outside Ctenophore Lake,* RMNH.POR.11260, RMNH.POR.11261, RMNH.POR.11262; *Gam Island, Reef flat,* RMNH.POR.11263; *Gam Island, Mangrove,* RMNH.POR.11264.

Description. External morphology. Globular sponges, size from 3 to 5 cm in diameter (Figs 9A, 10A, B). Surface highly hispid due to the projecting spicules, covered by numerous porocalices. Porocalices are bowl-shape, with rounded apertures, up to 4 × 5 mm and 5 mm deep, abundant; no cloaca; in preserved material some porocalices are closed.

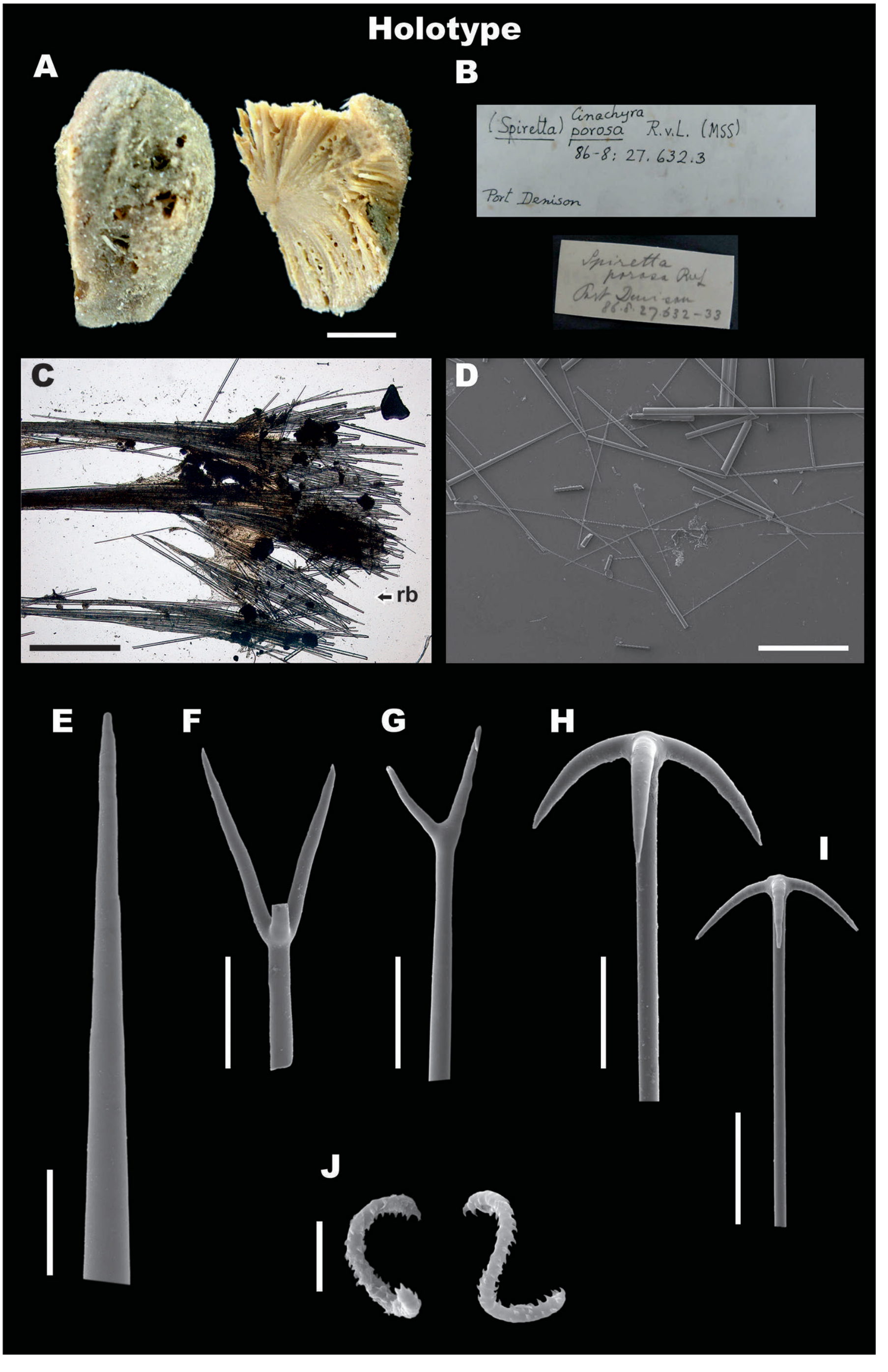

Figure 9. *Cinachyrella porosa*. Holotype NHMUK1886.8.29.632-633, Port Denison, Australia. **A** preserved material showing porocalices and internal structure **B** Labels of the type specimen **C** skeleton **D** electron micrograph showing oxea fragments and triaenes rhabds **E** oxea, end detail **F** protriaene **G** prodiaene **H, I** anatriaenes **J** sigmaspires. Scale bars: 1 cm (**A, C**); 500 µm (**D**); 50 µm (**E**); 40 µm (**F–I**); 5 µm (**J**).

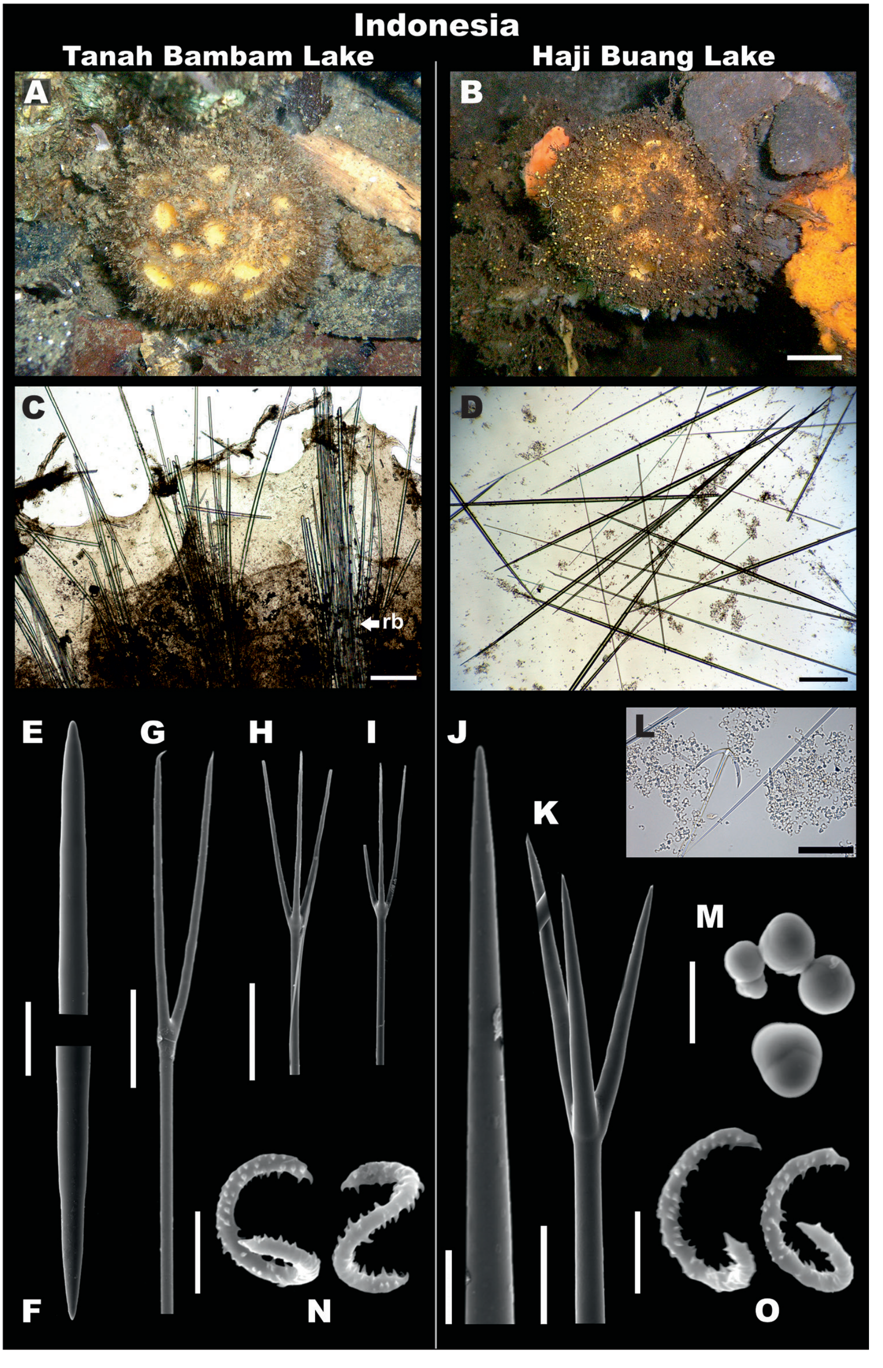

Figure 10. *Cinachyrella porosa* from Indonesia. A, C, E-I, N, RMNH.POR.11223, Tanah Bambam Lake. **B,D, J-M, O** RMNH.POR.11235, Haji Buang Lake **A-B** *In situ* photographs; **C** skeleton, showing radial bundles and triaenes **D** spicules in light microscope showing oxeas and triaenes rhabds **E, F** oxea, end details **G** prodiaene **H, I** protriaene **J** oxea, end detail **K** protriaene **L** anatriaene in light microscopy **M** spheres **N, O** sigmaspires. Scale bars: 500 µm (**C, D**); 20 µm (**E,F, J**); 40 µm (**G–I, K**); 100 µm (**L**); 5 µm (**M–O**).

Color generally yellow when alive (Figure 10A, B), which turns paler or even white-grey after preservation in ethanol (Figure 9A).

Skeleton. No cortex. Skeleton composed by bundles of oxeas and triaenes radiating from a central core (Figs 9C, 10C).

Megascleres. Measurements are shown in Table 6 for the holotype and Indonesian specimens. Holotype, oxeas 820–2553.2–3750 µm × 7.5–29.4–47.5 µm (Figure 9C-E); few anatriaenes (Figure 9H, I), with rhabd always broken 2.5–7.3–15 µm, cladi thin, with obtuse angles 50–67.6–100 µm × 30–42–60 µm × 2.5–5.6–7.5 µm; protriaenes less abundant (Figure 9F), with rhabd always broken up to 5800 µm × 5–7.3–12.5, probably tapering to dimensions < 1 µm, with thin and long cladi (25–44.4–65µm × 35–73–110µm × 5–5.1–7.5 µm); abundant prodiaenes with similar dimensions as protriaenes (Figure 9G).

Microscleres. No microxeas. Sigmaspires 5–8.6–12.5 µm in the holotype (Figure 9J) and 5–8.4–12.5 in the Indonesian specimens (Figure 10N, O), C-S shape; in some Indonesian specimens, silica spheres ranging from 3–7 µm in diameter can be present (Figure 10M).

Ecology. Occurs in reefs, mangroves, and marine lakes. Predominantly in shallow areas. Notably, a large population inhabit the marine lake of Tanah Bambam, where *C. porosa* was the dominant representative of moon sponges. This species produces 1–2 mm sized buds (Figure 8) and buds extensively in marine lakes habitats.

Distribution. According to the material examined in this revision, we observed that this species is widely distributed in the Indo-Pacific, from the Chagos archipelago, Sri Lanka, Australia, and Tonga Islands. In Indonesia, *C. porosa* has been collected in East Kalimantan, Java, Ternate, and West Papua.

Remarks. *Cinachyrella porosa* is distinguished from *C. australiensis* by the absence of acanthose microxea and smaller size of sigmaspires. The first species described with these two diagnostic characteristics was *Spiretta porosa* Lendenfeld, 1888, subsequently transferred to the genus *Tetilla* (Lendenfeld 1903) and included as a junior synonym of *C. australiensis* in both, Burton (1934) and WPD (2018). The detailed examination of the holotype of *C. porosa* suggests that this species should therefore be resurrected. Based on the careful examination of the holotypes of *C. albabidens* (Lendenfeld, 1907) and *C. albaobtusa* (Lendenfeld, 1907), and the descriptions and plates of *C. malaccensis* (Sollas, 1902) and *C. clavigera* (Hentschel, 1912), we coincide with the *porosa*-group recognized by Burton (1934). However, we disagree with the statement that intermediate forms can be found within the wide range of variation of *C. australiensis*, and therefore we consider *C. porosa* as a valid species clearly differentiated from *C. australiensis*. Lendenfeld (1907) recognized the difficulties to separate the three species of the alba-group, and his decision to discriminate them as different species was based on distant localities and slight differences on the abundance of triaenes. After the morphological analysis of the *C. albatridens* holotype, we consider that this species could also be a junior synonym of *C. porosa* because neither microxea nor other characters to separate this species were found. Although Burton (1934) did not consider *C. anomala* (Dendy, 1905) within the *porosa*-group, we suggest that a similar decision could be

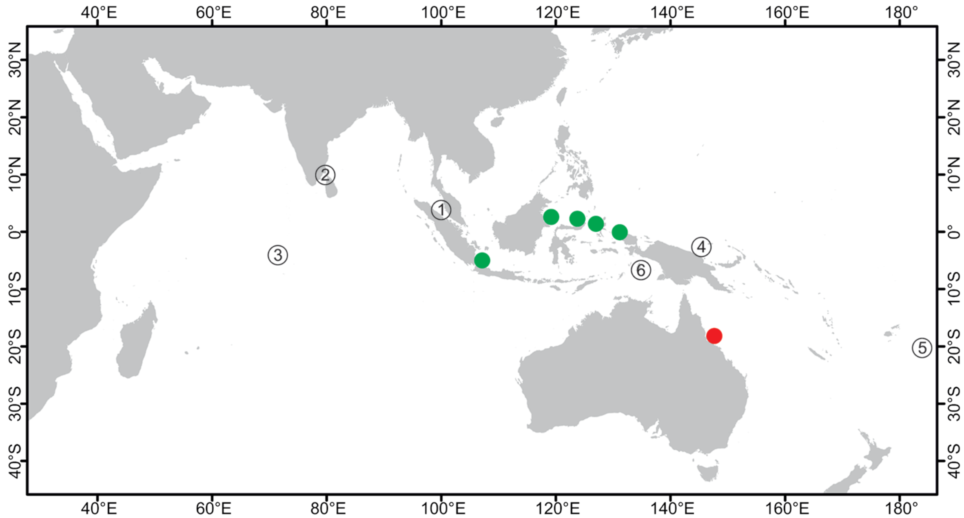

Figure 11. Distribution of *Cinachyrella porosa*. Red dot: type locality, *Spiretta porosa* Lendenfeld, 1888, Port Denison, Queensland, Australia. Green dots: Indonesian localities where the species was collected recently. Circled numbers: type localities of synonymized species **1** *Cinachyra malaccensis* Sollas, 1902, Malacca Strait, Malaysia **2** *Tetilla anomala* Dendy, 1905, Chilaw, Sri Lanka **3** *Cinachyra albatridens* Lendenfeld, 1907, Diego Garcia, Chagos Archipelago **4** *Cinachyra albaobtusa* Lendenfeld, 1907, Anachoreten (=Keniet) Islands, Papua New Guinea **5** *Cinachyra albabidens* Lendenfeld, 1907, Tonga Islands **6** *Tethya clavigera* Hentschel, 1912, Aru Island, Indonesia.

made based on our observations of the type specimen. Some of the Indonesian specimens have silica micro-spherules. Similar spherules have been described for species *C. anomala* and *C. hirsuta* (Dendy, 1905), as well as *Tetilla cinachyroides* (Hentschel 1911). Because *C. hirsuta* and *T. cinachyroides* contain acanthose microxea, they are synonimized with *C. australiensis*. The nature of these spherules has been discussed by Dendy (1905) and Lendenfeld (1907). Dendy (1905) suggests that the spherules are associated with mother cells, which probably would give origin to sigmaspires, or they can be considered as anomalous or incidental spicules. On the other hand, Lendenfeld (1907) estimated that spherules are the earlier stages of oxeas as described for *Tethya cranium* (see Lendenfeld 1907, plate 14 figs 11–15). Silica spherules are very variable within populations of the same species and among different genera in Tetillidae, suggesting that this character has no taxonomic value.

Cinachyrella paterifera **(Wilson, 1925)**
Figs 12, 13

Tetilla (Cinachyrella) paterifera Wilson, 1925: 375; plate 39, figs 6, 8; plate 48, fig. 4 (type seen).

Material examined. Holotype USNM21314, South of Tumindao Reef, Tibutu Island, Sibutu Group, Sulu Archipelago, Philippines, 18 m, 27 Feb 1908. **INDONESIA**. East Kalimantan, *Berau reef,* RMNH.POR.11207; RMNH.POR.11208; RMNH.POR.11209; RMNH.POR.11211. West Papua, *Wallace Lake,* RMNH.POR.11212, RMNH.POR.11213, RMNH.POR.11214; *Outside Wallace Lake,* RMNH.POR.11215; *Gam Island,* RMNH.POR.11216, RMNH.POR.11217, RMNH.POR.11218, RMNH.POR.11219, RMNH.POR.11220; *Ctenophore Lake,* RMNH.POR.11221.

Description. External morphology. Globular sponges, size from 5 to 7 cm in diameter attached to the substrate by a large peduncle/shaft 3 × 2.5 cm (Figure 12 A, B). Surface smooth to hispid due to the projecting spicules, covered by porocalices. Porocalices are bowl or pocket-shape, with rounded apertures, up to 5 × 7 mm and 2–4 mm deep; a central cloaca is located on the top, 15 × 12 mm in diameter and 10 mm deep. Color bright pink when alive, which turns slightly paler in ethanol. Skeleton composed by bundles of oxeas and triaenes radiating from a central core. No cortex.

Megascleres. The holotype and Indonesian measurements are shown in Table 6. Holotype, oxeas 1400–3011.5–4750 µm × 10–34.5–62.5 µm (Figure 12D, I); few anatriaenes (Figure 12L), with a thick, small, poorly developed cladi, 17.5–24.2–30 µm × 2–6.5–10 µm × 5–5.8–7.5 µm, rhabd slightly thicker in the middle 15–25 µm, and tapering to dimensions of < 1 µm.; two different types of protriaenes, first one rare, with thick and small cladi (Figure 12K), 30–32.5–35 µm × 22.5–31.3–40 µm × 7.5–7.5–7.5 µm, rhabd usually broken, up to 5000 × 10 µm, thicker in the middle 40 µm, and tapering to dimensions of < 1 µm, the second type smaller, very abundant around porocalices, with small cladi in acute angle (fork-shape), 7.5–12.5–17.5 µm × 12–15.5–20 µm × 2.5–2.5–2.5 µm, rhabd up to 820 × 2.5 µm; strongyles are common, although only broken spicules observed in the holotype (Figure 12J), Indonesian specimens are 1800–2545.8–3700 µm × 35–42.7–62.5 µm (Figure 12F); no calthrop-like triaenes.

Microscleres. No microxeas; sigmaspires 10–13.2–17.5 µm in the holotype (Figure 12N) and 10–14.8–20 µm in Indonesian material (Figure 12M); C-S shape.

Ecology. The species occurs mainly in reefs, and it is rare in marine lakes and mangroves. It usually inhabits sand bottoms, in which the penduncle serves as a support structure.

Distribution. Indonesia, including East Kalimantan and West Papua. It is also known from Sibutu Island in Philippines (Wilson 1925). Although it is found in a variety of habitats, *C. paterifera* is the least common species of *Cinachyrella* from Indonesia.

Remarks. *Cinachyrella paterifera* has a characteristic elongated peduncle, it is pink to violet colored, and it contains abnormal anatriaenes. Interestingly, Wilson (1925) described rare microxeas (250 × 2 µm) in one specimen of the type series, whilst they were very abundant in the other two types. After a detailed examination of the type specimen USNM 21314 and preparations from different parts of the individual sponge, no microxeas were observed, suggesting that this character is not diagnostic of the species. Although *C. tenuiviolacea* (Pulitzer-Finali 1982) from the Great Barrier Reef resembles *C. paterifera* in the distinctive pink to violet color and presence

Figure 12. *Cinachyrella paterifera*. **A, C, E-H, M** RMNH.POR.11207, Berau Reef, Indonesia (left side). **B, D, I-L, N** holotype USNM 21314, Timundao Reef, Sulu Archipelago, Philippines (right side) **A** specimen recently collected showing typical pink color, porocalices and stalk **B** Holotype, showing porocalices and stalk **C** skeleton showing radial bundles **D** spicules showing oxeas (ox) and strongyle (st), (scale bar 500 µm); **E** oxea, end detail **F** strongyle, end detail **G** protriaene **H** anatriaenes with short or abnormal cladus **I** oxea, end detail **J** strongyle, end detail **K** protriaenes **L** anatriaene with short or abnormal cladus **M, N** sigmaspires. Scale bars: 1 cm (**A, B**); 500 µm (**C, D**); 40 µm (**E–L**); 5 µm (**M, N**)

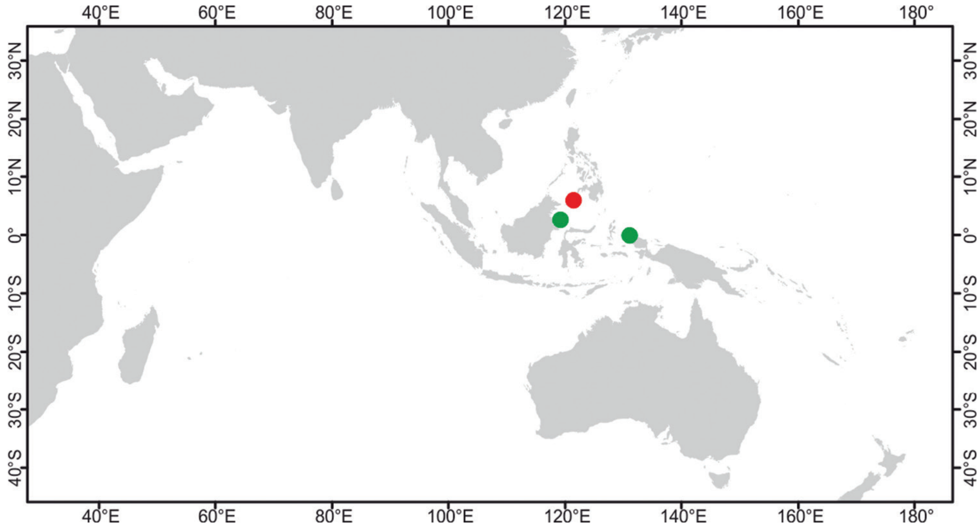

Figure 13. Distribution of *Cinachyrella paterifera*. Red dot: type locality, *Tetilla (Cinachyrella) paterifera* Wilson, 1925, Sibutu Island, Philippines. Green dots: Indonesian localities where the species was collected recently.

of abnormal anatriaenes, it remains to be investigated if these two species could be synonymized. We could not access type material from *C. tenuiviolacea*, and from the bad conditions of preservation noted by Pulitzer-Finali (1982) in his type specimen, it is not possible to determine whether the specimen has or does not have the peduncle characteristic of *C. paterifera*. The large numbers of hair-like protri- and prodiaenes around the porocalices of *C. paterifera*, resemble those described for *C. vaccinata* (Dendy, 1905), yet the *C. vaccinata* type contains acanthose microxea characteristic of *C. australiensis*. *Cinachyrella paterifera* share with *C. porosa* the absence of microxea, but they differ by the larger sigmaspires and abnormal protriaenes of *C. paterifera*. Indonesian specimens vary within the morphological range of the species. Specimens of this species belong to the same phylogenetic clade supporting its monophyly (Szitenberg et al. 2013; Schuster et al. 2017).

Identification key for Indonesian *Paratetilla* and *Cinachyrella* species

1	Porocalices present; calthrops	**2**
–	Porocalices present; no calthrops, all triaenes –if present– are long-shafted....	**4**
2	Trichodragmata present	***Paratetilla corrugata***
–	Trichodragmata not present	**3**
3	High numbers of porocalices, small size (up to 5 mm), brown color	***Paratetilla bacca***
–	Few porocalices, large size (7–15 mm), orange color, fleshy consistency	***Paratetilla arcifera***

4	Microxea present	**5**
–	Microxea not present	**6**
5	Acanthose microxea present (115–270 μm); sigmaspires 10–20 μm	***Cinachyrella australiensis***
–	Smooth microxea	***Cinachyrella schulzei*-group**
6	Small sigmaspires (5–10, few up to 12.5 μm), generally yellow color and ball-shape	***Cinachyrella porosa***
–	Large sigmaspires (10–20 μm), generally pink color, sometimes with peduncle to attach it to the substrate, pear-shape; protriaenes in two different classes; few anatriaenes with reduced and deformed cladi	***Cinachyrella paterifera***

Final remarks

Our results contribute to the understanding of the taxonomy and systematics of the Indo-Pacific tetillids. A review of the taxonomic history of the genus *Paratetilla* and the species *Cinachyrella australiensis*, showed some cases of misinterpreted synonyms, misidentifications and lack of detailed descriptions for some species. The concept of a single widespread species is refuted for *Paratetilla bacca* (Dendy 1922, Burton 1959) as well as for *Cinachyrella australiensis* (Burton 1934). A wide morphological variation within moon sponges was observed for specimens collected in Indonesia. Among our material, we recognize three *Paratetilla* and four *Cinachyrella* species occurring in Indonesia, inhabiting a variety of habitats such as marine lakes, coral reefs, and mangroves. We are resurrecting *P. arcifera* Wilson 1925 and *C. porosa* (Lendenfeld, 1888) as valid species. The majority of the holotypes were studied for the current study; the ones we did not review were either unavailable or the description of the text was clear and comprehensive.

The species of *Paratetilla* and *Cinachyrella* are clearly highly adaptable and widely distributed sponges. All species in the current study are distributed across Indonesia. It is remarkable that they are all sympatric, some species occuring together in the same marine lake. We have reviewed specimens from East Kalimantan, North Sulawesi, and West Papua. It is highly likely that there are more species in Indonesia in regions that have not been sampled as extensively. Further investigations into *Paratetilla* and *Cinachyrella* from the Molluccas, Nusa Tenggara, South Kalimantan, Eastern Papua, and also the virtually unexplored deep sea of Indonesia, will likely lead to the discovery of more species within these genera. Most species occur in all studied habitats (marine lakes, mangroves, and reefs) with a high degree of tolerance for high temperature and sedimentation, as has been observed in other families of sponges (Schönberg 2015). The exceptions to this high tolerance were *P. arcifera* and *C. paterifera,* which were only seen in reefs with little sedimentation or sediment resuspension. High budding was observed in specimens of *Cinachyrella australiensis* and *C. porosa* residing in marine lakes, while no budding was observed in the same species in the reefs. Singh and Thakur

(2015) revealed temperature as the most prominent factor regulating the intensity of budding in *Cinachyrella* cf. *cavernosa*.

Previous molecular phylogenetic studies indicate that *P. bacca, P. arcifera, C. porosa,* and *C. paterifera* are distinct monophyletic species, while *Cinachyrella australiensis* may consist of a species complex with morphologically cryptic species (Schuster et al. 2017). In the specimens that we identify as *C. australiensis* we do not find any consistent differences in spiculation to validate distinct species, in spite of the different haplotypes that are found within our specimens. Carella et al. (2016) also found that several well-supported subgroups within the *Cinachyrella* clade might correspond to subgenera. We were not able to distinguish multiple species with our set of *C. australiensis* specimens using standard morphological characters. Among the reviewed literature, we also observed that there is a tendency among people making inventories of reef species to name any yellow or yellow-orange tetillid ball *C. australiensis*. It is clear that the genus *Cinachyrella* and in particular the species *C. australiensis* require further analysis using either other molecular markers or morphological characters that go beyond the aims of the current study. We hope that our detailed study, images, and key will ensure that species from *Paratetilla and Cinachyrella* will be identified correctly based on morphological characters. It is important to understand the distinction between species, as there is a growing interest in natural products and other biobased studies from tetillids (e.g. Cleary et al. 2013, Mokhlesi et al. 2017, Zhang et al. 2017). We expect that the current study can provide a solid basis for subsequent species descriptions of Indo-Pacific species of the genera *Cinachyrella* and *Paratetilla.*

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Supplementary material 1

Table S1. Full collection details of each sample

Authors: Nadiezhda Santodomingo, Leontine E. Becking

Data type: species data

Link: https://doi.org/10.3897/zookeys.791.27546.suppl1

Supplementary material 2

Figure S1. Type material of *Tethya merguiensis*

Authors: Nadiezhda Santodomingo, Leontine E. Becking

Data type: multimedia

Explanation note: NHMUK 1894.11.16.17, Mergui Archipelago, Myanmar. **A** two slide preparations of the type specimen **B** skeleton, showing anatriaenes and oxeas **C** oxea, anatriaene, and protriaene **D** thin microxeas and sigmaspires **E** sigmaspires. Scale bars: 100 µm (**B, D**); 50 µm (**C**); 20 µm (**E**).

Link: https://doi.org/10.3897/zookeys.791.27546.suppl2

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DATA PAPER

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Marine invertebrate biodiversity from the Argentine Sea, South Western Atlantic

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Abstract

The list of marine invertebrate biodiversity living in the southern tip of South America is compiled. In particular, the living invertebrate organisms, reported in the literature for the Argentine Sea, were checked and summarized covering more than 8,000 km of coastline and marine platform. After an exhaustive literature review, the available information of two centuries of scientific contributions is summarized. Thus, almost 3,100 valid species are currently recognized as living in the Argentine Sea. Part of this dataset was uploaded to the OBIS database, as a product of the Census of Marine Life-NaGISA project. A list of 3,064 valid species, grouped into 1,662 genera distributed in 808 families and 23 phyla, was assessed. The best represented taxa were Arthropoda and Mollusca, contributing approximately with the 50% of the mentioned species in the literature. Cumulative species curves were analyzed in order to estimate the percentage of marine invertebrate biodiversity that is currently known. However, no model fit to our data, showing that the recorded species represent less than 50% of the expected marine invertebrate biodiversity for the Argentine Sea. The great surface of the Argentine Marine Platform (6,581,500 km^2) and the relative low effort in collecting and studying new species due to economical restrictions could explain the low fraction of described species. The training of new taxonomists, as well as, the support of projects that contribute to the knowledge of marine invertebrate biodiversity from South Western Atlantic is recommended.

Keywords

Argentina, Arthropoda, checklist, Mollusca, taxonomy

Project details

Project title: Marine Invertebrate Biodiversity from the Argentine Sea (South Western Atlantic).

Personnel: Gregorio Bigatti (data collector, data manager, project director); Javier H. Signorelli (collection identifier, data collector, data manager).

Funding: This project was partially supported by Census of Marine Life, Nagisa Project, SARCE, PICT 2014-640.

Study area descriptions: The Large Marine Ecosystems (LMEs) are regional units described for the conservation and management of living marine resources (Sherman 1991). The Argentine Sea belongs to LME 14 of South Western Atlantic and comprises coastal environments, continental shelf, slope and ocean basins, covering 6,581,500 km^2 of marine platform (http://www.plataformaargentina.gov.ar/en). In this area, two major marine currents coexist: the cold Malvinas and the warm Brazil currents (Boltovskoy 1979). The former, rich in nutrients, is generated from the Antarctic Circumpolar current, whereas the later moves southwards along the edge of the slope (Piola and Rivas 1997, Piola 2008). In the transition zone (from 30° to 46° S), different oceanographic processes allow a high biological production (Acha et al. 2004). From the biogeographical point of view, two zoogeographical provinces in the Argentine Sea are present. The Argentinean province extends from Cabo Frio, Brazil to Valdés peninsula, Argentina. The Magellanic province ranges from Chiloe Island, Chile, in the Pacific Ocean to the coasts of Valdés peninsula. However, in deeper waters, this biogeographical province extends further northwards to the state of Santa Catarina, Brazil (Woodward 1856, Cooke 1895, Ekman 1953, Scarabino 1977, Boschi et al. 1992, Briggs 1995, Boschi 2000a, 2000b, Spalding et al. 2007).

The Argentine coastline is more than 8,400 km in length (Venerus and Cedrola 2017). Over this large area, heterogeneous topography and variable climate can be observed. As stated by Costello et al. (2017), the oceans appear ideal for biodiversity due to unlimited water availability, large areas and less extreme temperatures respect to land. Although oceans contain more phyla and classes than land and fresh waters, only 16% of total described species are marine. Biodiversity of marine environments reaches a highest level in tropical regions, decreasing gradually towards higher latitudes (Fischer 1960, Roy et al. 1998, Engle and Summers 1999, Gray 2001, Mittelbach et al. 2007). This inverse tendency between biodiversity and latitude seems to be balanced by a higher biomass and endemism at higher latitudes (Boltovskoy et al. 2005). In the last years, some studies have been done in order to document these patterns in marine invertebrates from the South Western Atlantic (Astorga et al. 2003, Bertness et al. 2006, Diez 2006, López Gappa et al. 2006, López Gappa and Sueiro 2006, Carranza et al. 2009, Griffiths et al. 2009, Scarabino et al. 2016, Zelaya 2016, Alves et al. 2017, among others). Also, some international initiatives as NaGISA (Census of

Marine Life), or SARCE (South American Research Group on Coastal Ecosystems), contribute to the knowledge of the coastal marine biodiversity.

The first zoological observations on marine biodiversity from the Argentine Sea, occurred during the 19th century, when European and North American naturalists visited the South American coast (e.g. Voyage dans l'Amérique Méridionale; H.M.S. "Challenger"). These first expeditions allowed the publication of large compendiums and catalogues of marine fauna from South America (Dillwyn, 1817, Say, 1822, d´Orbigny, 1834-47, Reeve, 1843-78, E. A. Smith, 1881, 1885, among others). Subsequent local catalogues complemented these first observations with new additional data (Berg 1900, Bernasconi 1937, Carcelles 1944, Carcelles and Williamson 1951, Castellanos 1970, Escofet 1970, among others). During the second half of the 20th century, several Argentine marine expeditions contributed to increase knowledge on marine invertebrate biodiversity in Argentina [e.g. R/V "*Academik Knipovich* " (1967); R/V "*Almirante Saldanha*" (1966); R/V "*Atlantis II*", (1971); R/V "*El Austral*" (1966-1967); R/V "*Vema*", (1962); R/V "*Walther Herwig*" (1966-71)]. Recently (2009-2017), the R/V Puerto Deseado from the Argentinean National Research Council (CONICET) supported several field works, not only in the Argentine Sea, but also in the Antarctic Continent.

This work compiles and reviews the available information on marine invertebrate biodiversity in the Argentine Sea gathered after an exhaustive literature search.

Taxonomic coverage

The present dataset comprises 23 phyla, 808 families, 1,662 genera and 3,064 valid species. The most represented groups are Arthropoda and Mollusca with 746 (24.35%) and 862 (28.13 %) valid species, respectively (Table 1).

Taxonomic ranks

Phylum: Acanthocephala
Family: Polymorphidae
Genus: *Corynosoma*

Phylum: Annelida
Family: Ampharetidae, Aphroditidae, Arenicolidae, Capitellidae, Chaetopteridae, Chrysopetalidae, Cirratulidae, Cossuridae, Dorvilleidae, Echiuridae, Eunicidae, Flabelligeridae, Glyceridae, Goniadidae, Hesionidae, Histriobdellidae, Lumbrineridae, Maldanidae, Nephtyidae, Nereidae, Nereididae, Oenonidae, Onuphidae, Opheliidae, Orbinidae, Orbiniidae, Oweniidae, Paraonidae, Pectinariidae, Pholoidae, Phyllodocidae, Pilargidae, Piscicolidae, Poecilochaetidae, Polynoidae, Sabellariidae, Sabellidae, Scalibregmatidae, Serpulidae, Sigalionidae, Spionidae, Syllidae, Terebellidae, Travisiidae, Trichobranchidae, Tubificidae, unclassified Annelida 1, Urechidae

Table 1. Number of valid species registered in WoRMS (December 2017) (worldwide distributed) and those reported in the literature for the Argentine Sea.

Phylum	WoRMS		Argentine Sea			
	N° of species	%	N° of families	N° of genera	N° of species	%
Acanthocephala	522	0.30	1	1	2	0.07
Annelida	13949	7.93	48	141	200	6.53
Arthropoda	57104	32.46	213	459	746	24.35
Brachiopoda	426	0.24	4	8	10	0.33
Bryozoa	6111	3.47	79	150	332	10.84
Cephalorhyncha	236	0.13	2	3	3	0.10
Chaetognatha	131	0.07	1	1	1	0.03
Cnidaria	11645	6.62	68	132	224	7.31
Ctenophora	200	0.11	7	7	9	0.29
Dicyemida	122	0.07	2	2	3	0.10
Echinodermata	7332	4.17	48	116	181	5.91
Entoprocta	190	0.11	3	3	5	0.16
Hemichordata	130	0.07	1	1	1	0.03
Mollusca	47478	26.99	206	405	862	28.13
Nematoda	6893	3.92	30	64	113	3.69
Nematomorpha	5	0.00	1	1	1	0.03
Nemertea	1368	0.78	6	12	30	0.98
Phoronida	11	0.01	1	1	2	0.07
Platyhelminthes	12833	7.30	33	54	75	2.45
Porifera	8655	4.92	49	93	250	8.16
Rotifera	201	0.11	1	1	1	0.03
Sipuncula	156	0.09	3	6	9	0.29
Tardigrada	209	0.12	1	1	4	0.13
Total	**175,907**	**100**	**808**	**1,662**	**3,064**	**100**

Genus: *Abarenicola*, *Aglaophamus*, *Ampharete*, *Amphipolydora*, *Amphitrite*, *Anobothrus*, *Aphrodita*, *Arabella*, *Arctacama*, *Armandia*, *Artacama*, *Axiothella*, *Bathydrilus*, *Boccardia*, *Boccardiella*, *Capitella*, *Carazziella*, *Caulleriella*, *Chaetopterus*, *Cirratulus*, *Cirriformia*, *Cistenides*, *Clymenella*, *Cossura*, *Cryobdella*, *Diopatra*, *Dipolydora*, *Dispio*, *Drilonereis*, *Epigamia*, *Eteone*, *Eulalia*, *Eumida*, *Eunereis*, *Eunice*, *Eunoe*, *Euzonus*, *Exogone*, *Ficopomatus*, *Flabelligella*, *Flabelligera*, *Glycera*, *Glycinde*, *Goniada*, *Gymnonereis*, *Halosydna*, *Harmothoe*, *Hemipodia*, *Hermadion*, *Hermundura*, *Heteromastus*, *Hyalopomatus*, *Hydroides*, *Idanthyrsus*, *Kinbergonuphis*, *Laeonereis*, *Laetmonice*, *Lanice*, *Lanicides*, *Laubierpholoe*, *Leitoscoloplos*, *Levinsenia*, *Lumbrineris*, *Maldanella*, *Mammiphitime*, *Marphysa*, *Mercierella*, *Microspio*, *Nainereis*, *Neanthes*, *Neodexiospira*, *Nephtys*, *Nereis*, *Nicon*, *Ninoe*, *Notalia*, *Nothria*, *Notocirrus*, *Notomastus*, *Notopsilus*, *Onuphis*, *Ophelia*, *Ophelina*, *Ophioglycera*, *Oriopsis*, *Owenia*, *Paleanotus*, *Paralaeospira*, *Parapionosyllis*, *Paraprionospio*, *Parasabella*, *Perkinsiana*, *Petaloproctus*, *Pherusa*, *Phragmatopoma*, *Phyllochaetopterus*, *Phyllodoce*, *Phylo*, *Phynchospio*, *Pionosyllis*, *Piromis*, *Platynereis*, *Poecilochaetus*, *Polydora*, *Potamilla*, *Priono-*

spio, *Proceraea*, *Procerastea*, *Prochaetoparia*, *Protolaeospira*, *Romanchella*, *Sabella*, *Sabellaria*, *Salvatoria*, *Scalibregma*, *Schistomeringos*, *Scolecolepides*, *Scolelepis*, *Scoloplos*, *Serpula*, *Sigambra*, *Simplaria*, *Sphaerosyllis*, *Spio*, *Spiochaetopterus*, *Spiophanes*, *Spirorbis*, *Steggoa*, *Sthenelais*, *Stratiodrilus*, *Streblosoma*, *Syllidia*, *Syllis*, *Terebellides*, *Thalassema*, *Thelepus*, *Travisia*, *Trichobranchus*, *Typosyllis*, *Ungulites*, *Urechis*

Phylum: Arthropoda
Family: Acanthaspidiidae, Acanthephyridae, Acanthonotozomellidae, Aegidae, Aethridae, Alpheidae, Amaryllididae, Ameiridae, Ammotheidae, Ampithoidae, Ancorabolidae, Antarcturidae, Anthuridae, Aoridae, Apseudidae, Archaeobalanidae, Archaeocumatidae, Arcturidae, Aristeidae, Atelecyclidae, Austrarcturellidae, Austrobalanidae, Austrodecidae, Balanidae, Belliidae, Benthesicymidae, Blepharipodidae, Bodotriidae, Bopyridae, Branchinectidae, Bythocyprididae, Calanidae, Calappidae, Callianassidae, Callipallenidae, Campylonotidae, Cancridae, Canthocamptidae, Caprellidae, Carcinidae, Chaetiliidae, Chasmocarcinidae, Cheidae, Chthamalidae, Cirolanidae, Clausidiidae, Clausocalanidae, Cletodidae, Colomastigidae, Colossendeidae, Coronulidae, Corophiidae, Crangonidae, Cryptoniscidae, Cushmanideidae, Cyclopinidae, Cyllopodidae, Cymothoidae, Cyproideidae, Cytherideidae, Cytheruridae, Dactylopusiidae, Dendrogastridae, Desmosomatidae, Dexaminidae, Diastylidae, Diogenidae, Diosaccidae, Ectinosomatidae, Endeidae, Enteropsidae, Eophliantidae, Epialtidae, Ethusidae, Exoedicerotidae, Galenidae, Gammarellidae, Geryonidae, Gnathiidae, Grapsidae, Halacaridae, Halophilosciidae, Haploniscidae, Harpacticidae, Hemicytheridae, Hippidae, Hippolytidae, Holognathidae, Homolidae, Hyalellidae, Hyalidae, Hymenosomatidae, Hyssuridae, Idoteidae, Inachidae, Inachoididae, Iphimediidae, Ischnomesidae, Ischyroceridae, Janiridae, Joeropsididae, Lampropidae, Laophontidae, Latreilliidae, Leptanthuridae, Leptocytheridae, Leuconidae, Leucosiidae, Leucothoidae, Ligiidae, Liljeborgiidae, Limnoriidae, Lithodidae, Lophogastridae, Luciferidae, Lysianassidae, Macropipidae, Majidae, Melitidae, Miraciidae, Mithracidae, Munididae, Munnidae, Munnopsidae, Myicolidae, Mysidae, Nannastacidae, Nebaliidae, Nematocarcinidae, Neocytherideididae, Neotanaidae, Nephropidae, Nephropsidae, Normanellidae, Nymphonidae, Ochlesidae, Ocypodidae, Oedicerotidae, Oithonidae, Oplophoridae, Orthopsyllidae, Pachylasmatidae, Pachynidae, Paguridae, Palaemonidae, Pallenopsidae, Pandalidae, Panopeidae, Paracalanidae, Paradoxostomatidae, Paramunnidae, Paranthuridae, Parapaguridae, Parastenheliidae, Parthenopidae, Pasiphaeidae, Peltidiidae, Peltogastridae, Penaeidae, Peracarida, Petalophthalmidae, Photidae, Phoxocephalidae, Phoxocephalopsidae, Phoxychilidiidae, Pinnotheridae, Platyischnopidae, Platyschnopidae, Platyxanthidae, Polybiidae, Polychelidae, Pontocyprididae, Pontogeneiidae, Porcellanidae, Porcellidiidae, Portunidae, Processidae, Pseudidotheidae, Pseudotachidiidae, Rectarcturidae, Santiidae, Scalpellidae, Scyllaridae, Sebidae, Sergestidae, Serolidae, Sesarmidae, Solenoceridae, Sphaeromatidae, Squillidae, Staphylinidae, Stegocephalidae, Stenetriidae, Stenothoidae, Synopiidae, Talitridae, Tanaididae, Tegastidae, Tetrasquillidae,

Thalestridae, Tisbidae, Trachyleberididae, unclassified Arthropoda 2, Upogebiidae, Uristidae, Urothoidae, Varunidae, Xanthidae, Xestoleberididae, Ydianthidae, Zobrachoidae

