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ANÁLISE CLADÍSTICA E REVISÃO TAXONÔMICA DE *TOBIAS* SIMON, 1895 (ARANEAE, THOMISIDAE, STEPHANOPINAE)

Miguel Machado

DISSERTAÇÃO DE MESTRADO

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Orientador: Dr. Arno Antonio Lise

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Dissertação apresentada como requisito para a obtenção do título de Mestre em Zoologia pelo Programa de Pós-Graduação da Pontifícia Universidade Católica do Rio Grande do Sul.

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Aprovada em _________ de _________________________ de 2016

BANCA EXAMINADORA:

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Dr. Alexandre B. Bonaldo

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Dr. Ricardo Ott

ADVERTÊNCIA

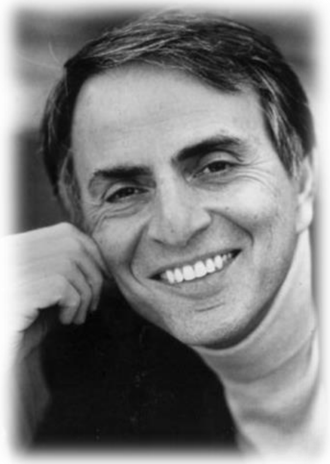
Esta dissertação não é uma publicação válida, conforme descrito no capítulo III do Código Internacional de Nomenclatura Zoológica. Portanto, nomes novos e mudanças taxonômicas propostas não possuem validade para fins de nomenclatura ou prioridade.

WARNING

This dissertation is not valid as a publication, as described in the chapter III of the International Code of Zoological Nomenclature. Therefore, taxonomic changes and new names proposed here are not valid for nomenclatural or priority purposes.

“I don’t want to believe. I want to know.”

Carl Sagan



To my beloved parents, Gilce Elenar Leite Machado and
Paulo Roberto da Silva.

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SUMÁRIO

APRESENTAÇÃO

Thomisidae Sundevall, 1833 é a sétima maior família de aranhas, contando atualmente com 175 gêneros e 2.154 espécies. Sua distribuição é cosmopolita, com representantes ocorrendo predominantemente em regiões de clima tropical e subtropical. Estas aranhas são caçadoras de emboscada, de hábitos diurnos e que não constroem teias. Usualmente os Thomisidae apresentam acentuado dimorfismo sexual, sendo os machos em geral menores que as fêmeas. Estas aranhas são popularmente conhecidas como “aranhas-caranguejo” em razão da maneira como se locomovem na vegetação e pela morfologia e disposição de suas pernas I e II: estendidas lateralmente (laterígradas) e geralmente maiores e mais robustas que as pernas III e IV.

Desde a proposição original de Thomisidae, aspectos relativos à sua sistemática têm sido alvo de constantes discussões, principalmente as relações intrafamiliares e os limites taxonômicos das subfamílias atualmente aceitas e de seus gêneros componentes. A posição taxonômica de diversos Stephanopinae Neotropicais ainda é incerta, deste modo, o presente estudo visou a realização de uma análise cladística aliada ao estudo taxonômico do gênero *Tobias*, que resultou por uma sinonímia para este gênero, o qual propomos ser sinônimo júnior de *Epicadus*. Uma nova diagnose é proposta para *Epicadus*, que após os atos taxonômicos aqui propostos, passa a ser composto por nove espécies: E. *camelinus* comb. nov., *E. caudatus* comb. nov., *E. granulatus*, *E. heterogaster*, *E. pulcher* comb. nov., *E. pustulosus* comb. nov., *E. rubripes*, *E. taczanowskii* comb. nov. e *E. trituberculatus* comb. nov.

O primeiro capítulo desta dissertação já está publicado na Zootaxa e é intitulado “Taxonomic notes on the crab spider genus *Tobias* Simon, 1895 (Araneae, Thomisidae, Stephanopinae)”. O segundo capítulo está escrito sob as normas da Zoological Journal of Linnean Society, periódico ao qual será submetido.

PRESENTATION

Thomisidae Sundevall, 1833 is the seventh largest family of spiders, currently comprising 175 genera and 2.154 species. Its distribution is worldwide with representatives occurring predominantly in tropical and subtropical regions. These spiders are ambush hunters with diurnal habits and do no build webs. Thomisids usually present a remarkable sexual dimorphism, being the males in general smaller than females and are popularly known as "crab spiders" due to the way they move on vegetation and by the morphology and disposition of the legs I e II: laterally disposed (laterigrade) and usually larger and stouter than legs III e IV.

Since the original proposition of Thomisidae much has been discussed about its systematics, specially its intrafamiliar relations and taxonomic boundaries of its subfamilies and component genera. The taxonomic position of many Neotropical Stephanopinae remain uncertain, therefore, the present study focused on a cladistics analysis allied to a taxonomic review of *Tobias*, which results in a synonymy for this genus which we propose as junior synonym of *Epicadus*. A new diagnosis is proposed for *Epicadus*, that after all taxonomic acts proposed here, is comprised by nine species: *E. camelinus* comb. nov., *E. caudatus* comb. nov., *E. granulatus*, *E. heterogaster*, *E. pulcher* comb. nov., *E. pustulosus* comb. nov., *E. rubripes*, *E. taczanowskii* comb. nov. and *E. trituberculatus* comb. nov.

The second chapter of this dissertation is already published in Zootaxa and is titled "Taxonomic notes on the crab spider genus *Tobias* Simon, 1895 (Araneae, Thomisidae, Stephanopinae)". The first chapter complies with the requirements of the Zoological Journal of Linnean Society, journal to which the article will be submitted.

RESUMO

Desde a proposição original de Thomisidae, muito se tem discutido a respeito de sua taxonomia e relações intrafamiliares. A subfamília Stephanopinae é formada por indivíduos caracterizados pela presença de dentes nas quelíceras e pernas anteriores maiores e mais robustas que as posteriores, no entanto, a monofilia deste grupamento não tem sido corroborada em fator dos caracteres diagnósticos dúbios e pelo grande número de gêneros que ainda não foram submetidos a estudos revisivos. No presente trabalho são apresentadas uma análise cladística e uma revisão taxonomica do gênero *Tobias* Simon, 1895. A análise é baseada em uma matriz com 29 táxons terminais (7 no grupo interno e 22 no grupo externo) e 87 caracteres morfológicos. A análise de pesagem implícita resultou em uma árvore mais parcimoniosa obtida em 16 grupos de distorção e com 294 passos, que suportam *Tobias* como um grupo parafilético com *Epicadus* Simon, 1895, e seu sinônimo júnior. *Onocolus* Simon, 1895 surgiu como grupo irmão de *Epicadus*. *Epicadus pulcher* Mello-Leitão, 1929 comb. nov. é considerado sinônimo sênior de *Epicadus epicadoides* Mello-Leitão comb. nov., 1944 e *Epicadus regius* Birabén, 1955 comb. nov., *Epicadus granulatus* Banks, 1909 é proposto como sinônimo sênior de *Epicadus inermis* Mello-Leitão, 1929 comb. nov., *Epicadus camelinus* (O. Pickard-Cambridge, 1869) comb. nov. é considerado sinônimo sênior de *Epicadus martinezi* Birabén, 1955 comb. nov. e *Epicadus trituberculatus* (Taczanowski, 1872) comb. nov. é considerado sinônimo sênior de *Epicadus paraguayensis* Mello-Leitão, 1929 comb. nov. e *Epicadus planus* Mello-Leitão, 1932. Novos registros de distribuição e redescrições são apresentados para as espécies supracitadas. As espécies anteriormente descritas em *Tobias*, *Epicadus caudatus* Mello-Leitão comb. nov., 1929 e *Epicadus pustulosus* Mello-Leitão, 1929 comb. nov., juntamente com *Epicadus heterogaster* (Guérin, 1829) e *Epicadus rubripes* Mello-Leitão, 1929 foram redescritas recentemente e portanto não foram incluídas no presente estudo. Após a análise cladística, *Epicadus* agora compreende 9 espécies.

ABSTRACT

Since the original proposition of Thomisidae, much has been discussed about its taxonomy and intra-family relations. The subfamily Stephanopinae comprises individuals characterized by the presence of cheliceral teeth and by the anterior legs stronger and larger than the posterior ones, however, the monophyly of this group has not been corroborated due their dubious diagnostic characters and by the lack of revisional studies on several of its component genera. A phylogenetic analysis followed by a morphological revision of the spider genus *Tobias* Simon, 1895 are performed. The analysis is based on a matrix with 29 terminal taxa (7 in ingroup and 22 in outgroup) scored for 87 morphological characters. The implied weighting analysis resulted in one most parcimonious tree with 294 steps obtained in 16 distortion groups, which support that *Tobias* is paraphyletic with *Epicadus* Simon, 1895, and considered its junior synonym. *Onocolus* Simon, 1895 emerge as the sister group of *Epicadus*. *Epicadus pulcher* Mello-Leitão, 1929 comb. nov. is considered senior synonym of *Epicadus epicadoides* Mello-Leitão comb. nov., 1944 and *Epicadus regius* Birabén, 1955 comb. nov., *Epicadus granulatus* Banks, 1909 is proposed as senior synonym of *Epicadus inermis* Mello-Leitão, 1929 comb. nov., *Epicadus camelinus* (O. Pickard-Cambridge, 1869) comb. nov. is considered senior synonym of *Epicadus martinezi* Birabén, 1955 comb. nov. and *Epicadus trituberculatus* (Taczanowski, 1872) comb. nov. is considered senior synonym of *Epicadus paraguayensis* Mello-Leitão, 1929 comb. nov. and *Epicadus planus* Mello-Leitão, 1932. New distribution records and redescriptions are provided. The species latter described in *Tobias*, *Epicadus caudatus* Mello-Leitão, 1929 comb. nov., *Epicadus pustulosus* Mello-Leitão comb. nov., 1929, and also the original species *Epicadus heterogaster* (Guérin, 1829) *and Epicadus rubripes* Mello-Leitão, 1924 were recently revised, thus, they were not described in the present study. After the cladistics analysis, *Epicadus* now comprises 9 species.