Genus: *Abyssianira*, *Acanthaspidia*, *Acanthephyra*, *Acanthocarpus*, *Acanthocyclus*, *Acantholobulus*, *Acanthonotozomoides*, *Acanthoserolis*, *Achelia*, *Achelous*, *Actaea*, *Acutiserolis*, *Advenogonium*, *Aega*, *Aegaeon*, *Aegla*, *Agauopsis*, *Allorostrata*, *Allosergestes*, *Allotanais*, *Alpheus*, *Alteutha*, *Amaryllis*, *Ambostracon*, *Ameira*, *Amonardia*, *Ampelisca*, *Amphiascoides*, *Amphiascopsis*, *Amphiascus*, *Amphibalanus*, *Ampithoe*, *Anacalliax*, *Anchistrocheles*, *Anchistylis*, *Ancinus*, *Andaniotes*, *Anoplodactylus*, *Antarctobiotus*, *Antarctomysis*, *Antarcturus*, *Antennuloniscus*, *Antennulosignum*, *Antiboreodiosaccus*, *Apohyale*, *Arcoscalpellum*, *Arenaeus*, *Argilloecia*, *Aristaeopsis*, *Armases*, *Artemesia*, *Arthromysis*, *Artystone*, *Astrurus*, *Atlantocuma*, *Atlantorchestoidea*, *Atlantoserolis*, *Atyloella*, *Atylus*, *Aurila*, *Austinixa*, *Australicythere*, *Austroaurila*, *Austrocytheridea*, *Austrodecus*, *Austrofilius*, *Austromegabalanus*, *Austronanus*, *Austropandalus*, *Austroregia*, *Balanus*, *Bathyporeiapus*, *Benthesicymus*, *Betaeus*, *Betamorpha*, *Bircenna*, *Bledius*, *Blepharipoda*, *Branchinecta*, *Brazilserolis*, *Briarosaccus*, *Bruzelia*, *Caecianiropsis*, *Caecocassidias*, *Caecognathia*, *Calanus*, *Callinectes*, *Callipallene*, *Callistocythere*, *Calyptraeotheres*, *Campylaspis*, *Campylonotus*, *Caprella*, *Carcinus*, *Cassidias*, *Cerapus*, *Ceratoserolis*, *Cetopirus*, *Chaceon*, *Chaetarcturus*, *Chasmocarcinus*, *Cheirimedon*, *Cheus*, *Chiriscus*, *Chono*, *Chorismus*, *Cilunculus*, *Cirolana*, *Claudicuma*, *Clausocalanus*, *Cleantis*, *Coenophthalmu*, *Colanthura*, *Collodes*, *Colomastix*, *Colossendeis*, *Compressoscalpellum*, *Coperonus*, *Copidognathus*, *Corystoides*, *Cristaserolis*, *Cumella*, *Cumellopsis*, *Curidia*, *Cushmanidea*, *Cyathura*, *Cyclaspis*, *Cyclopina*, *Cyllopus*, *Cymadusa*, *Cyrtograpsus*, *Cyrtoplax*, *Cytheropteron*, *Cytherura*, *Dactylopusia*, *Danielethus*, *Dardanus*, *Dendrogaster*, *Deosergestes*, *Diarthrodes*, *Diastylis*, *Disconectes*, *Dissodactylus*, *Dolichiscus*, *Drepanopus*, *Dynamenella*, *Dynoides*, *Ebalia*, *Ectinosoma*, *Edotia*, *Elminius*, *Emerita*, *Endeis*, *Enhydrosoma*, *Enhydrosomella*, *Enteropsis*, *Erikus*, *Ethusina*, *Eualus*, *Euchaetomera*, *Eudevenopus*, *Eudorella*, *Eugerdella*, *Eupelte*, *Eurycope*, *Eurypanopeus*, *Eurypodius*, *Eusergestes*, *Exhippolysmata*, *Exoediceropsis*, *Exosphaeroma*, *Fabia*, *Falklandia*, *Farfantepenaeus*, *Fissarcturus*, *Fistulobalanus*, *Fosterella*, *Frontoserolis*, *Fuegiphoxus*, *Funchalia*, *Gammaropsis*, *Gardinerosergia*, *Glyptonotus*, *Gnathia*, *Gondogeneia*, *Goodingius*, *Gracilimesus*, *Halacarellus*, *Halacarus*, *Halicarcinus*, *Haliophasma*, *Halophiloscia*, *Hansenomysis*, *Haplocheira*, *Harpacticus*, *Hemicyclops*, *Hemicythere*, *Hemicytherura*, *Hemilamprops*, *Hemingwayella*, *Henryhowella*, *Hepatus*, *Heterocythereis*, *Heterolaophonte*, *Heterosquilla*, *Hexapanopeus*, *Holostylis*, *Homola*, *Hyalella*, *Hyssura*, *Iais*, *Ianthopsis*, *Iathrippa*, *Idotea*, *Idyanthe*, *Ilyarachna*, *Iphimedia*, *Iphimediella*, *Ischyrocerus*, *Ischyromene*, *Isocladus*, *Isonebula*, *Jassa*, *Joeropsis*, *Laophonte*, *Laophontodes*, *Latreillia*, *Latreutes*, *Lebbeus*, *Lembos*, *Leptanthura*, *Leptocuma*, *Leptoserolis*, *Leptostylis*, *Leucippa*, *Leucon*, *Leucothoe*, *Leurocyclus*, *Libidoclaea*, *Libinia*, *Ligia*, *Liljeborgia*, *Limnoria*, *Linca*, *Liriopsis*, *Lissosabinea*, *Litarcturus*, *Lithodes*, *Lophogaster*, *Loxopagurus*, *Loxoreticulatum*, *Lucifer*, *Macrochiridotea*, *Macrochiridothea*, *Magellianira*, *Melita*, *Merhippolyte*, *Meridionalicythere*, *Meridiosignum*, *Mesochra*, *Mesorhoea*, *Metacarcinus*, *Metanephrops*, *Metatiron*, *Metharpinia*, *Microphoxus*, *Mixarcturus*, *Monocoro-*

phium, *Monoculopsis*, *Moruloidea*, *Munida*, *Munna*, *Munneurycope*, *Munnogonium*, *Myropsis*, *Mysidetes*, *Mysidopsis*, *Nannocalanus*, *Natatolana*, *Nauticaris*, *Neasellus*, *Neastacilla*, *Nebalia*, *Nematocarcinus*, *Neocytherideis*, *Neohelice*, *Neojaera*, *Neolithodes*, *Neomysis*, *Neosergestes*, *Neoserolis*, *Neotanais*, *Normanella*, *Nothochthalamus*, *Notiax*, *Notobalanus*, *Notocrangon*, *Notomegabalanus*, *Notopoma*, *Nymphon*, *Oculocytheropteron*, *Oithona*, *Omonana*, *Orchestia*, *Orchomenella*, *Ornatoscalpellum*, *Orthopsyllus*, *Ostrincola*, *Ovalipes*, *Pachycheles*, *Paguristes*, *Pagurus*, *Palaemon*, *Pallenopsis*, *Pandalopsis*, *Panoppeus*, *Pantomus*, *Papillosacythere*, *Paracalanus*, *Paracymothoa*, *Paradexamine*, *Paradoxapseudes*, *Paradoxostoma*, *Parafoxiphalus*, *Paralaophonte*, *Paralomis*, *Paramonoculopsis*, *Paramphiascella*, *Paramunna*, *Paranthura*, *Parapenaeus*, *Parasergestes*, *Paraserolis*, *Parastenhelia*, *Parategastes*, *Parathalestris*, *Parawaldeckia*, *Paridotea*, *Parione*, *Pariphimedia*, *Parthenope*, *Pasiphaea*, *Patagoniella*, *Peisos*, *Pelia*, *Peltarion*, *Penaeus*, *Pentacheles*, *Perissocope*, *Perissocytheridea*, *Persephona*, *Petalidium*, *Philocheras*, *Phoxocephalopsis*, *Phoxorgia*, *Pilumnoides*, *Pilumnus*, *Pinnaxodes*, *Pinnixa*, *Planes*, *Platidotea*, *Platorchestia*, *Platyisao*, *Pleoticus*, *Pleurosignum*, *Polycheria*, *Polyonix*, *Porcellana*, *Porcellidium*, *Poti*, *Prehensilosergia*, *Probolisca*, *Probopyrus*, *Procampylaspis*, *Processa*, *Procythereis*, *Proharpinia*, *Propagurus*, *Propontocypris*, *Pseudidothea*, *Pseudione*, *Pseudiphimediella*, *Pseudobranchiomysis*, *Pseudomma*, *Pterygosquilla*, *Pyromaia*, *Quetzogonium*, *Quinquelaophonte*, *Retarcturus*, *Rhombognathus*, *Riggia*, *Robertgurneya*, *Robertsonia*, *Rochinia*, *Santia*, *Scutellidium*, *Scyllarides*, *Seba*, *Semicytherura*, *Semixestoleberis*, *Septemserolis*, *Sergestes*, *Sergia*, *Sergio*, *Serolella*, *Serolis*, *Sinelobus*, *Socarnoides*, *Sphaeroma*, *Spinolambrus*, *Stenocionops*, *Stenorhynchus*, *Stereomastis*, *Stylicletodes*, *Stylopandalus*, *Styloptocuma*, *Sursumura*, *Sympagurus*, *Synerythrops*, *Syneurycope*, *Synidotea*, *Syrrhoe*, *Systellaspis*, *Tanais*, *Tanystylum*, *Tenupedunculus*, *Tetrachaelasma*, *Tetraxanthus*, *Thymops*, *Thymopsis*, *Thysanoserolis*, *Tigriopus*, *Tiron*, *Tisbe*, *Tmetonyx*, *Tonocote*, *Triantella*, *Tryphosites*, *Tumidotheres*, *Uca*, *Ultimachelium*, *Upogebia*, *Uristes*, *Uromunna*, *Urothoe*, *Vanhoeffenura*, *Victorhensenoides*, *Waiteolana*, *Xenanthura*, *Xestoleberis*, *Xigonus*, *Xiphopenaeus*, *Xouthous*, *Zausopsis*, *Zyzzigonium*

Phylum: Brachipoda
Family: Discinidae, Frieleiidae, Terebratellidae, Terebratulidae
Genus: *Aneboconcha*, *Dyscritosia*, *Liothyrella*, *Magellania*, *Neorhynchia*, *Pelagodiscus*, *Syntomaria*, *Terebratella*

Phylum: Bryozoa
Family: Adeonellidae, Adeonidae, Aeteidae, Alcyonidiiade, Arachnopusiidae, Aspidostomatidae, Beaniidae, Bifaxariidae, Bitectiporidae, Bryocryptellidae, Buffonellodidae, Bugulidae, Buskiidae, Calloporidae, Calvetiidae, Calwelliidae, Candidae, Catenicellidae, Cellaridae, Cellariidae, Celleporidae, Cerioporidae, Chaperiidae, Chorizoporidae, Crepidacanthidae, Cribilinidae, Cribrilinidae, Crisiidae, Cryptosulidae, Cupuladriidae, Diaperoeciidae, Diastoporidae, Electridae, Entalophoridae, Escharinidae, Exochellidae, Farciminariidae, Farrellidae, Favoelariidae,

Flustridae, Fredericellidae, Frondiporidae, Gigantoporidae, Haywardozoontidae, Hippoporidridae, Hippothoidae, Horneridae, Immergentiidae, Inversiulidae, Lacernidae, Lekythoporidae, Lichenoporidae, Lyroporidae, Membraniporidae, Microporellidae, Microporidae, Myriaporidae, Odmoneidae, Oncousoeciidae, Onichocellidae, Orbituliporidae, Phidoloporidae, Philodoporidae, Plagioeciidae, Porinidae, Pseudidmoneidae, Pustuloporidae, Romancheinidae, Romncheinidae, Schizoporellidae, Sclerodomidae, Scrupariidae, Smittinidae, Stomatoporidae, Tubuliporidae, Umbonulidae, unclassified Bryozoa 1, Vesicularidae, Walkeriidae

Genus: *Adeonella, Adeonellopsis, Aetea, Aimulosia, Alcyonidium, Alderina, Alloeoflustra, Amastigia, Amathia, Amphiblestrum, Andreella, Antarctothoa, Apiophragma, Arachnopusia, Aspericreta, Aspidostoma, Austroflustra, Beania, Bicrisia, Bientalophora, Bowerbankia, Buffonellodes, Bugula, Bugulina, Buskia, Caberea, Callopora, Calloporina, Calvetia, Camptoplites, Canda, Carbasea, Catadysis, Cellaria, Cellarinella, Celleporella, Celleporina, Chaperia, Chaperiopsis, Chartella, Chiastosella, Chondriovelum, Chorizopora, Codonellina, Columnella, Conopeum, Cookinella, Cornucopina, Crepidacantha, Crisia, Crisularia, Cryptostomaria, Cryptosula, Dartevellia, Diaperoecia, Discoporella, Disporella, Domosclerus, Electra, Ellisina, Escharina, Escharoides, Euginoma, Eurystrotos, Exochella, Farrella, Fasciculipora, Favostimosia, Fenestrulina, Figularia, Filisparsa, Flustrapora, Foveolaria, Galeopsis, Gigantopora, Gregarinidra, Haywardozoon, Hemismittoidea, Himantozoum, Hippadenella, Hippomonavella, Hippoporina, Hippothoa, Hornera, Ichthyaria, Idmidronea, Idmonea, Immergentia, Inversiula, Jolietina, Kenoaplousina, Lacerna, Lageneschara, Lichenopora, Mecynoecia, Melicerita, Membranicellaria, Membranipora, Menipea, Metroperiella, Micropora, Microporella, Monastesia, Myriapora, Neoflustra, Neothoa, Nevianipora, Notoplites, Odontoporella, Ogivalia, Orthoporidra, Orthoporidroides, Osthimosia, Paracellaria, Parafigularia, Parasmittina, Phonicosia, Plagioecia, Platonea, Platychelyna, Plesiothoa, Porella, Pseudidmonea, Retepora, Reteporella, Reteporellina, Romancheina, Salicornaria, Sclerodomus, Scruparia, Scrupocaberea, Scrupocellaria, Securiflustra, Sertella, Smittina, Smittoidea, Sphaerulobryozoon, Spiroporina, Stephanollona, Stomatopora, Stomhypselosaria, Talivittaticella, Tricellaria, Tubulipora, Turbicellepora, Turritigera, Umbonula, Villicharixa, Walkeria, Xylochotridens*

Phylum: Cephalorhyncha
Family: Echinoderidae, Priapulidae.
Genus: *Echinoderes*, *Priapulopsis*, *Priapulus*

Phylum: Chaetognatha
Family: Sagittidae
Genus: *Sagitta*

Phylum: Cnidaria
Family: Acontiophoridae, Actiniidae, Actinostolidae, Aglaopheniidae, Alcyoniidae, Andvakiidae, Anthoptilidae, Bathyphelliidae, Blackfordiidae, Boloceroididae,

Bougainvilliidae, Campanulariidae, Campanulinidae, Caryophylliidae, Clavulariidae, Corallimorphidae, Corymorphidae, Corynidae, Cyaneidae, Diadumenidae, Drymonematidae, Edwardsiidae, Epizoanthidae, Eudendriidae, Flabellidae, Halcampidae, Haleciidae, Haliplanellidae, Halipteridae, Haloclavidae, Halopteridae, Halopterididae, Hebellidae, Hormathiidae, Hydractiniidae, Hydridae, Isanthidae, Isididae, Isophellidae, Kirchenpaueriidae, Lafoeidae, Limnactiniidae, Lovenellidae, Lychnorhizidae, Metridiidae, Mitrocomidae, Niobiidae, Oceaniidae, Olindiidae, Pelagiidae, Pennatulidae, Periphyllidae, Phialellidae, Plumulariidae, Primnoidae, Renillidae, Rhodaliidae, Sagartiidae, Sertulariidae, Stomolophidae, Stylasteridae, Syntheciidae, Tetraplatidae, Thyroscyphidae, Tiarannidae, Tubulariidae, Ulmaridae, unclassified Cnidaria 1

Genus: *Abietinella*, *Acryptolaria*, *Actinauge*, *Actinostola*, *Actinothoe*, *Aglaophenia*, *Alcyonium*, *Amphianthus*, *Amphisbetia*, *Andvakia*, *Anemonia*, *Antholoba*, *Anthoptilum*, *Anthothoe*, *Armadillogorgia*, *Artemidactis*, *Atolla*, *Aulactinia*, *Aurelia*, *Austroneophellia*, *Billardia*, *Bimeria*, *Blackfordia*, *Bolocera*, *Boloceroides*, *Botryon*, *Bougainvillia*, *Boungainvillia*, *Bunodactis*, *Calliactis*, *Calycella*, *Campanularia*, *Caryophyllia*, *Chrysaora*, *Clytia*, *Corymorpha*, *Corynactis*, *Coryne*, *Desmonema*, *Diadumene*, *Drymonema*, *Dynamena*, *Echinisis*, *Ectopleura*, *Epiactis*, *Epizoanthus*, *Eucheilota*, *Eudendrium*, *Filellum*, *Flabellum*, *Glandulactis*, *Gonothyraea*, *Grammaria*, *Halecium*, *Halipteris*, *Halisiphonia*, *Halopteris*, *Harenactis*, *Hartlaubella*, *Hebella*, *Hormathia*, *Hybocodon*, *Hydra*, *Hydractinia*, *Hydrodendron*, *Inferiolabiata*, *Isoparactis*, *Isophellia*, *Isosicyonis*, *Isotealia*, *Kirchenpaueria*, *Lafoea*, *Limnactinia*, *Lychnorhiza*, *Lytocarpia*, *Mitrocomella*, *Monactis*, *Monastaechas*, *Nauthisoe*, *Nemertesia*, *Niobia*, *Obelia*, *Olindias*, *Orthopyxis*, *Oulactis*, *Parabunodactis*, *Parahalcampa*, *Paraisometridium*, *Paranthus*, *Paraphelliactis*, *Parascyphus*, *Parathuiaria*, *Pariactis*, *Peachia*, *Pennatula*, *Periphylla*, *Phacellophora*, *Phelliactis*, *Phelliogeton*, *Phialella*, *Phlyctenanthus*, *Phymactis*, *Plumarella*, *Plumularia*, *Pseudoparactis*, *Ramirezia*, *Renilla*, *Rhizogeton*, *Rhodalia*, *Rhodelinda*, *Sagartianthus*, *Sarsia*, *Schizotricha*, *Scolanthus*, *Sertularella*, *Sicyonis*, *Silicularia*, *Sporadopora*, *Stauroteca*, *Staurotheca*, *Stegella*, *Stegopoma*, *Stomolophus*, *Stygiomedusa*, *Stylaster*, *Symplectoscyphus*, *Synthecium*, *Tetraplatia*, *Tricnidactis*, *Urticina*, *Urticinopsis*, *Zoanthina*

Phylum: Ctenophora

Family: Atollidae, Beroidae, Cestidae, Lampeidae, Lyroctenidae, Mertensiidae, Pleurobrachiidae

Genus: *Beroe*, *Callianira*, *Cestum*, *Lampea*, *Lyrocteis*, *Mnemiopsis*, *Pleurobrachia*

Phylum: Dicyemida

Family: Conocyemidae, Dicyemidae

Genus: *Conocyema*, *Dicyema*

Phylum: Echinodermata

Family: Abertellidae, Aeropsidae, Amphilepididae, Amphiuridae, Antedonidae, Arbaciidae, Asteriidae, Asterinidae, Asterostomatidae, Astropectinidae, Benthopectinidae, Chiridotidae, Cidaridae, Ctenocidaridae, Ctenodiscidae, Cucumariidae, Echinasteridae, Echinidae, Elpidiidae, Ganeriidae, Goniasteridae, Goniopectinidae, Gorgonocephalidae, Heliasteridae, Korethrasteridae, Laetmogonidae, Luidiidae, Mellitidae, Odontasteridae, Ophiacanthidae, Ophiactidae, Ophiodermatidae, Ophiolepididae, Ophiomyxidae, Ophiuridae, Parechinidae, Phyllophoridae, Poraniidae, Prenasteridae, Pseudachasteridae, Psolidae, Pterasteridae, Schizasteridae, Solasteridae, Stichasteridae, Synallactidae, Temnopleuridae, Urechinidae

Genus: *Abatus*, *Abertella*, *Aceste*, *Achlyonice*, *Acodontaster*, *Allostichaster*, *Amphilepis*, *Amphiodia*, *Amphiophiura*, *Amphipholis*, *Amphipodia*, *Amphiura*, *Anasterias*, *Anteliaster*, *Arbacia*, *Asterina*, *Astrochlamys*, *Astrohamma*, *Astropecten*, *Astrotoma*, *Athyonidium*, *Austrocidaris*, *Bathybiaster*, *Bathyplotes*, *Brisaster*, *Calyptraster*, *Ceramaster*, *Cheiraster*, *Chiridota*, *Cladaster*, *Cladodactyla*, *Cosmasterias*, *Ctenodiscus*, *Cycethra*, *Delopatagus*, *Diplasterias*, *Diplodontias*, *Diplopteraster*, *Echinaster*, *Elpidia*, *Encope*, *Florometria*, *Ganeria*, *Glabraster*, *Gorgonocephalus*, *Hemioedema*, *Hemipholis*, *Henricia*, *Hippasteria*, *Hymenaster*, *Isometra*, *Labidiaster*, *Laetmogone*, *Leptychaster*, *Lethasterias*, *Lophaster*, *Loxechinus*, *Luidia*, *Luidiaster*, *Mediaster*, *Molpadiodemas*, *Neomilaster*, *Notocidaris*, *Odontaster*, *Ophiacantha*, *Ophiactis*, *Ophiocamax*, *Ophioceres*, *Ophiochondrus*, *Ophiocten*, *Ophiogona*, *Ophiolebella*, *Ophioleuce*, *Ophiolimna*, *Ophiolycus*, *Ophiomastus*, *Ophiomitrella*, *Ophiomusium*, *Ophiomyxa*, *Ophionotus*, *Ophioperla*, *Ophioplinthus*, *Ophioplocus*, *Ophiosparte*, *Ophiosteira*, *Ophiozonella*, *Ophiura*, *Pentactella*, *Pentamera*, *Peribolaster*, *Perissasterias*, *Perknaster*, *Porianopsis*, *Promachocrinus*, *Psalidaster*, *Pseudarchaster*, *Pseudechinus*, *Pseudocnus*, *Pseudostichopus*, *Psilaster*, *Psolidium*, *Psolus*, *Pteraster*, *Remaster*, *Scotoplanes*, *Sigmodota*, *Smilasterias*, *Solaster*, *Staurocucumis*, *Sterechinus*, *Taeniogyrus*, *Trachythyone*, *Tremaster*, *Tripylaster*, *Tripylus*, *Urechinus*

Phylum: Entoprocta
Family: Barentsiidae, Loxosomatidae, Pedicellinidae
Genus: *Barentsia*, *Loxosomella*, *Pedicellina*

Phylum: Hemichordata
Family: Rhabdopleuridae
Genus: Rhabdopleura

Phylum: Mollusca
Family: Acmaeidae, Acteocinidae, Acteonidae, Aeolidiidae, Anatomidae, Anomiidae, Aplustridae, Argonautidae, Astartidae, Barleeiidae, Bathydorididae, Bathyspinulidae, Borsoniidae, Buccinidae, Cadlinidae, Caecidae, Calliostomatidae, Callochitonidae, Calyptraeidae, Cancellariidae, Capulidae, Cardiidae, Carditidae, Cassidae, Cavoliniidae, Cerithiidae, Cetoconchidae, Chaetopleuridae, Chitonidae, Chromodorididae, Cingulopsidae, Cliidae, Clionidae, Cocculinidae, Cochlespiridae, Cochliopidae, Collonidae, Columbellidae, Condylocardiidae, Conidae, Corambidae, Corbulidae, Crassatellidae, Cuspidariidae, Cuvierinidae, Cyamiidae, Cy-

clochlamyidae, Cylichnidae, Cymbuliidae, Dentaliidae, Diaphanidae, Discodorididae, Donacidae, Dorididae, Dotidae, Drillidae, Drilliidae, Eatoniellidae, Eatonielllidae, Ellobiidae, Entalinidae, Enteroctopodidae, Epitoniidae, Eubranchidae, Eulimellinae, Eulimidae, Facelinidae, Fasciolariidae, Fissurellidae, Flabellinidae, Gadilidae, Gaimardiidae, Galeommatidae, Gastrochaenidae, Gonatidae, Goniodoridae, Goniodorididae, Hemiarthridae, Hermaeidae, Hiatellidae, Ischnochitonidae, Kellielidae, Lametilidae, Laonidae, Lasaeidae, Laternulidae, Lepetidae, Leptochitonidae, Limacinidae, Limapontiidae, Limidae, Limifossoridae, Limifossoridae, Limopsidae, Liotiidae, Littorinidae, Loliginidae, Lologinidae, Lottiidae, Lucinidae, Lyonsiellidae, Lyonsiidae, Mactridae, Malletiidae, Mangeliidae, Margaritidae, Marginellidae, Mathildidae, Mesodesmatidae, Montacutidae, Mopaliidae, Muricidae, Myidae, Mytilidae, Mytillidae, Nacellidae, Nassariidae, Naticidae, Neilonellidae, Neoleptonidae, Neomeniidae, Newtoniellidae, Notaeolidiidae, Nuculanidae, Nuculidae, Nystiellidae, Ocotpodidae, Octopodidae, Octopoidae, Olivellidae, Olividae, Omalogyridae, Ommastrephidae, Onchidorididae, Onychoteuthidae, Orbitestellidae, Ostreidae, Pandoridae, Pectinidae, Pendromidae, Peraclidae, Periplomatidae, Pharidae, Philinidae, Philobryidae, Pholadidae, Plakobranchidae, Planorbidae, Pleurobranchaeidae, Pleurobranchiidae, Plicatulidae, Pnemodermatidae, Polyceridae, Poromyidae, Propeamussiidae, Protocuspidariidae, Pseudomelatomidae, Pteriidae, Pulsellidae, Pyramidellidae, Pyroteuthidae, Ranellidae, Raphitomidae, Retusidae, Rhabdidae, Rissoidae, Sareptidae, Scissurellidae, Seguenziidae, Seguenzioidae, Semelidae, Siliculidae, Simrothiellidae, Siphonariidae, Skeneidae, Solariellidae, Solecurtidae, Solemyidae, Solenidae, Spiolidae, Tegulidae, Tellinidae, Terebridae, Teredinidae, Tergipedidae, Thraciidae, Thyasiridae, Tindariidae, Tofanellidae, Tonnidae, Tritoniidae, Trochidae, Turbinidae, Turritelidae, Ungulinidae, Vanikoridae, Velutinidae, Veneridae, Vesicomyidae, Volutidae, Volutomitridae, Wemersoniollidae, Yoldiidae

Genus: *Abra*, *Acanthina*, *Acanthodoris*, *Acanthopleura*, *Acesta*, *Acharax*, *Acmaea*, *Acteocina*, *Acteon*, *Adamussium*, *Adelomelon*, *Adipicola*, *Admete*, *Adontorhina*, *Adrana*, *Aeolidia*, *Aequipecten*, *Aesopus*, *Aforia*, *Agladrillia*, *Alia*, *Aloidis*, *Altenaeum*, *Alvania*, *Amarilladesma*, *Amauropsis*, *Amiantis*, *Amphissa*, *Anachis*, *Anatoma*, *Ancula*, *Angulus*, *Anomacme*, *Anomalocardia*, *Antistreptus*, *Aplysiopsis*, *Argeneuthria*, *Argentovoluta*, *Argobuccinum*, *Argonauta*, *Aspalima*, *Astarte*, *Asthenothaerus*, *Astyris*, *Atomiscala*, *Aulacomya*, *Austrochlamys*, *Austrocominella*, *Axinulus*, *Bankia*, *Barleeia*, *Bathydoris*, *Bathyspinula*, *Belalora*, *Bentheledone*, *Berghia*, *Berthella*, *Bostrycapulus*, *Brachidontes*, *Brachiodontes*, *Brevinucula*, *Brookula*, *Buccinanops*, *Cadlina*, *Cadulus*, *Caecum*, *Calliostoma*, *Callochiton*, *Capulus*, *Cardiomya*, *Carditamera*, *Carditella*, *Carditopsis*, *Carolesia*, *Catillopecten*, *Cavinetnea*, *Cavolinia*, *Cerithiella*, *Cerodrillia*, *Cetoconcha*, *Chaetopleura*, *Chlamys*, *Chrysallida*, *Clio*, *Clione*, *Cocculina*, *Conchoceles*, *Conus*, *Coralliophila*, *Corambe*, *Corbula*, *Coroniscala*, *Coronium*, *Crassinella*, *Crenella*, *Crepidula*, *Crepipatella*, *Cuspidaria*, *Cuthona*, *Cuvierina*, *Cyamiocardium*, *Cyamiun*, *Cyclocardia*, *Cyclochlamys*, *Cyclopecten*, *Cyclostrema*, *Cylichna*, *Cymbulia*, *Dacrydium*, *Dallocardia*, *Darina*, *Delectopecten*, *Dentalium*, *Dermatomya*, *Diaphana*, *Diaulula*, *Diodora*, *Diplodonta*, *Donax*, *Doris*, *Doryteuthis*, *Doto*, *Drillia*, *Duplicaria*, *Eatoniella*, *Eledone*, *Elysia*, *Emiliostraca*, *Ennucula*, *Ensis*, *Enteroctopus*, *Entodesma*, *Epicodakia*, *Epitonium*, *Ercolania*, *Eubranchus*, *Eulimastoma*, *Eulimella*, *Eulimostraca*, *Eumetula*, *Eurhomalea*, *Euspira*, *Eutivela*, *Falsilunatia*, *Falsimargarita*, *Falsitromina*, *Fictonoba*, *Fissidentalium*, *Fissurela*, *Fissurella*, *Fissurellidea*, *Flabellina*, *Flexopecten*, *Fuegotrophon*, *Fusitriton*, *Gaimardia*, *Gargamella*, *Geitodoris*, *Genaxinus*, *Glypteuthria*, *Gonatus*, *Graneledone*, *Halistylus*, *Harpovoluta*, *Haurakia*, *Hebetancylus*, *Heleobia*, *Hemiarthrum*, *Hemiliostraca*, *Hiatella*, *Holoplocamus*, *Homalopoma*, *Illex*, *Iothia*, *Ischnochiton*, *Jaspidella*, *Jukesena*, *Kellia*, *Kelliella*, *Kerguelenatica*, *Kidderia*, *Kurtiella*, *Laevilitorina*, *Lamellaria*, *Laona*, *Lasaea*, *Laternula*, *Laubiericoncha*, *Ledella*, *Lepidopleurus*, *Leptochiton*, *Leucosyrinx*, *Leukoma*, *Limacina*, *Limatula*, *Limea*, *Limifossor*, *Limopsis*, *Linucula*, *Lissarca*, *Lissotesta*, *Lithophaga*, *Littoridina*, *Lodderia*, *Loligo*, *Loripes*, *Lucapinella*, *Lucinoma*, *Luzonia*, *Lyonsia*, *Lyonsiella*, *Lyrodus*, *Macoma*, *Macromphalina*, *Mactra*, *Magallana*, *Malletia*, *Malvinasia*, *Mangelia*, *Margarella*, *Margarites*, *Marseniopsis*, *Martialia*, *Mathilda*, *Melanella*, *Mendicula*, *Meteuthria*, *Minicymbiola*, *Miomelon*, *Mitrella*, *Moroteuthis*, *Mulinia*, *Munditia*, *Muricopsis*, *Musculus*, *Muusoctopus*, *Muussoctopus*, *Mya*, *Myonera*, *Mysella*, *Mytilimeria*, *Mytilus*, *Nacella*, *Natica*, *Neilonella*, *Neobuccinum*, *Neolepton*, *Neomenia*, *Nettastoma*, *Newnesia*, *Notaeolidia*, *Notocochlis*, *Nucula*, *Nuculana*, *Nuttallochiton*, *Nuttalochiton*, *Octopus*, *Odontocymbiola*, *Odostomia*, *Oenopota*, *Okenia*, *Olivancillaria*, *Olivella*, *Omalogyra*, *Onoba*, *Onychoteuthis*, *Orbitestella*, *Ostrea*, *Pagodula*, *Pandora*, *Panopea*, *Papuliscala*, *Parabuccinum*, *Paradmete*, *Paraeuthria*, *Parathyasira*, *Pareuthria*, *Parficulina*, *Parmaphorella*, *Parvanachis*, *Parvaplustrum*, *Parviturbo*, *Patelloida*, *Pellilitorina*, *Pelseneeria*, *Peltodoris*, *Pendroma*, *Peracle*, *Periploma*, *Pertusiconcha*, *Perumytilus*, *Petricola*, *Phidiana*, *Philine*, *Philobrya*, *Phlyctiderma*, *Photinastoma*, *Photinula*, *Pisolamia*, *Pitar*, *Plawenia*, *Plaxiphora*, *Pleurobranchaea*, *Pleurotomella*, *Plicatula*, *Pododesmus*, *Policordia*, *Polycera*, *Polyschides*, *Pontiothauma*, *Poromya*, *Powellisetia*, *Prelametila*, *Prisogaster*, *Pristigloma*, *Probuccinum*, *Prodoris*, *Propebela*, *Propeleda*, *Prosipho*, *Protocuspidaria*, *Provocator*, *Prunum*, *Pseudokellia*, *Pteria*, *Pterigioteuthis*, *Pulsellum*, *Puncturella*, *Pupatonia*, *Pusillina*, *Pyrene*, *Pyrunculus*, *Raeta*, *Rapana*, *Retrotapes*, *Retusa*, *Rhabdus*, *Rhinoclama*, *Robsonella*, *Rocellaria*, *Rostanga*, *Savatieria*, *Scissurella*, *Scurria*, *Scutopus*, *Seguenzia*, *Semele*, *Semicassis*, *Semimytilus*, *Semirossia*, *Silicula*, *Sinezona*, *Sinuber*, *Siphonaria*, *Siphonodentalium*, *Skenella*, *Solariela*, *Solen*, *Sphenia*, *Spirotropis*, *Spongiobranchaea*, *Strigilla*, *Strombiformis*, *Tagelus*, *Tawera*, *Tectonatica*, *Tegula*, *Tellina*, *Terebra*, *Teredo*, *Thecacera*, *Thesbia*, *Thielea*, *Thracia*, *Thyasira*, *Tindaria*, *Toledonia*, *Tonicia*, *Tonna*, *Tractolira*, *Transempitar*, *Trenchia*, *Tritonia*, *Trochita*, *Tromina*, *Trophon*, *Trophonopsis*, *Tropidomya*, *Turbonilla*, *Turritella*, *Turritellopsis*, *Typhlodaphne*, *Tyrinna*, *Vesicomya*, *Volutomitra*, *Volvarina*, *Waldo*, *Wemersoniella*, *Xymenopsis*, *Yoldia*, *Yoldiella*, *Zeadmete*, *Zidona*, *Zygochlamys*

Phylum: Nematoda

Family: Acuariidae, Anisakidae, Anoplostomatidae, Anticomidae, Axonolaimidae, Camacolaimidae, Chromadoridae, Comesomatidae, Desmodoridae, Diplopeltidae, Draconematidae, Enchelidiidae, Enoplidae, Ethmolaimidae, Haliplectidae, Leptolaimidae, Leptosomatidae, Linhomoeidae, Microlaimidae, Monhysteridae, Monoposthiidae, Oncholaimidae, Phanodermatidae, Selachinematidae, Siphonolaimoidea, Sphaerolaimidae, Thoracostomopsidae, Tripyloididae, unclassified Nematoda 1, Xyalidae

Genus: *Anoplostoma*, *Anticoma*, *Aponema*, *Araeolaimus*, *Bathylaimus*, *Camacolaimus*, *Cantracaecum*, *Cervonema*, *Chromadora*, *Chromadorita*, *Comesoma*, *Contracaecum*, *Cosmocephalus*, *Crestanema*, *Daptonema*, *Deontostoma*, *Desmodora*, *Desmolaimus*, *Didelta*, *Diplolaimelloides*, *Draconema*, *Enoplus*, *Euchromadora*, *Eumorpholaimus*, *Eurystomina*, *Fenestrolaimus*, *Graphonema*, *Halichoanolaimus*, *Haliplectus*, *Hopperia*, *Laimella*, *Leptolaimus*, *Linhystera*, *Metalinhomoeus*, *Metoncholaimus*, *Microlaimus*, *Monhystera*, *Monoposthia*, *Neochromadora*, *Nudora*, *Odontophora*, *Oncholaimellus*, *Oncholaimus*, *Paraethmolaimus*, *Paralinhomoeus*, *Paramesacanthion*, *Paramonohystera*, *Parasaveljevia*, *Perspiria*, *Phanoderma*, *Pontonema*, *Prochromadora*, *Pseudocella*, *Pseudosteineria*, *Ptycholaimellus*, *Sabatieria*, *Siphonolaimus*, *Sphaerolaimus*, *Steineridora*, *Terschellingia*, *Theristus*, *Thoracostoma*, *Tripyloides*, *Viscosia*

Phylum: Nematomorpha
Family: Nectonematidae
Genus: *Nectonema*

Phylum: Nemertea
Family: Amphiporidae, Lineidae, Malacobdellidae, Panorhynchidae, Tetrastemmatidae, Valenciniidae
Genus: *Amphiporus*, *Baseodiscus*, *Cerebratulus*, *Gastropion*, *Huilkia*, *Lineus*, *Malacobdella*, *Panorhynchus*, *Parapolia*, *Parborlasia*, *Tetrastemma*, *Wiotkenia*

Phylum: Phoronida
Family: unclassified Phoronida
Genus: *Phoronis*

Phylum: Platyhelminthes
Family: Bdellouridae, Bothriocephalidae, Bucephalidae, Capsalidae, Cathetocephalidae, Diclidophoridae, Echeneibothriidae, Echinobothriidae, Echinostomatidae, Eutetrarhynchidae, Fecampiidae, Gyrocotylidae, Hemiuridae, Hexabothriidae, Lacistorhynchidae, Macrovalvitrematidae, Mazocraeidae, Meidiamidae, Microphallidae, Onchobothriidae, Opecoelidae, Paraberrapecidae, Phyllobothriidae, Plagiostomidae, Pterobothriidae, Rhinebothriidae, Sphyriocephalidae, Strigeidae, Taxa incertae sedis, Tentaculariidae, Tetrabothriidae, Triaenophoridae, Umagillidae.
Genus: *Acanthobothrium*, *Anonchocephalus*, *Anthobothrium*, *Bothriocephalus*, *Bucephalus*, *Calliobothrium*, *Callitetrarhynchus*, *Callorhynchocotyle*, *Cardiocephaloides*, *Cathetocephalus*, *Clestobothrium*, *Collastoma*, *Coronocestus*, *Crossobothrium*, *Dasyrhynchus*,

Diclidophora, *Dollfusiella*, *Echinostoma*, *Fecampia*, *Grillotia*, *Guidus*, *Gyrocotyle*, *Halysioncum*, *Hepatoxylon*, *Heteronybelinia*, *Kronborgia*, *Lacistorhynchus*, *Lecithochirium*, *Levinseniella*, *Macruricotyle*, *Maritrema*, *Mazocraes*, *Mecistobothrium*, *Meidiama*, *Microphallus*, *Neogrubea*, *Neomacrovalvitrema*, *Neopterinotrematoides*, *Nicolasia*, *Notomegarhynchus*, *Opecoeloides*, *Orygmatobothrium*, *Paraberrapex*, *Parachristianella*, *Parahemiurus*, *Plagiostomun*, *Prosorhynchoides*, *Pseudanthocotyloides*, *Pterobothrium*, *Rhinebothrium*, *Symcallio*, *Synsiphonium*, *Tetrabothrius*, *Tetrasepta*

Phylum: Porifera
Family: Acarnidae, Ancorinidae, Axinellidae, Baeriidae, Biemnidae, Callyspongiidae, Chalinidae, Clionaidae, Coelosphaeridae, Darwinellidae, Dendoricellidae, Dictyonellidae, Dysideidae, Esperiopsidae, Geodiidae, Grantiidae, Guitarridae, Halichondriidae, Halisarcidae, Hamacanthidae, Hyalonematidae, Hymedesmiidae, Isodictyidae, Latrunculiidae, Latrunculina, Leucaltidae, Leucascidae, Leucosoleniidae, Microcionidae, Mycalidae, Myxillidae, Niphatidae, Petrosiidae, Phellodermidae, Phloeodictyidae, Plakinidae, Polymastiidae, Raspailiidae, Rossellidae, Spongiidae, Spongillidae, Stelligeridae, Stylocordylidae, Suberitidae, Sycettidae, Tedaniidae, Tethyidae, Tetillidae, Thorectidae
Genus: *Amphilectus*, *Amphimedon*, *Artemisina*, *Auletta*, *Axinella*, *Biemna*, *Callyspongia*, *Calyx*, *Caulophacus*, *Chalinula*, *Cinachyra*, *Ciocalypta*, *Clathria*, *Cliona*, *Dasychalina*, *Dendrilla*, *Dictyonella*, *Dragmacidon*, *Dysidea*, *Echinoclathria*, *Ephydatia*, *Esperiopsis*, *Eurypon*, *Fibula*, *Fibulia*, *Gellius*, *Geodia*, *Grantia*, *Guitarra*, *Halichondria*, *Haliclona*, *Haliclonissa*, *Halicnemia*, *Halisarca*, *Hamacantha*, *Hemigellius*, *Hyalonema*, *Hymedesmia*, *Hymenancora*, *Hymeniacidon*, *Hyrtios*, *Inflatella*, *Iophon*, *Isodictya*, *Latrunculia*, *Leucandra*, *Leucascus*, *Leucettusa*, *Leuconia*, *Leucosolenia*, *Lissodendoryx*, *Megaciella*, *Microxina*, *Mycale*, *Myxilla*, *Neopetrosia*, *Oceanapia*, *Pachychalina*, *Pachychalina*, *Petrosia*, *Phakellia*, *Phelloderma*, *Phorbas*, *Pione*, *Plakina*, *Plicatellopsis*, *Polymastia*, *Pseudosuberites*, *Pyloderma*, *Radiospongilla*, *Raspailia*, *Rhizaxinella*, *Rossella*, *Scalarispongia*, *Scopalina*, *Semisuberites*, *Spongia*, *Spongosorites*, *Stelletta*, *Stelodoryx*, *Stylocordyla*, *Suberites*, *Sycon*, *Tedania*, *Tentorium*, *Tethya*, *Tethyopsis*, *Tetilla*, *Topsentia*, *Trochospongilla*, *Ulosa*, *Volzia*

Phylum: Rotifera
Family: Philodinidae
Genus: *Anomopus*

Phylum: Sipuncula
Family: Golfingiidae, Phascolionidae, Themistidae
Genus: *Golfingia*, *Nephasoma*, *Nephastoma*, *Onchnesoma*, *Phascolion*, *Themiste*

Phylum: Tardigrada
Family: Batillipedidae
Genus: *Batillipes*

Methods

Spatial coverage: The spatial coverage of this project ranged from 35°51'16.98'S/ 55°40'20.27'W to 55°11'27.81'S/ 66°7'6.21'W. It comprises coastal environments, the continental shelf and slope, and ocean basins (Argentine Marine Platform).

Literature survey and quality control description: A comprehensive literature review was carried out. It included scientific publications, technical reports, and uploaded data to OBIS database during the NaGISA (Census of Marine Life) and SARCE projects. The reviewed literature allowed the compilation of marine invertebrate taxa reported by the Argentine Sea.The taxonomic status of the taxa were contrasted with updated literature, and corroborated using World Register of Marine Species databases (WoRMS 2017). Thus, the number of phyla, families, genera, and current valid species combinations are reported. However, no taxonomic revisions of the cited species were undertaken. These results provide an updated checklist of marine invertebrate knowledge on the Argentine Sea. For each phylum, the percentage of valid species living in the Argentine Sea was compared with the global percentage reported by WoRMS (http://www.marinespecies.org/aphia.php?p=stats). This analysis allowed us to assess the status of knowledge for each phylum in a global and regional context.

Data resources. The dataset herein reported has been revised and updated from a published dataset as part of a larger project through OBIS, as a result of the Census of Marine Life-NaGISA project [Marine Invertebrate from Argentina, Uruguay and Chile. v1.4. ArOBIS Centro Nacional Patagónico. Dataset/Occurrence. http://arobis.cenpat-conicet.gob.ar:8081/resource?r=arobis-marineinvertebrate].

Data Analysis: A cumulative species analysis was carried out to estimate the status of knowledge of marine invertebrate biodiversity of Argentine Sea. This study was done by using the Clench model ($v2 = (a*v1)/(1+(b*v1))$), applied by Jimenez-Valverde and Hortal (2003). In this work, we defined as effort units the number of species described per year from 1758 to 2017. In this analysis, only the valid species were considered. Each dot in Figure 1 represents the year when the valid species was described (and subsequently reported in the literature as living in the Argentine Sea). The number of described valid species per year in the region was tested using the Statistica 5.1 program, with the Simplex & Quasi-Newton adjust model. In case of no data fitting the Clench model, another one would be used.

Object name: Darwin Core Archive Marine Invertebrate from Argentina, Uruguay and Chile (in part).
Character encoding: UTF-8
Format name: Darwin Core Archive format.
Format version: 1.0
Distribution: http://arobis.cenpat-conicet.gob.ar:8081/resource?r=arobis-marineinvertebrate
Publication date of data: 2016-11-17
Language: English

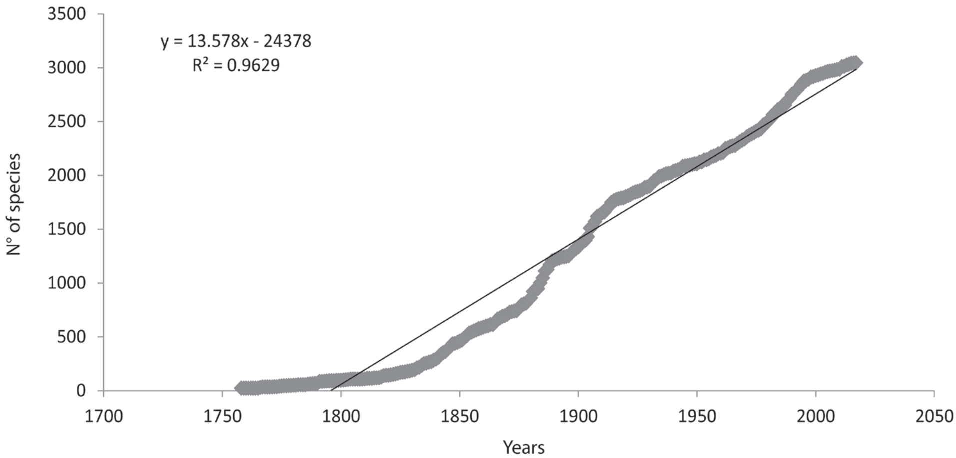

Figure 1. Cumulative curve for valid marine invertebrate species reported as living in the Argentine Sea (South Western Atlantic). Each dot in the figure represents the year when the taxa was described (and subsequently reported in the literature as living in the Argentine Sea).

Metadata language: English
Date of metadata creation: 2015-09-07
Hierarchy level: Dataset

Discussion

The large surface of the Argentinean Marine Platform and Coasts, together with the low number of valid reported species of marine invertebrates, denote that more research is required to increase the knowledge of this group in the South Western Atlantic Ocean and particularly, in the Argentine Sea. The data here compiled did not fit to the Clench model (y= (a*x)/1+b*x)). The obtained curve was y = ((6.33037*x)/(1+ ((-0.00198)*x)); R=0.98121. As the value of b is almost zero, the obtained curve could be considered as linear. When fitting the data to a linear curve, the formula was y= 13.578x – 24378 (R^2 = 0.9629). This could be attributable to the fact that species mentioned in the literature for the Argentine Sea would be less than 50% of the expected marine invertebrate species present in the region (Fig. 1).

During the last two centuries, an average of twelve species had been described per year as living in the Argentine Sea. At the beginning of the 19th century, the descriptions were completely based on material collected by European and North American expeditions (Fig. 2). The creation of the Museo Argentino de Ciencias Naturales (MACN) in 1812 contributed to increase the knowledge and descriptions of marine invertebrates (Penchaszadeh 2012). By the end of the 19th century and the beginning of 20th two "golden periods" were observed (1879-1888 and 1899-1908). During these two periods the amount of described species was considerably increased probably associated to global marine expeditions. One of them was undoubtedly the "Challenger Expedition" of 1873-76, which described more that 4,000 new species over the world. The reports of this expedition are considered as one of the greatest progresses in the knowledge of the world´s natural history. By the end of the 20th century, another pulse, of almost 450 species, was newly described for Argentine waters, in the period 1979-1998 (Fig. 2). This fact could be probably associated to the consolidation of specialists in taxonomy in Argentina and the return of scientists exiled during the military dictatorship (1976-1983). During these 20 years (1979–1998) 30 % of the Nematoda, Bryozoa and Brachiopoda registered in Argentine waters were described. However, the phyla Mollusca and Arthropoda were still the most represented groups during that period. Finally, in the last years (beginning of 21st century), new species are being described, mainly promoted by the scientific system of Argentina (MINCyT, CONICET), international projects (Census of Marine Life) and open access databases (OBIS, WoRMS). Nonetheless, the knowledge of marine invertebrate biodiversity is still low in the region.