On the the crab spider genus *Epicadus* Simon, 1895: cladistics analysis and taxonomic review supports a synonymy for *Tobias* Simon, 1895 (Araneae, Thomisidae)

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A phylogenetic analysis followed by a morphological revision of the spider genus *Tobias* Simon, 1895 are performed. The analysis is based on a matrix with 29 terminal taxa (7 in ingroup and 22 in outgroup) scored for 87 morphological characters. The implied weighting analysis resulted in one most parcimonious tree with 303 steps obtained in six distortion groups, which support that *Tobias* is paraphyletic with *Epicadus* Simon, 1895 and considered its junior synonym. *Onocolus* Simon, 1895 emerge as the sister group of *Epicadus*. *Epicadus pulcher* Mello-Leitão, 1929 **comb. nov.** is considered senior synonym of *Epicadus epicadoides* Mello-Leitão **comb. nov.**, 1944 and *Epicadus regius* Birabén, 1955 **comb. nov.**, *Epicadus granulatus* Banks, 1909 is proposed as senior synonym of *Epicadus inermis* Mello-Leitão, 1929 **comb. nov.**, *Epicadus camelinus* (O. Pickard-Cambridge, 1869) **comb. nov.** is considered senior synonym of *Epicadus martinezi* Birabén, 1955 **comb. nov.** and *Epicadus trituberculatus* (Taczanowski, 1872) **comb. nov.** is considered senior synonym of *Epicadus paraguayensis* Mello-Leitão, 1929 **comb. nov.** and *Epicadus planus* Mello-Leitão, 1932. New distribution records and redescriptions are provided and the above species, both with *Epicadus caudatus* Mello-Leitão **comb. nov.**, 1929, *Epicadus pustulosus* Mello-Leitão, 1929 **comb. nov.**, *Epicadus heterogaster* (Guérin, 1829) and *Epicadus rubripes* Mello-Leitão, 1929 form *Epicadus*, which now on comprises eleven species.

ADDITIONAL KEYWORDS: *Epicadus* – Neotropical – phylogeny – taxonomy – Stephanopinae

INTRODUCTION

Thomisidae Sundevall, 1833 is the seventh largest family of spiders, currently comprising 175 genera and 2.155 species (World Spider Catalog, 2015). Thomisids are worldwide distributed, with most of their representatives occurring in tropical and subtropical regions (World Spider Catalog, 2015). These spiders are diurnal ambush-hunters and do not build webs. Some species of the genera *Amyciaea* Simon, 1885, *Aphantochilus* O.P.-Cambridge, 1870 and *Bucranium* O.P.-Cambridge 1881 are ant-mimic. Other species change the color of the body in order to camouflage themselves in flowers or leafs, as *Epicadus heterogaster* Guérin 1829 (Comstock, 1948; Foelix, 2010; Heiling, 2003; Silva-Moreira & Machado, 2016).

Thomisids also are known as "crab spiders" due their laterigrad legs and by the way they move at the vegetation (Dippenaar-Schoeman & Jocqué, 1997). The legs I and II in Thomisidae are usually larger and stronger than legs III and IV, being the tibiae and metatarsi ventrally armed with strong macrosetae (Mello-Leitão, 1929; Dippenaar-Schoeman & Jocqué, 1997; Foelix, 2010). Thomisidae members also present a short and convex carapace, conical chelicerae and four pairs of eyes arranged in two heterogeneous curved rows, being the lateral eyes usually larger than the median ones and located on tubercles (Foelix, 2010; Mello-Leitão, 1929). The sexual dimorphism is common in the family, in which males are generally smaller than females (Comstock, 1948; Dippenaar-Schoeman & Jocqué, 1997).

Since the proposition of Thomisidae, several authors have discussed the aspects related to its systematic (Simon, 1895; Roewer, 1954; Ono, 1988, Benjamin *et al.* 2008; Benjamin, 2011, Teixeira *et al.* 2014). The classifications originally made by Simon (1895) were adapted by Ono (1988), who discussed about the relation between the subfamilies of Thomisidae. Ono (1988) proposed a dendrogram presenting possible “synapomorphies” for Thomisidae subfamilies and its relations. Seven subfamilies were recognized by Ono (1988): Aphantochilinae, Bominae, Dietinae, Stephanopinae, Stiphropodinae, Strophiinae and Thomisinae. After that, the last study on intra-family relations in Thomisidae were performed by Teixeira *et al.* (2014), who synonymize Strophiinae to Aphantochilinae. Stephanopinae was considered the basal group in Thomisidae due to the presence of cheliceral teeth (Ono, 1988), comprising spiders usually characterized by the parallel endites, short and truncated labium, robust anterior legs armed with ventral macrosetae at tibiae and metatarsi and by the PME well developed, generally larger than the PLE (Mello-Leitão, 1929; Ono, 1988). Although these characteristics group most of the current members of the Stephanopinae, recently Benjamin et al. (2008) and Benjamin (2011), proposed respectively a molecular and a morphological phylogeny for Thomisidae. In both studies this subfamily was not recovered as a monophyletic group. The presence of cheliceral teeth, a character which was thought to be synapomorphic/diagnostic for these group (Ono, 1988; Wunderlich, 2004), in fact seem to be a plesiomorphy (Benjamin, 2011). Benjamin (2011) also highlights that many genera of Stephanopinae need to be reviewed, especially those of Australia, New Zealand and the New World.

In the Neotropics, many species of Stephanopinae were described by Simon (1895) and Mello-Leitão (1929). Since then, taxonomic revisions on this group were performed by Lise (1973, 1979 a, 1979 b, 1980 a, 1980 b), 1981, 2005), Bonaldo and Lise (2001) and Benjamin (2013). However, most of the abovementioned works focused on the genus *Onocolus* Simon, 1895, meanwhile other close genus proposed by Simon (1895) still with their original descriptions and diagnosis. There is at least five genera that are believed to be close related in Stephanopinae, whose boundaries are extremely obscure: *Tobias* Simon 1895, *Epicadus* Simon, 1895 *Epicadinus* Simon 1895, *Onocolus* Simon 1895 and *Rejanellus* Lise 2005. Lise (2005) and Silva-Moreira & Machado (2016) made brief comments about this issue and evinced the need to undertake a phylogenetic analysis on this group. The boundaries that distinguishes those genera are still blurred and their diagnosis/ description are very poor and lacking of good distinctive characters.

Tobias Simon, 1895 was proposed to include the species *Stephanopsis camelina* O. Pickard-Cambridge, 1869 (designated as type-species), *Thomisus cornutus* Taczanowski, 1872, *T. quinquetuberculatus* Taczanowski, 1872 and *T. rugosus* Taczanowski, 1872. In the original description, Simon (1895) stated that the species of *Tobias* are related to *Onocolus* Simon, 1895 by the anterior eye row strongly recurved and by the smaller median eyes, close to the lateral ones, but differs from that genus by the carapace slightly longer and higher on the posterior region, higher clypeus and elevated abdomen with lateral and median projections. The type species, *T. camelinus* (O. pickard-Cambridge, 1869) was described from Amazonas, northern Brazil, based on an adult female labelled “Amazon; Bates, 1861” and characterized by the following characters: cephalothorax short, broad and elevated on its thoracic portion; tegument covered by many small setiferous tubercles; anterior eye row very recurved with median eyes smaller than the lateral ones; posterior eye row slightly procurved with median eyes larger than the lateral eyes; ocular quadrangle longer than wide; legs I and II very robust, with two lines of setiferous tubercles on ventral surface of femura; tibiae and metatarsi with two lines of strong macrosetae; opisthosoma with five projections, posterior with bifid and round apexes. Despite these characteristics, the taxonomic status of *Tobias* always seemed uncertain due its resemblance with other Stephanopinae genera.

Most of the species of *Tobias* were described by Mello-Leitão (1929), however, its descriptions are not elucidative, usually lacking diagnostic characters or illustrations. The species are known only from their original descriptions and the diagnosis of the genus is poor, therefore, in the present paper we present a taxonomic review and also a cladistics analysis of *Tobias* to test its monophyly and relation with others close Stephanopinae genera. The synonyms, new combinations, redescriptions of the valid species and representations of its epigynum and palps in major details are hereinafter.