The Kingdom Animalia comprises 29 invertebrate phyla (WoRMS), however, only six phyla have not been recorded as living in the Argentine Sea (Table 1). These are Cycliophora, Gastrotricha, Gnathostomulida, Orthonectida, Placozoa and Xenacoelomorpha. The phylum Arthropoda and Mollusca constitute around 50 % of the reported marine invertebrates. However, the percentage of Argentinean marine Arthropoda is lower compared to the global knowledge, revealing that this group is far to be resolved in the region. In contrast to that, the mollusks percentage is more consistent. Some groups as Bryozoa, Cnidaria, Porifera and Echinodermata exceed the global registered percentage reported by WoRMS (2017). The observed percentage of the phylum Ne-

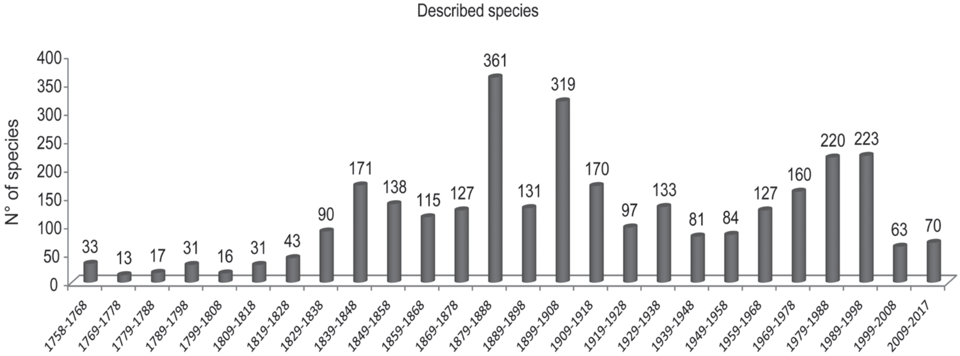

Figure 2. Number of valid marine invertebrate species described per decade that were subsequently mentioned in the literature as living in the Argentine Sea.

mertea coincides with the worldwide registered in WoRMS. Nevertheless, only 30 species have been reported as living in the southwestern Atlantic, suggesting that the number of known nemertean is still low. In addition, 70% of Nemertea species was described in the Northern Hemisphere (Kajihara et al. 2008). This could indicate that new Argentinean nemerteans could be described in the future. Research focused on marine invertebrate biodiversity in Argentina is currently growing. Additionally, some young researchers on invertebrate taxonomy are being trained towards a scientific career. On the other hand, the financial support provided by the government is still scarce.

A distribution analysis of the species is a complex issue, due to, in several cases, the literature examined named "Argentine Sea" or "Argentine Coast" as a locality. This is the case of 955 records of species cited for the Argentine Sea without a precise locality. However, distribution patterns by provinces were made excluding those 955 records and estimating the percentage for the main taxonomic groups in order to elucidate hot spots in the Argentine Sea (Fig. 3). It is clear that the Magellan region is the most studied region of the Argentine Sea with 1166 (55%) mentioned species in the literature followed by the Buenos Aires province coast with 526 (25 %). Few records were exclusively mentioned for the Río Negro Province in the literature; only 29 (1,5 %) species were named for this area. Santa Cruz and Chubut provinces, with 251 (12 %) and 137 (6,5 %) reported species respectively, present more species than Río Negro but the number of reported species is still low compared to Tierra del Fuego and Buenos Aires provinces. In general terms, the phylum Mollusca and Arthropoda were the most mentioned groups along the Argentine Sea. Nevertheless, the phylum Nematoda in the Santa Cruz province and Annelida (mostly Polychaeta) in Chubut, were widely studied (Fig. 3). The fact that more species are described in the southern region of the Argentine Sea could be attributable to the concentration of oceanographic campaigns that were performed by international initiatives when travel to Antartica or passing from Pacific to Atlantic Ocean (around Tierra del Fuego and Southern Islands). The major biodiversity encountered in the southern tip of the Southwest Atlantic also could be attributable to an inverse biodiversity pattern that was previously registerd in Southwest Atlantic higher latitudes for some intertidal rocky shore invertebrates (Palomo et al 2011) or other taxa as asellote isopods (Doti et al. 2014). The increasing in biodiversity in high latitudes could also be attributable to the presence of high extentions of hard bottoms that permit the settlement of invertebrates and the fact that most Magellanic species that occur in southern Chile extend to the Southwest Atlantic (Lopez Gappa et al. 2006).

In Argentina, the main factors that modify benthic communities are habitat degradation and disturbance, urban development, dredging and resuspension of sediment, establishment of ports, tourism-associated impact, global and local aquatic contamination sources, and fisheries (Bigatti and Penchaszadeh 2008). Notably, bottom trawling dominates coastal and deep-sea fishing in the Argentine platform. This fishery produces a large number of discards of benthic invertebrates, accounting up to 80 % of the catch (Orensanz et al. 2008). In order to provide an adequate management of the natural resources, studies on coastal management, conservation and

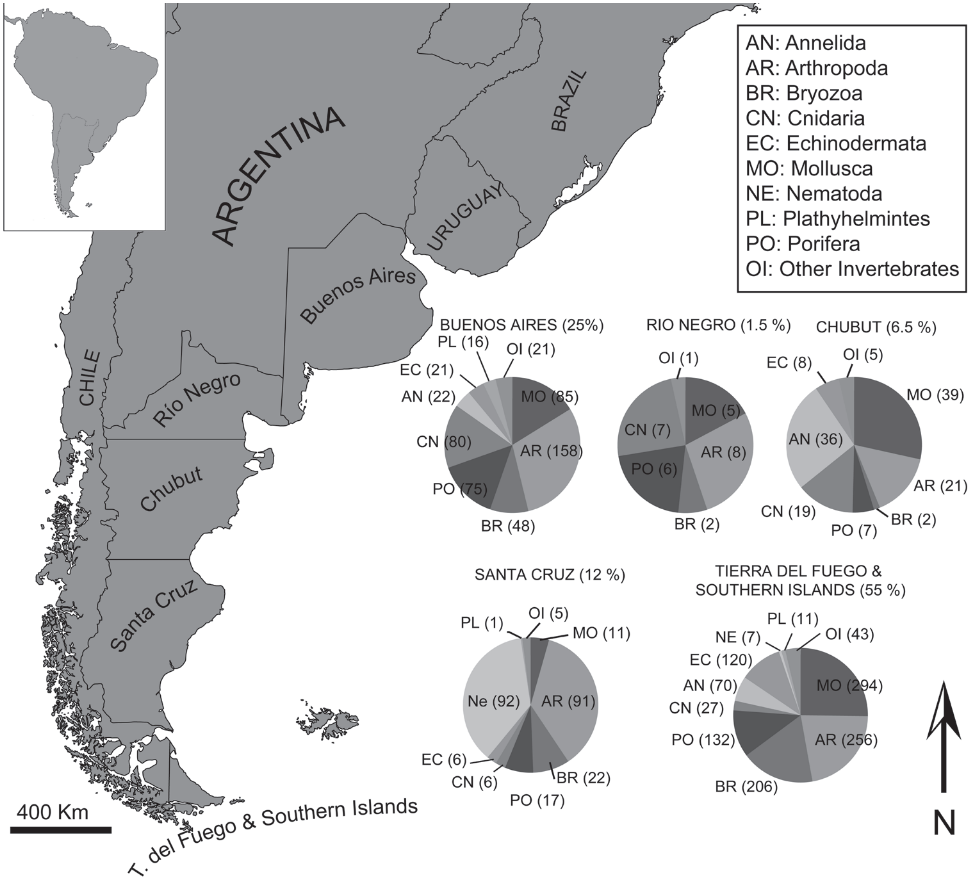

Figure 3. Distribution of main taxonomic marine invertebrate groups. The parenthesys after the province indicates the percentage of species mentioned as living in each province. The parenthesys after the phyllum initials indicates the number of species mentioned in the literature.

distribution patterns have been carried out (Sullivan and Bustamante 1999, Barragán et al. 2003, Cusson and Bourget 2005, Cañete et al. 2008, Miloslavich et al. 2011, among others).

Finally, biological invasions of different organisms (algae, mollusks, hydroids, bryozoans, ascidiaceans and crustaceans) have negatively affected local marine biodiversity, as well as, regional economy (Orensanz et al. 2002, Penchaszadeh et al. 2005, Bigatti and Penchaszadeh, 2008, Schwindt 2008). A total of 28 marine exotic species and 43 cryptic species have been reported as living in the Argentine Sea (Orensanz et al. 2002), while the number is increasing in the last years. The impact of biological invasions constitutes a serious problem to marine invertebrate biodiversity in Argentine Sea and consequently affects descriptions of new species, even before of their description. The results of this checklist suggest the importance of studies focused on marine invertebrate biodiversity in the southern tip of South America, where some hot spots, as the Protected Marine Area Burdwood bank, harbor great abundance and diversity of endemic species (Miloslavich et al 2011). New studies on marine invertebrate biodiversity will provide consistent data for the generation of management policies tending to create new marine protected areas and the conservation of the species´habitats.

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Supplementary material 1

List of Valid species reported as living in the Argentine Sea

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Data type: occurence

Link: https://doi.org/10.3897/zookeys.791.22587.suppl1

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RESEARCH ARTICLE

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Five new coexisting species of copepod crustaceans of the genus *Spaniomolgus* (Poecilostomatoida: Rhynchomolgidae), symbionts of the stony coral *Stylophora pistillata* (Scleractinia)

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Abstract

Spaniomolgus is a symbiotic genus of copepods of the poecilostomatoid family Rhynchomolgidae and is known to be associated with shallow-water reef-building hermatypic corals. Three species of this genus were previously found only in washings of *Acropora* and *Stylophora* in northern Madagascar. Four coral morphotypes of *Stylophora pistillata* (Pocilloporidae) were collected by SCUBA at 1 to 28 m depth in five sites in the Saudi Arabian Red Sea in 2013. Copepods found on these colonies were studied using light, confocal and scanning electron microscopy. Five new, and one known, species of the genus *Spaniomolgus* were discovered in washings and inside the galls of the hermatypic coral *S. pistillata*. The description of these new species (*Spaniomolgus globus* **sp. n.**, *S. stylophorus* **sp. n.**, *S. dentatus* **sp. n.**, *S. maculatus* **sp. n.**, and *S. acutus* **sp. n.**) and a key for the identification of all of its congeners is provided herein.

Keywords

Copepoda, Crustacea, symbiosis, biodiversity, Pocilloporidae, coral reefs, Red Sea

Introduction

Rhynchomolgidae Humes and Stock, 1973 is one of the largest families of poecilostomatoid copepods comprising over 250 species living in association with various marine invertebrates (Ho and Kim 2001; Boxshall and Halsey 2004). There are 44 genera in the family Rhynchomolgidae with the genus *Doridicola* Leydig, 1853 being the largest in the family and comprising 52 species (Ho and Ivanenko 2013, Walter and Boxshall 2018). Thirty-eight genera of the family include only up to six species. One of these small genera, *Spaniomolgus* Humes & Stock, 1973, consists of three species: the type species *S. compositus* (Humes & Frost, 1964), *S. geminus* (Humes & Ho, 1968) and *S. crassus* (Humes & Ho, 1968), all previously attributed to the genus *Lichomolgus* Thorell, 1859. *Spaniomolgus* are found in association with scleractinians of the genera *Acropora* Oken, 1815, *Seriatopora* Lamarck, 1816, and *Stylophora* Schweigger, 1820 from Madagascar (Humes and Ho 1968, Humes and Stock 1972, 1973). There have been no records of *Spaniomolgus* since the revision of the lichomolgoid complex (Humes and Stock 1972, 1973) and until the discovery of an unidentified species of *Spaniomolgus* living in modified polyps (galls) of *Stylophora pistillata* Esper, 1797 in the Red Sea (Ivanenko et al. 2014, Shelyakin et al. 2018).

Branching corals of *Stylophora pistillata* are widely distributed around the Indo-Pacific and are phenotypically plastic, i.e., morphological variation across different habitats, depths, and geographic regions can be observed. The latest study based on seven DNA loci demonstrated that *Stylophora* corals from the Red Sea belong to a single molecular clade, and that morphospecies of *Stylophora pistillata*, *S. danae* Milne Edwards & Haime, 1850, *S. subseriata* (Ehrenberg, 1834), and *S. kuehlmanni* Scheer & Pillai, 1983 from the Red Sea are now considered as synonyms of *S. pistillata* (Arrigoni et al. 2016).

This paper describes five new species of *Spaniomolgus* living in symbiosis with four morphotypes of *Stylophora pistillata* from the Red Sea. Comments on the relationships with other congeners are given, and a key to the species of the genus *Spaniomolgus* is presented.

Materials and methods

The sampling was undertaken in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST). Permissions for KAUST to undertake the research were obtained from the appropriate governmental agencies of the Kingdom of Saudi Arabia.

Four colonies of *Stylophora pistillata* from the Thuwal reefs in the central Red Sea and one colony from the reef close to Al Lith in the southern Red Sea were sampled (distance between the sampling locations is about 280 km) (Fig. 1, Table 1). The map was created using Python scripts (Jones et al. 2001), labels were included using the software Adobe Photoshop CS4 (Adobe Systems, San Jose, CA, USA). The coral colonies were collected using a hammer and chisel, and encased in sealed plastic bags while snorkeling and SCUBA diving at depths ranging from 1 to 28 m. The coral samples

Table 1. Sampling localities in the Red Sea.

Specimen of the coral host	Species	Coordinates	Locality	Depth (m)	Date
SA13-12	*Stylophora pistillata*	22°12'4.30"N, 38°57'31.40"E	Thuwal	1	24.04.2013
SA13-25	*Stylophora pistillata* (morphotype *subseriata*)	22°19'9.26"N, 38°51'15.78"E	Thuwal	10.4	25.04.2013
SA13-31	*Stylophora pistillata* (morphotype *danae*)	22°20'23.45"N, 38°50'52.33"E	Thuwal	28	26.04.2013
SA13-61	*Stylophora pistillata*	22°03'48.5"N, 38°45'51.2"E	Thuwal	1	29.04.2013
SA13-72	*Stylophora pistillata* (morphotype *mordax*)	20°08'02.1"N, 40°05'58.86"E	Al Lith	2.5	03.05.2013

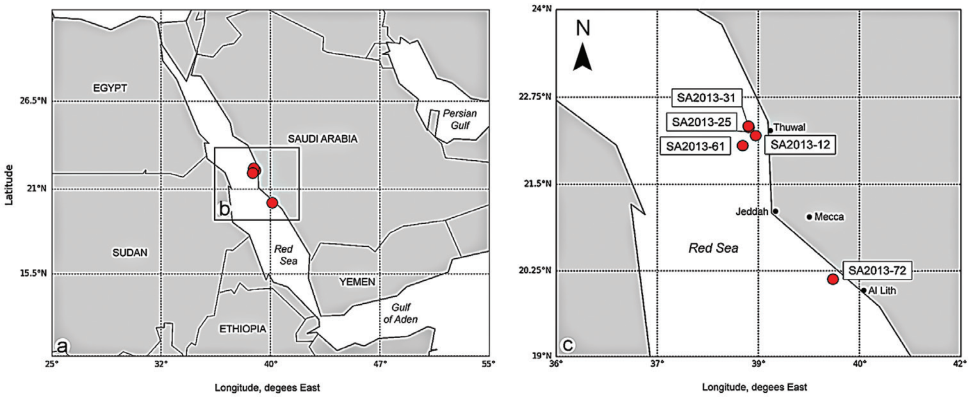

Figure 1. a–c Sampling localities and study area in the Red Sea (Saudi Arabia). The red circles indicate sampling localities of the indicated samples of *Stylophora pistillata* (see Table 1).

were rinsed on board as follows: 96% ethanol was added to each sample until the overall solution reached a concentration 10% to relax the animals attached to the coral. After 15 minutes, the samples were shaken, and the water with the detached symbionts was filtered through a 100 µm sieve. Copepods were sorted under a Carl Zeiss™ Stemi 2000-C stereomicroscope. Coral colonies were also examined for copepods in modified corallites and galls. Galls were dissected, and copepods were extracted from inhabited polyps using entomological needles and preserved in 96% ethanol.

In the lab, copepods were dissected in lactic acid and then stained with Chlorazol black E (Sigma C-1144) for contrast enhancement (Ivanenko and Defaye 2004). Specimens were then examined as temporary mounts in lactophenol and later sealed with Entellan as permanent mounts. The coral hosts (Fig. 2) were bleached in sodium hypochlorite for 48 h, rinsed with fresh water, dried and photographed. The copepods were kept in 2 mL vials in 96% ethanol with a small drop of glycerol.

For confocal microscopy, exoskeletons were individually transferred to distilled water and then stained with Fuchsin (Ivanenko et al. 2012; Corgosinho et al. 2018).

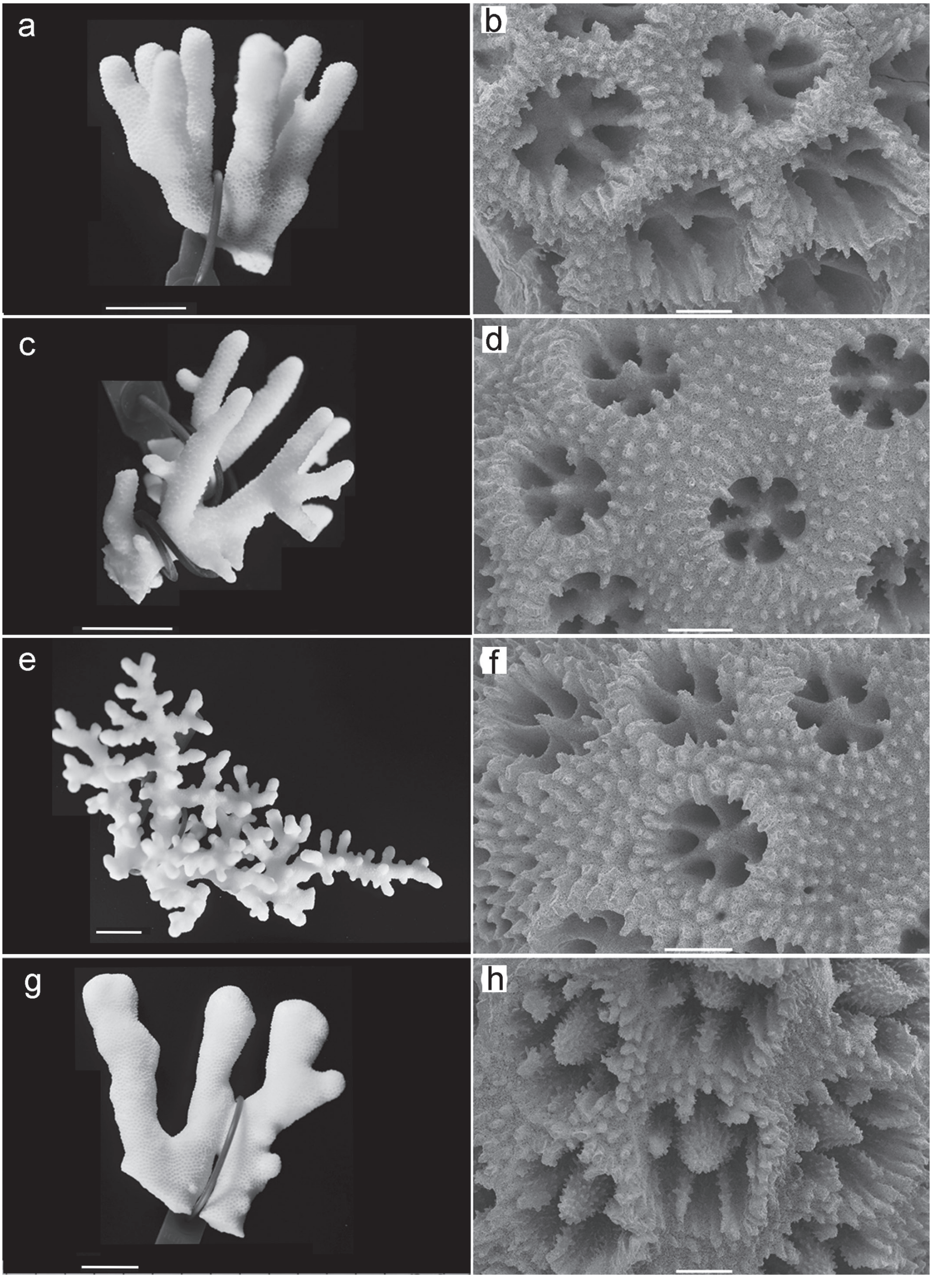

Figure 2. *Stylophora pistillata*, coral skeletons and corallite structures (SEM). **a, b** Specimen SA13-12 **c, d** Morphotype *subseriata*, specimen SA13-25 **e, f** Morphotype *danae* SA13-31 **g, h** Morphotype *mordax*, specimen SA13-61. Scale bars: 20 mm (**a, c, e, g**); 0.5 mm (**b, d, f, h**).

The copepods were inspected using an inverted Nikon A1 confocal laser scanning microscope (CLSM, Nikon Corporation, Tokyo, Japan) at Lomonosov Moscow State University, using a 40× oil immersion objective and lasers with wavelengths of 532 and 640 nm. The laser power was set to 60%. The amplitude offset and detector gain were manually adjusted. CLSM image stacks were obtained throughout the whole animal, and the scanning software was adjusted to perform the optimal number of scans. Image size was set for 2000×2000 dpi and the reconstruction of the external anatomy was obtained by maximum projection. The final images were adjusted for contrast and brightness using the software Adobe Photoshop CS4.

All figures were prepared using a Leica DM5500B differential interference microscope equipped with a camera lucida. The armature formula of swimming legs 1–4 follows Sewell (1949), spines are indicated by Roman numerals and setae by Arabic numerals. Mean body length (MBL) of copepods was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami.

For scanning electron microscopy (SEM), copepods were dehydrated through increasing ethanol concentrations, critical point dried, mounted on aluminium stubs, coated with gold, and examined in a CamScan SEM (CamScan Electron Optics Ltd, London, UK) at the Faculty of Biology of Lomonosov Moscow State University. The bleached fragments of corals were mounted on metal stands using glue, coated with a conductive gold film and examined with the same SEM.

Type specimens of copepods are deposited in the collection of the Zoological Museum of Lomonosov Moscow State University (ZMMU). The coral hosts are deposited in the collection of King Abdullah University of Science and Technology (KAUST).

Results

Five new and one described species of the genus *Spaniomolgus* were found in washings and inside of polyps of four morphotypes of the hermatypic coral *Stylophora pistillata* collected from five sites (Table 1, Fig. 1) at depths ranging from 1 to 28 m. The description of the five new species (*Spaniomolgus globus* sp. n., *S. stylophorus* sp. n., *S. dentatus* sp. n., *S. maculatus* sp. n., and *S. acutus* sp. n.) is provided herein.

Taxonomy

Poecilostomatoida Thorell, 1859
Family Rhynchomolgidae Humes & Stock, 1973

Genus *Spaniomolgus* Humes & Stock, 1973

Type species. *Lichomolgus compositus* Humes & Frost, 1964 now regarded as a synonym of *Spaniomolgus compositus* (Humes & Frost, 1964), by original designation.

Other species. *Spaniomolgus geminus* (Humes & Ho, 1968), *S. crassus* (Humes & Ho, 1968), *S. globus* sp. n., *S. stylophorus* sp. n., *S. dentatus* sp. n., *S. maculatus* sp. n., *S. acutus* sp. n.

Remarks. The publication by Humes and Stock in 1972 of a list of new taxa, including *Spaniomolgus* and Rhynchomolgidae, without diagnoses of the new taxa is considering by us as interrupted and continued in 1973 (ICZN 1999: Art. 10.1.1); therefore the publication date of the genus becomes 1973.

Spaniomolgus globus sp. n.

http://zoobank.org/9EC98428-E87D-4854-B2C7-7BEAA59DF14A

Figs 3, 4

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°03'48.5"N, 38°45'51.2"E.

Material examined. 1 ♀ holotype (ZMMU Me-1209) and 3 ♀♀ paratypes (ZMMU Me-1210) from tubular-shaped modification of corallites of *Stylophora pistillata* (KAUST SA2013-61) collected at 1 m depth.

Etymology. The specific Latin epithet *globus*, globe, refers to the body shape in life when the urosome forms an s-shaped flexure.

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 3a). Total body length ranging from 1.1 to 1.5 mm (mean = 1.3 mm, n = 4); width ranging from 580 to 600 µm (mean = 590 µm, n = 4). Prosome consists of cephalothorax (first pedigerous somite incompletely separated by an indistinct furrow) and three free pedigerous somites. Rostral area covered with hyaline setules (not figured). Second and third pedigerous somites with epimeral areas slightly angular. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome s-shaped when alive, with the genital double-somite drawn forward under the metasome and the postgenital somites in line with the prosome (Fig. 3a); 5-segmented, comprising fifth pedigerous somite, genital double-somite, and three free abdominal somites (Fig. 3b). In dorsal view, only the postgenital somites are visible. Leg 5-bearing somite bell-shaped, slightly wider than long.

Genital double-somite (Fig. 3b) narrow, squarish (200 × 200 µm); its dorsal length (120 µm) much shorter than its ventral length (200 µm). Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening); lateral margins nearly parallel. Each genital area with two minute setae (Fig. 3b). Egg sac unknown. Width and length of three postgenital somites, 120 × 180, 85 × 130 and 105 × 120 µm from anterior to posterior.

Caudal rami (Fig. 3b) elongated, 180 × 45 µm, 4.0 times longer than wide. With six setae relatively short and naked. Outer lateral seta 52 µm, outermost terminal seta 41 µm, innermost terminal seta 47 µm. Two median terminal setae broadened, 58 µm (outer) and 52 µm (inner) in length. Dorsal seta 35 µm.

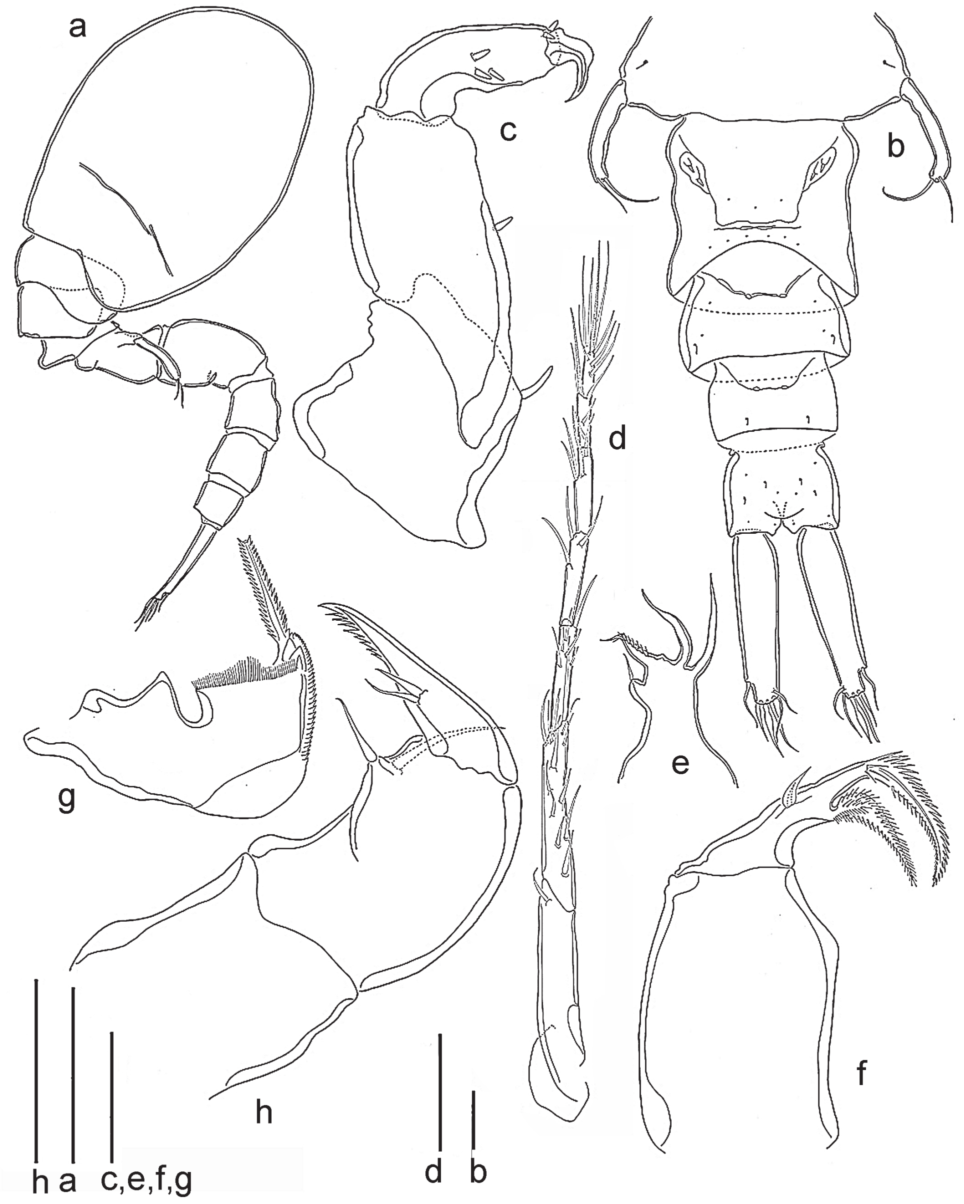

Figure 3. *Spaniomolgus globus* sp. n., female. **a** Habitus lateral **b** Urosome dorsal **c** Antenna **d** Antennule **e** Maxillule **f** Maxilla **g** Mandible **h** Maxilliped. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–h**).

Antennule (Fig. 3d) 7-segmented, segments 67, 97, 41, 39, 35, 21 and 20 µm long respectively (measured along their posterior margin). Armature formula as follows: 1, 13, 6, 3, 4 and 1 aesthetasc, 3 and 1 aesthetasc and 7 (two of them joined at the base) and 1 aesthetasc. All setae relatively short and naked.

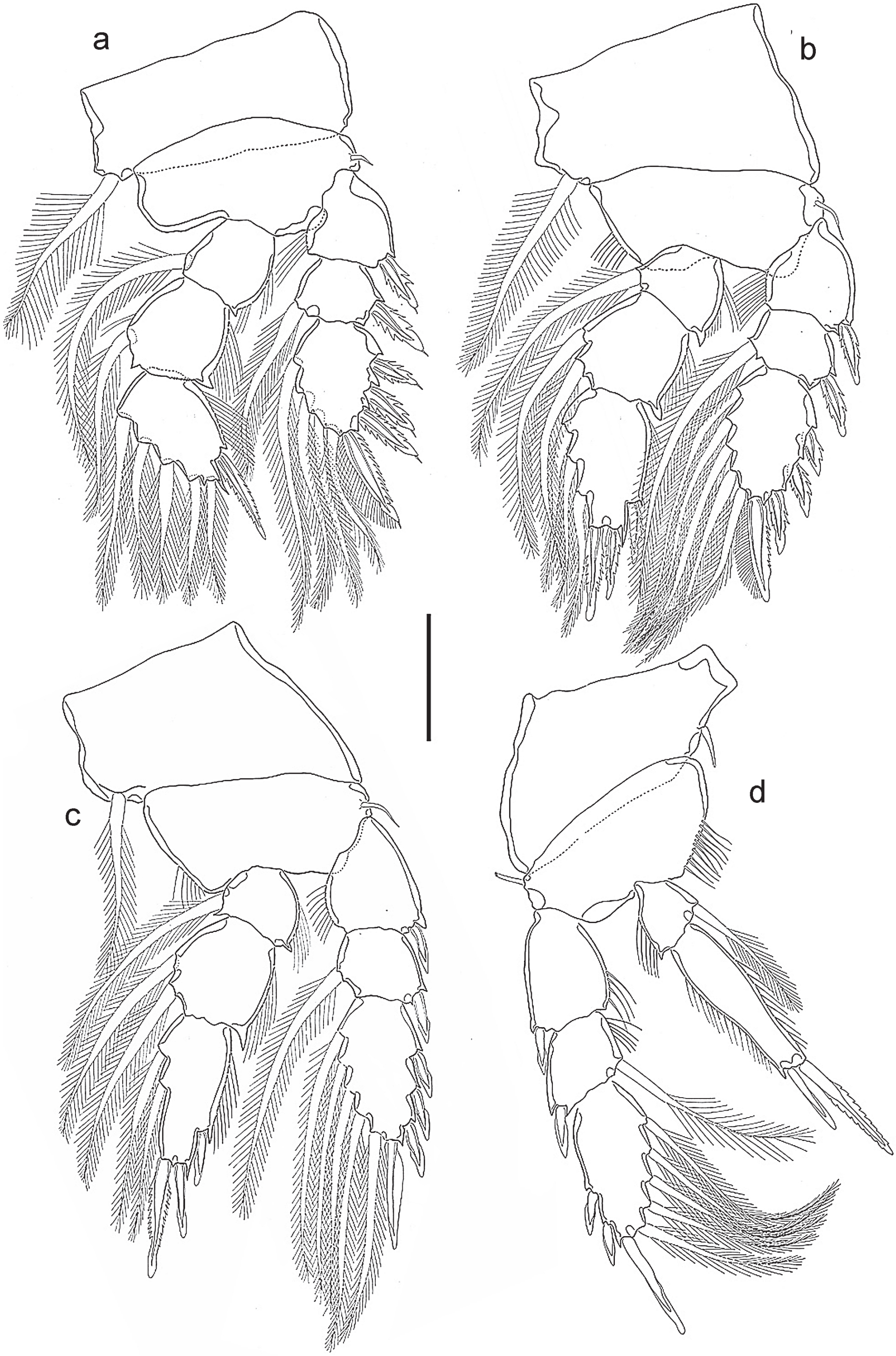

Figure 4. *Spaniomolgus globus* sp. n., female. **a** Leg 1 **b** Leg 2 **c** Leg 3 **d** Leg 4 Scale bar: 50 µm.

Antenna (Fig. 3c) 3-segmented; first segment 81µm long with small terminal hyaline seta; second segment 113 µm long with similar seta medially; third segment (formed by fusion of original segments 3 and 4 in *Lichomolgus*) 63 µm long with three hyaline setae medially (representing the usual three setae on penultimate segment in *Lichomolgus*) and two apical hyaline setae. Small recurved terminal claw 32 µm long. Length ratio of second to third segment (measured along inner margin) 2.1:1.

Mandible (Fig. 3g). Basal region with a rounded hyaline expansion and a distal row of small teeth on inner margin, and a fringe of setules on the outer margin. Terminal lash long, denticulated.

Maxillule (Fig. 3e) a single segment with a small seta and three hyaline prolongations (seemingly not articulated), one of them ornamented with setules.

Maxilla (Fig. 3f) 2-segmented; proximal segment unarmed; distal segment with a small seta medially, and two setiform processes apically, one barbed, the other with spinules.

Maxilliped (Fig. 3h) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like denticulated distally, with two setae medially.

Legs 1–4 (Fig. 4a-d) with 3-segmented rami except for 2-segmented leg 4 endopod. Inner coxal seta long and plumose in legs 1–3, short and naked in leg 4. Outer basal seta short and naked in all legs. Endopod of leg 4 reaching beyond middle of third exopodal segment; with two terminal spines unequal in length, outer 32 µm long, inner 55 µm long, the latter spines with hyaline. Outer spines on leg 4 exopod with smooth lamellae. Armature formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–0	I-0; I-1; III,I,4	0–1; 0–1; I,1,4
Leg 2	0–1	1–0	I-0; I-1; III,I,5	0–1; 0–2; I,II,3
Leg 3	0–1	1–0	I-0; I-1; III,I,5	0–1; 0–2; I,II,2
Leg 4	0–1	1–0	I-0; I-1; II,I,5	0–1; 0,II,0

Fifth leg (Fig. 3b) with protopod incorporated into somite; outer basal smooth seta minute. Free exopodal segment long, slender and recurved, 6.7 times as long as wide, bearing two apical setae unequal in length, innermost more than twice the length of outer one.

Sixth leg (Fig. 3b) represented by two very small articulated spines near attachment of eggs sacs.

Male unknown.

***Spaniomolgus dentatus* sp. n.**
http://zoobank.org/4A6D3CC9-2492-4092-82D8-38F95675696A
Fig. 5

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°03'48.5"N, 38°45'51.2"E.

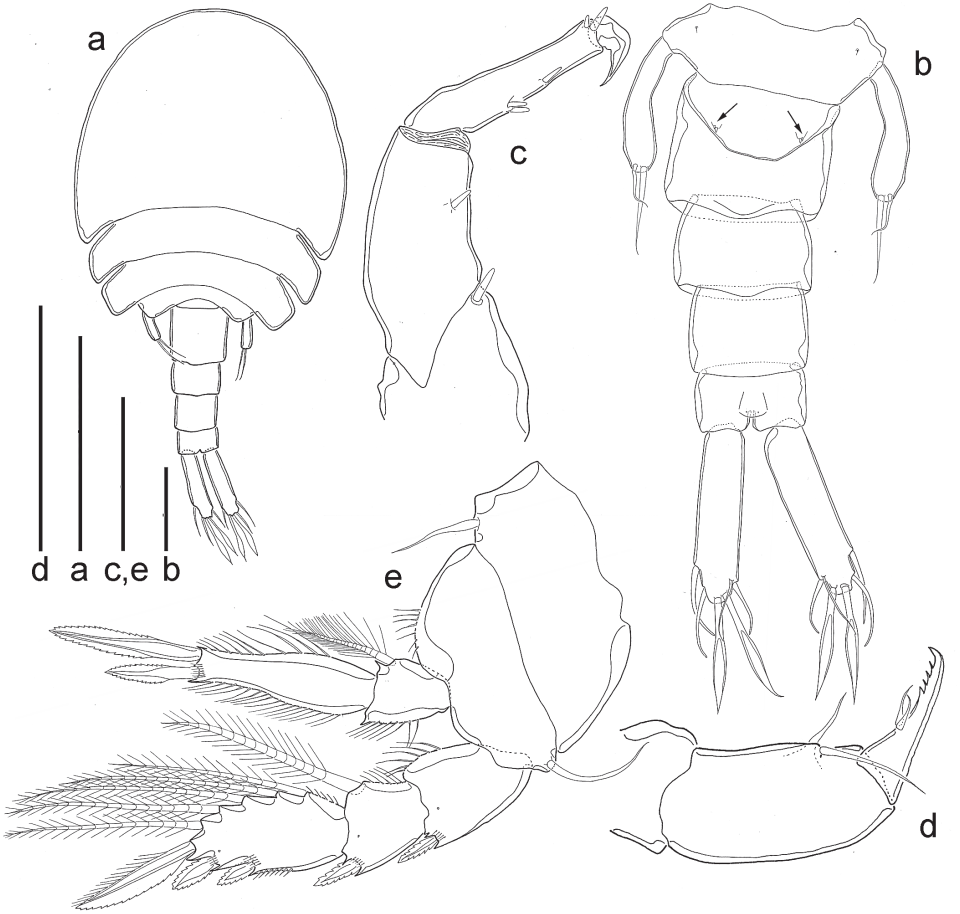

Figure 5. *Spaniomolgus dentatus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal (Leg 6 arrowed) **c** Antenna **d** Maxilliped **e** Leg 4. Scale bars: 300 μm (**a**); 100 μm (**b**); 50 μm (**c–e**).

Material examined. 1 ♀ holotype (ZMMU Me-1213) and 1 ♀ paratype (ZMMU Me-1214) from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) collected at 28 m depth.

Etymology. The specific name from the Latin *dentatus*, refers to the denticulated margin of the maxillipedal claw.

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 5a). Body length 750 μm and maximum width 390 μm. Prosome comprising cephalothorax and three free pedigerous somites. Second and third pedigerous somites with slightly rectangular epimeral areas. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 6b). Leg 5-bearing somite wider than long.

Genital double-somite (Fig. 5b) slightly longer than wide (95 × 83 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform elements (Fig. 5b). Egg sac unknown. Three postgenital somites 55 × 83, 53 × 72 and 39 × 67 µm from anterior to posterior.

Caudal rami (Fig. 5b) elongated, 108 × 25 µm, 4.3 times as long as wide. With six setae; all setae relatively short and naked. Outer lateral seta 44 µm, outermost terminal seta 41 µm, innermost terminal seta 33 µm. Two median terminal setae broadened, 72 µm (outer) and 66 µm (inner) in length. Dorsal seta 39 µm.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 5c) 3-segmented; first segment 53 µm long with small terminal hyaline seta; second segment 68 µm long with seta medially; third segment 60 µm long with three hyaline setae medially and two apical hyaline setae, small recurved terminal claw 24 µm long. Second and third segments measured along inner margin subequal in length.

Maxilliped (Fig. 5d) 3-segmented. First segment unarmed; second segment slightly elongated, with two naked inner setae; third segment claw-like, denticulate distally, with two setae medially.

Leg 4 (Fig. 5e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta naked. Endopod reaching beyond middle of third exopodal segment; second segment with two apical spines unequal in length, outer 30 µm long, inner 50 µm long, the latter spines with hyaline and weakly serrated margins. Outer spines of exopod with barbed lamellae.

Fifth leg (Fig. 5b) with protopod incorporated into somite; outer basal seta not observed. Free segment long, slender and recurved, 4.2 times as long as wide, bearing two apical setae unequal in length, inner most about twice as long as outer one.

Sixth leg (arrowed in Fig. 5b) represented by two very small articulated projections near attachment of eggs sacs.

Male unknown.

***Spaniomolgus maculatus* sp. n.**
http://zoobank.org/3269010E-C96D-4F9B-8FBB-4189C01F6455
Fig. 6

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°19'09.26"N, 38°51'15.78"E.

Material examined. 1 ♀ holotype (ZMMU Me-1215) and 1 ♀ paratype (ZMMU Me-1216) from *Stylophora pistillata* (morphotype *S. subseriata*) (KAUST SA2013-25) collected at 10.4 m depth; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) (22°03'48.5"N, 38°45'51.2"E) collected at 28 m depth.

Etymology. The specific Latin epithet *maculatus* refers to the maculate body surface, light brown when alive.

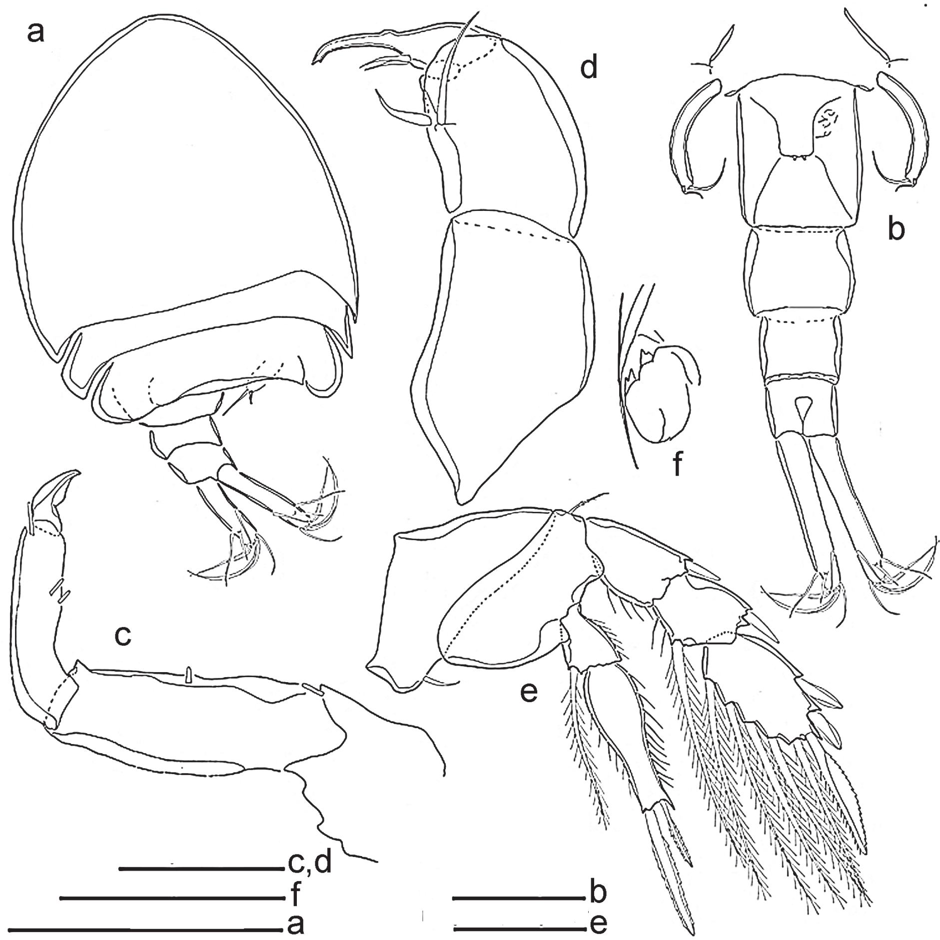

Figure 6. *Spaniomolgus maculatus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4 **f** Genital area. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–f**).

Description. Adult female.

Body cyclopiform; oval cephalothorax slightly pointed on top and cylindrical urosome (Fig. 6a). Mean body length 710 µm (with range of 700 – 720 µm) and mean maximum width 315 µm (with range of 270 – 360 µm), based on two specimens. Prosome comprising cephalothorax and three free pedigerous somites. Second pedigerous somite with epimeral area slightly angular and third pedigerous somite with epimeral area rounded. Fourth pedigerous somite smaller than preceding ones, almost invisible in dorsal view.

Urosome s-shaped when alive, with the genital double-somite drawn forward under the metasome and the postgenital somites retained in line with the prosome. Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 6b). In dorsal view, only the postgenital somites visible. Leg

5-bearing somite slightly wider than long. Genital double-somite (Fig. 6b) narrow, slightly longer than wide (108 × 92 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two very small articulated projections (Fig. 6f). Egg sac unknown. Three postgenital somites 67 × 83, 50 × 63 and 42 × 54 µm from anterior to posterior.

Caudal rami (Fig. 6b) elongated, 125 × 21 µm, 5.0 times longer than wide. With six setae, all short and naked. Outer lateral seta 42 µm, outermost terminal seta 54 µm, inner lateral seta 33 µm, innermost terminal seta 37 µm, median terminal setae 71 µm in length. Dorsal seta 20 µm.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 6c) 3-segmented; first segment 45 µm long with small hyaline apical seta; second segment 87 µm long with one hyaline seta medially; third segment 55 µm long with two hyaline setae medially, and one apical hyaline seta, with small recurved terminal claw 22 µm long. Length ratio of second to third segments (measured along inner margin) 1.7:1.

Maxilliped (Fig. 6d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like, with two setae medially equal in length; apex with pore.

Leg 4 (Fig. 6e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta short and naked, outer basal seta short and plumose. Endopod reaching beyond middle of third exopodal segment; with two distal spines unequal in length, outer 30 µm long, inner 50 µm long, the latter spines with hyaline and weakly serrated margins. Outer spines of exopod with smooth lamellae.