MATERIAL AND METHODS

Choise of terminal taxa

The data matrix includes 29 terminal taxa, seven of which are in-group species and 22 out-group species. In order to test the monophyly of *Tobias*, the choice of the out-group was based on the groups proposed by Simon (1895) and the clades by Benjamin *et al.* (2008). Of the four groups proposed by Simon (1895) for 'Stephanopsinae' (Stephanopseae, Hedaneae, Stephanopoideae and Phrynarachneae), *Tobias* was included in 'Stephanopseae' group. Therefore, all other genera of this group were included in the outgroup of this analysis, being *Onocolus*, *Epicadus*, *Epicadinus* and *Rejanellus* represented by two species each, and all other genera represented by only one species. Such outgroup choice is due to the striking morphological resemblance and blurred boundaries between the above genera and *Tobias*. Some of these genera were included in the phylogenetic analysis made by Benjamin (2008), who proposed the clades *Borboropactus*, *Epidius* and *Stephanopis* and *Thomisus*. Insofar as the first clades are composed by species of 'Stephanopseae' *sensu* Simon, 1895, *Tmarus polyandrus* Mello-Leitão, 1929 was chosen to root the tree, as *Tmarus* Simon, 1875 was considered as being part of the *Thomisus* clade (Benjamin, 2008). The following species were selected: *Tmarus polyandrus* Simon, 1875, *Stephanopoides sexmaculata* Mello-Leitão, 1929, *Synalus angustus* (L. Koch, 1876), *Stephanopis ditissima* (Nicolet, 1849), *Sidymella* *lucida* (Keyserling, 1880), *Rejanellus pallescens* (Bryant, 1940), *Rejanellus mutchleri* (Petrunkevitch, 1930), *Phrynarachne ceylonica* (O. Pickard-Cambridge, 1884), *Onocolus infelix* Mello-Leitão, 1941, *Onocolus intermedius* (Mello-Leitão, 1929), *Isala punctata* L. Koch, 1876, *Hedana ocellata* Thorell, 1890, *Epidius pallidus* (Thorell, 1890), *Epicadus heterogaster* (Guérin, 1829), *Epicadus rubripes* Mello-Leitão, 1924, *Epicadinus trispinosus* (Taczanowski, 1872), *Epicadinus spinipes* (Blackwall, 1862), *Coenypha edwardsi* (Nicolet, 1849), *Borboropactus* sp., *Stephanopis quinquetuberculata* (Taczanowski, 1872) and *Stephanopis* sp.; ingroup: *Tobias camelinus* (O. Pickard-Cambridge, 1869), *Tobias caudatus* Mello-leitão, 1929, *Tobias inermis* Mello-Leitão, 1929, *Tobias pulcher* Mello-Leitão, 1929, *Tobias pustulosus* Mello-Leitão, 1929, *Tobias taczanowskii* Roewer, 1951 and *Tobias trituberculatus* (Taczanowski, 1872).

The examined material are deposited in Muséum National D' Histoire Naturelle, Paris (MNHN, C. Rollard), Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCTP, A.A. Lise), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ, G. Giribet and L. Liebensperger), Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ, A. B. Kury), Museu Paraense Emílio Goeldi, Belém (MPEG, A. B. Bonaldo), Museo de La Plata, La Plata (MLPA, L. A. Pereira) and Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN, R. Ott), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto-da-Rocha) and Instituto Butantan, São Paulo (IBSP, A. D. Brescovit). Photos were taken in a Multipurpose Zoom Microscope Nikon AZ100M and scanning electron microscopy was conducted with a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (CEMM) of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS). Geographic coordinates for map construction were extracted directly from labels. When necessary, the geographic coordinates were obtained on the Global Gazetteer Online (available at http://www.fallingrain.com/world/index.html).

Character survey

Some characters were adapted from Ono (1988), Benjamin (2011) and Ramírez (2014), but most of the characters are proposed in this study (See appendix 1). The analysis was based on a matrix of 87 characters (See appendix 2). In order to avoid the artificial inflation of the consistency index, all autapomorphies were previously excluded (Bryant, 1995).

The terminology used in this study follows Machado *et al.* (2015) and Silva-Moreira & Machado (2016). All measurements are in millimeters and the abbreviations related to the eyes diameter, interdistances and median ocular quadrangle follows the standard pattern used in arachnology. The left palp of males were represented in retrolateral and ventral view. The epigynum was detached from the abdomen and illustrated in ventral and dorsal view. The term "primary spermatecae" is used to designate the structures where the fertilization ducts are connected and "secondary spermatecae" to structures attached to copulatory ducts (Bonaldo, 2000).

Anatomical abbreviations: ALE, Anterior lateral eyes; AME, Anterior median eyes; CD, copulatory duct; CO copulatory opening; CV, superior curve of the copulatory duct; FD, fertilization ducts FeT, Femoral tubercles; MS Medial spire; DTA, Distal tibial apophysis; PLE, Posterior lateral eyes; PME, Posterior median eyes; RTA, Retrolateral tibial apophysis; Ps, primary spermatecae; Ss, secondary spermatheca; SPt, sensorial pits; MPP median posterior abdominal projection; ULP, upper lateral abdominal projection; LLP, lower lateral abdominal projection; LBL, longitudinal black line; TWS, thoracic white spot; TF, tegular furrow.

Parsimony analysis

The character matrix were assembled in MESQUITE 3.04 (Maddison & Maddison, 2015). All characters were treated as non-additive and discrete. We choose to refrain the use of continuous characters because of the few specimens available for many terminal taxa. Furthermore, unequivocal gaps could not been recognized between the character states (measurements) to justify the codification of continuous characters as discrete.