Fifth leg (Fig. 6b) with protopod incorporated into somite; outer basal smooth seta short. Free segment long, slender and recurved, 7.6 times as long as wide, bearing two apical setae unequal in length, inner most about twice as long as outer one.

Male unknown.

***Spaniomolgus acutus* sp. n.**

http://zoobank.org/10C25D5C-ED4B-4234-B6BA-F0B3988225B7

Fig. 7

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°19'9.26"N, 38°51'15.78"E.

Material examined. 1 ♀ holotype (ZMMU Me-1217) and 1 ♀ paratype (ZMMU Me-1218) from *Stylophora pistillata* (morphotype *S. subseriata*) (KAUST SA2013-25) collected at 10.4 m depth; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) (22°03'48.5"N, 38°45'51.2"E) collected at 28 m depth.

Etymology. The specific Latin epithet *acutus*, pointed, refers to the pointed epimeral areas of the second and third pedigerous somites.

Description. Adult female.

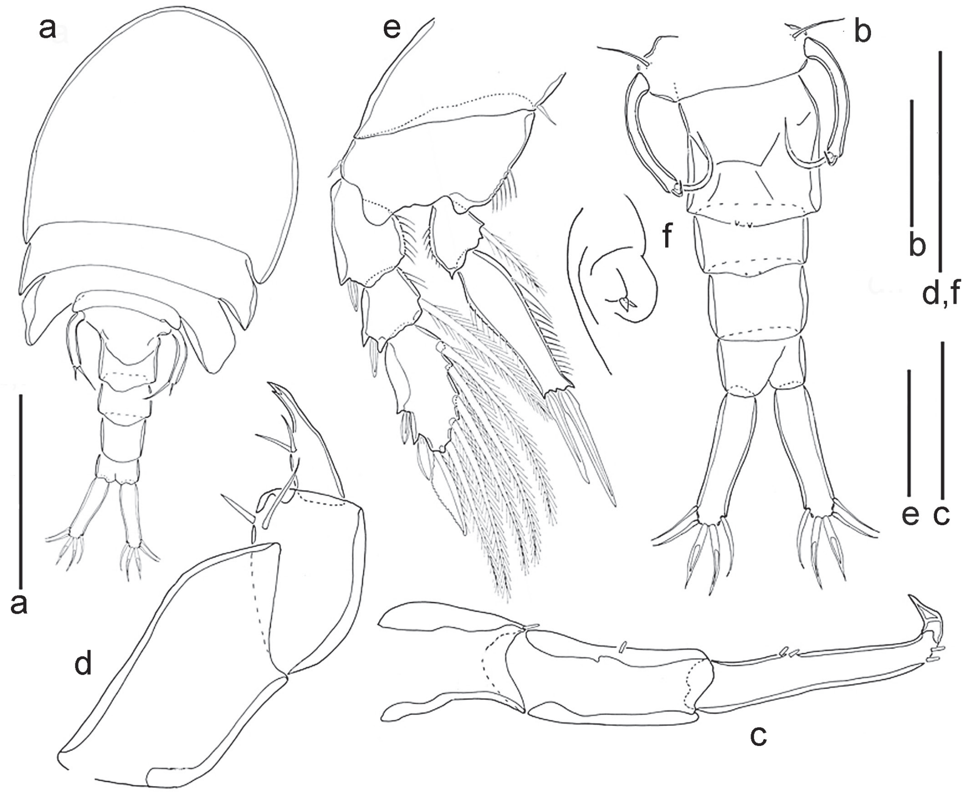

Figure 7. *Spaniomolgus acutus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4 **f** Genital area. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm (**c–f**).

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Fig. 7a). Mean body length 855 µm (with range of 850 – 860 µm) and mean maximum width 365 µm (with range of 320 – 410 µm), based on two specimens. Prosome comprising cephalothorax and three free pedigerous somites. Second and third pedigerous somites with epimeral areas pointed. Fourth pedigerous somite smaller than preceding ones, its epimeral areas much less expanded.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 7b). Leg 5-bearing somite slightly wider than long. Genital double-somite (Fig. 7b) narrow, slightly longer than wide (107 × 100 µm); lateral margins nearly parallel. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform elements (Fig. 7f). Egg sac unknown. Three postgenital somites 48 × 89, 52 × 78 and 40 × 70 µm from anterior to posterior.

Caudal rami (Fig. 7b) elongated, 111 × 30 µm, 3.7 times longer than wide. With five setae, all relatively short and naked. Outer lateral seta 44 µm, outermost terminal seta 41 µm, innermost terminal seta 48 µm. Two median terminal setae broadened, 52 µm (outer) and 59 µm (inner) in length. Dorsal seta not observed.

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. c) 3-segmented; first segment 48µm long with small terminal hyaline seta; second segment 60 µm long, with similar seta medially; third segment 76 µm long, with two hyaline setae medially, and two apical hyaline setae, with small recurved terminal claw 20 µm long. Length ratio of second to third segments (measured along inner margin) 1:1.2.

Maxilliped (Fig. 7d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third claw-like segment with two setae medially, and a tooth subapically.

Leg 4 (Fig. 7e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta short and naked. Endopod reaching tip of third exopodal segment, with two apical spines unequal in length, outer 39 µm long, inner 52 µm long, the latter spines with hyaline and smooth margins. Outer spines on leg 4 exopod with smooth lamellae.

Fifth leg (Fig. 7b) with protopod incorporated into somite; outer basal seta smooth. Free segment long, slender and recurved, 9.3 times as long as wide, bearing two apical setae unequal in length, inner most 3.6 times the length of outer one.

Sixth leg (Fig. 7f) represented by two very small articulated projections near attachment of eggs sacs.

Male unknown.

***Spaniomolgus stylophorus* sp. n.**
http://zoobank.org/56C93061-E2C5-47E5-8A3C-977D264B169E
Figs 8, 9 b–d

Type locality. Saudi Arabian Red Sea, reef near Thuwal, 22°12'04.30"N, 38°57'31.40"E.

Material examined. 1 ♀ holotype (ZMMU Me-1211) and 1 ♀ paratype (ZMMU Me-1212) from *Stylophora pistillata* (KAUST SA2013-12) collected at 1 m depth in the inner part of the reef; 1 additional ♀ from *Stylophora pistillata* (morphotype *S. danae*) (KAUST SA2013-31) collected at 28 m depth in the outer part of reef (22°20'23.45"N, 38°50'52.33"E).

Etymology. The specific epithet *stylophorus* refers to the host name *Stylophora.*

Description. Adult female.

Body cyclopiform, with oval cephalothorax and cylindrical urosome (Figs 8a, 9b). Mean body length 1.15 mm (with range of 1.1 – 1.2 mm) and mean maximum width 365 µm (with range of 320 – 410 µm), based on two specimens. Somite bearing leg 1 completely separated from cephalosome. Epimeral areas of metasomal somites slightly angular. Fourth pedigerous somite smaller than preceding ones, its epimeral areas not visible in dorsal view.

Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite and three free abdominal somites (Fig. 8b). In dorsal view, only the postgenital somites visible. Leg 5-bearing somite slightly wider than long. Genital double-somite (Fig. 8b) bell-

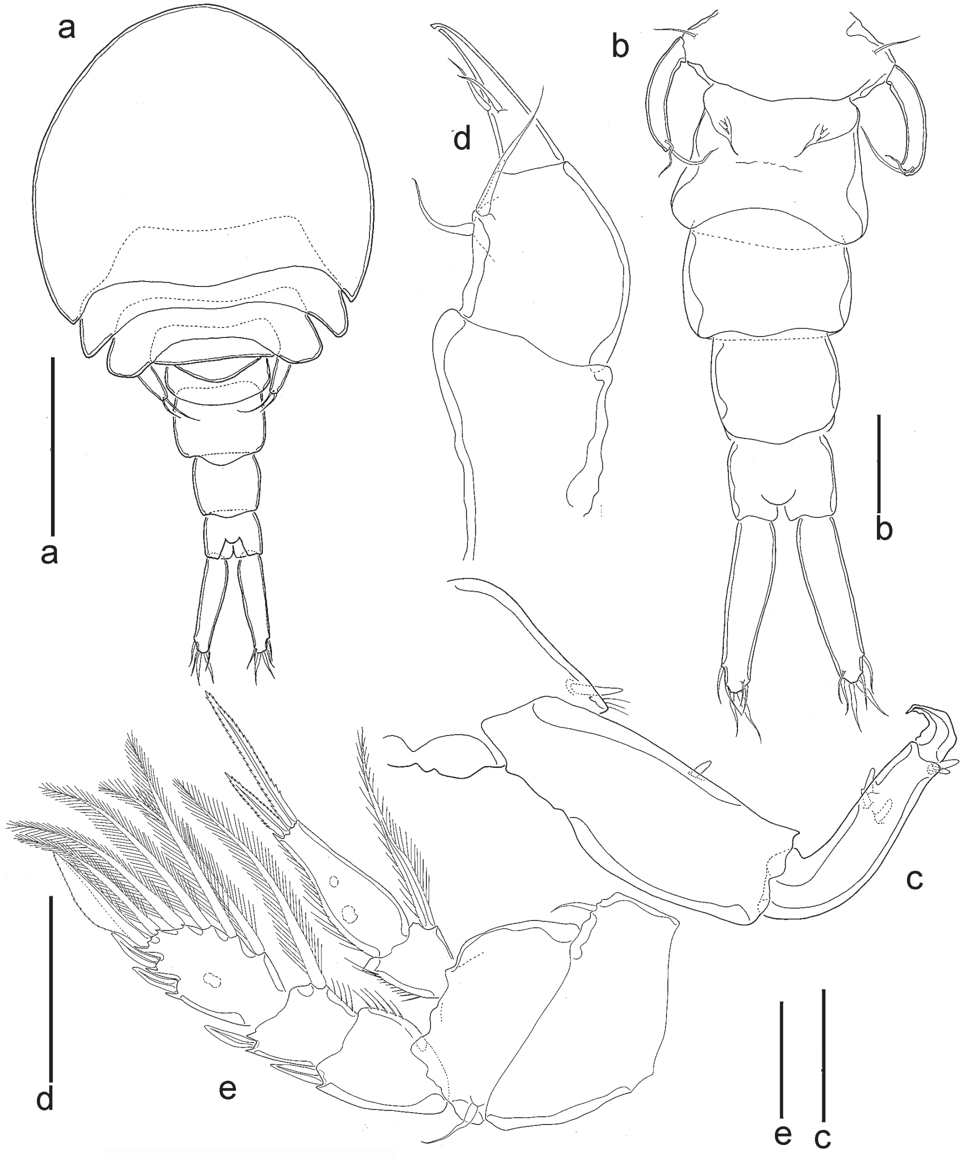

Figure 8. *Spaniomolgus stylophorus* sp. n., female. **a** Habitus dorsal **b** Urosome dorsal **c** Antenna **d** Maxilliped **e** Leg 4. Scale bars: 300 µm (**a**); 100 µm (**b**); 50 µm(**c–e**).

shaped; 170 µm minimum width (anterior half), 220 µm maximum width (posterior half) and 155 µm long; shorter dorsally than ventrally. Paired genital apertures bipartite, each comprising ventrolateral copulatory pore and dorsolateral gonopore (oviduct opening). Each genital area with two minute spiniform setae (Fig. 8b). Egg sac unknown. Three postgenital somites 120 × 180, 120 × 130 and 94 × 110 µm from anterior to posterior.

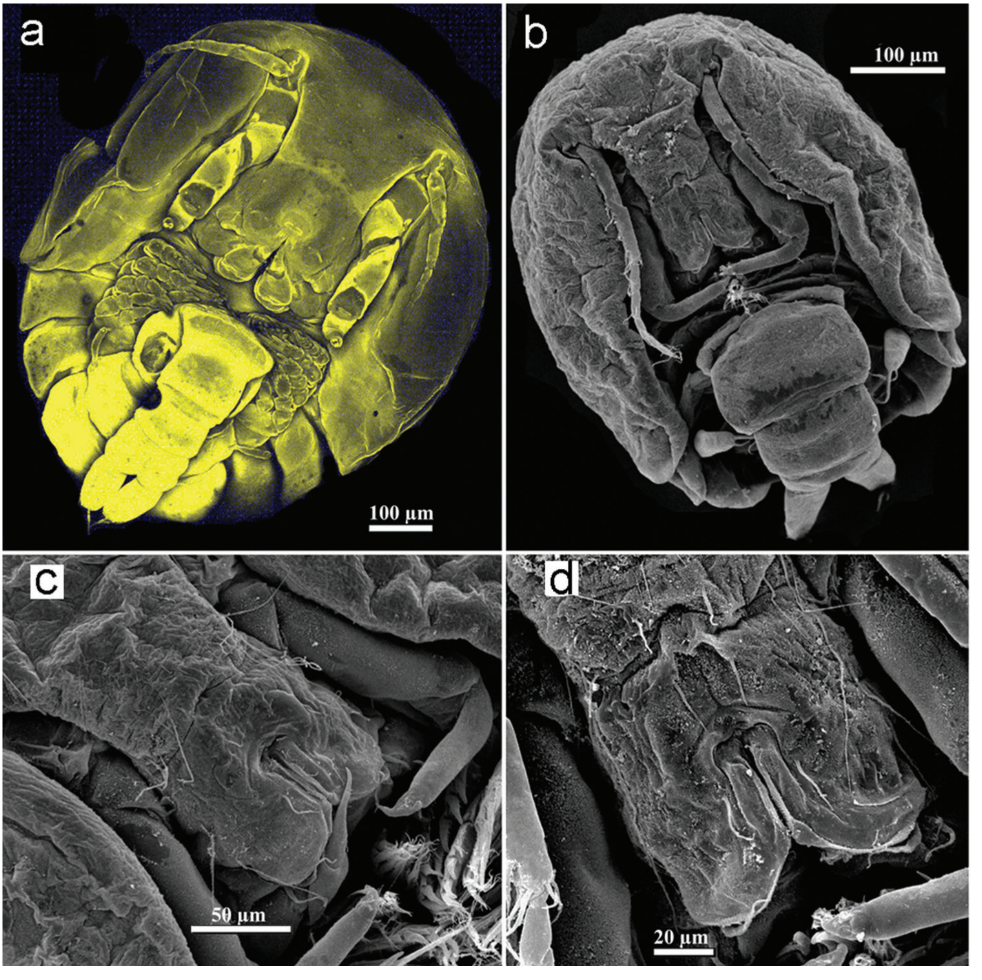

Figure 9. *Spaniomolgus,* females. **a** *S. crassus* (Humes & Ho, 1968), confocal photo. *S. stylophorus* sp. n., SEM **b** Habitus ventral **c** Rostral area **d** Labrum.

Caudal rami (Fig. 8b) elongated, 200 × 45 µm, 4.4 times as long as wide. With six setae, all relatively short and naked. Outer lateral seta 40 µm, outermost terminal seta 40 µm, innermost terminal seta 30 µm. Two median terminal setae broadened, 50 µm (outer) and 60 µm (inner) in length. Dorsal seta 25 µm.

Rostral area with hyaline setules (Fig. 9c, d).

Antennule, mandible, maxillule, maxilla and armature formula for legs 1–4 as for *Spaniomolgus globus* sp. n.

Antenna (Fig. 8c) 3-segmented; first segment 80µm long with small terminal hyaline seta; second segment 115 µm long with a seta medially; third segment 78 µm long with three hyaline setae medially, and two apical hyaline setae, with small recurved terminal claw 30 µm long. Length ratio of second to third segments (measured along inner margin) 1.5:1.

Maxilliped (Fig. 8d) 3-segmented; first segment unarmed; second segment robust, with two naked inner setae; third segment claw-like, with two setae medially equal in length; apex with pore.

Leg 4 (Fig. 8e) with 3-segmented exopod and 2-segmented endopod. Inner coxal seta and outer basal seta short and naked. Endopod reaching beyond middle of third exopodal segment, with two apical spines unequal in length, outer 38 µm and inner 70 µm, the latter spines with hyaline and serrated margins. Outer spines of exopod with smooth lamellae.

Leg 5 (Fig. 8b) with protopod incorporated into somite; outer basal seta naked. Free segment long, slender and recurved, 5.0 times as long as wide, bearing two apical setae unequal in length, inner most more than twice the length of outer one.

Male unknown.

***Spaniomolgus crassus* (Humes & Ho, 1968)**
Fig. 9a

Material examined. 2 ♀♀ found in tubular-shaped modification of corallites of *Stylophora pistillata* (morphotype *S. mordax*) (KAUST SA2013-72) collected on a reef near Al Lith at 2.5 m depth (20°08'02"N, 40°05'59"E).

Discussion

Taxonomy

Designation of the genus *Spaniomolgus* Humes & Stock, 1973 was based on three previously known species of *Lichomolgus* copepods associated with scleractinian corals: the type species *S. compositus*, *S. geminus*, and *S. crassus* from northern Madagascar (Humes and Frost 1964, Humes and Ho 1968). The finding of five new species and *S. crassus* in the Red Sea is the first record since 1968. Although *Spaniomolgus* is a rather homogenous genus, there are differences among its eight species.

The body has a broadened and thickened prosome in *S. crassus* and *S. globus,* but it is moderately widened, and the epimeral areas of the second and third pedigerous somites are slightly rectangular or angular in *S. stylophorus*, *S. geminus*, *S. compositus*, *S. dentatus*, *S. maculatus,* and *S. acutus*. Another key character to separate the species of *Spaniomolgus* is the body organization. For example, the first pedigerous somite is clearly set off from the cephalosome in *S. crassus* and *S. stylophorus,* incompletely separated from the cephalosome by an indistinct furrow in *S. geminus*, *S. compositus,* and *S. globus*, and completely fused to the cephalosome in *S. dentatus, S. maculatus*, and *S. acutus*.

The antennules are very similar in all eight species, with the only difference being the presence of an extra seta in the sixth segment in *S. globus*, *S. stylophorus*, *S. dentatus*, *S. maculatus*, and *S. acutus*.

The antenna of all species, except for *S. maculatus* and *S. acutus*, have the same armature formula (1,1,3+2+claw). *Spaniomolgus maculatus* and *S. acutus* have a reduced armature of 1,1,2+1+claw and 1,1,2+2+claw, respectively. The length ratio of the second and the third segments of the antenna can be also used for species delimitation. For example, the length ratio of the two distal antennary segments is 1.1:1 in *S. crassus*, *S. geminus*, *S. compositus,* and *S. dentatus*, but 1.5:1 in *S. stylophorus*, 1.7:1 in *S. maculatus*, 2.1:1 in *S. globus* (2.1: 1), and 1:1.2 in *S. acutus.*

The maxillules of *S. globus*, *S. stylophorus*, *S. dentatus*, *S. maculatus,* and *S. acutus* are represented by a single segment bearing a small seta and three hyaline prolongations without evident articulation. However, according to Humes and Frost (1964) and Humes and Ho (1968), the maxillule shows four hyaline prolongations without articulation in *S. geminus*, *S. compositus,* and *S. crassus*. The condition of the maxillulary projections of the latter three species needs to be reassessed because the articulation of one of these elements was probably overlooked.

As for the maxilliped, small interspecific differences in the third claw-like segment were detected. The margin of the claw has three very small subterminal spinules in *S. geminus*, *S. compositus,* and *S. crassus,* but it is smooth and with an apical pore in *S. stylophorus* and *S. maculatus*. The distal half of the claw's margin is denticulated in *S. globus* and *S. dentatus;* but with as single subapical tooth in *S. acutus*.

The armature of the legs is the same for the eight species; only the ornamentation of the fourth leg varies among the species. The exopodal spines have barbed lamellae in *S. geminus*, *S. compositus*, *S. dentatus*, *S. maculatus*, and *S. acutus*, but they are smooth in *S. crassus*, *S. globus*, and *S. stylophorus*. With respect to the terminal spines of the second endopodal segment, they are hyaline and smooth in *S. acutus* and *S. crassus*, but serrated in *S. stylophorus*, *S. dentatus*, *S. maculatus*, *S. compositus,* and *S. geminus*. In *S. globus* the outer terminal spine is serrated and the inner one is smooth.

The genital double-somite, generally rather narrow, can be present in three different shapes. In *S. crassus, S. compositus,* and *S. geminus* it is wider in its anterior third than in its posterior two-thirds; it is longer than wide with almost parallel margins in *S. dentatus, S. maculatus* and *S. acutus*, and completely square and bell-shaped in *S. globus* and *S. stylophorus* (wider in its posterior part).

The fifth leg in all species shows a long, slender and recurved segment of exopod with two apical setae. The length:width ratio of the free segment varies among the species, it is 10.5 times as long as wide in *S. geminus*, 9.3 times in *S. acutus,* 7.9 times in *S. compositus*, 7.6 times in *S. maculatus*, 6.7 times in *S. globus*, 6.3 times in *S. crassus*, 5.0 times in *S. stylophorus*, and 4.2 times in *S. dentatus*. Noteworthy, the outer basal seta of is minute in *S. globus* and has not been observed in *S. dentatus*.

The length:width ratio of the caudal rami, characteristically elongated in all the species, is also variable. The caudal rami are 9.1 times as long as wide in *S. geminus*, 5.0 times in *S. compositus* and *S. maculatus*, between 4.0 and 4.5 times in *S. globus*, *S. stylophorus* and *S. dentatus*, 3.7 times in *S. acutus*, and 2.8 times in *S. crassus*. The eight species present six terminal setae that are characteristically short and naked, except for *S. acutus* in which the dorsal seta has not been observed.

Key to species of the genus *Spaniomolgus* Humes & Stock, 1973 (females)

1 First pedigerous somite completely separated from cephalothorax **2**
– First pedigerous somite not completely separated from the cephalothorax **3**
2 Prosome unusually broadened and thickened; caudal rami 2.8 times as long as wide; length ratio of second to third segments of the antenna 1.1:1; terminal claw of maxilliped with subterminal spinules ....***S. crassus*** **(Humes & Ho, 1968)**
– Prosome broad; caudal rami 4.4 times as long as wide; length ratio of second to third segments of the antenna 1.5:1; terminal claw of maxilliped with apical pore ....***S. stylophorus*** **sp. n.**
3 First pedigerous somite incompletely separated from cephalosome by an indistinct furrow **4**
– Cephalosome fully incorporating first pedigerous somite **6**
4 Caudal rami greatly elongated, 9.1 times as long as wide; outer exopodal spines of fourth leg with barbed lamellae; free segment of fifth leg 10.5 times as long as wide.. ***S. geminus*** **(Humes & Ho, 1968)**
– Caudal rami 5.0 times as long as wide or less **5**
5 Caudal rami 5.0 times as long as wide; length ratio of second to third segment of the antenna 1.1:1; outer exopodal spines of fourth leg with barbed lamellae; free segment of fifth leg 7.9 times as long as wide............ ***S. compositus*** **(Humes & Frost, 1964)**
– Caudal rami 4.0 times as long as wide; length ratio of second to third segment of the antenna 2.1:1; outer exopodal spines of fourth leg with smooth lamellae; free segment of fifth leg 6.7 times as long as wide ....***S. globus*** **sp. n.**
6 Outer exopodal spines of fourth leg with barbed lamellae; caudal rami 4.3 times as long as wide; length ratio of second to third segment of the antenna 1:1; free segment of fifth leg 4.2 times as long as wide................................ ***S. dentatus*** **sp. n.**
– Outer exopodal spines of fourth leg with smooth lamellae **7**
7 Caudal rami 5.0 times as long as wide; length ratio of second to third segment of the antenna 1.7:1; free segment of fifth leg 7.6 times as long as wide; terminal claw of maxilliped with apical pore .... ***S. maculatus*** **sp. n.**
– Caudal rami 3.7 times as long as wide; length ratio of second to third segment of the antenna 1:1.2; free segment of fifth leg 9.3 times as long as wide; terminal claw of maxilliped with a tooth subapically ....***S. acutus*** **sp. n.**

Hosts

Spaniomolgus compositus found by Humes and Frost (1964) in washings of *Stylophora subseriata,* and *Spaniomolgus crassus* and S. *geminus* reported by Humes and Ho (1968) from washings of *Stylophora mordax* (Dana, 1846) should be now considered as co-occurring symbionts of one coral host, *Stylophora pistillata.* We assume that the coral indicated by Humes and Frost (1964) as *Seriatopora subseriata* is actually *Stylophora subseriata* (Ehrenberg, 1834) as the name *Seriatopora subseriata* is not valid. Thus, all eight species of *Spaniomolgus* reported in the present paper are now considered as associates of a single host species, *Stylophora pistillata*.

Ecological comments

The scleractinian coral *Stylophora* is considered to be one of the main Indo-Pacific reef-framework builders and is one of the dominant species in shallow-water reef environments exposed to strong wave action (Veron 2000). *Stylophora pistillata* hosts a great variety of copepods, including highly transformed xarifiids, which live in the gastrovascular cavities of the polyps. These symbiotic copepods were first noticed by Dr. Sebastian A. Gerlach during the Xarifa Expedition to the Red Sea and the Maldives Archipelago in 1957–1958 (Humes 1985a). Since then, copepods of three different orders have been found in association with this scleractinian coral: one species of Harpacticoida, *Alteuthellopsis corallina* Humes, 1981 (Peltidiidae, ectosymbiotic), three species of Siphonostomatoida, *Asteropontius corallophilus* Stock, 1966, *A. magnisetiger* Kim, 2010, *Gascardama longisiphonata* Kim, 2010, and seven species of Poecilostomatoida (Stock 1966, Humes 1981, Kim 2010). Among these poecilostomatoid copepods, five endosymbiotic species belong to the family Xarifiidae, *Xarifia decorata* Humes & Ho, 1968, *X. dissona* Humes, 1985, *X. lissa* Humes & Ho, 1968, *X. obesa* Humes & Ho, 1968, and *X. lissa* Humes & Ho, 1968, and three ectosymbiotic species belong to the family Rhynchomolgidae, *S. crassus*, *S. compositus*, and *S. geminus* (Humes and Frost 1964, Humes and Ho 1968, Humes 1985b).

Though coral-associated copepods have been studied for a considerable period of time, there remains a scarcity of data on their biology and ecology (Humes 1994, Ho 2001, Cheng et al. 2016, Ivanenko et al. 2018). Relationships between copepods and their hosts remain poorly studied due to the microscopic size of these crustaceans making *in situ* observations difficult. There are only few studies that include information about the interactions between copepods and corals (e.g. Ivanenko et al. 2014, Shelyakin et al. 2018).

Recent experiments by Cheng and Dai (2009) showed the ability of xarifiid copepods to get inside of the polyp of *S. pistillata* and to stay there as a symbiont. These copepods can make a polyp open its mouth either by releasing specific chemicals which induce feeding behaviour or act as muscle relaxants. However, it is still unclear which mechanism is actually utilized. It is also unknown if other coral species may be infected in a similar manner. Gall-inducing copepods are another example of coral hosts being affected by copepods. These copepods appear to attach to the soft tissues of the coral, and by disturbing it with their swimming legs, elicit the defence mechanism of a coral to grow a calcareous barrier (Dojiri 1988, Ivanenko et al. 2014). The multifocal purple spots syndrome of sea fans, which was thought to be caused by a fungous pathogen, appears to be induced by endoparasitic copepods sitting in the tissue outgrowths (Ivanenko et al. 2017).

It is often unclear whether copepods should be classified as parasites, because of the absence of rigorous experimental documentation. If we want to study copepod-coral relationships, it is crucial to know which copepod species are involved in symbiosis and what is their effect on the host. Therefore, it is important to provide detailed descriptions as well as identification keys for all copepod species associated with corals, so species composition and abundance of copepod communities can be tracked and used as a bioindicator for environmental changes and coral health (Ho 2001, Zeppilli et al. 2015, 2018).

Moreover, most of the symbiotic copepods depend entirely on the well-being of their hosts, and with the loss of corals during the recent bleaching events, many species of copepods associated with these corals could disappear, some even before being described. For instance, reefs close to Al Lith in the central Red Sea, where some of our samples were collected, were severely affected by the major bleaching event of 2015–2016 (Monroe et al. 2018, Osman et al. 2018). Most of the colonies of *S. pistillata* at the Al Lith reefs and about 20% of colonies at the Thuwal reefs were bleached and died (Monroe et al. 2018, Osman et al. 2018, personal observations of V.N. Ivanenko and S.V. Mudrova in May 2017). Therefore, abundance and diversity of copepods could have also been strongly affected, and some of the species collected from the reefs near Al Lith may already be gone from this region.

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RESEARCH ARTICLE

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Description of a new species of *Saissetia* from China (Hemiptera, Coccomorpha, Coccidae)

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Abstract

The adult female of a new species of soft scale *Saissetia puerensis* Zhang & Feng, **sp. n.** is described and illustrated from the genus *Saissetia* Deplanche, 1859. This species was collected on *Lithocarpus uvariifolius* (Hance) in Yunnan province, China. A key is provided to separate adult females of all *Saissetia* species known from China. A table is provided showing the distribution of *Saissetia* in various zoogeographical regions throughout the world.

Keywords

Coccinae, distribution, *Saissetia*, soft scale insect, taxonomy

Introduction

Soft scale insects, the third largest family of the Coccoidea, are distributed around the world, and currently include 169 genera and 1183 species (García Morales 2018). Most of them are pests of agricultural and horticultural crops. One species of soft scale, *Ericerus pela* which provides wax, an important industrial raw material, is considered to be beneficial in industry (Fang and Wang 2012; Henderson and Hodgson 2005).

The genus *Saissetia*, described by Deplanche in 1859, is a member of the tribe Saissetiini, subfamily Coccinae, and includes 44 species from around the world (Tang 1991; García Morales 2018). Six species of *Saissetia* have been recorded in China (García Morales 2018).

In this paper, the adult female of a new species *Saissetia puerensis* Zhang & Feng, sp. n. is described and illustrated. In addition, the genus *Saissetia* is described and a key is provided to separate the six species of *Saissetia* currently known from China. A list of *Saissetia* species throughout the world and their distributions in various zoogeographical regions is presented in Table 1.

Materials and methods

All specimens were collected from Yunnan province in China, and mounted according to the methods described by Hodgson and Henderson (2000). The morphological terminology describing the mounted specimens primarily follows the nomenclature developed by Hodgson (1994). A Nikon compound microscope was used to examine specimens and an Olympus BH–2 stereoscopic microscope was used to draw illustrations from mounted adult female specimens. Measurements of all characters were recorded in micrometers (μm) or millimeters (mm).

All specimens were deposited in the Northwest A&F University, Yangling, Shaanxi, China (**NWAFU**).

Taxonomy

Genus *Saissetia* Deplanche, 1859

Saissetia Deplanche, 1859: 6.
Bernardia Ashmead, 1891: 100.

Type species. *Lecanium coffeae* Walker, 1852.

Generic diagnosis. Adult female. Body oval, slightly or distinctly convex, H-shaped ridge distinctively present on dorsal surface. ***Dorsum.*** Derm membranous, oval or polygonal areolations. Dorsal setae coniform; dorsal tubercles present or absent; dorsal tubular ducts absent; anal plate triangular, with obvious discal seta. ***Margin.*** Marginal setae branched or apex pointed; stigmatic spines of three setae, the median spine longer than others; stigmatic cleft shallow or deep. **Venter.** Antennae of 6–8 segments; legs well developed, with tibio-tarsal articulation sclerosis (except in *S. neglecta*); spiracular disc-pores with 5–6 loculi; pregenital disc-pores with 10–12 loculi, present around anal plate, some on abdominal segment, a few pregenital disc-pores extend to thorax; ventral tubular ducts present in submargin.

Saissetia puerensis **Zhang & Feng, sp. n.**
http://zoobank.org/9910C83A-8F63-464E-9181-DEEB352340FF
Figure 1

Material examined. Holotype: adult female. CHINA, Yunnan, Puer. 24. vii. 2017, on *Lithocarpus uvariifolius* (Hance) Rehd, Na Zhang (NWAFU). **Paratypes:** two adult females mounted on different slides, data same as holotype.

Diagnosis. The adult female of *S. puerensis* can be diagnosed by the combination of the following features: (1) body convex and sclerotized, distinct H-shaped ridge present on dorsum surface; (2) dorsal tubercles present; (3) dorsal tubular ducts absent; (4) dorsal setae tapered; (5) antennae 8 segments; (6) legs well developed, with tibio-tarsal articulation and articulation sclerosis; (7) spiracular disc-pores present in a rather broad band 7–8 pores wide; (8) anal plates with a discal seta; (9) ano-genital fold with four or five pairs of setae; (10) four types of ventral tubular ducts: (i) type I present on medial submarginal area and inner and medial submarginal area of posterior abdominal segments, some scattered on inner submarginal area mingling with type II, some on outer submarginal area mingling with type III, (ii) type II present mainly on inner submarginal area, few present on procoxa and mesocoxa, and a few ducts present near antennae and mouthparts, some mingling with type I in medial submarginal area, (iii) type III present on outer broad submarginal area, some ducts present in inner submarginal area, (iv) type IV present on anal cleft and broad submarginal band mingling with t types I, II and III, most present on posterior abdominal segments, few ducts present on mesocoxa; (11) pregenital disc-pores, 10–11 loculi, mainly with ten loculi, abundant around anal opening, some extending in transverse bands on abdominal segments, and some laterad of metacoxa and mesocoxa.

Description. *Appearance in life*. Pre-reproductive adult female: Body elongate-oval, dorsum greenish. Mature adult female: Body oval, dorsum reddish-brown, convex and sclerotized, distinct H-shaped ridge present on dorsum surface.

***Slide-mounted specimens*:** Body oval, 1.5–2.3mm long, 1.0–1.5mm wide, margin with a distinct indentation at each stigmatic cleft; anal cleft 1/8–1/10 body length.

***Dorsum*:** Derm membranous or slight sclerotized. Dermal areolations well developed, with one dorsal microductule. Dorsal setae 5.3–7.8 µm long, tapered, apex slightly curved, with a well-developed basal socket, scattered all over the dorsum. Dorsal tubercles present on submarginal area, 2–5 on head, 0–2 between stigmatic clefts, 2–3 between posterior stigmatic cleft and anal cleft. Preopercular pores small, 2.7–4.5 µm wide, 14–26 in front of anal plates. Dorsal tubular ducts absent. Anal plates together quadrate, 139.6–155.1 µm long, 67.5–78.1 µm wide, outer angle slightly obtuse; posterolateral margin slightly longer than anterolateral: anterolateral margin 84.5–100.9 µm long, posterolateral margin 103.5–122.3 µm long; posterolateral margin slightly convex and anterolateral margin slightly concave, with four apical setae and a discal seta; supporting bars not contacted with each other. Ano-genital fold with four or five pairs of setae, 37.1–60.7 µm long, present along anterior margin; three pairs

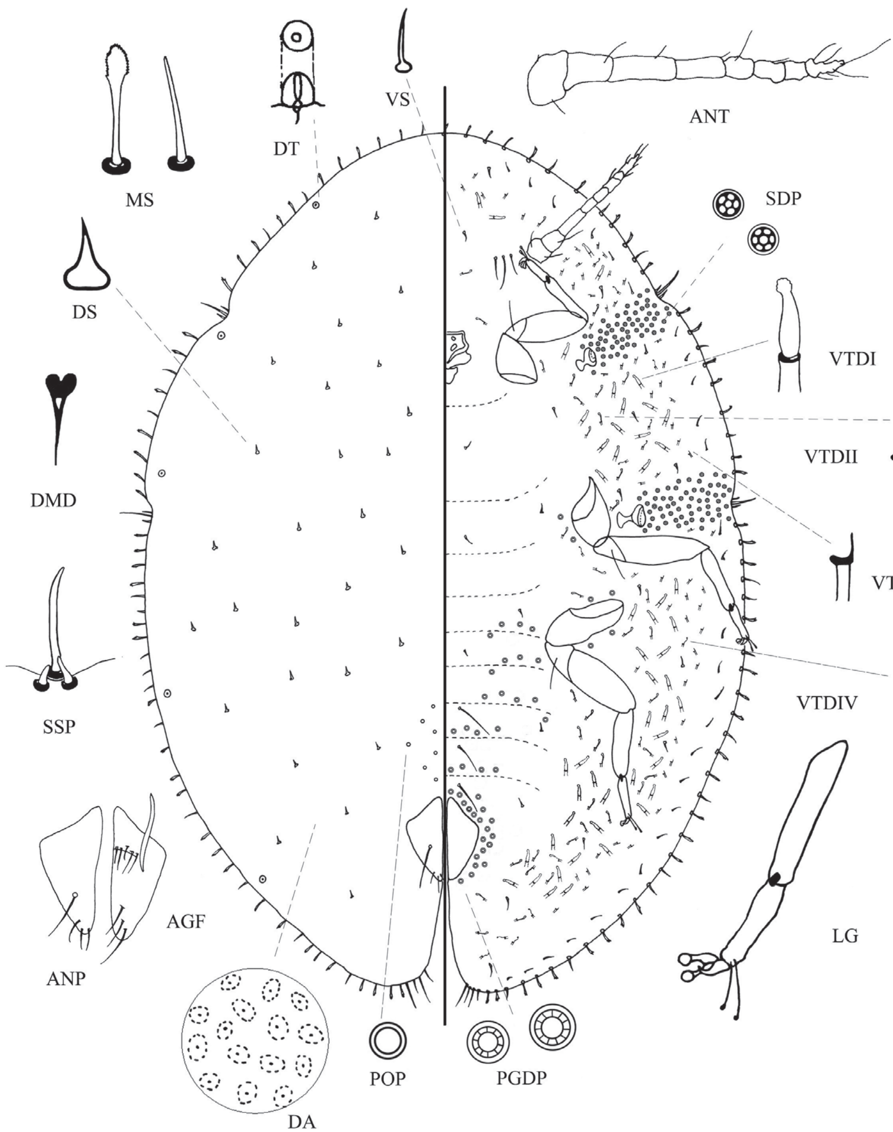

Figure 1. *Saissetia puerensis* Zhang & Feng, sp. n., adult female. The dorsal surface is depicted on the left side and the ventral surface on the right side, with enlargements of some important characters shown around the main illustration. Abbreviations: **AGF** ano-genital fold **ANP** anal plates **ANT** antenna **DA** dermal areolations **DMD** dorsal microduct **DS** dorsal seta **DT** dorsal tubercles **LG** tibio-tarsus of hind leg **MS** marginal setae **PGDP** pregenital disc-pore **POP** preopercular pores **SDP** spiracle disc-pore **SSP** stigmatic spine **VTD** ventral tubular ducts of types I-IV **VS** ventral setae.

of setae, 28.6–57.2 µm long, present along lateral margin. Anal ring subcircular, with four pairs of setae, 163.1–189.4 µm long. Eyespots near margin.

***Margin*:** Marginal setae, 12.8–44.1 µm long, branched, straight or curved, a few spinous, all with well-developed basal sockets, with 36–46 setae between anterior clefts, 12–16 setae between each anterior cleft and posterior cleft, and 27–35 setae between each posterior cleft and anal cleft; some over 50 µm around anal cleft. Stigmatic cleft distinct and deep, with three stigmatic spines: one medial spine, 60.3–65.9 µm long, blunt, slightly curved apex and broadly based; lateral spines, 15.5–21.2 µm long, stout, straight; median four to five times longer than laterals.

***Venter*:** Derm membranous. Antennae 8 segments, 328.6–357.2 µm long, the third segment longest; with three pairs of interantennal setae, 21.4–88.5 µm long. Spiracular disc-pores, with 5–6 loculi, mainly with five loculi, occasionally six loculi, each about 3.2–4.9 µm wide; present in a rather broad band 7–8 pores wide between stigmatic cleft and each spiracle; 30–66 pores in each anterior spiracle band and 45–93 pores in each posterior band. Legs well developed, slender, with tibio-tarsal articulation and articulation sclerosis; claws without denticle; tarsal digitules and claw digitules both with knobbed apices, but tarsal digitules longer and thinner than claw digitules, tarsal digitules length 49.5–66.7 µm, claw digitules length 27.2–36.0 µm; dimensions of metathoracic leg: coxa 105.2–135.4 µm, trochanter+ femur 182.3–230.3 µm, tibia + tarsus 229.6–249.8 µm, tibia about two times longer than tarsus, claw 21.4–27.9 µm. Pregenital disc-pores, 10–11 loculi, mainly with ten loculi, occasionally 11 loculi, each about 3.8–5.9 µm wide; abundant around anal opening, some extending in transverse bands on abdominal segments, and some laterad of metacoxa and mesocoxa; with three pairs of long pregenital setae, each 95.7–138.3 µm long. There are four types of ventral tubular ducts:

Type I: a duct with large terminal gland, inner ductule almost as wide and long as outer ductule; present on medial submarginal area and inner and medial submarginal area of posterior abdominal segments, some scattered on inner submarginal area mingling with type II, some on outer submarginal area mingling with type III.

Type II: inner ductule almost twice as long as outer ductule, inner ductule thinner than outer ductule, but not filamentous, with a well-developed terminal gland; present mainly on inner submarginal area, few present on procoxa and mesocoxa, and a few ducts present near antennae and mouthparts, some mingling with type I in medial submarginal area.

Type III: outer ductule of this type slightly shorter than type I, a filamentous inner ductule without terminal gland; present on outer broad submarginal area, some ducts present in inner submarginal area.

Type IV: inner ductule almost two times as long as outer ductule, a filamentous inner ductule with a ball-shaped terminal gland; present on anal cleft and broad submarginal band mingling with t types I, II, and III, most present on posterior abdominal segments, few ducts present on mesocoxa. Ventral tubular ducts distributed irregularly; a few are scattered near anal cleft, becoming progressively more frequent anteriorly. Submarginal setae present in a single row, each 7.5–14.2 µm long; other ventral setae slender, each 7.9–18.6 µm long, quite sparsely distributed.

Etymology. The species epithet *puerensis* is a noun in apposition, referring to the place where this new species was collected.

Host. *Lithocarpus uvariifolius* (Hance) Rehd in China.

Distribution. China (Yunnan).

Key to adult females of *Saissetia* occurring in China

1	Stigmatic spines 4–7 setae	***S. vivipara* Williams &Watson, 1990**
–	Stigmatic spines 3 setae	**2**
2	Ventral tubular ducts with a broad inner ductule present in submarginal area	**3**
–	Ventral tubular ducts with a broad inner ductule absent in submarginal area	**5**
3	Marginal setae fine; dorsal submarginal tubercles absent	***S. bobuae* Takahashi, 1935**
–	Marginal setae branched; dorsal submarginal tubercles present	**4**
4	Ventral tubular ducts of 3 types distributed regularly in a submarginal band (*type I* distributed on medial submarginal area, *type II* distributed on inner submarginal area and *type III* distributed on outer submarginal area); Spiracular band 2–3 pores wide	***S. coffeae* (Walker), 1852**
–	Ventral tubular ducts of 4 types distributed irregularly in a submarginal band (the distribution of *types I*, *II*, *III and IV* is irregular, *type I* mingling with *type II* on inner submarginal area and mingling with *type III* on outer submarginal area); Spiracular band 7–8 pores wide	***S. puerensis* sp. n.**
5	Marginal setae between each anterior cleft and posterior cleft number 15–23	***S. miranda* (Cockerell & Parrott), 1899**
–	Marginal setae between each anterior cleft and posterior cleft number 4–12	**6**
6	Marginal setae branched; anal ring with four pairs of setae	***S. neglecta* De Lotto, 1969**
–	Marginal setae fine; anal ring with three pairs of setae	***S. oleae* (Olivier), 1791**

Discussion

This species is considered to be close to *Saissetia coffeae* (Choi and Lee 2017) and they share some distinct characteristics: 1) more than one type of ventral tubular duct; 2) anal plate with a discal seta; 3) three pairs of setae present along lateral margin; and 4) anal ring subcircular, with four pairs of setae.

However, *S. puerensis* can be distinguished by the possession of the following features (character states of *S. coffeae* in parenthesis): 1) four types of ventral tubular ducts (three); 2) ventral tubular ducts distributed irregularly, especially on posterior abdominal segments, type I mingling with type II (regularly); 3) type II not present on medial thorax (present); 4) inner ductule of type II ventral tubular ducts almost twice as long as outer ductule (inner ductule as long as outer ductule); 5) spiracle in a rather broad band 7–8 pores wide (2–3); 6) preopercular pores 14–26 in front of anal plates (5–14); and 7) ano-genital fold with four or five pairs of setae (three).

Lithocarpus uvariifolius (Hance) Rehd is the only plant known to be a host for *S. puerensis*. Heavy infestations of this pest cause a sooty mold to build up, which reduces photosynthesis and stunts the growth of the plant. *L. uvariifolius* is only known from China (Wu et al. 1999), and *S. puerensis* may therefore be restricted to this country. Further studies are required to determine if *S. puerensis* has other host plants and occurs in other countries.

World distribution of *Saissetia* species (Table 1)

Table 1 is based on information from ScaleNet which has not been published previously. Only *S. coffeae*, *S. miranda*, and *S. oleae* have worldwide distributions. The highest numbers of species are found in the Ethiopian and Neotropical regions, with 50.0% and 43.2% respectively; 40.9% of species occur only in the Ethiopian region and 34.1% only in the Neotropical region. The Nearctic region has fewest species, with only 9.1%.

Table 1. *Saissetia* species of the world: a simple list with indications of distribution by zoogeographical regions. Abbreviations: Pa = Palaearctic, Na = Nearctic, Et = Ethiopian, Or = Oriental, Au = Australian and Oceanic, Nt = Neotropical.

Species	Et	Nt	Or	Au	Pa	Na
S. absona	+					
S. anonae		+				
S. auriculata		+				
S. bobuae			+			
S. carnosa	+					
S. cassiniae				+		
S. cerei					+	
S. chimanimanae	+					
S. chitonoides	+					
S. coffeae	+	+	+	+	+	+
S. discoides		+				
S. dura		+				
S. ficinum					+	
S. glanulosa		+				
S. hurae		+				
S. infrequens		+				
S. jocunda	+					
S. lucida		+				
S. malagassa	+					
S. minensis		+				
S. miranda	+	+	+	+	+	+
S. mirifica				+		
S. monotes	+					
S. munroi	+					
S. neglecta		+	+	+		+
S. nigrella	+					
S. oleae	+	+	+	+	+	+
S. opulenta	+					
S. orbiculata	+					
S. persimilis	+					
S. poinsettiae	+					
S. privigna	+		+		+	
S. reticulata		+				
S. sclerotica	+					
S. scutata		+				

Species	Et	Nt	Or	Au	Pa	Na
S. socialis		+				
S. somereni	+					
S. subpatelliformis	+					
S. tolucana		+				
S. velfozoi		+				
S. vivipara			+	+		
S. xerophila	+					
S. zanthoxylum		+				
S. zanzibarensis	+					

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RESEARCH ARTICLE

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Sixteen new species of the genus *Pseudopoda* Jäger, 2000 from China, Myanmar, and Thailand (Sparassidae, Heteropodinae)

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Abstract
Sixteen new species of *Pseudopoda* Jäger, 2000 (Sparassidae, Heteropodinae) are described. Among them, eight species were collected from China: *P. chayuensis* Zhao & Li, **sp. n.** (♂), *P. conaensis* Zhao & Li, **sp. n.** (♂), *P. medogensis* Zhao & Li, **sp. n.** (♂), *P. nyingchiensis* Zhao & Li, **sp. n.** (♂), *P. shacunensis* Zhao & Li, **sp. n.** (♂), *P. shuo* Zhao & Li, **sp. n.** (♂♀), *P. yuanjiangensis* Zhao & Li, **sp. n.** (♀) and *P. zixiensis* Zhao & Li, **sp. n.** (♂); seven from Myanmar: *P. colubrina* Zhao & Li, **sp. n.** (♂♀), *P. daxing* Zhao & Li, **sp. n.** (♂), *P. gexiao* Zhao & Li, **sp. n.** (♂), *P. putaoensis* Zhao & Li, **sp. n.** (♂), *P. subbirmanica* Zhao & Li, **sp. n.** (♂♀), *P. titan* Zhao & Li, **sp. n.** (♂♀), *P. xia* Zhao & Li, **sp. n.** (♂); and one from Thailand: *P. maeklongensis* Zhao & Li, **sp. n.** (♂). A distribution map of the new species is also provided.

Keywords
Description, huntsman spiders, taxonomy

Introduction

Pseudopoda Jäger, 2000 is currently the third largest genus in the family Sparassidae Bertkau, 1872, containing 124 known species. A molecular phylogeny of Sparassidae asserted that *Pseudopoda* belongs to the subfamily Heteropodinae, and is closely related to *Heteropoda* Latreille, 1804 and *Sinopoda* Jäger, 1999 (Moradmand et al. 2014). Along with the description of 49 new species from Himalayas and adjacent mountains, Jäger (2001) proposed six species-groups mainly according to the features of male pedipalp and female epigyne: *P. diversipunctata*-group, *P. latembola*-group, *P. martensi*-group, *P. parvipunctata*-group, *P. prompta*-group and *P. schwendingeri*-group. Based on both molecular and morphological characteristics, Zhang et al. (2017) proposed the seventh species group: *P. daliensis*-group and described three new species from Yunnan, China.

Currently, all of the *Pseudopoda* species are found in Asian countries: Bhutan, China, India, Indonesia, Japan, Laos, Myanmar, Nepal, Pakistan, Thailand, and Vietnam. To date, 54 species have been reported from China, while 14 from Myanmar and six species from Thailand (World Spider Catalog 2018). A considerable number of them are recorded from high altitude mountain regions, such as the Himalayas and Yunnan-Guizhou Plateau in China. Most of the *Pseudopoda* species exhibit very small-ranged distributions, but a high local diversity. A previous research explored on the application of DNA barcoding in taxonomic assessment in this genus, and indicated there is a greater species diversity remaining to be discovered (Cao et al. 2016). Here, we described 16 newly discovered species collected from southern China (Yunnan Province, Jiangxi Province and Tibet Autonomous Region), northern Myanmar (Kachin State), and Thailand (Tak Province).

Material and methods

All specimens were examined and measured with a Leica M205C stereomicroscope. Images of male pedipalps and female epigynes were taken with an Olympus C7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus BX51 compound light microscope after removing them from the spiders' bodies. Images of bodies were taken with an Olympus C7070 camera mounted on an Olympus SZX12 dissecting microscope. Epigynes were cleaned and treated in trypsin and if necessary, in boiling solution of potassium hydroxide (KOH) before taking images of the vulvae. All images were assembled using Helicon Focus 6.7.1 software.

All measurements are in millimeters. Leg formula, spination, and measurements of palp and legs follow Jäger and Vedel (2007). Arising points of tegular appendices (i.e. embolus, conductor) are given as 'clock positions' on the left palp in ventral view. When the left palp is lost or incomplete, the images of right palp will be taken and flipped horizontally for the sake of comparison. In this case, the right palp will be treated as the left one.

Abbreviations used in the text and figures are given below:

AB anterior bands of epigynal field
ALE anterior lateral eye
AME anterior median eye
BP basal part of embolic projection
C conductor
CH clypeus height
CO copulatory opening
dRTA dorsal part/branch of RTA
DS dorsal shield of prosoma
E embolus

EP	embolic projection	**RTA**	retrolateral tibial apophysis
FD	fertilization duct	**S**	sperm duct
FW	first winding	**SP**	spermatheca
H	hump on tegulum	**ST**	subtegulum
LL	lateral lobe of epigyne	**T**	tegulum
OS	opisthosoma	**TE**	tip of embolus
PI	posterior incision of LL	**TP**	tegular protrusion
PLE	posterior lateral eye	**vRTA**	ventral part/branch of RTA.
PME	posterior median eye		

All material studied are deposited in the Institute of Zoology, Chinese Academy of Sciences (**IZCAS**) in Beijing, China.

Taxonomy

Family Sparassidae Bertkau, 1872

Subfamily Heteropodinae Thorell, 1873

Genus *Pseudopoda* Jäger, 2000

Type Species. *Sarotes promptus* O. Pickard-Cambridge, 1885

Diagnosis. Exclusively distributed in Asia. Small to large Heteropodinae. Male palp with membranous conductor (but sometimes absent), embolus at least in its basal part broadened and flattened, RTA arising basally or mesially from tibia; female epigyne with lateral lobes rising distantly beyond epigastric furrow, and in most cases covering median septum (modified from Jäger 2000).

Pseudopoda chayuensis Zhao & Li, sp. n.

http://zoobank.org/16E0E430-38B3-4913-A1C0-08A3ACA430FB
Figs 1, 2, 37

Type material. Holotype ♂: China, Tibet Autonomous Region, Nyingchi Prefecture, Chayu County, Walong, 28°35.092'N, 98°07.384'E, 3680 m, VIII 2013, J. Liu.

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

Diagnosis. Medium-sized *Pseudopoda* species. Male resembles *P. gongschana* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 6, figs 10–15) and *P. platembola* Jäger, 2001 (see Jäger 2001: 57, figure 35a–e) by: 1. embolus sickle-shaped, tapering very moderately (Figure 2A); 2. dRTA well developed and finger-like, curving distally (Figure 1A–C). It can be distinguished from the two congeners by the following combination of characters: 1. embolic projection near the tip of embolus, making the tip look

Figure 1. *Pseudopoda chayuensis* Zhao & Li, sp. n., right palp of male holotype, horizontally flipped for the sake of comparison. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

somewhat incised (Figure 1A; embolic projection absent in *P. platembola*); 2. embolus curving more intensely than in *P. gongschana* (Figure 2A).

Description. Male (holotype). Body length 10.7, DS length 4.3, DS width 4.1, OS length 6.4, OS width 3.4. Eyes: AME 0.16, ALE 0.24, PME 0.16, PLE 0.30, AME-

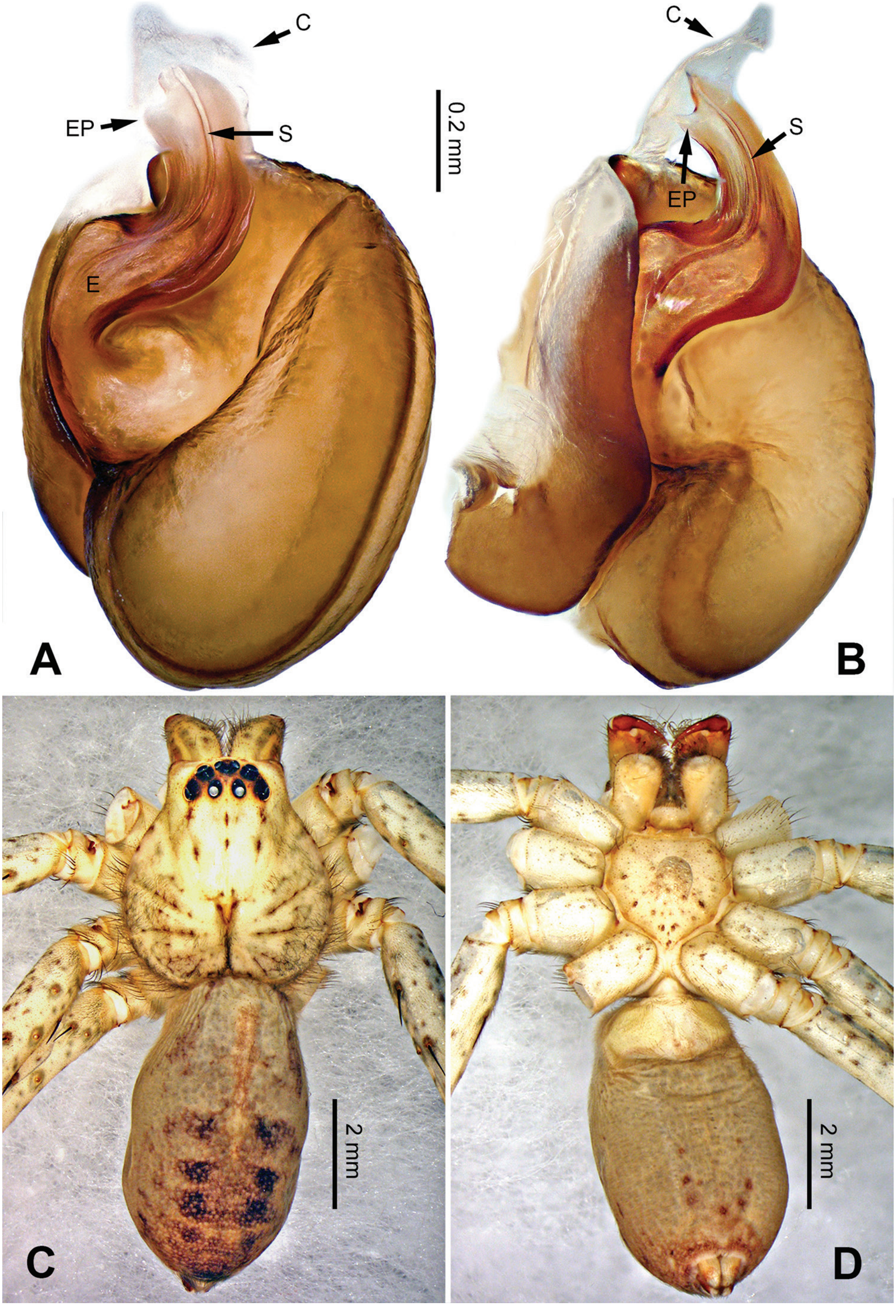

Figure 2. *Pseudopoda chayuensis* Zhao & Li, sp. n., male holotype. Right bulb horizontally flipped for the sake of comparison. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

AME 0.20, AME-ALE 0.10, PME-PME 0.33, PME-PLE 0.33, AME-PME 0.41, ALE-PLE 0.33, CH AME 0.32, CH ALE 0.24. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2111; legs: femur I-III 323, IV 331; patella I-IV 001; tibia I-IV 2126; metatarsus I-II 2024, III 3025, IV 3037. Measurements of palp and legs: palp - (-, 1.0, 1.4, -, 2.4), leg I 26.3 (7.0, 2.5, 7.0, 7.5, 2.3), leg II 28.3 (7.5, 2.5, 8.0, 8.0, 2.3), leg III 23.2 (6.8, 2.3, 6.1, 6.1, 1.9), leg IV 25.7 (7.0, 2.1, 6.8, 7.5, 2.3). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 15 denticles.

Palp as in diagnosis. Cymbium distally slender and elongated, with a small retrobasal projection in ventral view. RTA arising basally to mesially from tibia, vRTA thumb-like, shorter than dRTA (Figure 1A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus sickle-shaped, arising from tegulum at 10 o'clock position. The embolus tapering and very moderately curved. Embolic projection emerging at the prolateral margin of embolus as a blunt hump. Conductor arising from tegulum at 12 o'clock position, slightly leaning prolaterally and covering the tip of embolus (Figure 2A, B).

Coloration in ethanol: carapace yellow. Radial furrows and fovea dark brown. Dorsal opisthosoma brown with black pattern. Legs yellowish brown, with reddish brown dots and patches (Figure 2C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda colubrina Zhao & Li, sp. n.

http://zoobank.org/8EDAFE92-8991-4BD0-A68F-C3895F419AB5
Figs 3–5, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, road to Ziradum Village, 27°33.617'N, 97°06.567'E, 1003 m, 8 V 2017, J. Wu & Z. Chen. **Paratype:** 1 ♀, same locality as holotype, 13 XII 2016, J. Wu.

Etymology. The specific name is derived from the Latin word *colubrinus, -a, -um*, meaning 'serpentine, winding', and referring to the shape of embolus in this species, which coils at the basal part and erects distally and looks like an alarmed snake; adjective.

Diagnosis. Small to median-sized *Pseudopoda* species. Male resembles *P. wu* Jäger, Li & Krehenwinkel, 2015 (see Jäger et al. 2015: 384, figs 115–129) and *P. tji* Jäger, 2015 (see Jäger 2015: 333, figs 1–15, 91) by: 1. embolus robust but twisted, forming loops (Figure 4A, B; rarely seem in other *Pseudopoda* spp.); 2. conductor absent (Figure 4A, B). It can be easily distinguished from the two congeners by the following combination of characters: 1. only basal part of embolus twisted, distal part elongated and mildly bent (Figure 4A, B; distal part coiled in *P. tji* and *P. wu*); 2. tegulum occupying two third of alveolus (Figure 3B; covering whole or most of alveolus in *P. tji* and *P. wu*).

Female resembles *P. hyatti* Jäger, 2001 (see Jäger 2001: 72, figs 41j–m, 84) by: 1. posterior part of lateral lobes surpassing the epigastric furrow; 2. loops of internal duct system mainly winding near the central axis, running transversally (Figure 5A, B, E).

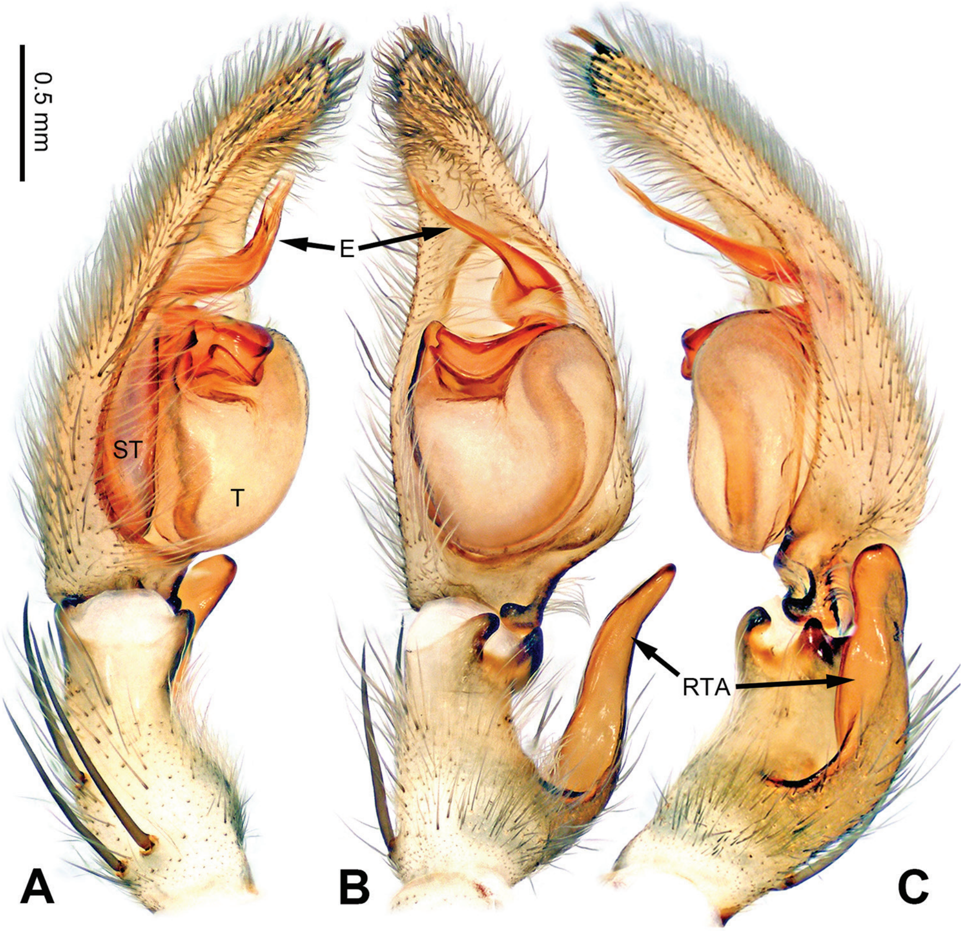

Figure 3. *Pseudopoda colubrina* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

It can be distinguished from the latter by the following combination of characters: 1. copulatory opening located at the middle to posterior part of epigyne (Figure 5A; located near the anterior margin of lateral lobe in *P. hyatti*); 2. anterior margin of epigynal field truncated, anterior bands absent (Figure 5A; anterior margin of epigynal field trilobate with short anterior bands in *P. hyatti*).

Description. Male (holotype). Body length 8.8, DS length 4.3, DS width 4.1, OS length 4.5, OS width 4.0. Eyes: AME 0.17, ALE 0.34, PME 0.29, PLE 0.28, AME-AME 0.23, AME-ALE 0.09, PME-PME 0.16, PME-PLE 0.33, AME-PME 0.37, ALE-PLE 0.32, CH AME 0.60, CH ALE 0.39. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2101; legs: femur I-II 323, III 322, IV 321; patella I-IV 101; tibia I-II 2026, III 2126, IV 2026; metatarsus I-II 1014, III 2025, IV 3036. Measurements of palp and legs: palp 6.3 (2.0, 0.9, 1.1, -, 2.3), leg I 20.4 (5.8, 2.0, 5.9, 4.9, 1.8), leg II 22.1 (6.1, 2.3, 6.4, 5.4, 1.9), leg III 16.7 (5.0, 1.8, 4.5, 4.0, 1.4), leg IV 19.6 (5.6, 1.7,

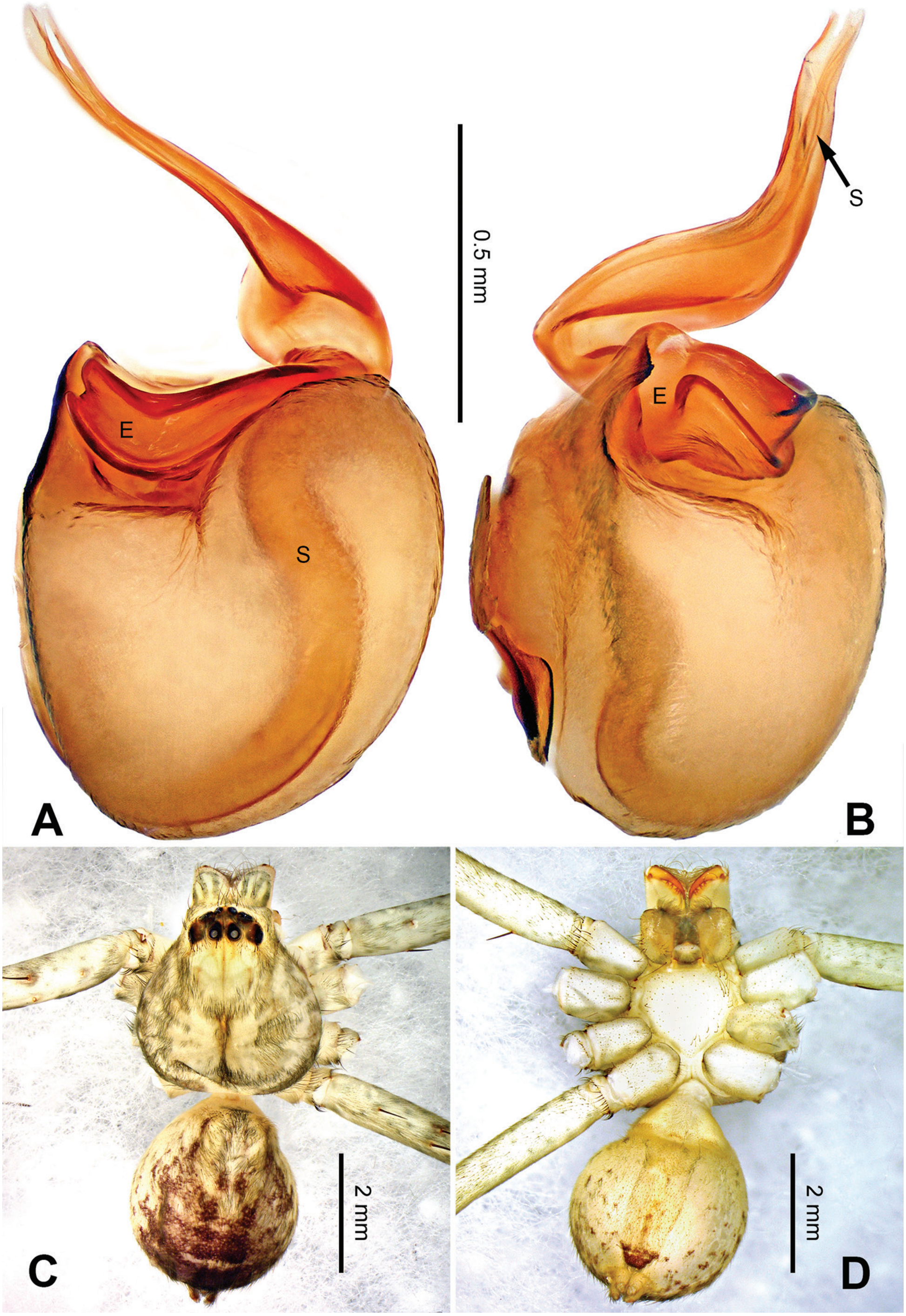

Figure 4. *Pseudopoda colubrina* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B.**

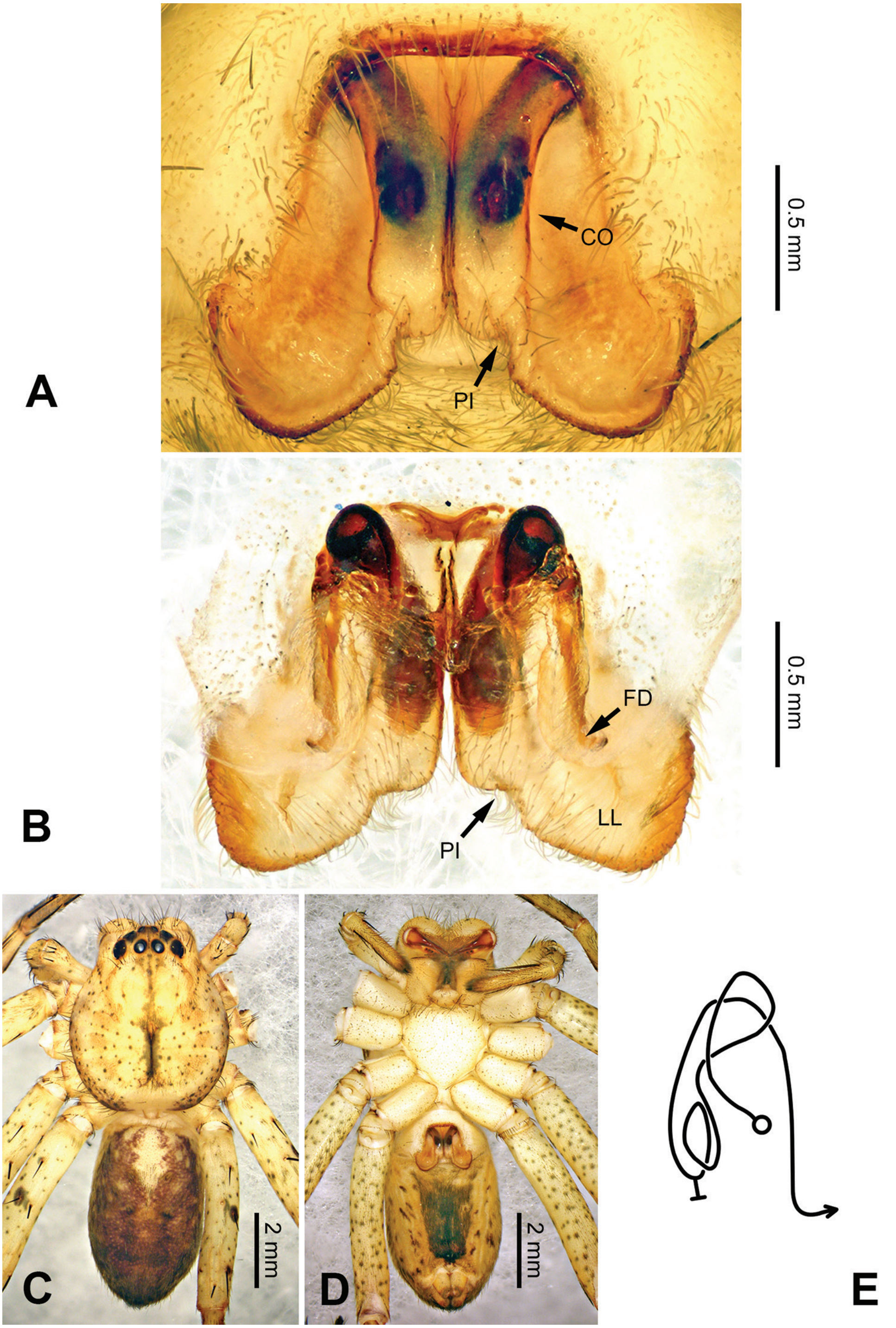

Figure 5. *Pseudopoda colubrina* Zhao & Li, sp. n., paratype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

5.0, 5.5, 1.8). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 21 denticles.

Palp as in diagnosis. Cymbium slender, tip slightly bent prolaterally, with a distinct retrobasal bulge. RTA arising basally from tibia, simple but elongated, blunt in retrolateral view (Figure 3A–C). Sperm duct bending near the top of tegulum, then running submarginally retrolaterally in tegulum. Basal part of embolus with distinct double rims. Tip of embolus pointing distally prolaterally. Conductor completely absent, like a few other species (e.g. *P. ashcharya* Jäger & Kulkarni, 2016) (Figure 4A, B).

Coloration in ethanol: carapace yellowish. Radial furrows and fovea darker brown. Dorsal opisthosoma reddish brown. Legs yellowish, with randomly distributed brown dots (Figure 4C, D).

Female (paratype). Body length 10.0, DS length 4.9, DS width 4.3, OS length 5.1, OS width 3.2. Eyes: AME 0.22, ALE 0.33, PME 0.25, PLE 0.31, AME-AME 0.20, AME-ALE 0.04, PME-PME 0.20, PME-PLE 0.41, AME-PME 0.40, ALE-PLE 0.37, CH AME 0.51, CH ALE 0.41. Leg formula: II-IV-I-III. Spination: palp 131, 101, 2121, 1014; legs: femur I-II 323, III 322, IV 321; patella I-IV 101; tibia I-IV 2026; metatarsus I 1014, II-III 2024, IV 3036. Measurements of palp and legs: palp 5.3 (1.6, 0.7, 1.0, -, 2.0), leg I 17.6 (4.9, 2.0, 5.0, 4.2, 1.5), leg II 19.2 (5.5, 2.2, 5.5, 4.4, 1.6), leg III 14.9 (4.4, 1.8, 3.9, 3.4, 1.4), leg IV 18.1 (5.5, 1.8, 4.5, 4.6, 1.7). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 20 denticles.

Epigyne as in diagnosis. Epigynal field with nearly equal length in transverse and longitudinal axis. Lateral lobes longer in longitudinal axis. Median margin of lateral lobes touching each other medially. Internal duct system with loops looming through the lateral lobes in ventral view (Figure 5A). A pair of small appendages present (Figure 5E).

Coloration in ethanol: As in male, but generally darker with more dots and patches (Figure 5C, D).

Distribution. Known only from the type locality.

Pseudopoda conaensis **Zhao & Li, sp. n.**

http://zoobank.org/532C598C-FB21-4DB2-A3B0-8788DF9343E1
Figs 6, 7, 37

Type material. Holotype ♂: China, Tibet Autonomous Region, Shannan Prefecture, Cona County, Lewang Bridge to Simuzha Scenic Area, roadside and scenic area, 27°49.571'N, 91°43.756'E, 2793 m, 1 VI 2016, J. Wu.

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

Diagnosis. Small-sized *Pseudopoda* species. Male resembles *P. roganda* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 18, figs 63–65) and *P. bibulba* (Xu & Yin, 2000) (see Jäger and Vedel 2007: 15, figs 44–59) by: 1. tegulum protruded proximally in

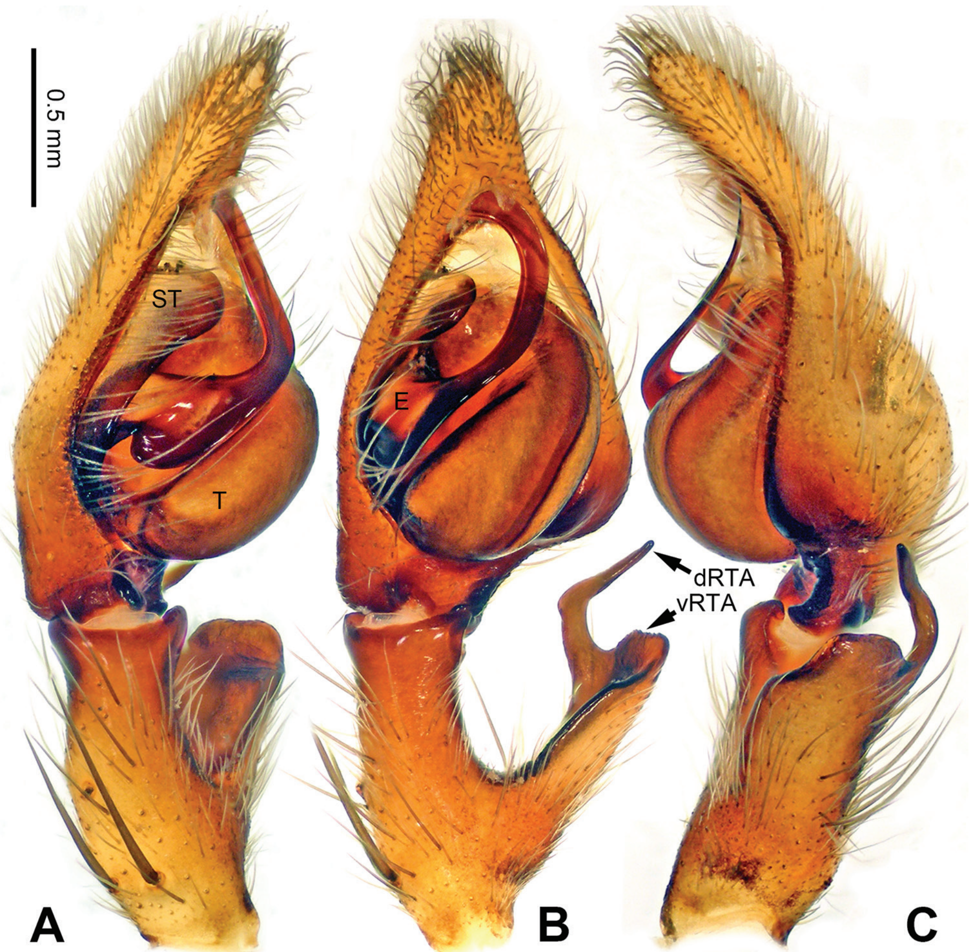

Figure 6. *Pseudopoda conaensis* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

retrolateral view; 2. embolus nearly the same width throughout (Figure 7A, B). It can be distinguished from the two congeners by the following combination of characters: 1. basal part of embolus broad (Figure 7B); 2. RTA well developed, dRTA finger-like, bending sharply; vRTA broad, with indention (Figure 6B, C; single-branched RTA in *P. bibulba*; dRTA almost straight in *P. roganda*).

Description. Male (holotype). Body length 8.3, DS length 3.8, DS width 3.1, OS length 4.5, OS width 2.5. Eyes: AME 0.17, ALE 0.25, PME 0.19, PLE 0.26, AME-AME 0.17, AME-ALE 0.06, PME-PME 0.19, PME-PLE 0.30, AME-PME 0.26, ALE-PLE 0.22, CH AME 0.36, CH ALE 0.26. Spination: palp 131, 101, 2101; legs: femur I-II 323, IV 321; patella I-IV 000; tibia I 1026, II-IV 2026; metatarsus I-II 1014, III 3025, IV 3037. Measurements of palp and legs: palp 5.8 (2.0, 0.8, 1.2, -, 1.8), leg I 15.2 (4.0, 1.8, 4.2, 3.8, 1.4), leg II 16.0 (4.3, 1.9, 4.3, 4.0, 1.5), leg III - (-,

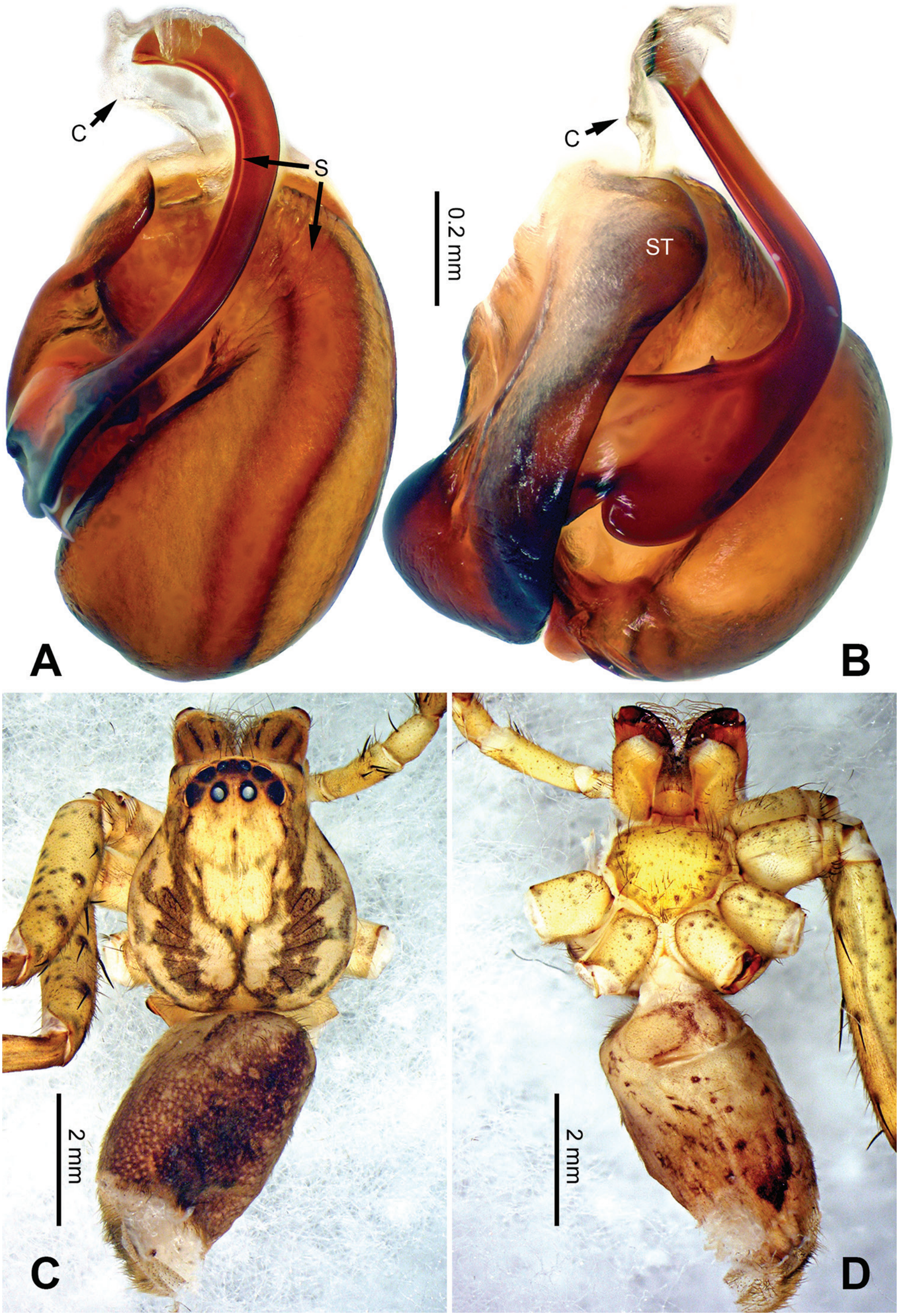

Figure 7. *Pseudopoda conaensis* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

1.4, 3.7, 3.6, 1.3), leg IV 15.6 (4.3, 1.6, 3.8, 4.3, 1.6). Promargin of chelicerae with three teeth, retromargin with five teeth. Cheliceral furrow with ca. 22 denticles.

Palp as in diagnosis. Cymbium relatively widened, with distinct retrolateral bulge beside bulb. RTA arising basally from tibia, well developed. Subtegulum extended, covering the base of conductor in prolateral view (Figure 6A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus long, sickle-shaped, arising from tegulum at 9 o'clock position. Conductor arising from tegulum at 12 o'clock position, leaning prolaterally and covering the tip of embolus (Figure 7A, B).

Coloration in ethanol: carapace yellowish brown, with a pair of dark longitudinal lateral bands. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown. Legs yellowish brown, with darker brown dots and patches (Figure 7C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda daxing Zhao & Li, sp. n.

http://zoobank.org/993762C9-E4AD-4119-A5D4-4957CD18634A
Figs 8, 9, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, road to Ziradum Village, 27°33.617'N, 97°06.567'E, 1003 m, 13 XII 2016, J. Wu.

Etymology. The specific name is derived from the Chinese Pinyin word for 'large size' (dà xíng), referring to the relatively large body size of the species; noun in apposition.

Diagnosis. Median-sized *Pseudopoda* species. Male resembles those of *P. contraria* Jäger & Vedel, 2007 (Jäger and Vedel 2007: 31, figs 114–119) and *P. semiannulata* Zhang, Zhang & Zhang, 2013 (see Zhang et al. 2013a: 279, figs 13–24) by: 1. embolus extremely expanded, covering nearly half of tegulum; 2. embolus plate-like, with embolic projection on its prolateral margin (Figure 9A, B). It can be distinguished from the two congeners by the following combination of characters: 1. sperm duct running near the prolateral margin of embolus (Figure 9A, B; running near the retrolateral margin in *P. contraria*); 2. tip of embolus and embolic projection slightly bent, pointing distally (Figure 9A; both much more strongly bent in *P. semiannulata*, tip of embolus pointing prolaterally, embolic projection pointing basally).

Description. Male (holotype). Body length 12.4, DS length 6.0, DS width 5.4, OS length 6.4, OS width 3.2. Eyes: AME 0.30, ALE 0.41, PME 0.36, PLE 0.37, AME-AME 0.22, AME-ALE 0.08, PME-PME, 0.26, PME-PLE 0.46, AME-PME 0.44, ALE-PLE 0.43, CH AME 0.57, CH ALE 0.41. Leg formula: II-IV-I-III. Spination: palp 131, 101, 2111; legs: femur I-III 323, IV 321; patella I-IV 001; tibia I-IV 2026; metatarsus I-II 1014, III 2024, IV 3036. Measurements of palp and legs: palp 9.4 (3.1, 1.4, 1.8, -, 3.1), leg I 29.3 (8.3, 3.0, 7.8, 7.8, 2.4), leg II 32.1 (8.7, 3.2, 9.0, 8.5, 2.7), leg III 25.1 (8.0, 2.6, 6.5, 6.0, 2.0), leg IV 29.4 (8.5, 2.5, 7.3, 8.5, 2.6). Pro-

Figure 8. *Pseudopoda daxing* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

margin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 25 denticles.

Palp as in diagnosis. Cymbium slender, with retrolateral bulge. RTA arising basally to mesially from tibia, dRTA hook-like, vRTA broad (Figure 8A–C). Sperm duct running submarginally retrolaterally in tegulum, then near the prolateral margin of embolus, meandering like a river flowing around mountains. Embolus arising from tegulum at 9

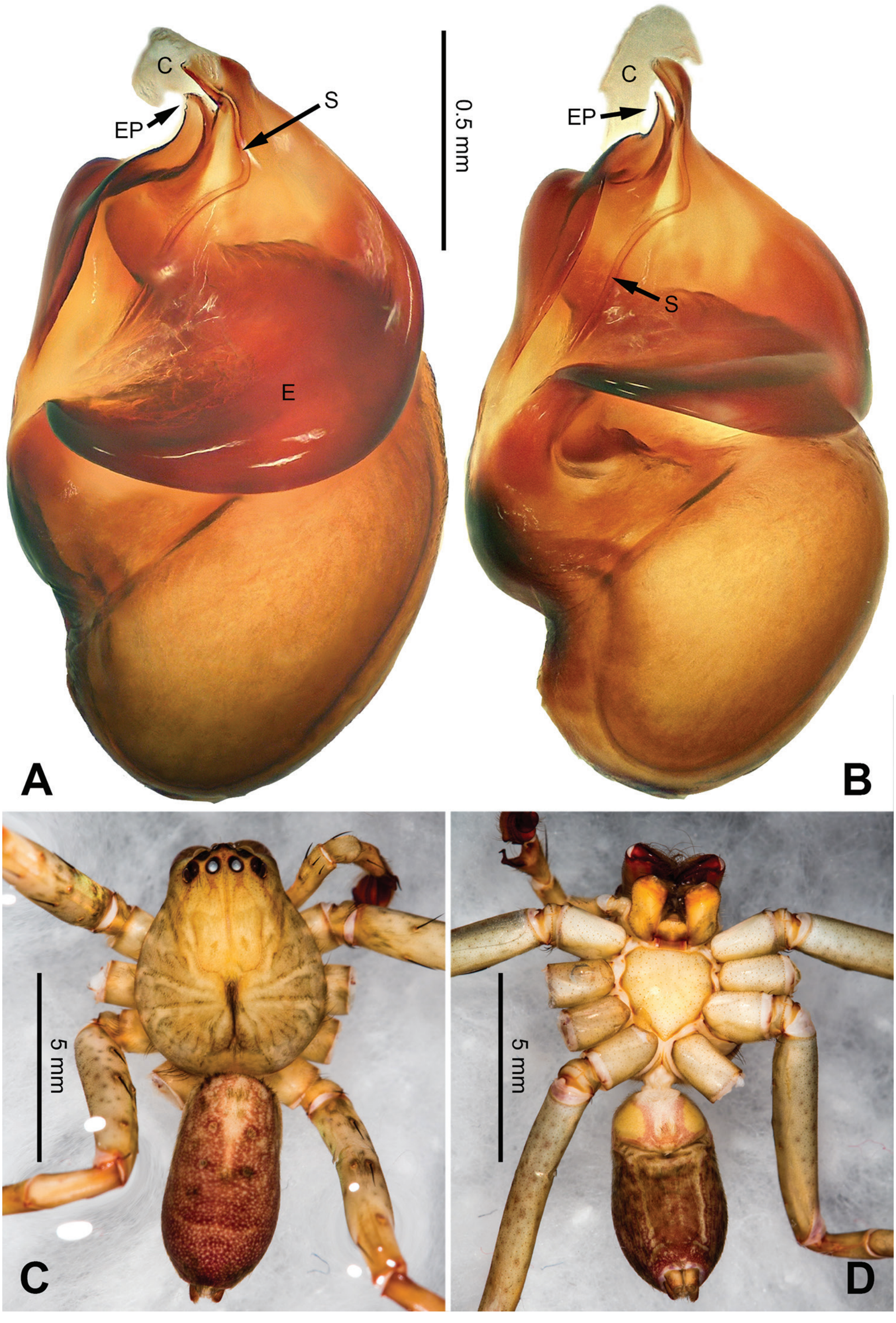

Figure 9. *Pseudopoda daxing* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

o'clock position. Conductor arising from tegulum at 12 o'clock position, leaning prolaterally (Figure 9A, B).

Coloration in ethanol: carapace yellowish brown. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown. Ventral opisthosoma with a pair of longitudinal bright lines. Legs yellowish brown, with randomly distributed brown dots (Figure 9C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda gexiao Zhao & Li, sp. n.

http://zoobank.org/388B9242-F83E-49EE-B8C8-C03F8C1B7336

Figs 10, 11, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, Hponkanrazi Wildlife Sanctuary roadside between Camp 1 to Camp 2, 27°36.067'N, 96°59.367'E, 1714 m, 10 V 2017, J. Wu & Z. Chen. **Paratype:** 1 ♂, same locality as holotype, 17 XII 2016, J. Wu.

Etymology. The specific name is derived from the Chinese Pinyin word for 'small-size' (gè xiǎo), referring to the relatively small body size of the species; noun in apposition.

Diagnosis. Small sized *Pseudopoda* species. Male resembles *P. exigua* (Fox, 1938) (see Jäger 2001: 87, figure 47h–l), *P. grahami* (Fox, 1936) (see Chen and Gao 1990: 156, figure 200a–b) and *P. amelia* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 12, figs 32–37) by: basal part of embolus broad, while the distal part tapering gradually and becoming filiform at distal end (Figure 11A). It can be distinguished from the three congeners by the following combination of characters: 1. RTA arising mesially from tibia, dividing into dRTA and vRTA (Figure 10B, C; arising basally in *P. grahami*; single-branched RTA in *P. exigua*); 2. tip of embolus bent with its end pointing distally retrolaterally (Figure 11A; bent and pointing prolaterally in *P. amelia*).

Description. Male (measurements of holotype first, those for paratype in parentheses). Body length 5.9 (5.4), DS length 2.8 (3.0), DS width 2.6 (2.6), OS length 3.1 (2.4), OS width 2.0 (1.7). Eyes: AME 0.16 (0.14), ALE 0.26 (0.25), PME 0.15 (0.19), PLE 0.28 (0.25), AME-AME 0.12 (0.13), AME-ALE 0.02 (0.06), PME-PME 0.19 (0.16), PME-PLE 0.21 (0.29), AME-PME 0.26 (0.32), ALE-PLE 0.15 (0.22), CH AME 0.20 (0.21), CH ALE 0.20 (0.15). Spination: palp 131, 101, 2111; legs: femur II-III 323, IV 321; patella I-IV 001; tibia I-III 2026, IV 2126; metatarsus I-II 1014, III 3035, IV 3036. Measurements of palp and legs: palp 3.9 (4.1) (1.1, 0.6, 0.9, -, 1.3), leg I - (-, 1.3, 2.8, 2.5, 1.1), leg II 11.2 (11.4) (3.2, 1.2, 3, 2.6, 1.2), leg III - (10.2) (-, -, -, -, -), leg IV - (11.2) (-, 1.0, 2.7, 3.1, 1.2). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 25 denticles.