The Heuristic search for most parsimonious trees was carried out in TNT 1.1 (Goloboff *et al.* 2008a). Character optimization and tree editing were implemented in Winclada ver. ASADO 1.89 (Nixon, 1999 – 2004). The dataset was submitted to two different methodologies: in the first one, the characters were equally weighted and the search parameters consisted in 5.000 replications starting from a random tree, using TBR and retaining up to 20 trees per replication, subjecting the resulting trees to a new TBR turn (hold 100.000; mult 5.000; keep/ 20); in the second analysis, we use implied weighing method (Goloboff, 1993; Goloboff *et al.* 2008) following the script proposed by Mirande

(2009) (See the output in appendix 3). In the latter we set 16 distortion groups, from 50% to 90% of fit, and performed 5 hits of search using the default parameters. Branch supports for both methodologies were estimated through Bremer decay index (Bremer, 1994) and Relative Bremer support, with the values calculated after ten turns and searching for suboptimal trees with 1 to 10 steps longer than the optimal tree. Up to 100.000 suboptimal trees were retained during each turn, according to the search methodology proposed by Teixeira *et al.* (2014).

RESULTS

From all 29 species, 21 were scored for both males and females, one was scored only for the female and seven for males. The equally weighted analysis resulted in 2 most parsimonious trees and is partially resolved, showing a basal politomy between most clades (Fig. 1). The clades *Stephanopis, Thomisus* and *Epidius*, proposed by Benjamin *et al*. (2008) and Benjamin (2011), were recovered and all species of *Tobias* composed a clade with *E. heterogaster* and *E. rubripes*, showing that currently *Tobias* is paraphyletic; *Onocolus* emerged as sister group of *Epicadus* (Fig. 1).

The implied weighted analysis showed that the 16 distortion groups obtained just one most parsimonious tree, with best fit obtained in nine K values (3.804, 4.294, 4.876, 5.577, 6.439, 7.522, 8.927, 10.820 and 13.511). All those trees presented the same topology, considered as the most congruent ones (fit = 11.505, length = 294) (Fig. 2). In the outgroup relations, the genus *Stephanopis* showed to be paraphyletic, presenting two different lineages; *S. lucida* emerged as the basal species of all remaining Stephanopinae that present some type of conical projection on opisthosoma. A clade formed by *Epicadinus* + *Epicadus* + *Onocolus* showed a grouping that corroborates previous taxonomic observations, and it is supported by two non-ambiguous synapomorphies related to male genitalia (shape of the RTA and presence of DTA – chars. 77 and 78 respectively). *Epicadinus* seems to be the basal member of the clade and sister of all remaining genera. The ingroup relations shows *Tobias* emerging in paraphyly with *Epicadus*, which is considered the senior synonym and presented two different lineages: the "*pustulosus* clade", formed by *E. granulatus*, *E. pustulosus* comb. nov. and *E. caudatus* comb. nov. and the "*heterogaster* clade", comprising *E. taczanowskii* comb. nov., *E. pulcher* comb. nov., *E. trituberculatus* comb. nov., *E. camelinus* comb. nov., *E. rubripes* and *E. heterogaster.*

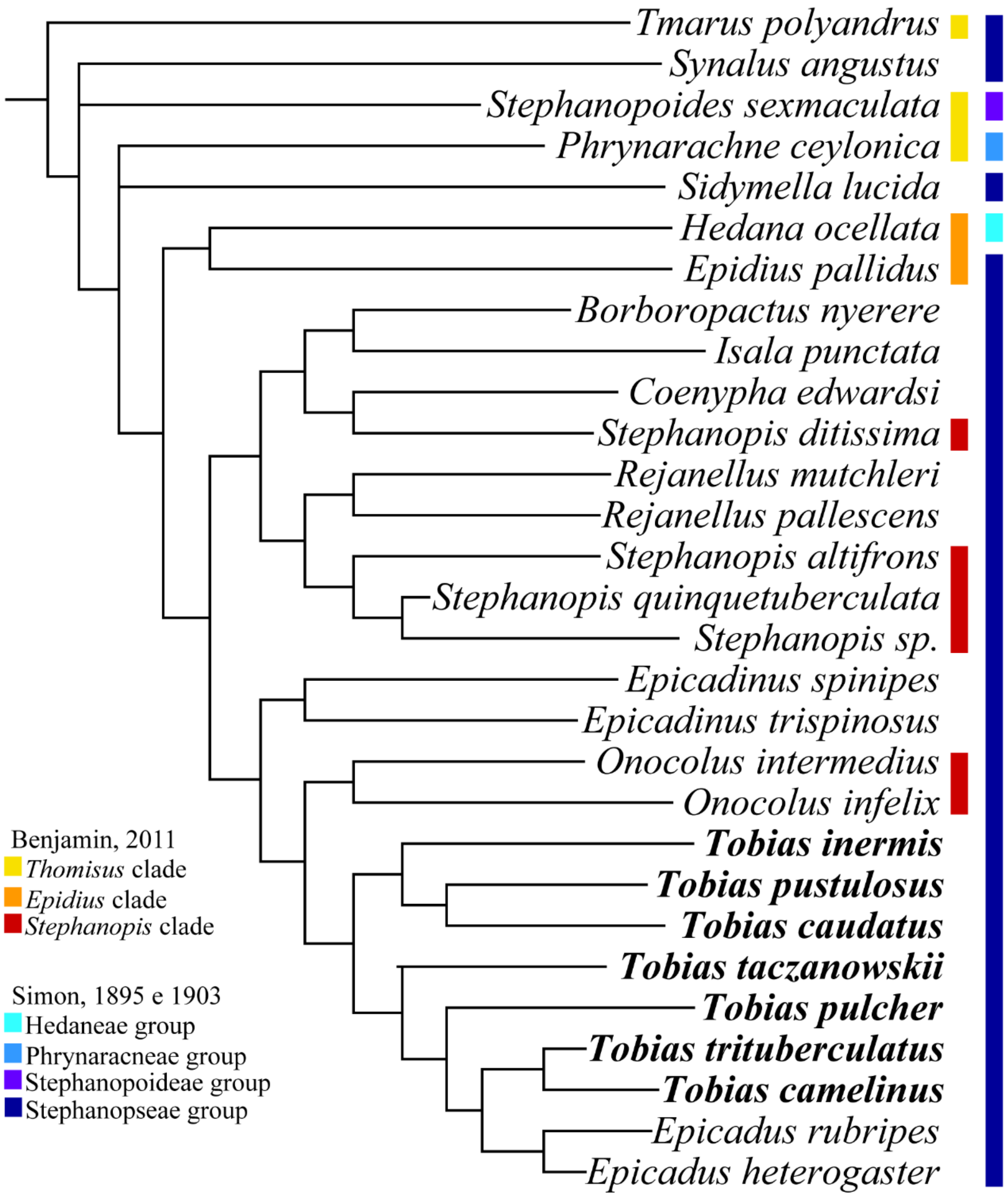

Figure 1. Strict consensus of the two most parcimonious trees under equally weighted analysis (length: 294 steps; CI=33; RI=64). Beside are the classical systematic groups proposed by Simon (1895; 1897) and the clades erected by Benjamin (2011).