Palp as in diagnosis. Retrolateral margin of cymbium swollen. Distal part of cymbium sub-triangular. RTA arising mesially to distally from tibia, dRTA needle-like, while vRTA broad (Figure 10A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus sickle-shaped, arising from tegulum at 9 o'clock

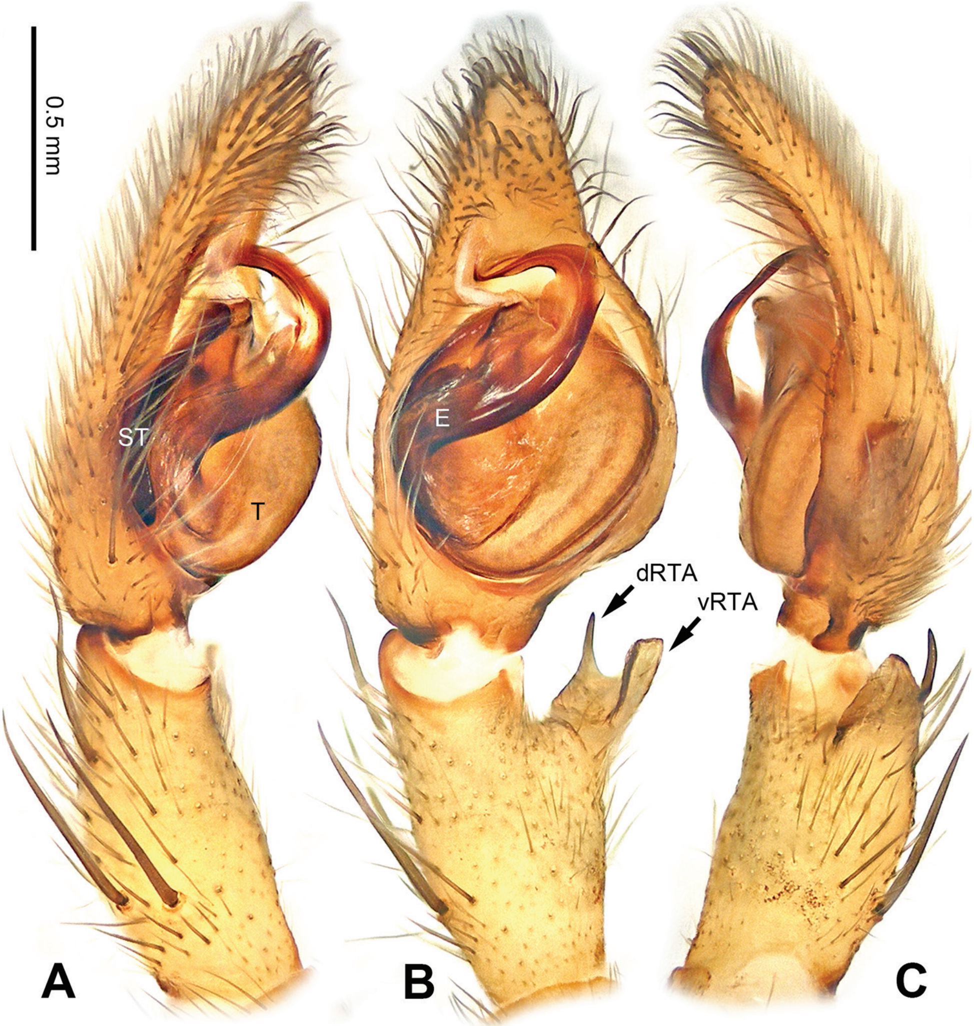

Figure 10. *Pseudopoda gexiao* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

position. Basal part of embolus broad, then tapering as it runs and coils, resulting in a filiform tip. Conductor arising from tegulum at 11 o'clock position, leaning prolaterally and then bent in a right angle, with its end covering the tip of embolus (Figure 11A, B).

Coloration in ethanol: carapace yellow, with a pair of dark longitudinal lateral bands. Dorsal opisthosoma reddish brown with a bright transverse band in the posterior half. Legs yellowish brown, with reddish brown dots and patches (Figure 11C, D).

Female. Unknown.

Distribution. Known only from the type locality.

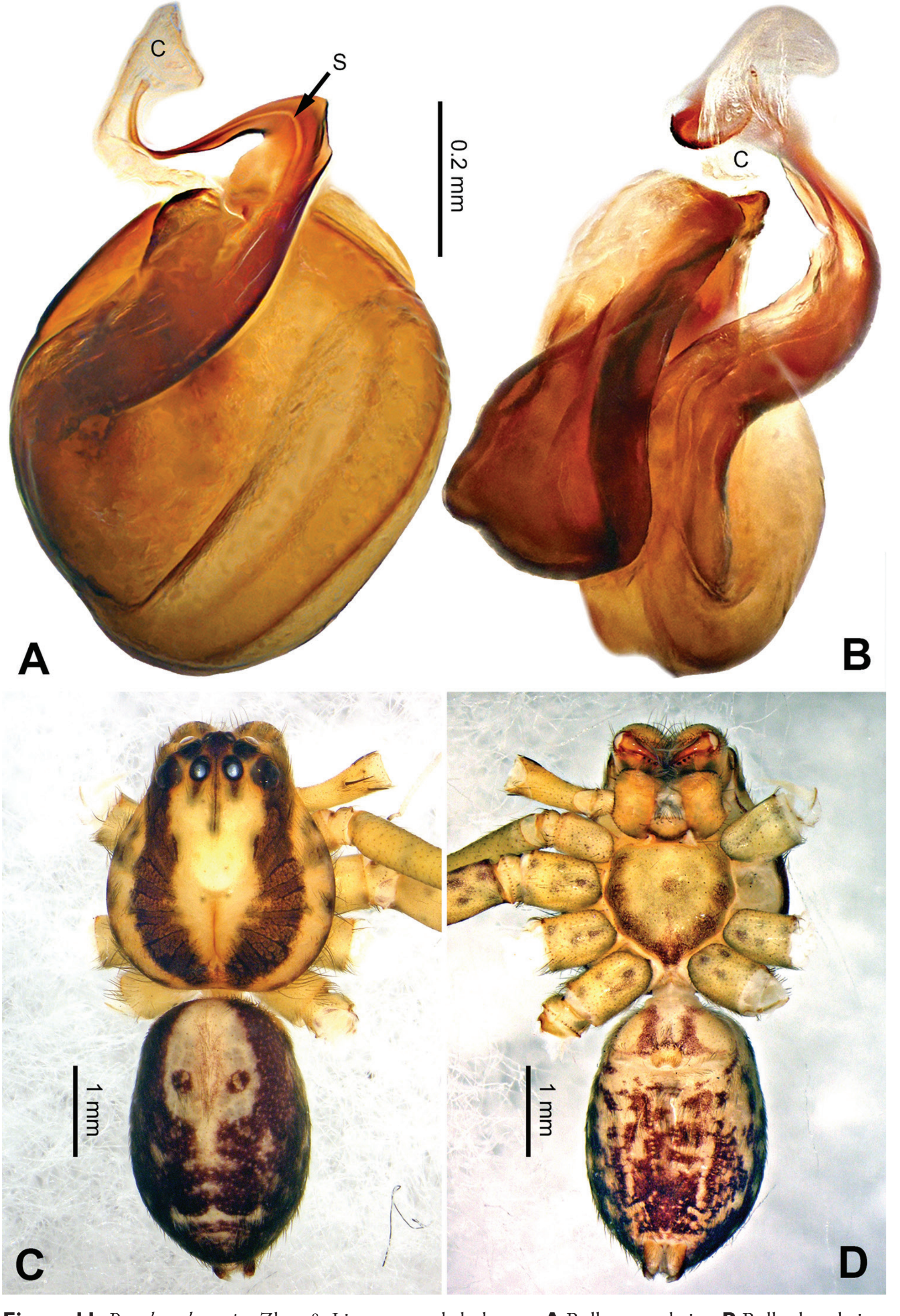

Figure 11. *Pseudopoda gexiao* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A**, **B**.

Pseudopoda maeklongensis **Zhao & Li, sp. n.**
http://zoobank.org/5317C261-04E4-443F-A4BB-B2F8EACB0048
Figs 12, 13, 37

Type material. Holotype ♂: Thailand, Tak Province, Umphang District, Mae Klong Subdistrict, field, 16°14.642'N, 98°59.914'E, 1228 m, 17 XI 2016, H. Zhao, Y. Li & Z. Chen.

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

Diagnosis. Small-sized *Pseudopoda* species. Male has long spiral embolus that resembles *P. parvipunctata* Jäger, 2001 (see Jäger 2001: 94, figure 49e–l) and *P. spirembolus* Jäger & Ono, 2002 (see Jäger and Ono 2002: 112, figs 11–14). It can be distinguished from the two congeners by the following combination of characters: 1. tegulum small, leaning towards the retrolateral margin of cymbium (Figure 12B); 2. embolic projection long, arising from the basal part of embolus at 9 o'clock position, forming a semicircle with its basal part running along with embolus and covering a part of it like a sheath (Figure 13A, B; absent in *P. spirembolus* and *P. parvipunctata*);

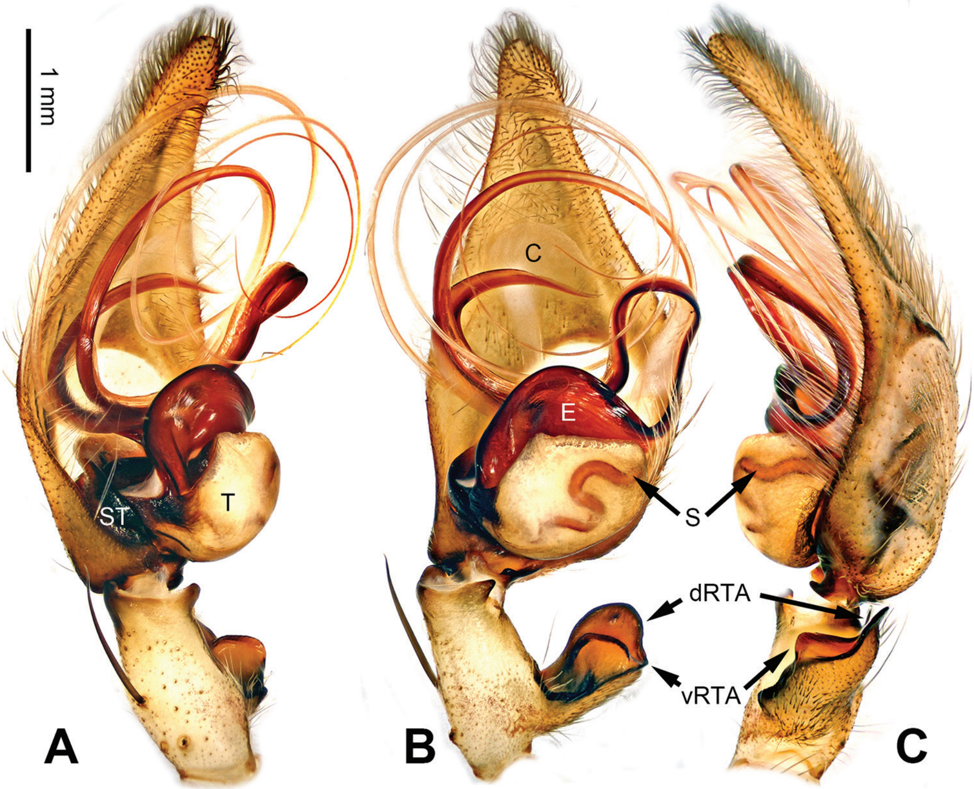

Figure 12. *Pseudopoda maeklongensis* Zhao & Li, sp. n., right palp of male holotype, horizontally flipped for the sake of comparison. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

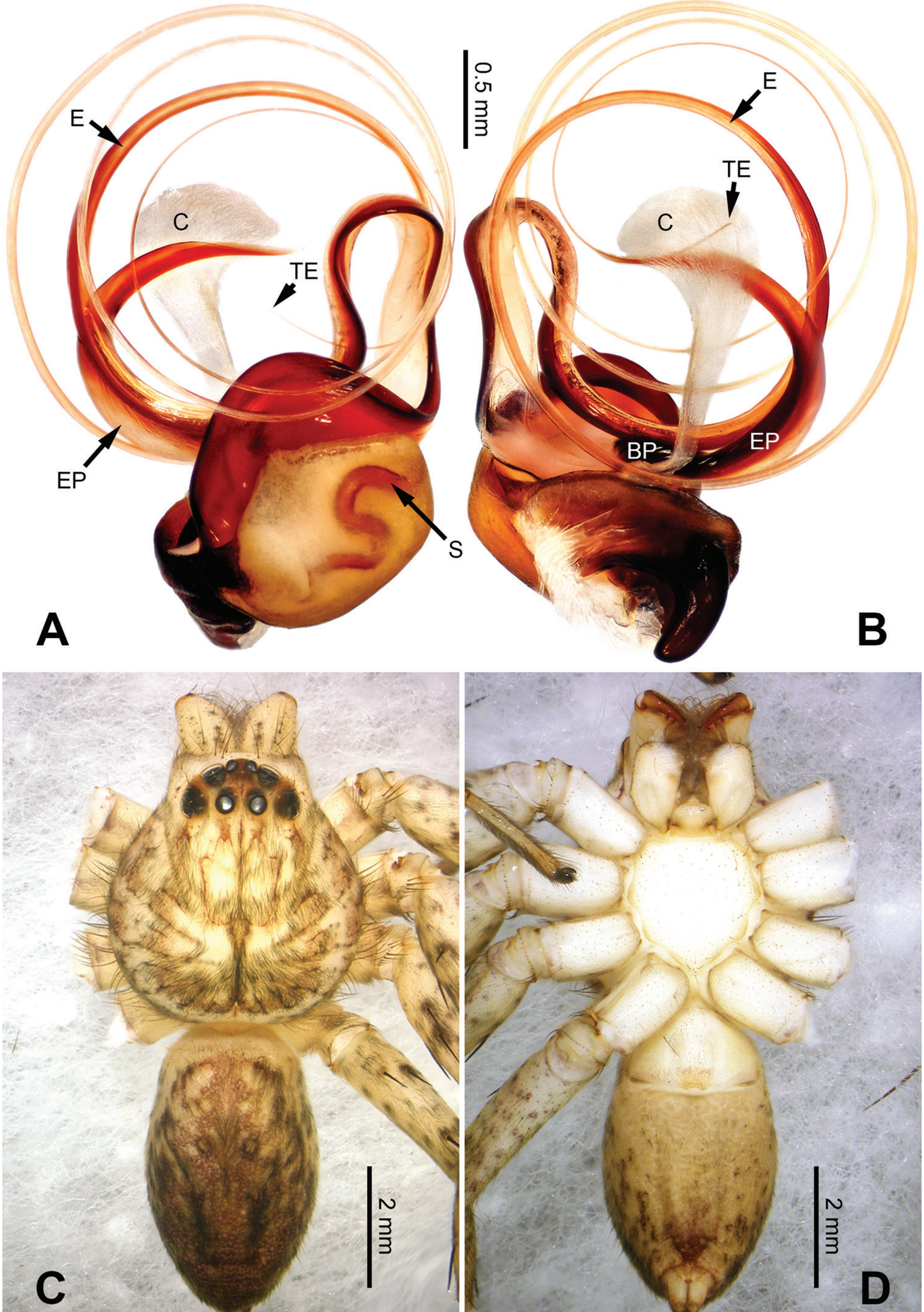

Figure 13. *Pseudopoda maeklongensis* Zhao & Li, sp. n., male holotype. Right bulb horizontally flipped for the sake of comparison. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

3. embolus extremely long, forming five loops (Figure 13A, B; forming three loops in *P. spirembolus*; two in *P. parvipunctata*); 4. cymbium flattened and broadened without any bulges (Figure 12A–C; elongated and with one bulge on the retrolateral margin in *P. parvipunctata*; broadened and with one bulge on the retrolateral margin in *P. spirembolus*).

Description. Male (holotype). Body length 9.3, DS length 4.4, DS width 4.0, OS length 4.9, OS width 2.8. Eyes: AME 0.21, ALE 0.37, PME 0.26, PLE 0.38, AME-AME 0.16, AME-ALE 0.03, PME-PME 0.22, PME-PLE 0.36, AME-PME 0.43, ALE-PLE 0.32, CH AME 0.45, CH ALE 0.38. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2101; legs: femur I-II 323, III 333, IV 331; patella I-IV 101; tibia I-IV 2026; metatarsus I-II 1014, III 2024, IV 3037. Measurements of palp and legs: palp 8.4 (3.0, 0.8, 1.2, -, 3.4), leg I 21.9 (5.9, 2.4, 6.4, 5.4, 1.8), leg II 23.4 (6.4, 2.5, 6.7, 5.8, 2), leg III 17.2 (5.1, 1.8, 4.8, 4.1, 1.4) leg IV 21.5 (6.2, 1.8, 5.5, 6.2, 1.8). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 38 denticles.

Palp as in diagnosis. Cymbium large. RTA arising basally from tibia. Both vRTA and dRTA flattened and blunt in ventral view (Figure 12A–C). Sperm duct S-shaped, running retrolaterally in tegulum. Embolus arising from tegulum at 9 o'clock position, extremely elongated. Conductor large and elongated, arising from the tegulum at 10 to 12 o'clock position (Figure 13A, B).

Coloration in ethanol: carapace yellow. Radial furrows and fovea brown. Dorsal opisthosoma yellowish to reddish brown. Legs yellow, with randomly distributed brown dots (Figure 13C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda medogensis Zhao & Li, sp. n.

http://zoobank.org/9C23B103-6026-4856-9CC2-E2874772F9FA

Figs 14, 15, 37

Type material. Holotype ♂: China, Tibet Autonomous Region, Nyingchi Prefecture, Medog County, 8 km of the road of Beibeng to Gelin, 29°14.660'N, 95°11.442'E, 1235 m, 11 VIII 2017, M. Xu.

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

Diagnosis. Median-sized *Pseudopoda* species. Male resembles *P. obtusa* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 25, figs 91–96) by: embolus broadened at its median part, distal part narrow and curved with embolic projection emerging prolaterally (Figure 15A, B). It can be distinguished from the latter by the following combination of characters: 1. RTA simple and pointed (Figure 14A–C; RTA with humps and blunt apices in *P. obtusa*); 2.distal part of embolus longer, bending more intensely than in *P. obtusa* (Figure 15A, B); 3. two embolic projections on the prolateral margin of distal embolus, the proximal one translucent (Figure 15A; only one on the same margin in *P. obtusa*).

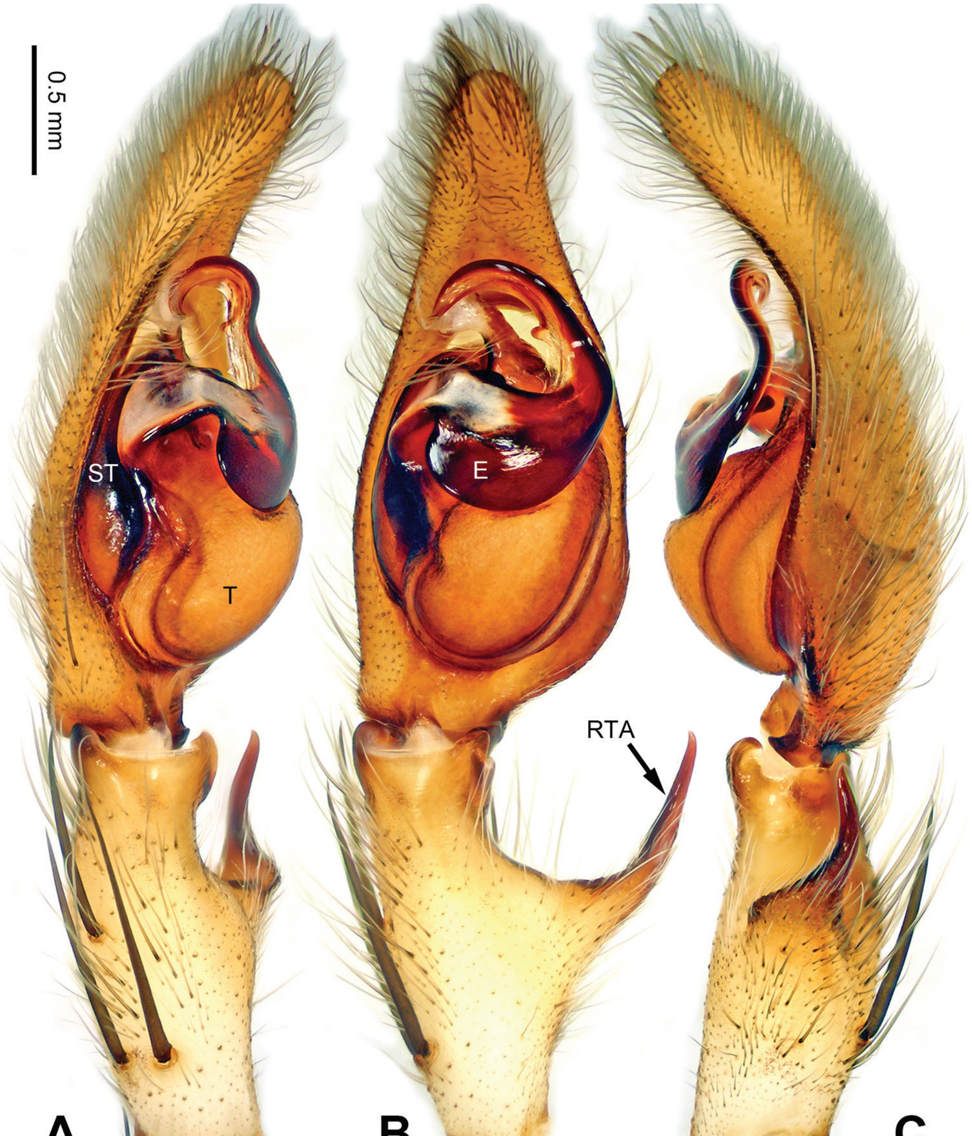

Figure 14. *Pseudopoda medogensis* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

Description. Male (holotype). Body length 10.4, DS length 5.1, DS width 4.7, OS length 5.3, OS width 3.2. Eyes: AME 0.25, ALE 0.40, PME 0.22, PLE 0.35, AME-AME 0.19, AME-ALE 0.06, PME-PME 0.28, PME-PLE 0.40, AME-PME 0.40, ALE-PLE 0.40, CH AME 0.39, CH ALE 0.33. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2100; legs: femur I-III 323, IV 322; patella I-IV 101; tibia I

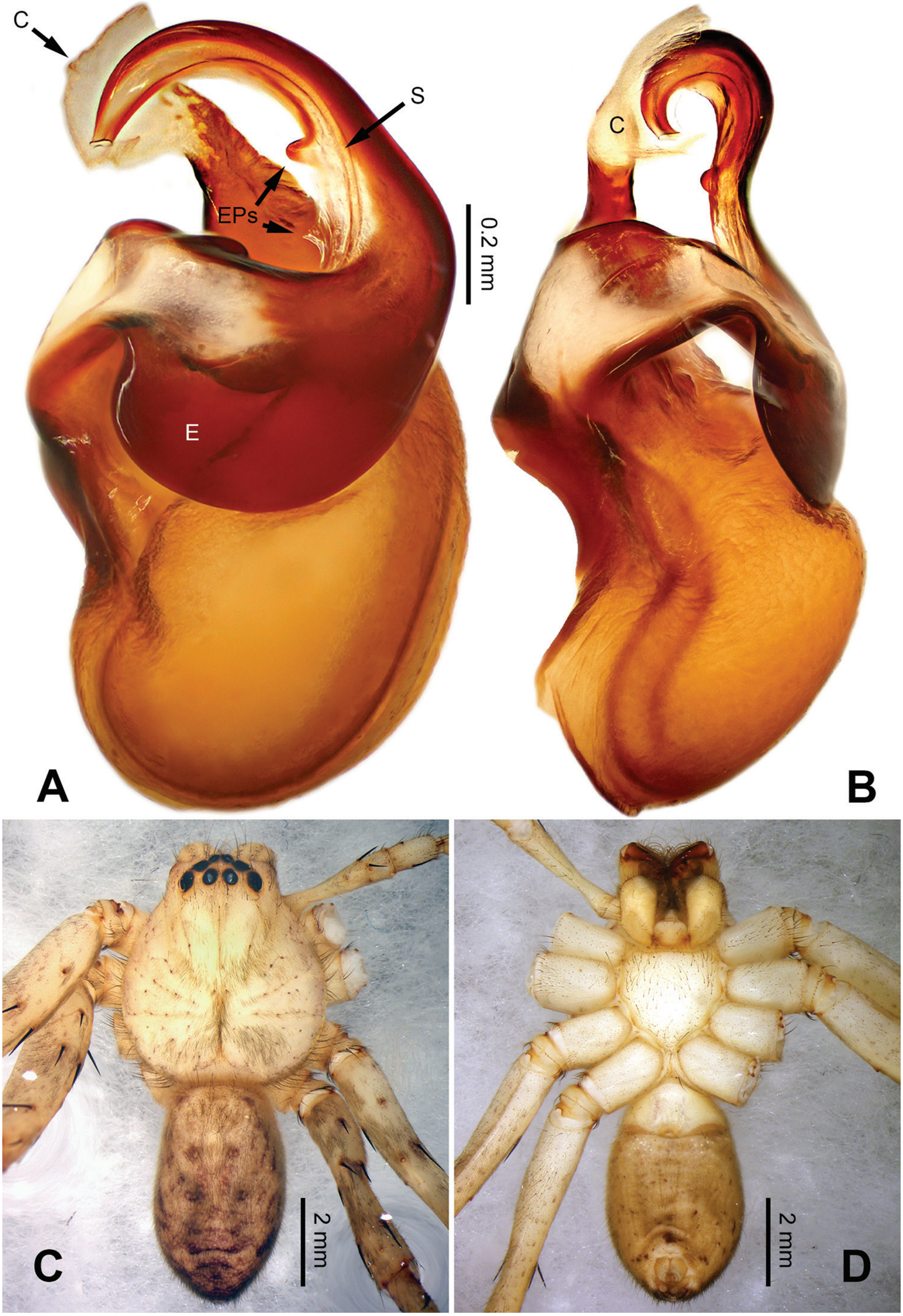

Figure 15. *Pseudopoda medogensis* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

2126, II 3236, III-IV 2226; metatarsus I-II 1014, III 2025, IV 3037. Measurements of palp and legs: palp 8.6 (3.1, 1.3, 1.6, -, 2.6), leg I 28.2 (7.8, 2.8, 8.0, 7.2, 2.4), leg II 30.8 (8.2, 3.1, 8.8, 8.0, 2.7), leg III 23.9 (6.8, 2.5, 6.7, 6.0, 1.9), leg IV 26.0 (7.3, 2.5, 6.9, 7.0, 2.3). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 35 denticles.

Palp as in diagnosis. Cymbium slender. RTA almost straight, arising mesially from tibia (Figure 14A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus arising from tegulum at 10 to 11 o'clock position with its basal part broadened. Distal part of embolus curved intensely, with its tip pointing at the base of embolus. Conductor arising from tegulum at 11 o'clock position (Figure 15A, B).

Coloration in ethanol: carapace bright brown. Radial furrows and fovea darker. Dorsal opisthosoma dark brown with black pattern. Legs bright brown, with dark brown patches (Figure 15C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda nyingchiensis **Zhao & Li, sp. n.**
http://zoobank.org/42C87FCE-E01A-47E0-9177-30A531AC9673
Figs 16, 17, 37

Type material. Holotype ♂: China, Tibet Autonomous Region, Nyingchi Prefecture, between Sejila Moution to Bayi Town, 29°33.790'N, 94°34.247'E, 3847 m, 13 VI 2016, J. Wu.

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

Diagnosis. Median-sized *Pseudopoda* species. Male resembles *P. gogona* Jäger, 2001 (see Jäger 2001: 58, figure 36a–e) and *P. gibberosa* Zhang, Zhang & Zhang, 2013 (see Zhang et al. 2013a: 274, figs 1–12) by: embolus sickle-shaped, with blunt embolic projection, tip pointing prolaterally (Figure 17A, B). It can be distinguished by: RTA well developed, divided into dRTA and vRTA, dRTA finger-like, elongated and curved (Figure 16B, C; dRTA distinctly shorter in *P. gogona* and *P. gibberosa*).

Description. Male (holotype). Body length 9.9, DS length 4.8, DS width 4.3, OS length 5.1, OS width 3.3. Eyes: AME 0.19, ALE 0.25, PME 0.20, PLE 0.32, AME-AME 0.20, AME-ALE 0.10, PME-PME 0.28, PME-PLE 0.38, AME-PME 0.38, ALE-PLE 0.34, CH AME 0.31, CH ALE 0.26. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2111; legs: femur I-III 323, IV 331; patella I-III 001, IV 000; tibia I-IV 2026; metatarsus I-II 2024, III 3035, IV 3037. Measurements of palp and legs: palp 7.2 (2.5, 1.1, 1.3, -, 2.3), leg I 23.5 (6.0, 2.5, 6.3, 6.7, 2.0), leg II 25.6 (6.6, 2.6, 7.0, 7.3, 2.1), leg III 21.8 (6.0, 2.3, 5.8, 6.0, 1.7), leg IV 23.4 (6.3, 2.2, 5.9, 7.0, 2.0). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 18 denticles.

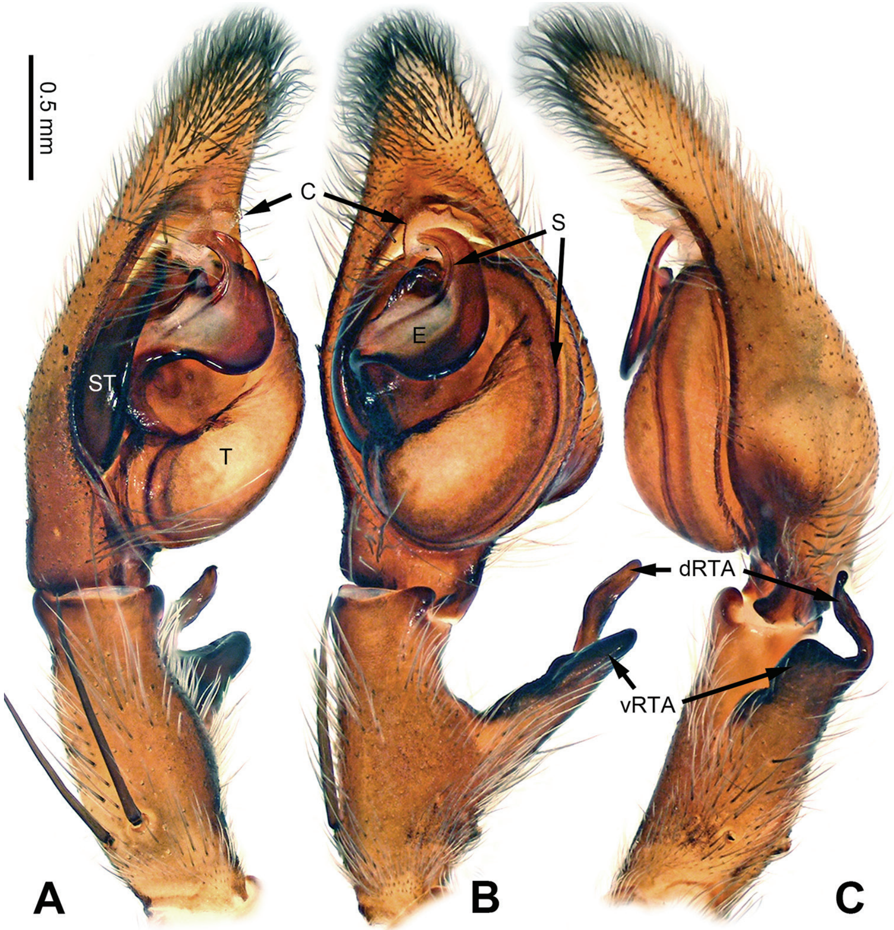

Figure 16. *Pseudopoda nyingchiensis* Zhao & Li, sp. n., right palp of male holotype, horizontally flipped for the sake of comparison. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

Palp as in diagnosis. Retrolateral margin of cymbium swollen. RTA arising basally to mesially from tibia, vRTA broad in retrolateral view (Figure16A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus arising from tegulum at 9 o'clock position. Conductor arising from tegulum at 12 o'clock position, slightly leaning prolaterally to cover the tip of embolus (Figure 17A, B).

Coloration in ethanol: carapace yellowish. Radial furrows and fovea brown. Dorsal opisthosoma brown. Legs yellowish brown, with randomly distributed dark brown dots (Figure 17C, D).

Female. Unknown.

Distribution. Known only from the type locality.

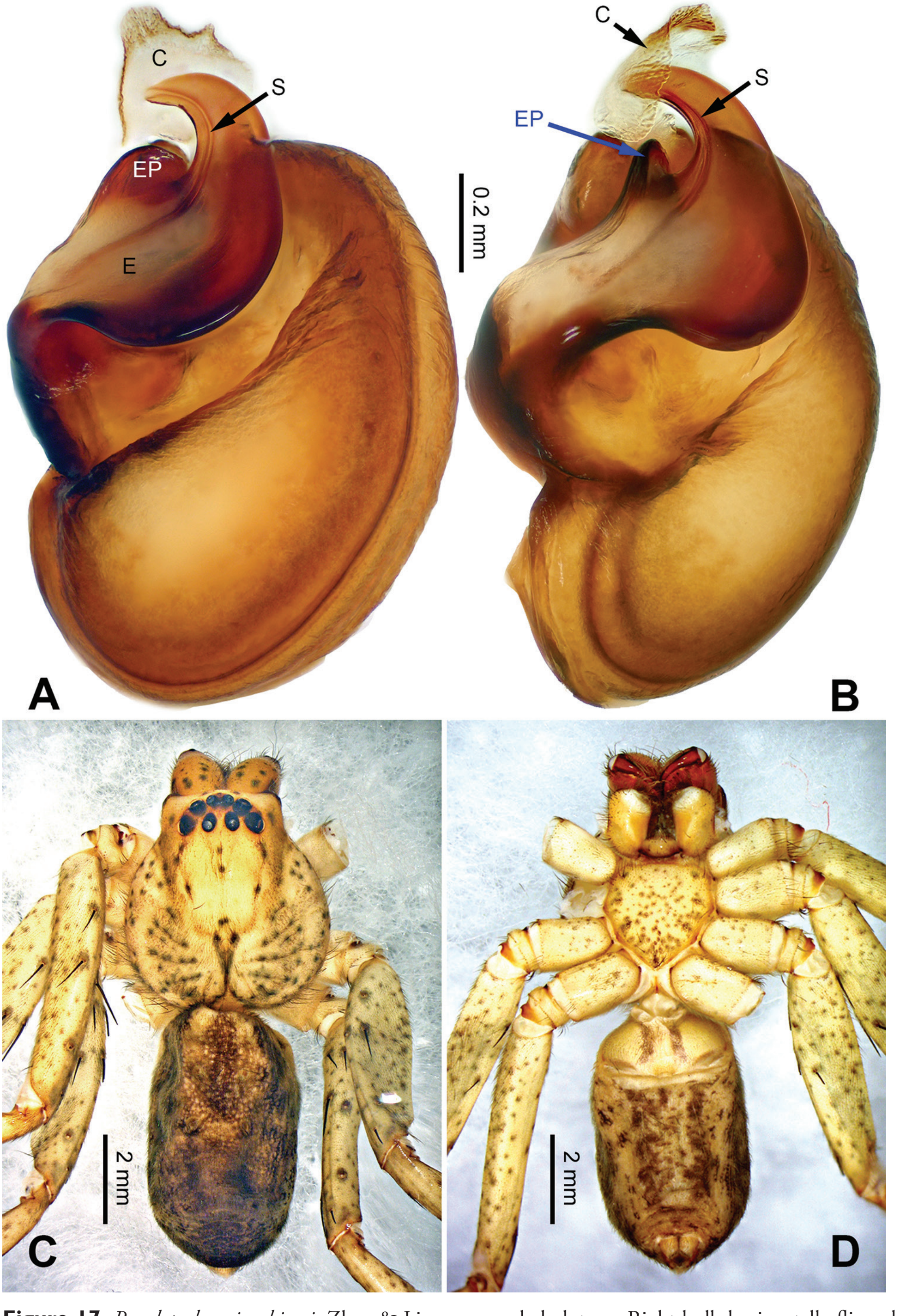

Figure 17. *Pseudopoda nyingchiensis* Zhao & Li, sp. n., male holotype. Right bulb horizontally flipped for the sake of comparison. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

Pseudopoda putaoensis **Zhao & Li, sp. n.**
http://zoobank.org/068BE24A-D6EB-4B24-B535-537D603F6B17
Figs 18, 19, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, Hponkanrazi Wildlife Sanctuary roadside between Camp 2 to Camp 3, 27°37.150'N, 96°58.917'E, 2806 m, 16 XII 2016, J. Wu.

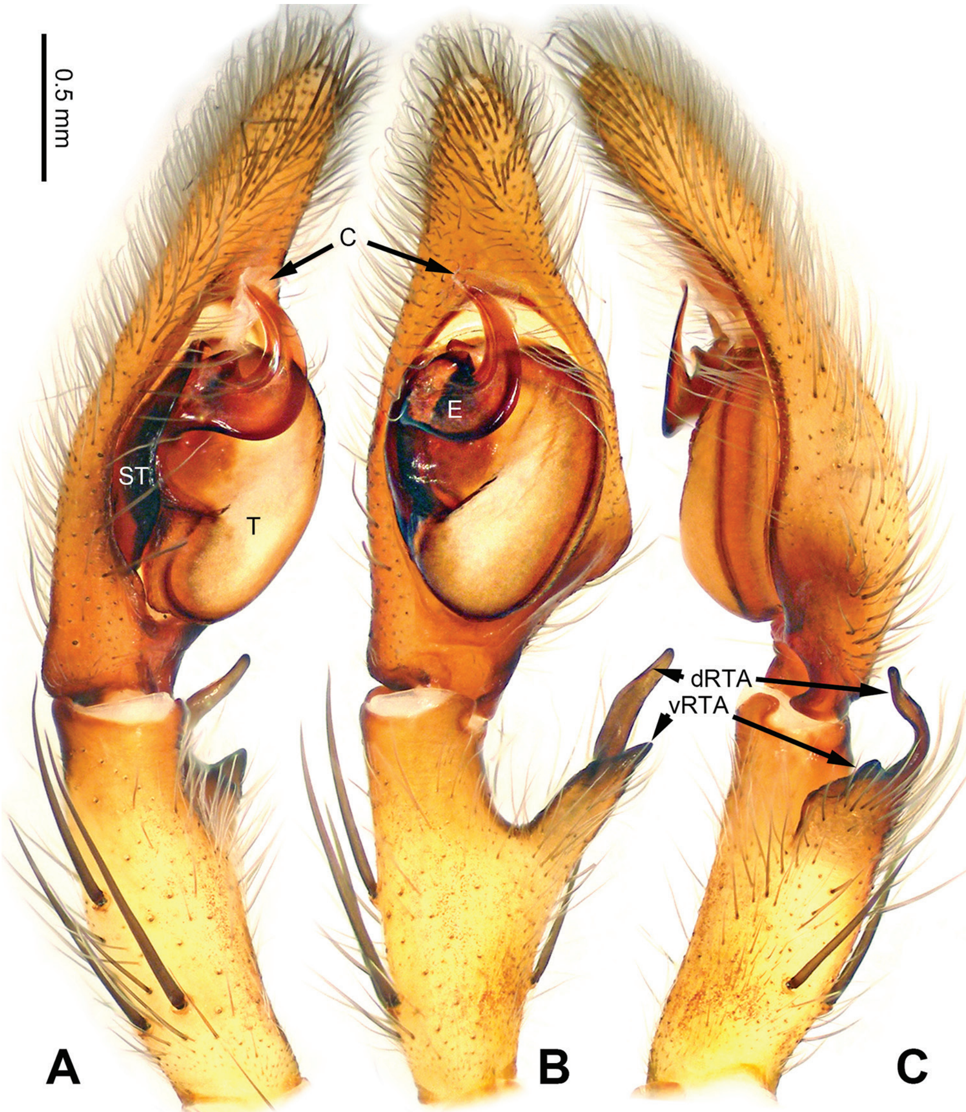

Figure 18. *Pseudopoda putaoensis* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

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

Diagnosis. Median-sized *Pseudopoda* species. Male resembles *P. platembola* Jäger, 2001 (see Jäger 2001: 57, figure 35a–e), *P. nyingchiensis* Zhao & Li, sp. n. (see Figs 16–17) and *P. huberi* Jäger, 2015 (see Jäger 2015: 346, figs 84–90, 97) by: 1. dRTA finger-like (Figure 18B, C); 2. embolus sickle-shaped (Figure 19A, B). It can be distinguished from the three congeners by the following combination of characters: 1. embolic projection pronounced, emerging from the prolateral margin of embolus (Figure 19A, B; absent in *P. platembola*); 2. cymbium slender and elongated (Figure 18B; shorter and wider in *P. nyingchiensis* Zhao & Li, sp. n. and *P. platembola*); 3. flange absent near the tip of embolus (present in *P. huberi*).

Description. Male (holotype). Body length 9.9, DS length 4.7, DS width 4.1, OS length 5.2, OS width 3.0. Eyes: AME 0.19, ALE 0.31, PME 0.19, PLE 0.31, AME-AME 0.19, AME-ALE 0.12, PME-PME 0.29, PME-PLE 0.38, AME-PME 0.36, ALE-PLE 0.28, CH AME 0.35, CH ALE 0.30. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2111, legs: femur I-II 323, III 322, IV 331; patella I-III 101, IV 000; tibia I-II 2226, III-IV 2126; metatarsus I-II 2024, III 3025, IV 3036. Measurements of palp and legs: palp 7.6 (2.6, 1.3, 1.5, -, 2.2), leg I 24.5 (6.5, 2.3, 6.5, 7.0, 2.2), leg II 26.8 (7.0, 2.6, 7.1, 7.8, 2.3), leg III 22.3 (5.6, 2.2, 6.0, 6.3, 1.9), leg IV 23.8 (6.2, 2.1, 6.1, 7.2, 2.2). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 30 denticles.

Palp as in diagnosis. Cymbium elongated, retrolateral bulge present. RTA arising mesially from tibia, vRTA broad and humble in retrolateral view (Figure 18A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus arising from tegulum at 10 o'clock position. Embolic projection broad and sub-triangular. Conductor arising from tegulum at 12 o'clock position, slightly leaning prolaterally to cover the tip of embolus (Figure 19A, B).

Coloration in ethanol: carapace yellowish. Radial furrows and fovea brown. Dorsal opisthosoma brown. Legs yellowish brown, with randomly distributed dark brown dots (Figure 19C, D).

Female. Unknown.

Distribution. Known only from the type locality.

***Pseudopoda shacunensis* Zhao & Li, sp. n.**

http://zoobank.org/A81F9E0F-CD1C-42AC-B2E0-E5D95AC5EC98
Figs 20, 21, 37

Type material. Holotype ♂: China, Jiangxi Province, Ji'an city, Taihe County, Shacun Town, Chayuan Village, Guangshiyan, 26°31.214'N, 115°06.616'E, 3124 m, 3 V 2013, Y. Luo & J. Liu.

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

Diagnosis. Small-sized *Pseudopoda* species. Male resembles *P. lushanensis* (Wang, 1990) (see Quan et al. 2014: 559, figs 4A–F, 5A–G), *P. martensi* Jäger, 2001 (see Jäger 2001: 66,

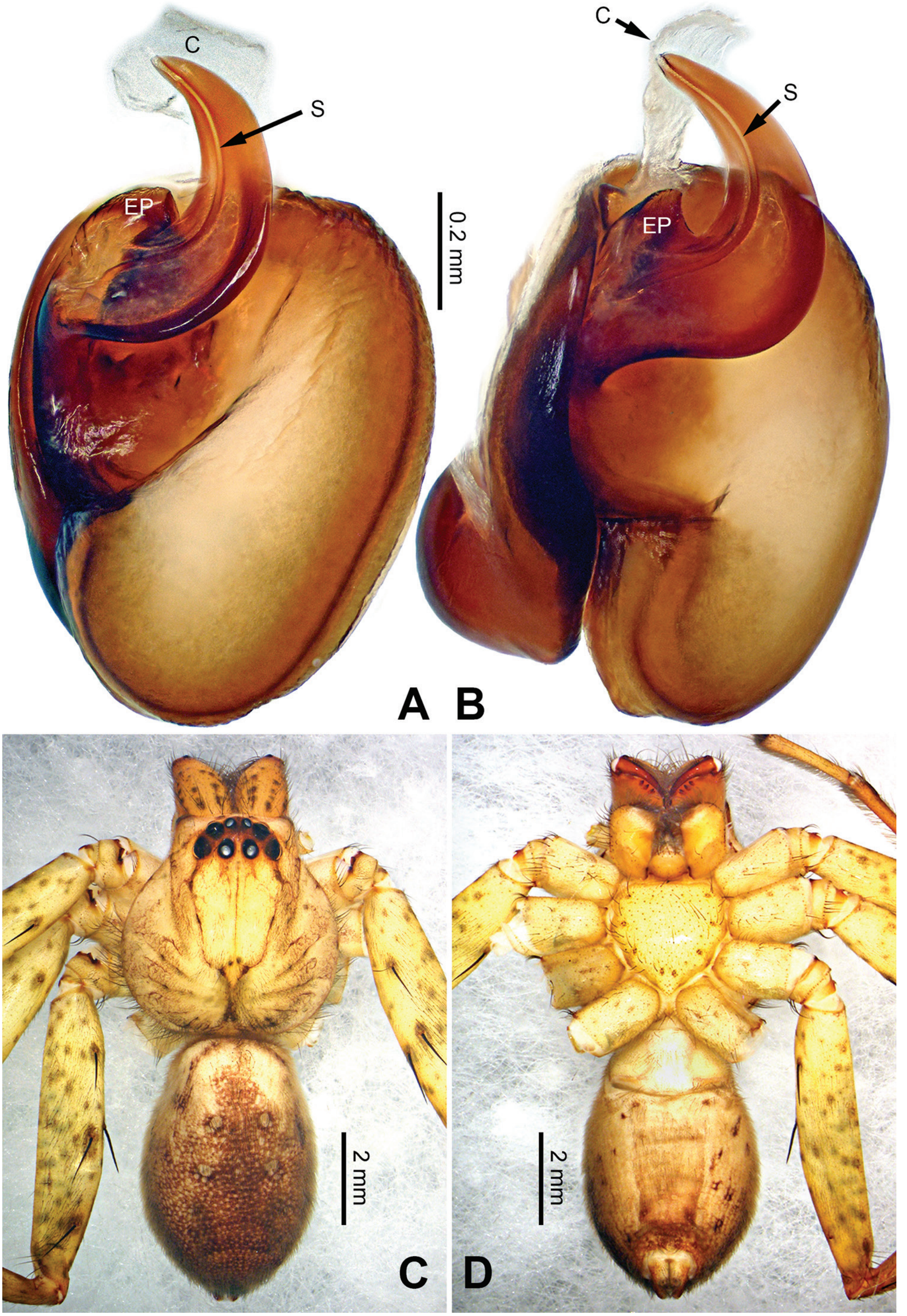

Figure 19. *Pseudopoda putaoensis* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

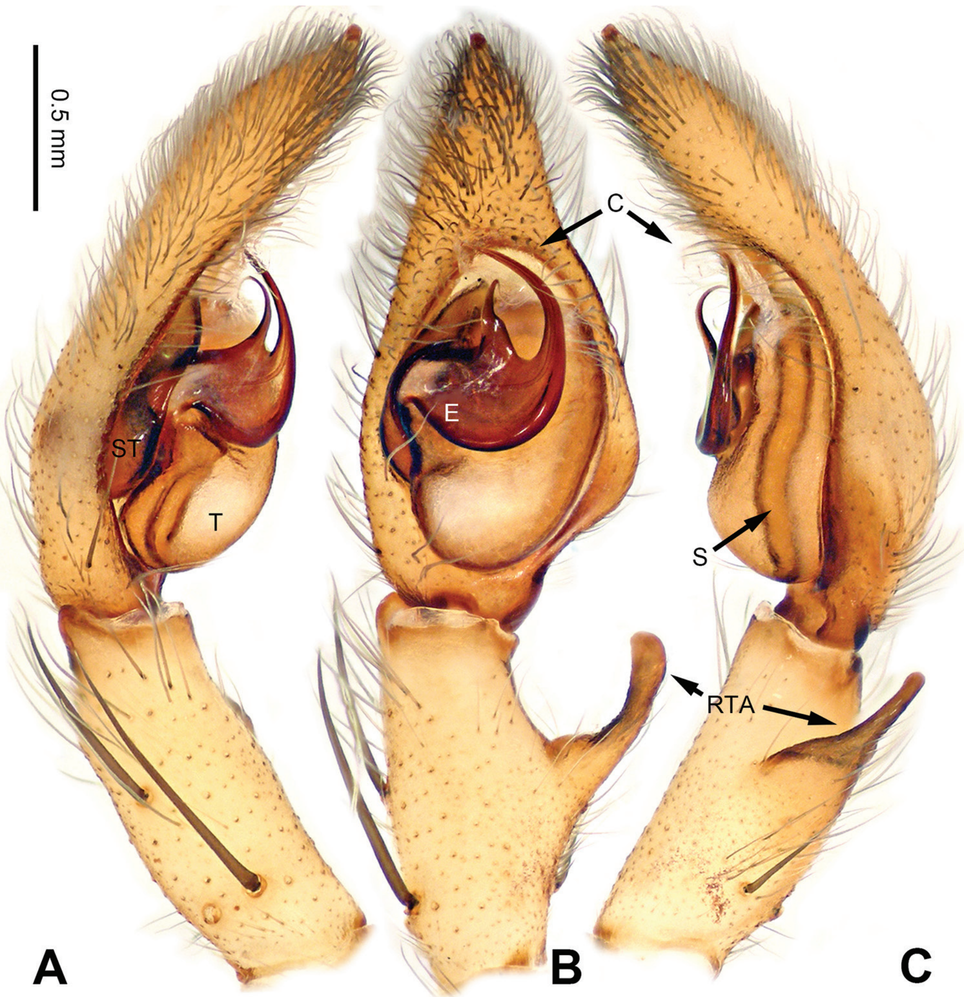

Figure 20. *Pseudopoda shacunensis* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

figs 3a–h, 39a–l, 84) and *P. hyatti* Jäger, 2001 (see Jäger 2001: 72, figs 41j–m, 84) by: 1. embolus sickle-shaped, its distal part filiform (Figure 21A, B); 2. RTA arising mesially from tibia, single-branched (Figure 20B, C). It can be distinguished by the elongated embolic projection curved backwards dorsally, with its tip ending near the base of conductor (Figure 21A, B; absent in *P. lushanensis*; significantly shorter in *P. hyatti* and *P. martensi*).

Description. Male (holotype). Body length 6.8, DS length 3.4, DS width 3.3, OS length 3.4, OS width 2.5. Eyes: AME 0.20, ALE 0.25, PME 0.20, PLE 0.25, AME-AME 0.18, AME-ALE 0.06, PME-PME 0.24, PME-PLE 0.30, AME-PME 0.31, ALE-PLE 0.27, CH AME 0.30, CH PLE, 0.28. Spination: palp 131, 101, 2111; legs: femur III 323, IV 321; patella III-IV 001; tibia III-IV 2126; metatarsus III 3025, IV 3035.

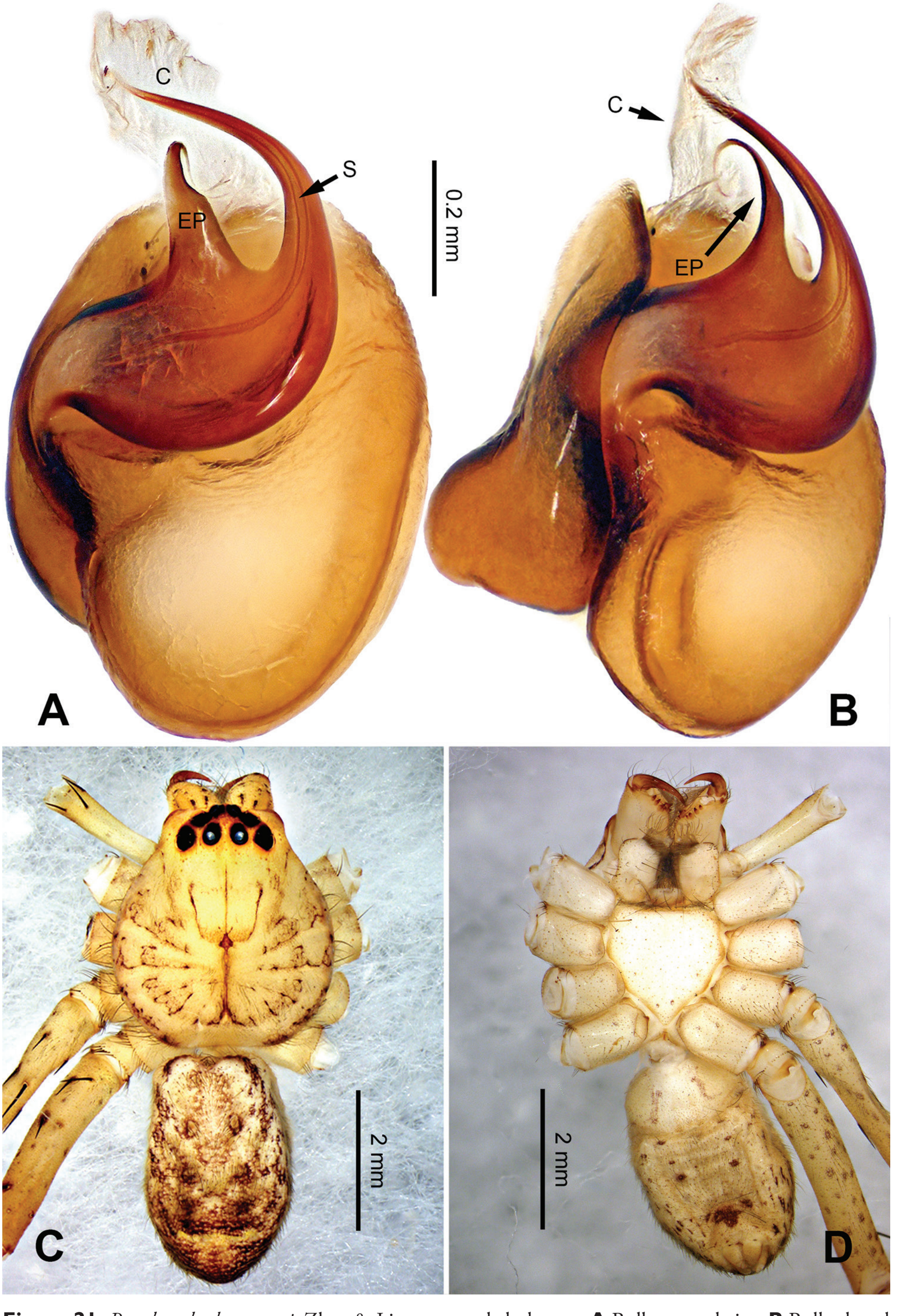

Figure 21. *Pseudopoda shacunensis* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

Measurements of palp and legs: palp 5.4 (1.8, 0.8, 1.1, -, 1.7), leg I -, leg II -, leg III 14.3 (4.0, 1.4, 4.0, 3.6, 1.3), leg IV 16.7 (4.3, 1.4, 4.5, 5.0, 1.5). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 24 denticles.

Palp as in diagnosis. RTA arising mesially from tibia (Figure 20A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus arising from tegulum at 9–10 o'clock position with its basal part broadened and its distal part filiform. Embolic projection arising mesially from embolus, steeply narrowed at its distal half. Distal part of embolic projection filiform, curved, and running backwards to the tegulum. Conductor arising from tegulum at 12 o'clock position, leaning prolaterally and covering the tip of embolus (Figure 21A, B).

Coloration in ethanol: carapace yellow. Radial furrows and fovea dark brown. Dorsal opisthosoma bright brown with reddish brown pattern composed of dense reddish brown dots. Legs yellow, with reddish brown dots and patches (Figure 21C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda shuo **Zhao & Li, sp. n.**

http://zoobank.org/2F891F63-2912-4965-B878-B5FB105EE0D2
Figs 22–24, 37

Type material. Holotype ♂: China, Tibet Autonomous Region, Nyingchi Prefecture, Medog County, 44 km of the road of Bomi to Medog, 29°42.516'N, 95°34.650'E, 2787 m, 30 VIII 2015, J. Wu. **Paratype:** 1 ♀, same data as holotype.

Etymology. The specific name is derived from the Chinese Pinyin word for 'gigantism' (shuò), referring to the relatively larger bulb on male palp than other *Pseudopoda* species; noun in apposition.

Diagnosis. Small-sized *Pseudopoda* species. Male resembles *P. zhangi* Fu & Zhu, 2008 (see Fu and Zhu 2008: 657, figs 1–5), *P. gogona* Jäger, 2001 (see Jäger 2001: 58, figure 36a–e), *P. gibberosa* Zhang, Zhang & Zhang, 2013 (see Zhang et al. 2013a: 274, figs 1–12) and *P. acuminata* Zhang, Zhang & Zhang, 2013 (see Zhang et al. 2013b: 39, figs 1–17) by: 1. tip of embolus sickle-shaped and directing prolaterally (Figure 23A, B); 2. RTA dividing into dRTA and vRTA, dRTA hook-like rather than finger-like (Figure 22B, C). It can be distinguished from the four congeners by the following combination of characters: 1. cymbium shortened, while tegulum swollen, covering a prominently bigger proportion of cymbium in ventral view than in *P. zhangi*, *P. gogona,* and *P. acuminata* (Figure 22B); 2. embolic projection as a small hump on the basal part of embolus (Figure 23A, B; pointed and near the tip of embolus in *P. acuminata*; at the same position but far more distinct in *P. gibberosa*); 3. single hump arising from tegulum near the base of conductor, humble, almost entirely covered by embolus in ventral view (Figure 23A, B; more distinct and clearly visible in ventral view in *P. zhangi*).

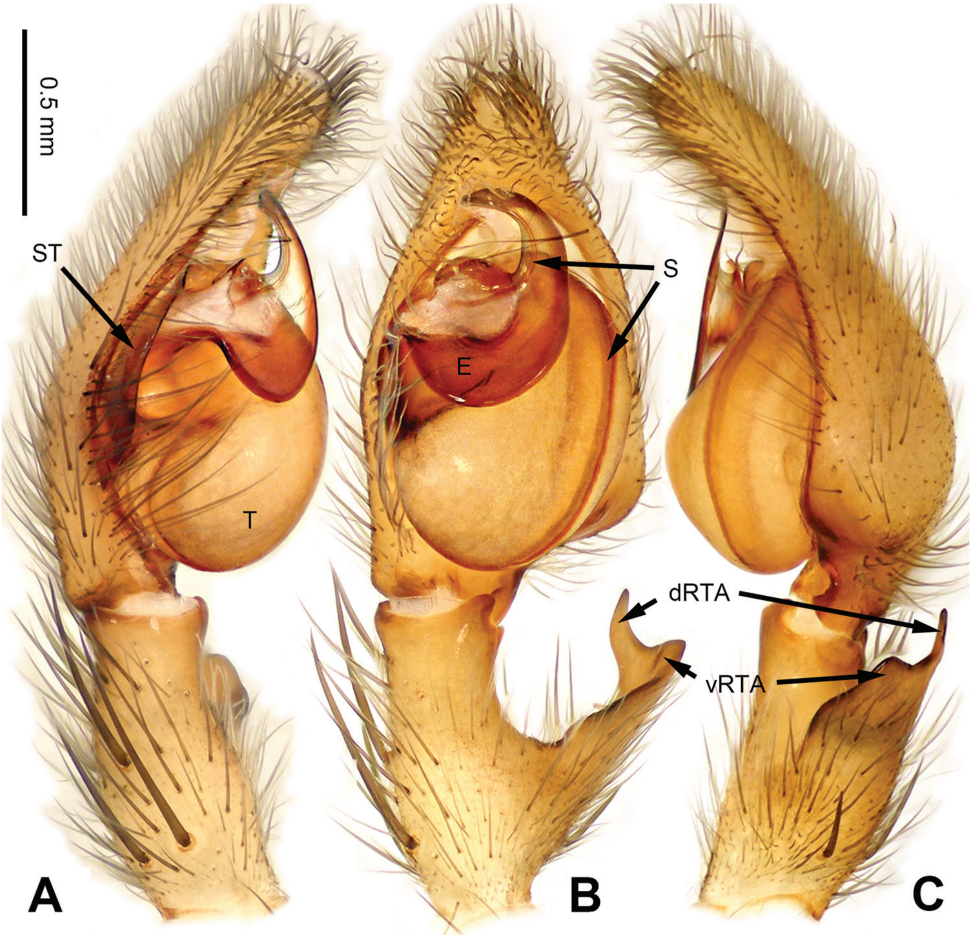

Figure 22. *Pseudopoda shuo* Zhao & Li, sp. n., right palp of male holotype, horizontally flipped for the sake of comparison. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

Female can be distinguished from other *Pseudopoda* species except *P. contraria* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 31, figs 114–119) and *P. zhangi* Fu & Zhu, 2008 (see Fu and Zhu 2008: 657, figs 1–5) by: 1. lateral lobes crescent-shaped (Figure 24A, B); 2. internal duct system with loops looming in ventral view as dark shades near the median margin of lateral lobes (Figure 24A); 3. posterior part of first winding of internal duct system hidden in lateral lobes in dorsal view (Figure 24B). It can be distinguished from the two congeners by the following combination of characters: 1. anterior bands poorly developed (Figure 24A; more distinct in *P. contraria*); 2. median margin of lateral lobe intensely curved, extending in the anterior half of epigynal field (Figure 24A, B; moderately curved in *P. zhangi*).

Description. Male (holotype). Body length 6.5, DS length 3.3, DS width 2.9, OS length 3.2, OS width 2.0. Eyes: AME 0.14, ALE 0.25, PME 0.17, PLE 0.22, AME-

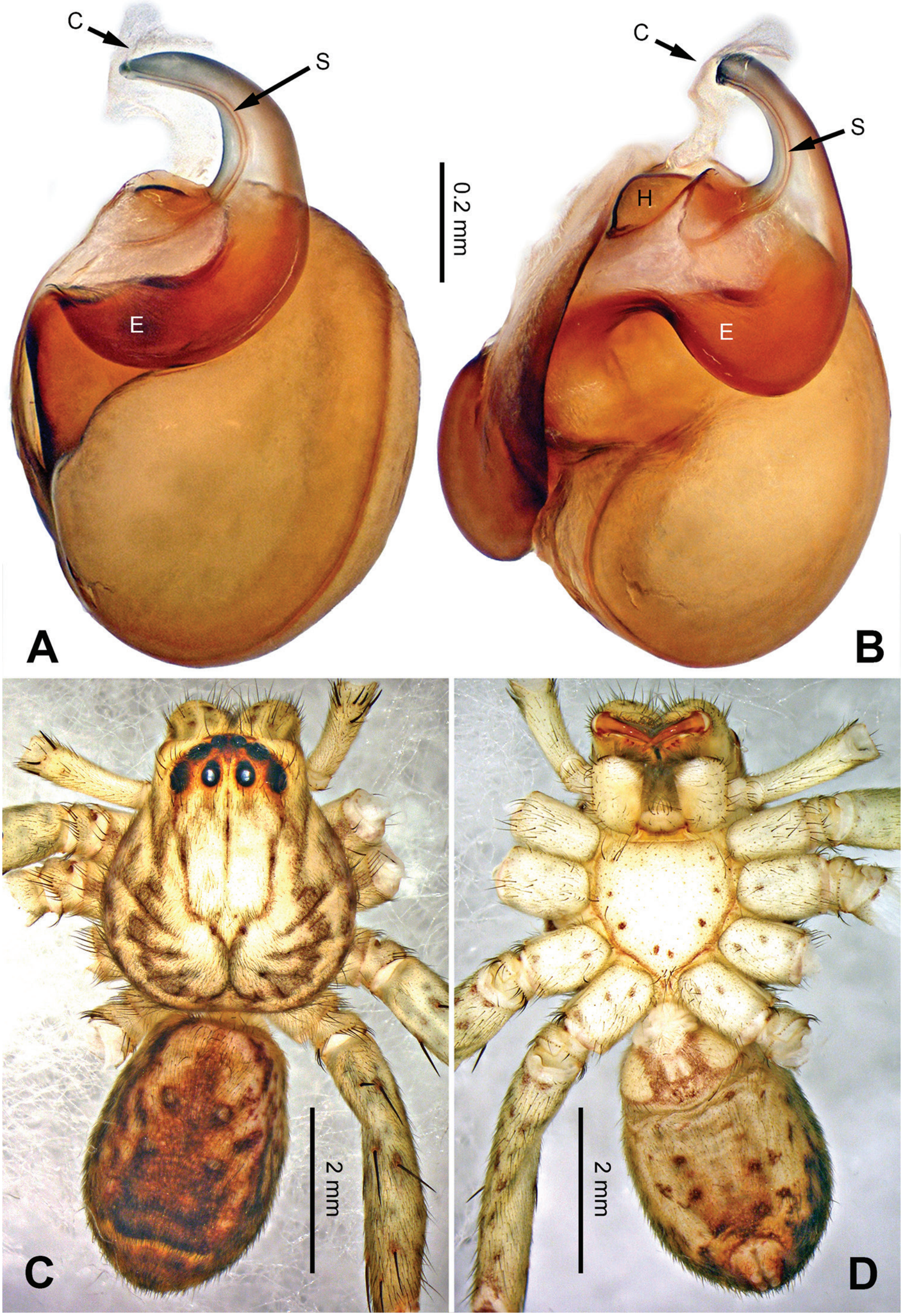

Figure 23. *Pseudopoda shuo* Zhao & Li, sp. n., male holotype. Right bulb horizontally flipped for the sake of comparison. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

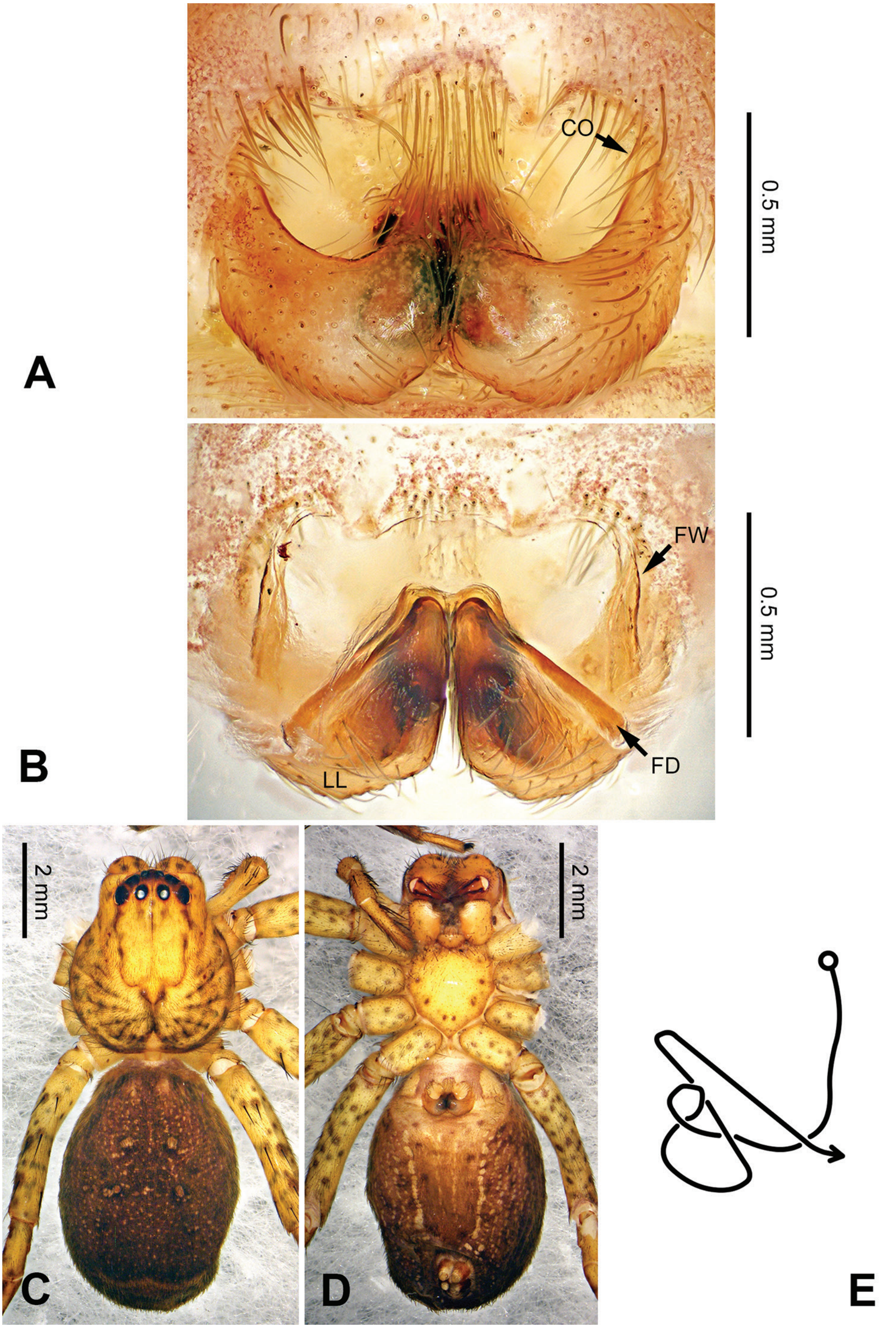

Figure 24. *Pseudopoda shuo* Zhao & Li, sp. n., paratype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

AME 0.12, AME-ALE 0.03, PME-PME 0.20, PME-PLE 0.30, AME-PME 0.28, ALE-PLE 0.24, CH AME 0.28, CH ALE 0.24. Leg formula: II-IV-I-III. Spination: palp 131, 101, 2111; legs: femur I-III 323, IV 332; patella I-III 001, IV 000; tibia I-IV 2026; metatarsus I-II 2024, III 3025, IV 3037. Measurements of palp and legs: palp - (-, 0.7, 0.9, -, 1.6), leg I 12.5 (3.5, 1.5, 3.3, 3.1, 1.1), leg II 13.1 (3.7, 1.5, 3.3, 3.1, 1.1), leg III 11.7 (3.4, 1.4, 3.0, 2.9, 1.0), leg IV 12.9 (3.6, 1.2, 3.3, 3.5, 1.3). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 25 denticles.

Palp as in diagnosis. Cymbium relatively shortened compared to other *Pseudopoda* species. RTA arising basally from tibia (Figure 22A–C). Sperm duct running submarginally and retrolaterally in tegulum. Embolus arising from tegulum at 10–11 o'clock position. Angle between the tip of embolus and the broad part of embolus is ca. 180°. Conductor arising from tegulum at 12 o'clock position (Figure 23A, B).

Coloration in ethanol: carapace bright brown with dark brown lateral bands. Radial furrows and fovea darker. Dorsal opisthosoma reddish brown with black pattern and a bright transverse band in the posterior half. Legs bright brown, with reddish brown patches (Figure 23C, D).

Female (paratype). Body length 8.8, DS length 3.8, DS width 3.3, OS length 5.0, OS width 3.5. Eyes: AME 0.14, ALE 0.24, PME 0.16, PLE 0.30, AME-AME 0.18, AME-ALE 0.21, PME-PME 0.25, PME-PLE 0.30, AME-PME 0.33, ALE-PLE 0.16, CH AME 0.28, CH ALE 0.24. Leg formula: II-IV-I-III. Spination: palp 131, 101, 1014, 2121; legs: femur I-III 323, IV 331; patella I-IV 000; tibia I-III 2026, IV 2025; metatarsus I-II 2024, III 3025, IV 3037. Measurements of palp and legs: palp 4.1 (1.5, 0.5, 0.7, -, 1.4), leg I 11.5 (3.4, 1.5, 3.0, 2.6, 1.0), leg II 12.2 (3.6, 1.6, 3.2, 2.8, 1.0), leg III 10.6 (3.2, 1.3, 2.8, 2.4, 0.9), leg IV 11.9 (3.5, 1.3, 2.9, 3.1, 1.1). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 28 denticles.

Epigyne as in diagnosis. Epigynal field longer in transverse axis, with poorly developed anterior bands and trilobate anterior margin. Lateral lobes longer in transverse axis, curved. Median margin of lateral lobe converged, with the posterior part V-shaped. Posterior incision of lateral lobe indistinct or absent (Figure 24A, B).

Coloration in ethanol: as in male, but generally darker. Ventral opisthosoma with a pair of bright, longitudinal, dashed lines (Figure 24C, D).

Distribution. Known only from the type locality.

Pseudopoda subbirmanica Zhao & Li, sp. n.

http://zoobank.org/0B4CC01D-0EC4-4F4B-997B-B44E75B53DC1

Figs 25–27, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, Hponkanrazi Wildlife Sanctuary roadside between Camp 1 to Camp 2, 27°36.550'N, 96°58.850'E, 2252 m, 17 XII 2016, J. Wu. **Paratypes:** 1 ♂, same locality as holotype, 14 V 2017, Z. Chen & J. Wu; 1 ♀, same locality as holotype, 18 V 2017.

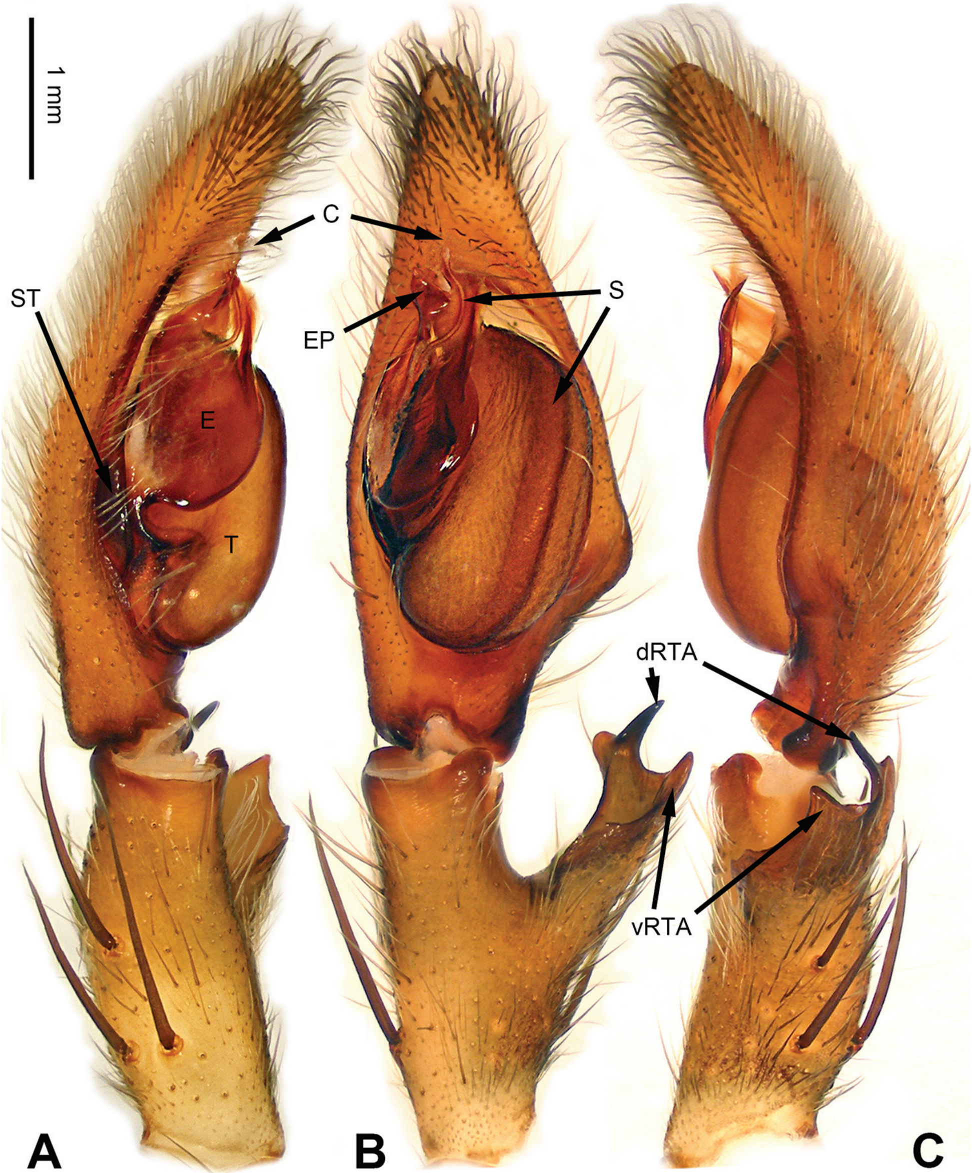

Figure 25. *Pseudopoda subbirmanica* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

Etymology. The specific name refers to the similarity of its female individual to *P. birmanica* Jäger, 2001; adjective.

Diagnosis. Small to median-sized *Pseudopoda* species. Male resembles *P. digitata* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 29, figs 105–113) by: embolus with prolateral projection near the tip (Figure 26A, B). It can be distinguished from the latter

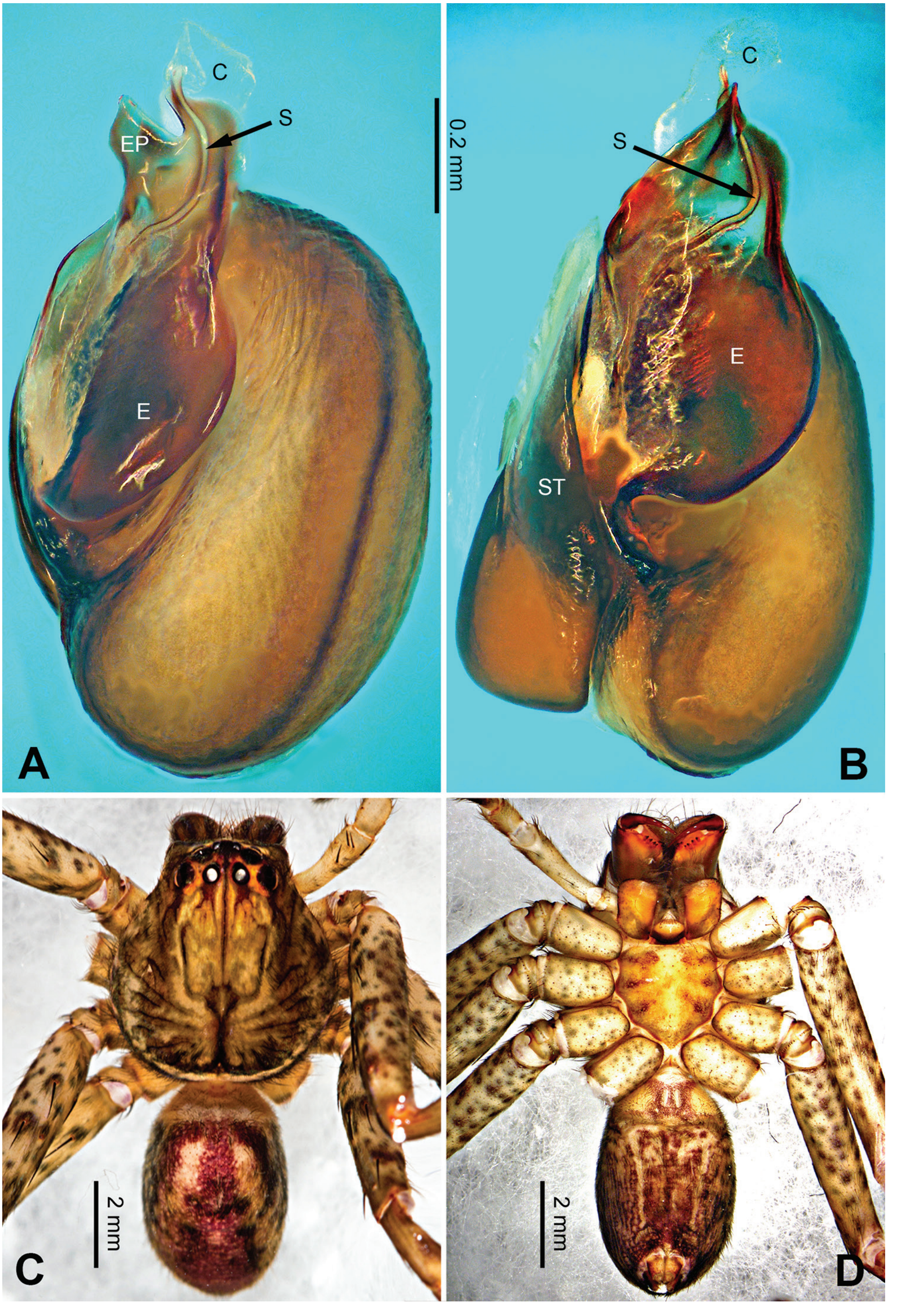

Figure 26. *Pseudopoda subbirmanica* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

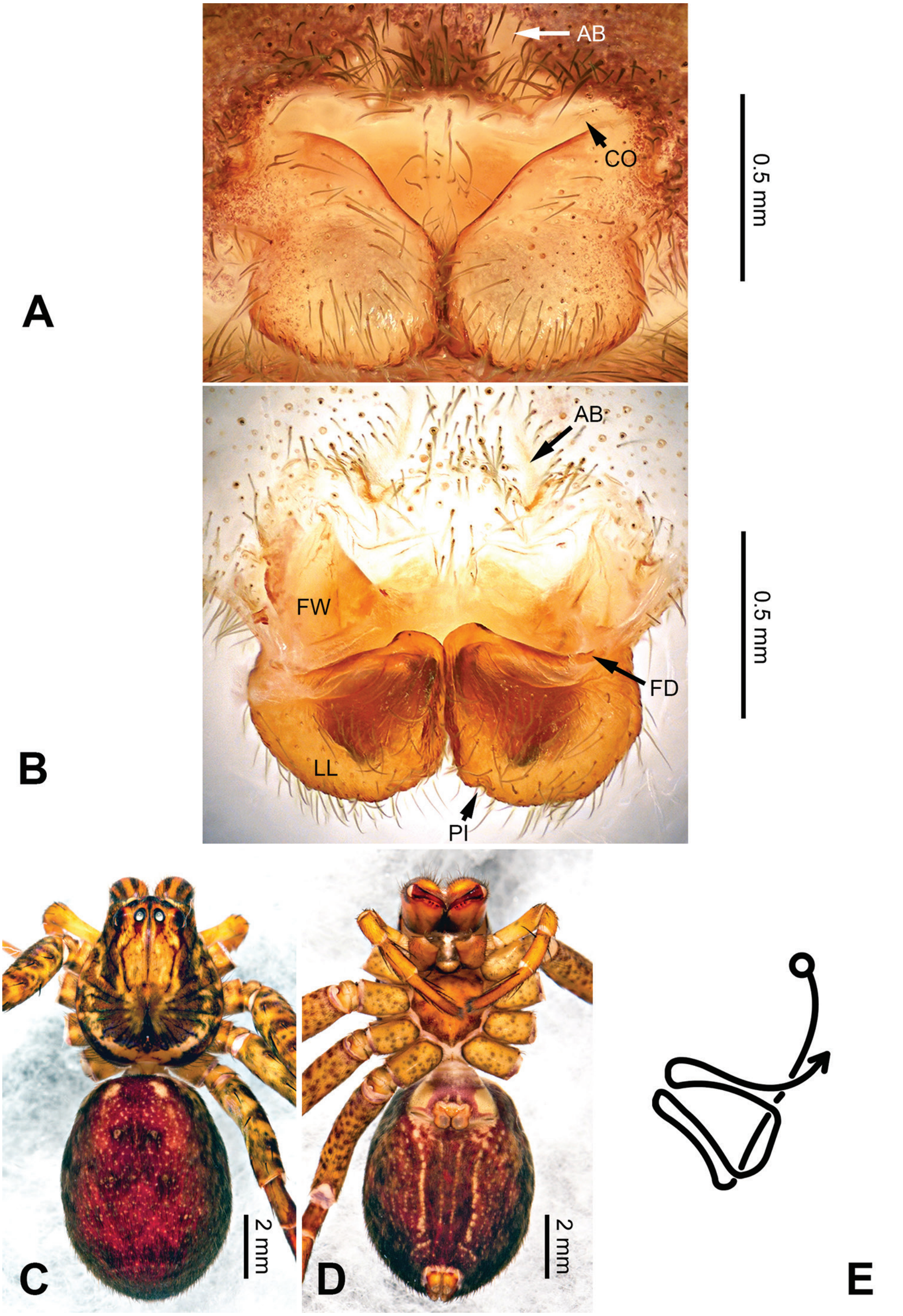

Figure 27. *Pseudopoda subbirmanica* Zhao & Li, sp. n., paratype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

by the following combination of characters: 1. tip of embolus pointed (Figure 26A, B; broad and blunt in *P. digitata*); 2. dRTA with a prolateral protrusion (Figure 25B, C).

Female extremely resembles *P. birmanica* Jäger, 2001 (see Jäger 2001: 75, figure 43a–c) with slight differences in their internal duct systems. For example, the female of *P. subbirmanica* Zhao & Li, sp. n. lacks an anterior loop near the fertilization duct, which is present in *P. birmanica* (Figure 27B, E).

Description. Male (holotype). Body length 9.3, DS length 5, DS width 4.5, OS length 4.3, OS width 3.0. Eyes: AME 0.16, ALE 0.33, PME 0.24, PLE 0.38, AME-AME 0.25, AME-ALE 0.13, PME-PME 0.24, PME-PLE 0.40, AME-PME 0.44, ALE-PLE 0.40, CH AME 0.48, CH ALE 0.37. Leg formula: IV-II-I-III. Spination: palp 131, 101, 2111; legs: femur I-III 323, IV 321; patella I-IV 001; tibia I-IV 2026; metatarsus I-II 1014, III 3035, IV 3037. Measurements of palp and legs: palp 6.9 (2.3, 1.1, 1.3, -, 2.2), leg I 20.3 (5.8, 2.0, 5.6, 5.3, 1.6), leg II 20.5 (5.9, 2.0, 5.8, 5.1, 1.7), leg III 18.6 (5.4, 2.0, 5.0, 4.6, 1.6), leg IV 20.6 (6.0, 1.8, 5.4, 5.4, 2.0). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 20 denticles.

Palp as in diagnosis. Cymbium slender. RTA arising mesially from tibia (Figure 25A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus broad and nearly sickle-shaped, arising from tegulum at 9 o'clock position. Tip of embolus tapering and bending slightly. Conductor arising from tegulum at 12 o'clock position (Figure 26A, B).

Coloration in ethanol: carapace yellowish brown. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown. Ventral opisthosoma with a pair of light transverse bands. Legs yellowish brown, with randomly distributed reddish brown dots (Figure 26C, D).

Female (paratype). Body length 12.2, DS length 5.1, DS width 4.8, OS length 7.1, OS width 5.1. Eyes: AME 0.16, ALE 0.29, PME 0.26, PLE 0.34, AME-AME 0.19, AME-ALE 0.08, PME-PME 0.26, PME-PLE 0.44, AME-PME 0.46, ALE-PLE 0.32, CH AME 0.36, CH ALE 0.30. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2121, 1014; legs: femur I-II 323, III 322, IV 331; patella I-IV 001; tibia I-IV 2026; metatarsus I-II 1014, III 3025, IV 3037. Measurements of palp and legs: palp 6.1 (1.8, 1.1, 1.2, -, 2.0), leg I 15.4 (4.3, 2.0, 4.1, 3.6, 1.4), leg II 16.1 (4.5, 1.9, 4.3, 3.8, 1.6), leg III 14.1 (4.3, 1.8, 3.4, 3.2, 1.4), leg IV 14.8 (4.1, 1.6, 3.6, 4.0, 1.5). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 25 denticles.

Epigyne as in diagnosis. Epigynal field longer in transverse axis. Anterior bands distinct, anterior margin slightly trilobate. Lateral lobes longer in transverse axis. Median margin of lateral lobes converged on the central axis, with anterior part V-shaped. Anterior margin of lateral lobe directed forward and then laterally (Figure 27A). Half of first winding of internal duct system hidden behind lateral lobe in dorsal view (Figure 27B). Loops of internal duct system (spermatheca) sub-triangular (Figure 27B, E).

Coloration in ethanol: as in male, but generally darker. Carapace with dark pattern (Figure 27C, D).

Distribution. Known only from the type locality.

***Pseudopoda titan* Zhao & Li, sp. n.**
http://zoobank.org/D3CCBE41-AE88-4583-9BE6-4EC20DEA3366
Figs 28–30, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, Hponkanrazi Wildlife Sanctuary, roadside between Camp 2 to Camp 3, 27°36.867'N, 96°58.933'E, 2491 m, 15 XII 2016, J. Wu. **Paratype:** 1 ♀, same locality as holotype, 12 V 2017, J. Wu & Z. Chen.

Etymology. The specific name is derived from the name of giants in Greek myth, referring to the gigantic size of this species; noun in apposition.

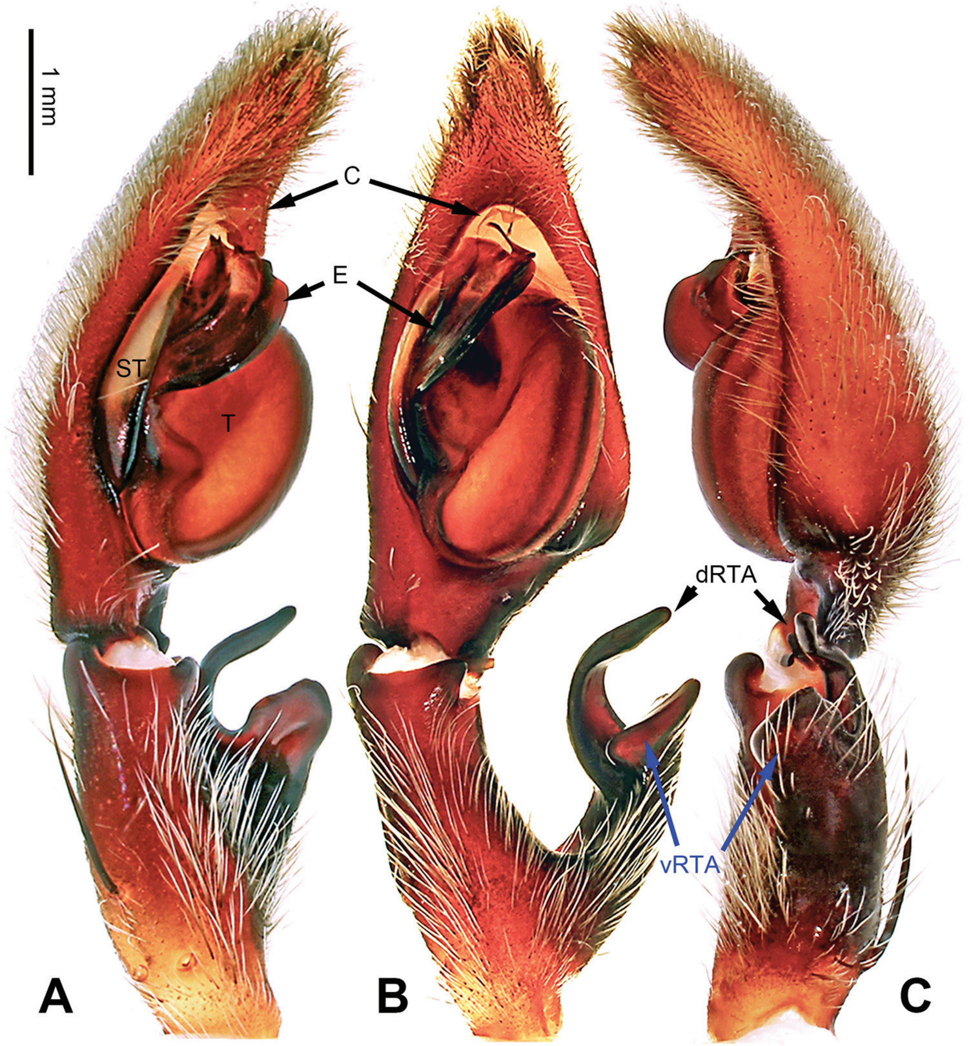

Figure 28. *Pseudopoda titan* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

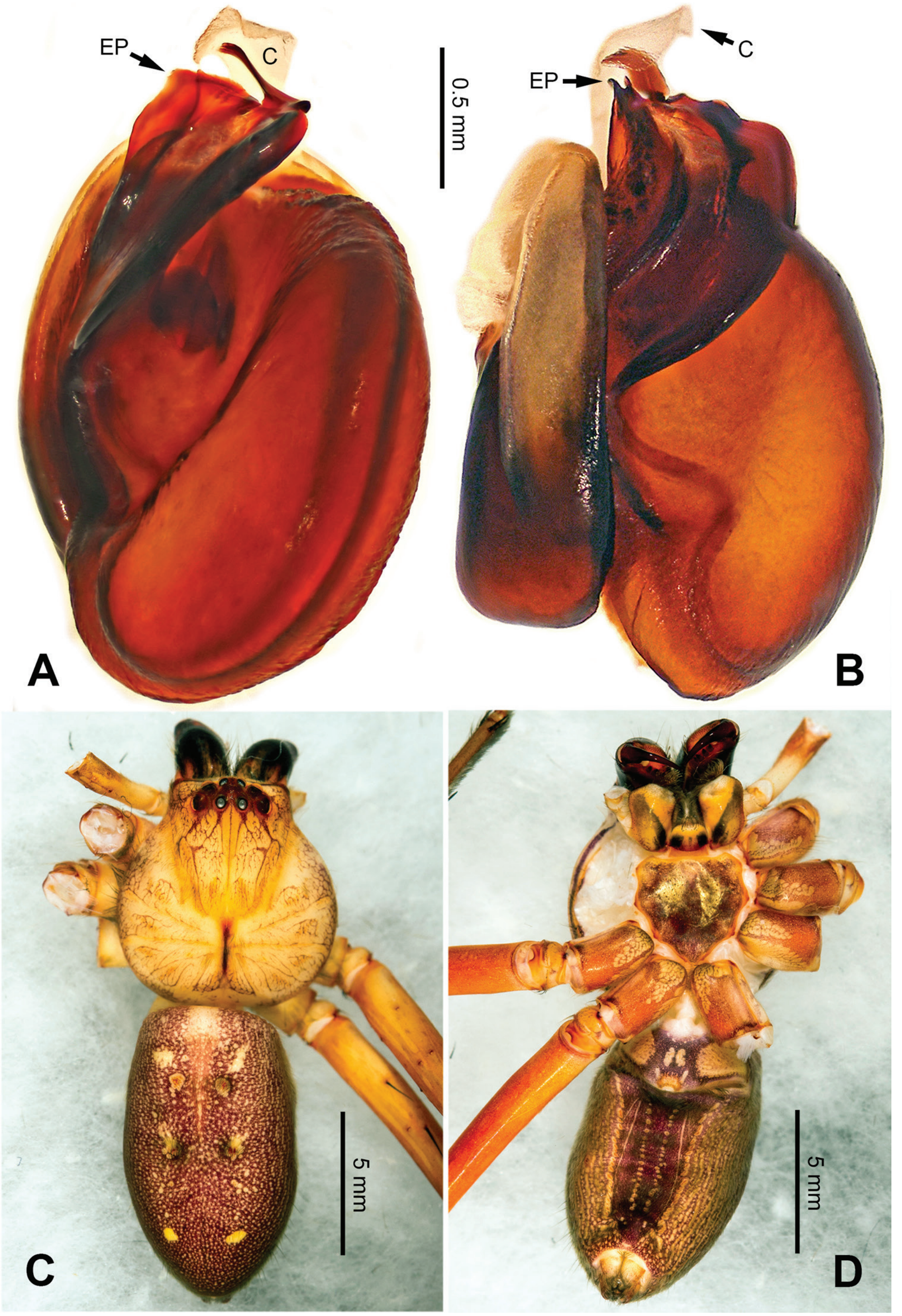

Figure 29. *Pseudopoda titan* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

Diagnosis. Large-sized *Pseudopoda* species. Male resembles *P. emei* Zhang, Zhang & Zhang, 2013 (see Zhang et al. 2013b: 44, figs 18–33), *P. namkhan* Jäger, Pathoumthong & Vedel, 2006 (see Jäger et al. 2006: 222, figs 20–28, 35–40) and *P. mediana* Quan, Zhong & Liu, 2014 (see Quan et al. 2014: 562, figs 6A–C, 7A–C, 8A–D, 9A–C) by: tip of embolus sharply curved and pointing prolaterally (Figure 29A, B). It can be distinguished from the three congeners by the following combination of characters: 1. dRTA well developed, curved, and finger-like (Figure 28A–C; straight and significantly shorter in *P. emei* and *P. mediana*; broadened in *P. namkhan*); 2. tip of embolus slightly broadened (Figure 29B; filiform in *P. emei*); 3. significantly larger in body size.

Female resembles those of *P. gemina* Jäger, Pathoumthong & Vedel, 2006 (see Jäger et al. 2006: 222, figs 14–19, 33–34) and *P. recta* Jäger & Ono, 2001 (see Jäger and Ono 2001: 25, figs 17–22) by: 1. median margin of lateral lobe converged (Figure 30A); 2. slender loops of internal duct system running transversally (Figure 30E). It can be distinguished from the two congeners by the following combination of characters: 1. posterior incisions of lateral lobes distinct (Figure 30A, B; absent in *P. recta* and *P. gemina*); 2. converging part of anterior margins of lateral lobes T-shaped (Figure 30A).

Description. Male (holotype). Body length 19.0, DS length 9.0, DS width 8.0, OS length 10.0, OS width 6.5. Eyes: AME 0.29, ALE 0.38, PME 0.33, PLE 0.38, AME-AME 0.30, AME-ALE 0.13, PME-PME 0.38, PME-PLE 0.60, AME-PME 0.46, ALE-ALE 0.38, CH AME 0.31, CH ALE 0.38. Leg formula: II-I-IV-III. Spination: palp 131, 101, 3100; legs: femur I-III 323, IV 321; patella I-II 101, III-IV 100; tibia I-III 2226, IV 2126; metatarsus I-II 1014, III 2025, IV 2424. Measurements of palp and legs: palp 14.4 (5.1, 2.1, 2.8, -, 4.5), leg I 48.2 (11.5, 4.5, 13.5, 14.0, 4.7), leg II 52.1 (13.5, 4.7, 14.0, 15.0, 4.7), leg III 37.6 (11, 3.7, 10.0, 9.5, 3.4), leg IV 40.6 (11.0, 3.6, 11.0, 11.0, 4.0). Promargin of chelicerae with three teeth, retromargin with four teeth, cheliceral furrow with ca. 30 denticles.

Palp as in diagnosis. Cymbium slender, with distinct retrolateral bulge beside bulb. RTA arising basally from tibia (Figure 28A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus arising from tegulum at 10 o'clock position, broad, almost straight in ventral view. Tip of embolus leaf-like, sharply curved, and pointing prolaterally. Embolic projection present as two additional triangular rims near the tip. Conductor arising from the tegulum at 12 to 1 o'clock position (Figure 29A, B).

Coloration in ethanol: carapace yellowish brown. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown, with white dots and yellow patches. Legs orange. Ventral opisthosoma with two pairs of longitudinal lines composed of orange dots (Figure 29C, D).

Female (paratype). Body length 19.0, DS length 9.0, DS width 8.0, OS length 10.0, OS width 6.5. Eyes: AME 0.40, ALE 0.43, PME 0.30, PLE 0.43, AME-AME 0.34, AME-ALE 0.19, PME-PME 0.46, PME-PLE 0.68, AME-PME 0.53, ALE-PLE 0.47, CH AME 0.47, CH ALE 0.47. Leg formula: II-I-IV-III. Spination: palp 131, 101, 3110, 2020; legs: femur I-III 323, IV 321; patella I-II 101, III-IV 100; tibia I-II 2226, III-IV 2126; metatarsus I-II 1014, III 2024, IV 2037. Measurements of palp and legs: palp 12.6 (4.0, 2.0, 2.6, -, 4.0), leg I 37.5 (11.5, 4.1, 10.0, 9.0, 2.9), leg II

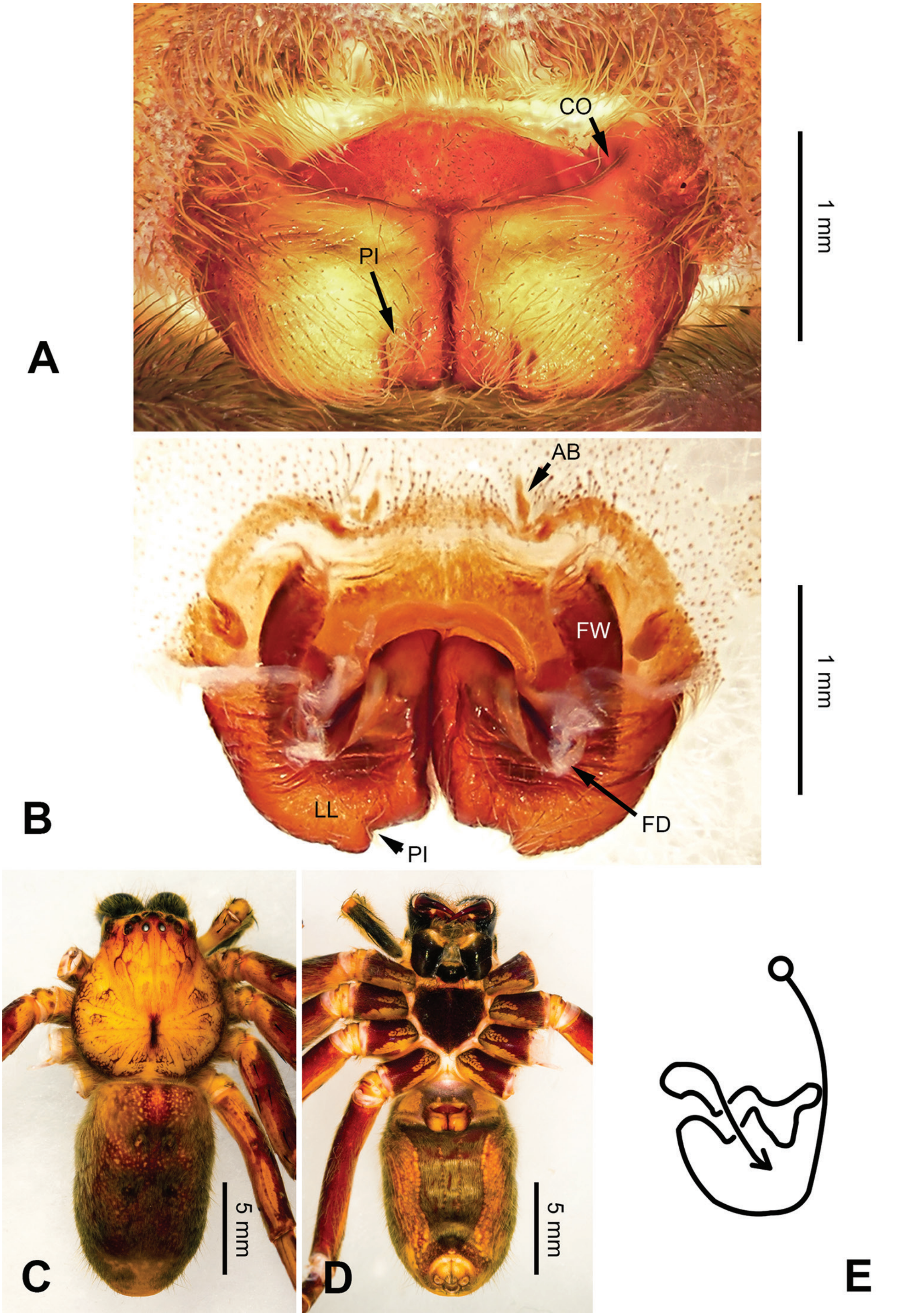

Figure 30. *Pseudopoda titan* Zhao & Li, sp. n., paratype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

40.2 (11.5, 4.2, 11.5, 10.0, 3.0), leg III 29.1 (8.5, 3.3, 8.0, 6.5, 2.8), leg IV 30.1 (9.0, 3.0, 8.0, 7.5, 2.6). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 30 denticles.

Epigyne as in diagnosis. Epigynal field longer in transverse axis, with distinct anterior bands and trilobate anterior margin. Lateral lobes longer in transverse axis, subrectangular but narrower laterally. Posterior incision of lateral lobe distinct, near the posterior meeting point of lateral lobes (Figure 30A). Lateral loops of internal duct system running transversally, covered by first winding in dorsal view (Figure 30B, E).

Coloration in ethanol: as in male but generally darker (Figure 30C, D).

Distribution. Known only from the type locality.

Pseudopoda xia Zhao & Li, sp. n.

http://zoobank.org/0BDB0064-B929-45F0-A6B8-A0BD071F6F56

Figs 31, 32, 37

Type material. Holotype ♂: Myanmar, Kachin State, Putao, around Ziradum Village, 27°33.465'N, 97°06.580'E, 1051 m, 8 V 2017, J. Wu & Z. Chen.

Etymology. The specific name is derived from the Chinese Pinyin word 'jimpness' (xiá), referring to the narrow abdomen of this species; noun in apposition.

Diagnosis. Small-sized *Pseudopoda* species. Male resembles *P. brauni* Jäger, 2001 (see Jäger 2001: 44, figs 26d–g, 27a–d), *P. trisuliensis* Jäger, 2001 (see Jäger 2001: 42, figure 28f–j), *P. prompta* (O. Pickard-Cambridge, 1885) (see Jäger 2000: 63, figs 1–15) and *P. confusa* Jäger, Pathoumthong & Vedel, 2006 (see Jäger et al. 2006: 220, figs 1–13, 29–32) by: embolus running near the prolateral margin of tegulum in ventral view. It can be distinguished from the four congeners by the following combination of characters: 1. RTA simple, with only one apex (Figure 31B, C; RTA with two apices in *P. confusa*); 2. tegulum with a distinct sub-triangular protrusion near the retrolateral margin (Figure 32A; absent in *P. prompta* and *P. confusa*; a blunt hump present on tegulum near the basal part of embolus in *P. trisuliensis* and *P. brauni*); 3. embolus with an extra rim running along the distal part of it (Figure 32B; absent or indistinct in *P. prompta* and *P. confusa*).

Description. Male (holotype). Body length 7.6, DS length 3.1, DS width 3.2, OS length 4.5, OS width 2.2. Eyes: AME 0.15, ALE 0.19, PME 0.15, PLE 0.21, AME-AME 0.12, AME-ALE 0.06, PME-PME 0.14, PME-PLE 0.25, AME-PME 0.21, ALE-PLE 0.24, CH AME 0.16, CH ALE 0.10. Leg formula: I-II-IV-III. Spination: palp 131, 101, 2101; legs: femur I-III 323, IV 322; patella I-II 101, III-IV 001; tibia I 2226, II-III 2116, IV 2126; metatarsus I 1014, II 0014, III 2024, IV 3026. Measurements of palp and legs: palp 5.8 (1.9, 0.9, 1.0, -, 2.0), leg I 28.6 (7.5, 1.8, 8.2, 8.5, 2.6), leg II 26.3 (7.5, .18, 7.0, 7.5, 2.5), leg III 19.1 (5.5, 1.3, 5.2, 5.5, 1.6), leg IV 25.5 (7.0, 2.0, 6.8, 7.5, 2.2). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 15 denticles.

Palp as in diagnosis. Cymbium slender, slightly elongated distally. RTA arising basally from tibia (Figure 31A–C). Tegulum with an additional ridge emerging basally,

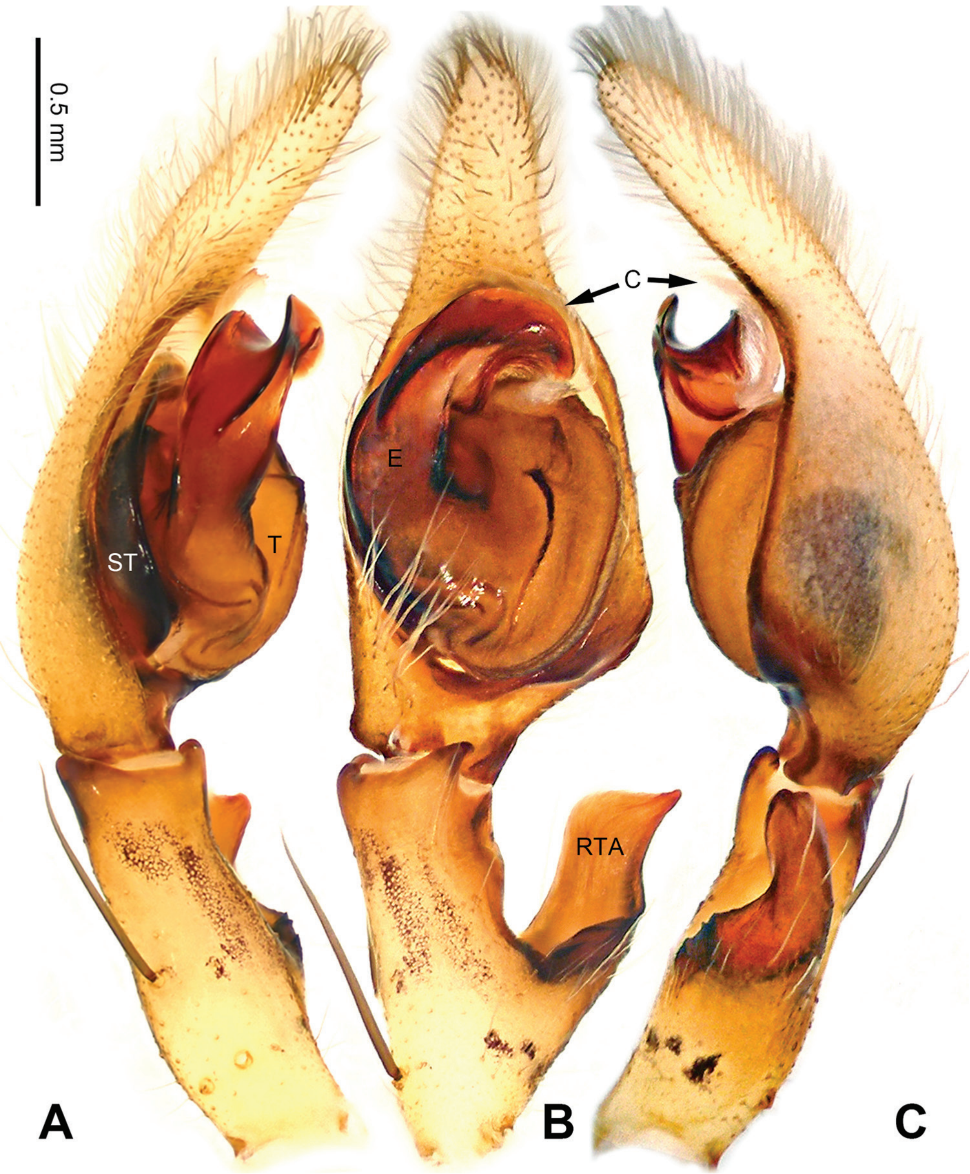

Figure 31. *Pseudopoda xia* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

and running distally, ending with a sub-triangular protrusion pointing at the basal part of embolus. Sperm duct running submarginally retrolaterally in tegulum, visible near the base of embolus as an S-shaped duct. Embolus arising from tegulum at 9 to 10 o'clock position. Wrinkles present below the distal part on embolus. Tip of embolus with indention. Conductor arising from tegulum at 1 to 2 o'clock position, slender, bent basally and then directed prolaterally (Figure 32A, B).

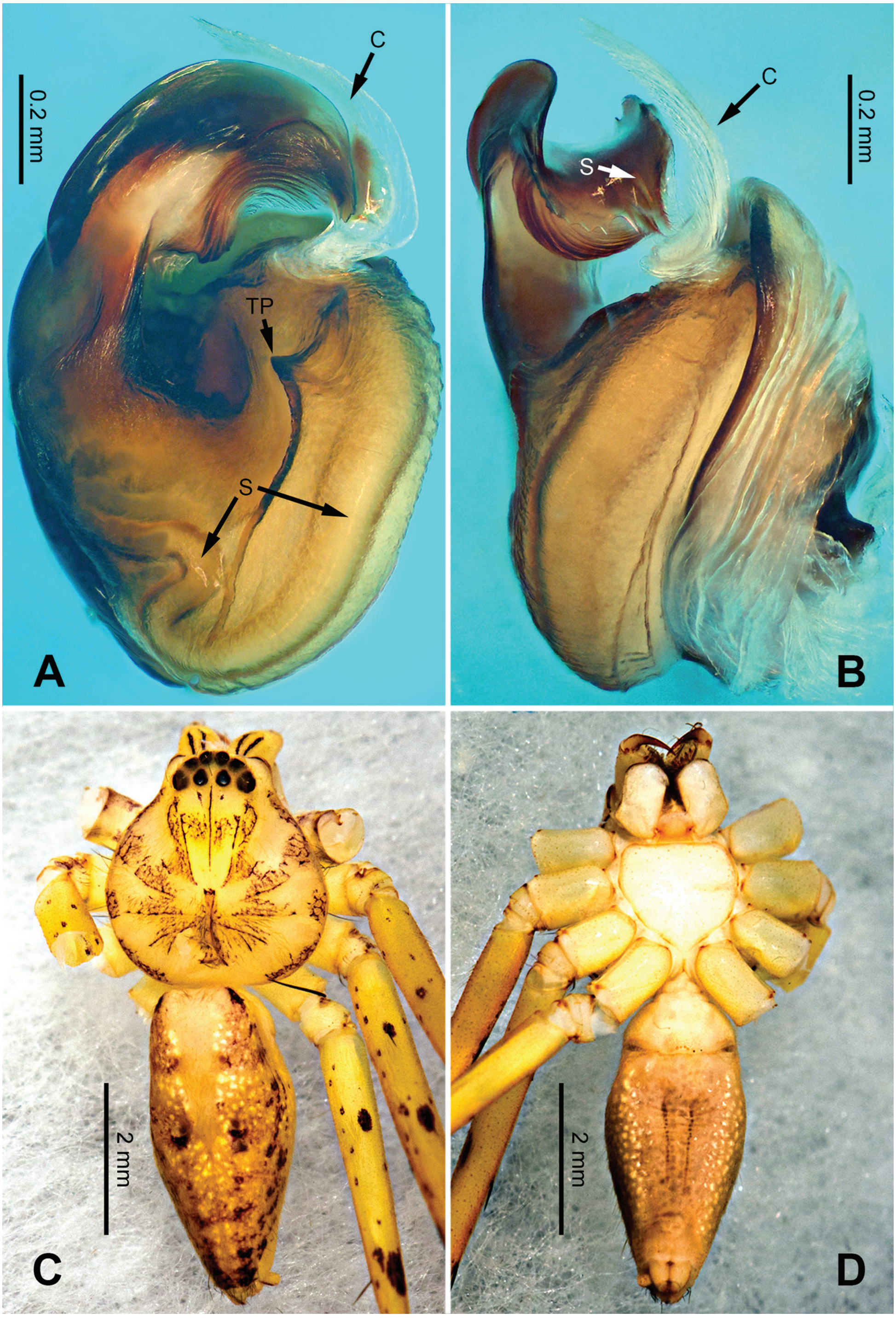

Figure 32. *Pseudopoda xia* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view.

Coloration in ethanol: carapace yellow. Radial furrows and fovea black. Dorsal opisthosoma orange, with black pattern and white dots. Ventral opisthosoma with a pair of longitudinal white bands. Legs yellow to orange, with randomly distributed black dots and patches (Figure 32C, D).

Female. Unknown.

Distribution. Known only from the type locality.

Pseudopoda yuanjiangensis Zhao & Li, sp. n.

http://zoobank.org/DD1ABF58-C8DB-4E7C-AEC3-B66ADC60EF51

Figs 33, 37

Type material. Holotype ♀: China, Yunnan Province, Yuxi City, Yuanjiang County, Yangchajie Village Nature Reserve, 23°39.632'N, 101°45.564'E, 2114 m, 4 VI 2015, Z. Chen & F. Li.

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

Diagnosis. Small to median-sized *Pseudopoda* species. Female resembles *P. bibulba* (Xu & Yin, 2000) (see Jäger and Vedel 2007: 15, figs 44–59) by: internal duct system with distinct lateral loops visible through cuticle in ventral view as rounded patches (Figure 33A). It can be distinguished from the latter species by the following combination of characters: 1. anterior bands distinct (Figure 33A; absent in *P. bibulba*); 2. lateral lobes much longer in transverse axis, with anterior margins bending posteriolaterally (Figure 33A; anterior margins bending anteriolaterally and then directed medially in *P. bibulba*).

Description. Female (holotype). Body length 8.5, DS length 2.8, DS width 2.7, OS length 5.7, OS width 4.0. Eyes: AME 0.18, ALE 0.28, PME 0.21, PLE 0.32, AME-AME 0.19, AME-ALE 0.11, PME-PME 0.28, PME-PLE 0.37, AME-PME 0.40, ALE-PLE 0.31, CH AME 0.35, CH ALE 0.30. Leg formula: II-I-IV-III. Spination: palp 131, 101, 2121, 1004; legs: femur I-II 323, III 322, IV 331; patella I-IV 001; tibia I-III 2026, IV 2025; metatarsus I-II 2024, III 3025, IV 3037. Measurements of palp and legs: palp 5.8 (1.7, 1.0, 1.3, -, 1.8), leg I 13.9 (4.0, 1.9, 3.5, 3.2, 1.3), leg II 15.2 (4.3, 2.1, 4.0, 3.4, 1.4), leg III 12.3 (3.7, 1.6, 3.1, 2.8, 1.1), leg IV 13.4 (4.1, 1.6, 3.3, 3.2, 1.2). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 38 denticles.

Epigyne as in diagnosis. Epigynal field longer in transverse axis, with anterior bands and trilobate anterior margin. Lateral lobes slightly converged on the central axis. Posterior incision of lateral lobe distinct, near the meeting point of lateral lobes. (Figure 33A, B).

Coloration in ethanol: carapace yellowish brown. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown, with a bright transverse band in the posterior half. Legs yellowish brown, with randomly distributed reddish brown dots (Figure 33C, D).

Male. Unknown.

Distribution. Known only from the type locality.

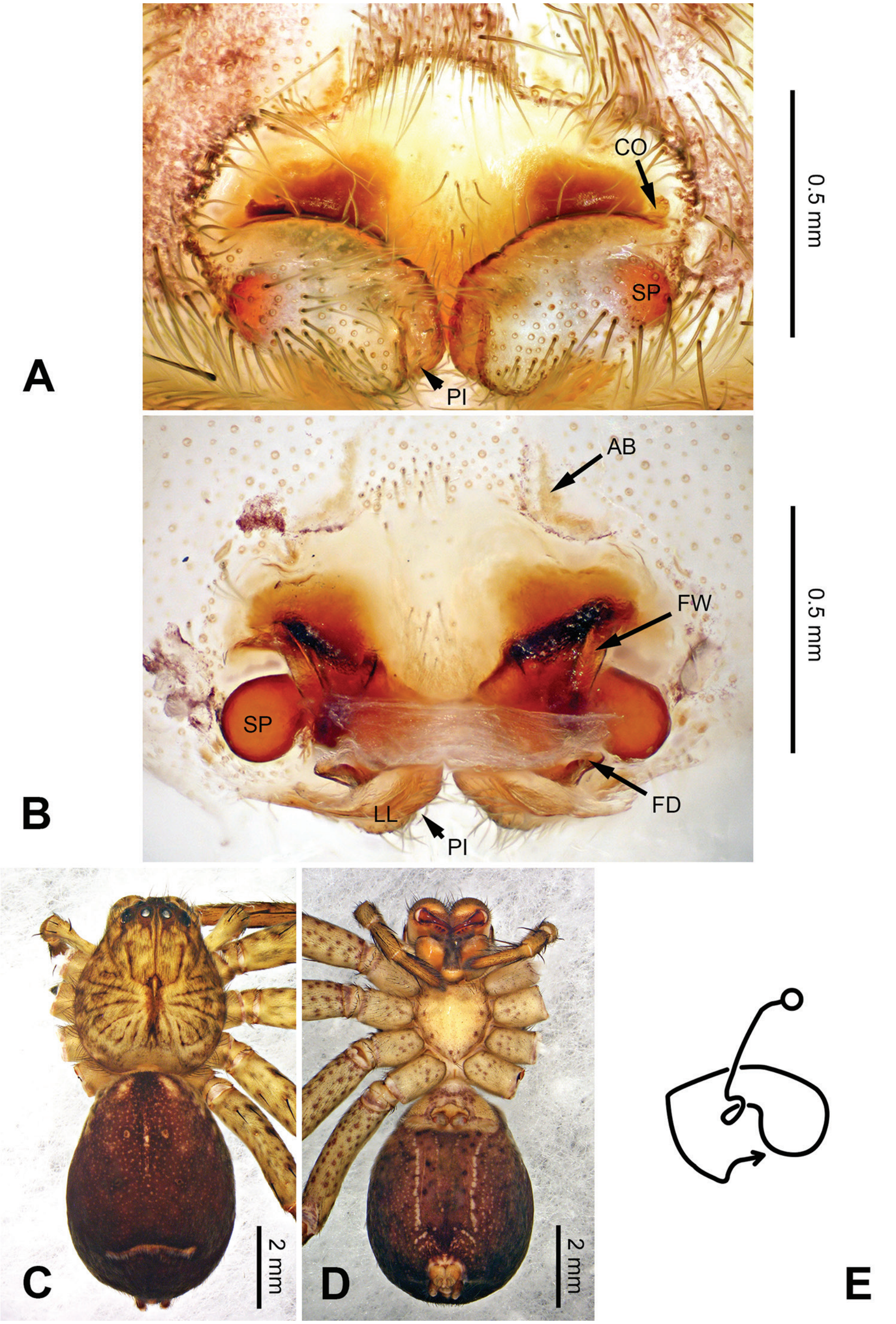

Figure 33. *Pseudopoda yuanjiangensis* Zhao & Li, sp. n., female holotype. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

Pseudopoda zixiensis **Zhao & Li, sp. n.**
http://zoobank.org/81384BB2-DF83-472F-B7ED-82BC432366F9
Figs 34–37

Type material. Holotype ♂: China, Yunnan Province, Chuxiong City, Zixi Mountain, 25°00.602'N, 101°24.386'E, 2445 m, VI 2017, Z. Chen. **Paratype:** 1♀, same data as holotype.

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

Diagnosis. Median-sized *Pseudopoda* species. Male resembles *P. sinapophysis* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 3, figs 1–6) and *P. mediana* Quan, Zhong & Liu, 2014 (see Quan et al. 2014: 562, figs 6A–C, 7A–C, 8A–D, 9A–C) by: embolus is curved, with its tip pointing back dorsally (Figure 35B). It can be distinguished from the two congeners by the following combination of characters: 1. cymbium short and blunt (Figure 34B; elongated and slender in *P. sinapophysis* and *P. mediana*); 2. prolateral rim of embolus extended and forming an embolic projection near the tip (Figure 35A, B); 3. dRTA finger-like (Figure 34A–C; broadened in *P. mediana*).

Female resembles *P. cangschana* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 19, figs 66–72), *P. gongschana* Jäger & Vedel, 2007 (see Jäger and Vedel 2007: 6, figs 10–15) and *P. albolineata* Jäger, 2001 (see Jäger 2001: 83, fig. 46a–o) in ventral view by the similar shape of lateral lobes, but can be distinguished from the three congeners by the following combination of characters: 1. lateral loops of internal duct system (spermathecae) distinct, visible in dorsal view (Figure 36B; spermatheca hidden behind first winding in *P. gongschana*); 2. first winding strongly bent (Figure 36B, E; almost straight in *P. cangschana* and *P. albolineata*).

Description. Male (holotype). Body length 10.5, DS length 5.0, DS width 4.4, OS length 5.5, OS width 3.2. Eyes: AME 0.17, ALE 0.29, PME 0.22, PLE 0.32, AME-AME 0.17, AME-ALE 0.08, PME-PME 0.26, PME-PLE 0.40, AME-PME 0.37, ALE-PLE 0.35, CH AME 0.38, CH ALE 0.30. Spination: palp 131, 101, 2111; legs: femur III 323, IV 331; patella III-IV 101; tibia III-IV 2026; metatarsus III 3025, IV 3037. Measurements of palp and legs: palp 7.3 (2.5, 1.1, 1.4, -, 2.3), leg I -, leg II -, leg III 19.6 (5.4, 2.2, 5.3, 5.1, 1.6), leg IV 21.9 (6.0, 2.1, 5.5, 6.5, 1.8). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 25 denticles.

Palp as in diagnosis. Cymbium sub-triangular, with distinct retrolateral bulge. RTA arising basally to mesially from tibia, vRTA humble and broad (Figure 34A–C). Sperm duct running submarginally retrolaterally in tegulum. Embolus broad and sickle-shaped, arising from tegulum at 10 o'clock position. Conductor arising from tegulum at 12 o'clock position, leaning slightly prolaterally (Figure 35A, B).

Coloration in ethanol: carapace yellowish brown. Radial furrows and fovea dark brown. Dorsal opisthosoma reddish brown. Ventral opisthosoma with a pair of bright longitudinal lines. Legs yellowish brown, with randomly distributed reddish brown dots (Figure 35C, D).

Female (paratype). Body length 11.5, DS length 5.5, DS width 4.7, OS length 6.0, OS width 4.2. Eyes: AME 0.21, ALE 0.32, PME 0.24, PLE 0.32, AME-AME 0.25, AME-ALE 0.13, PME-PME 0.33, PME-PLE 0.50, AME-PME 0.43, ALE-PLE

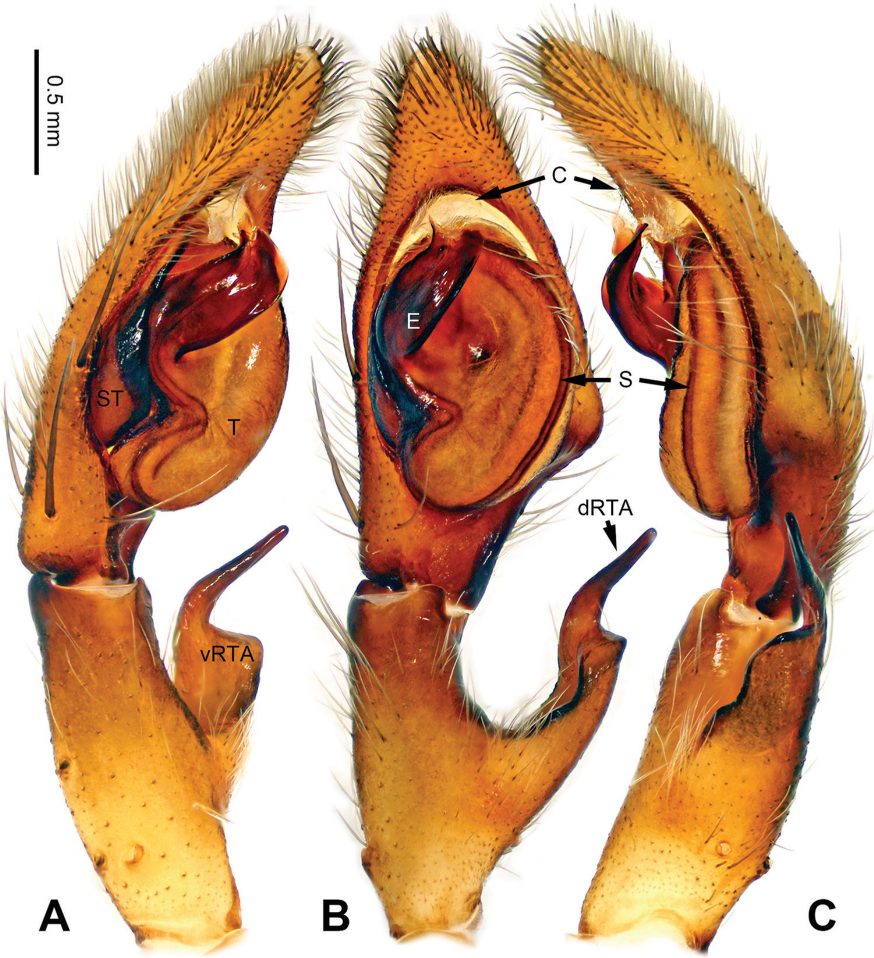

Figure 34. *Pseudopoda zixiensis* Zhao & Li, sp. n., left palp of male holotype. **A** Prolateral view **B** Ventral view **C** Retrolateral view. Scale bar equal for **A, B, C**.

0.42, CH AME 0.50, CH ALE 0.33. Spination: palp 131, 101, 2121, 1014; legs: femur II 323, III 322, IV 331; patella II-IV 001; tibia II-III 2026, IV 2025; metatarsus I-II 1014, III 3015, IV 3037. Measurements of palp and legs: palp 7.2 (2.2, 1.2, 1.6, -, 2.2), leg I - (-, -, -, 4.0, 1.6), leg II 18.5 (5.3, 2.7, 4.6, 4.3, 1.6), leg III 15.3 (4.5, 2.1,4.0, 3.4, 1.3), leg IV 17.4 (5.0, 2.0, 4.3, 4.5, 1.6). Promargin of chelicerae with three teeth, retromargin with four teeth. Cheliceral furrow with ca. 30 denticles.

Epigyne as in diagnosis. Epigynal field with nearly equal length in transverse and longitudinal axis. Anterior bands distinct, anterior margin slightly trilobate. Lateral lobes longer in longitudinal axis. Lateral lobes converged on the central axis, with both anterior and posterior part V-shaped. Spermathecae exposed in dorsal view. Spermathecae oval, with coiling ducts embedded (Figure 36B, E).

Coloration in ethanol: as in male, but generally darker (Figure 36C, D).

Distribution. Known only from the type locality.

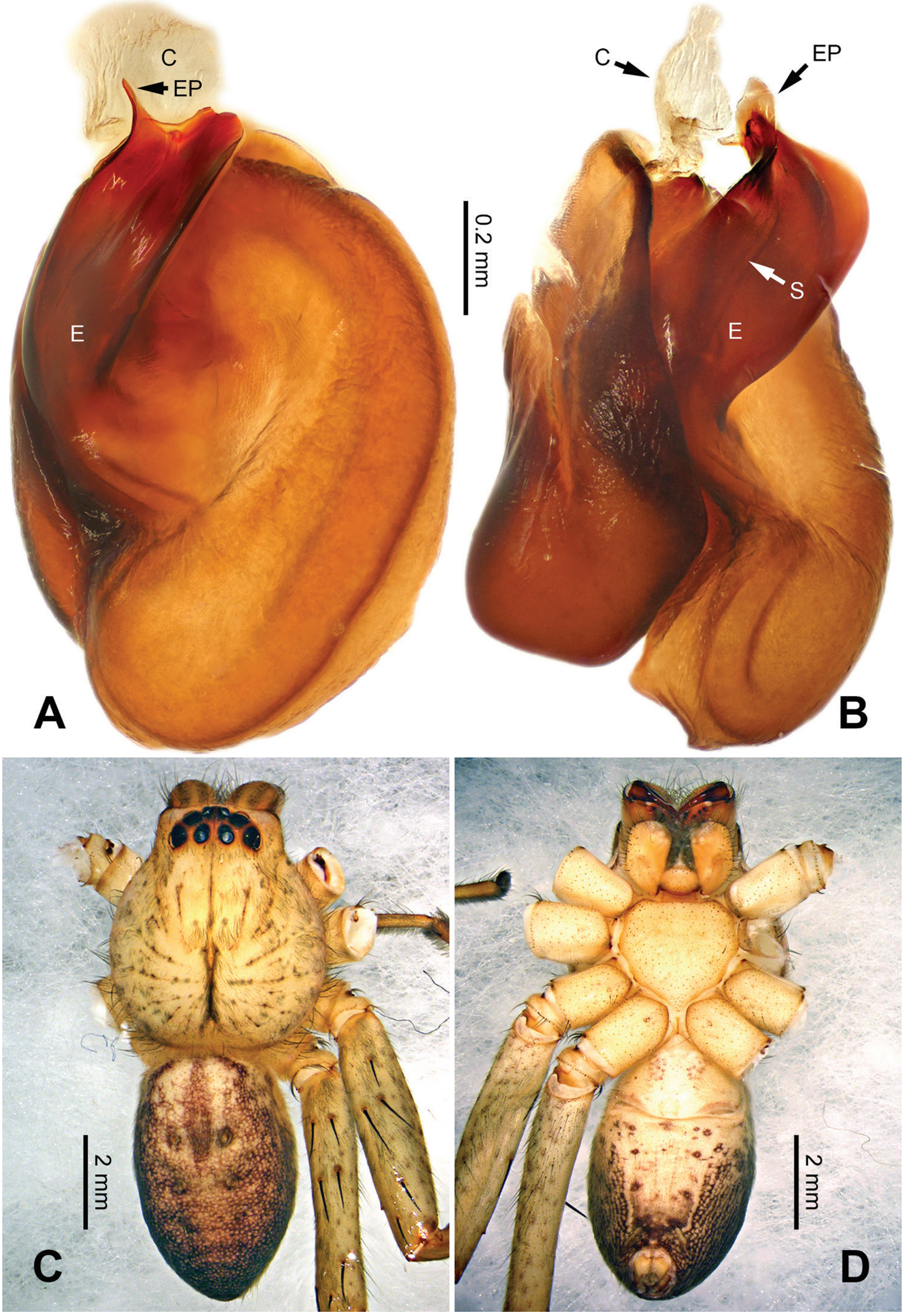

Figure 35. *Pseudopoda zixiensis* Zhao & Li, sp. n., male holotype. **A** Bulb, ventral view **B** Bulb, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view. Scale bar equal for **A, B**.

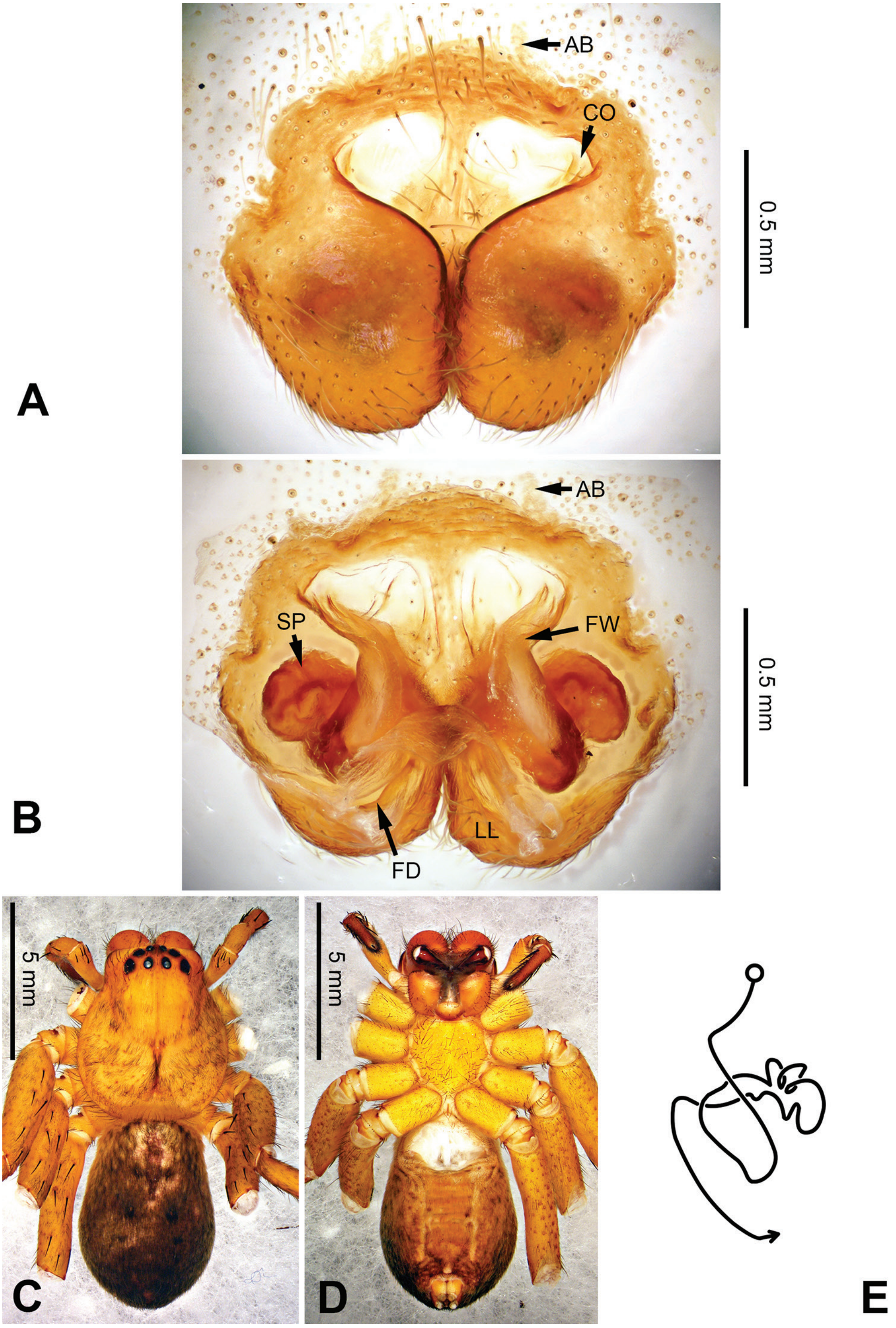

Figure 36. *Pseudopoda zixiensis* Zhao & Li, sp. n., paratype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Habitus, dorsal view **D** Habitus, ventral view **E** Schematic course of internal duct system, dorsal view.

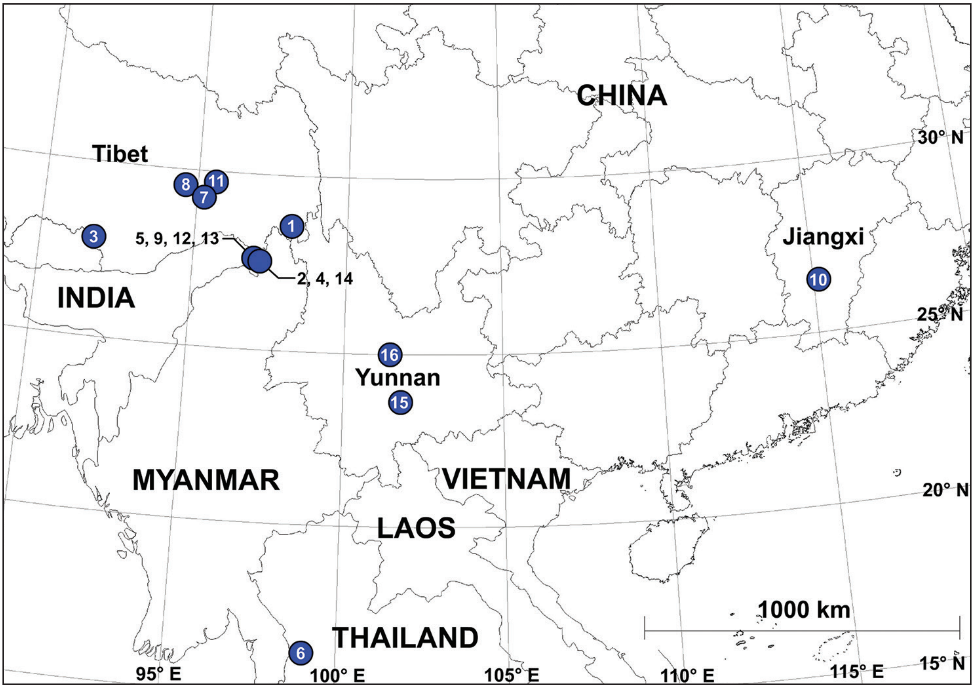

Figure 37. Distribution map of the sixteen new species from the genus *Pseudopoda*. The numbers represent the different species **1** *P. chayuensis* Zhao & Li, sp. n. **2** *P. colubrina* Zhao & Li, sp. n. **3** *P. conaensis* Zhao & Li, sp. n. **4** *P. daxing* Zhao & Li, sp. n. **5** *P. gexiao* Zhao & Li, sp. n. **6** *P. maeklongensis* Zhao & Li, sp. n. **7** *P. medogensis* Zhao & Li, sp. n. **8** *P. nyingchiensis* Zhao & Li, sp. n. **9** *P. putaoensis* Zhao & Li, sp. n. **10** *P. shacunensis* Zhao & Li, sp. n. **11** *P. shuo* Zhao & Li, sp. n. **12** *P. subbirmanica* Zhao & Li, sp. n. **13** *P. titan* Zhao & Li, sp. n. **14** *P. xia* Zhao & Li, sp. n. **15** *P. yuanjiangensis* Zhao & Li, sp. n. **16** *P. zixiensis* Zhao & Li, sp. n.

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