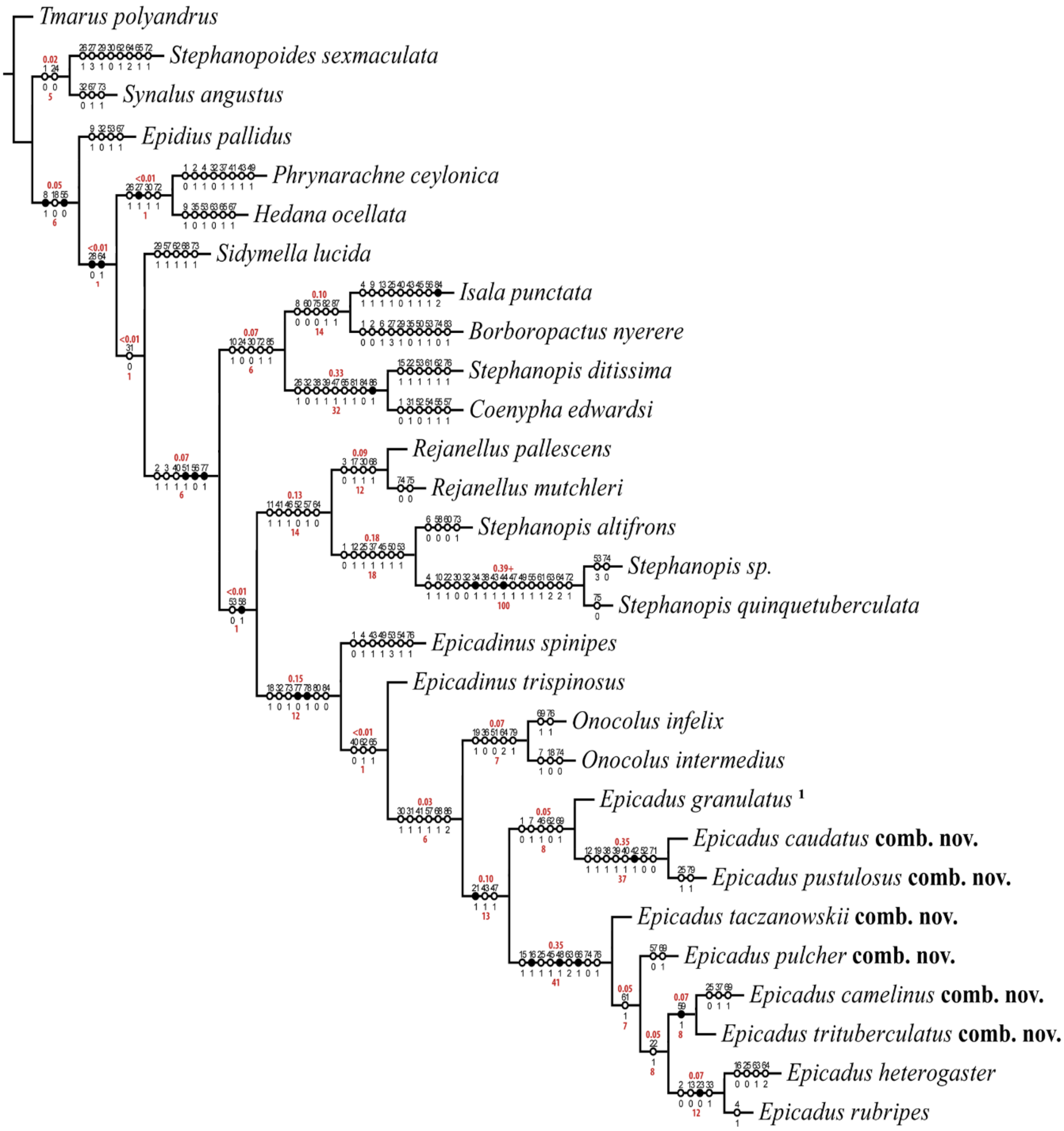

Figure 2. Most stable tree after implied weitghed analysis (K values: 3.804, 4.294, 4.876, 5.577, 6.439, 7.522, 8.927, 10.820 and 13.511; fit = 11.505, length = 294); numbers above branches indicate absolut Bremer Support values, below branches, relative Bremer Support; 1* *Epicadus granulatus* is the senior synonym of *Tobias inermis* represented in Fig.1.

DISCUSSION

Outgroup relations

The outgroup relations are partially concordant with previous hypotheses provided by Benjamin *et al*. (2008) and Benjamin (2011) by refute the groups originally proposed by Simon (1895) and supporting the hypothesis that *Borboropactus* belongs to a lineage apart from other 'Stephanopseae'. The *Stephanopis* clade, erected by Benjamin (2011), includes the genera *Onocolus*, *Stephanopi*s and *Sidymella*. However, in the present study the genus *Stephanopis* emerged as paraphyletic, presenting two different lineages. The relative Bremer index reveals a strong branch support for the relation between *C. edwardsi* and *S. ditissima*. This result, allied to the undoubtful similarities of the genitalia and coincident geographical distribution (World Spider Catalogue, 2015), indicates that possibly these two species are cogeneric. We even may infer that these tenuous bounderies are also expressed in the crossed taxonomic history between both genera, once *Coenypha* is endemic from Chile and was erected by Simon (1895) to include an older species that was once part of *Stephanopis*: *C. edwardsi* Nicolet, 1849. This latter one is related to the Chilean species *S. ditissima* by several characters related to male and female genitalia: presence of a median septum in the epigynum (char. 65), presence of a tegular ridge (char. 81), similar resting position of the embolus (char. 84) and its long and laminar form (char. 86) (which is synapomorphic for this particular clade). The other lineage of *Stephanopis* is formed by species from the Amazon and Atlantic Forest which present oval tegulum and short and filiform embolus, which is closer to what is found in the type species *S. altifrons*. These evidence suggest that probably the Chilean species of *Stephanopis* described by Nicolet, and species of *Coenypha*, may be synonyms. Futhermore, the Australian *Stephanopis* probably constitute a different genus from the Neotropical ones, however, this can only be verified under an extensive taxonomic review and phylogenetic analysis.

The genera *Onocolus* and *Epicadinus* form a clade with *Epicadus*, corroborating previous taxonomic observations, and is supported by two synapomorphies related to the male genitalia: canoe-shaped RTA (char. 77) and presence of DTA (char. 78). The presence of a long RTA sharing the same basis with the DTA in *Onocolus* was pointed by Lise (1981) in the taxonomic revision of the genus. Comparisons with the illustrations of the dorsal view of the female genitalia of some *Onocolus* species also provide the recognition of homologous structures disposed in the same ways, like the upper curve of the copulatory ducts which are enlarged and form a secondary spermatecae.

There is no revisional studies on *Epicadinus* and very few is know about this genus, however, the genitalia of both males and females present certain similarities with what is observed in *Epicadus* (Fig. 22D). Moreover, one of the diagnostic characteristics of *Epicadinus* is the presence of vertical projections in the eye mound (char. 34), a character that appear as a homoplasy shared with *E. heterogaster* (Fig. 14C) and *E. rubripes*.

Ingroup relations

The present study provides interesting results about the current taxonomic status of *Tobias* and relations between other Stephanopinae genera. *Tobias* emerged from this analysis as a paraphyletic group, being related with *Epicadus*. The clade was supported by one unambiguous synapomorphy (thoracic portion of prosoma higher than cephalic portion – char. 21; Figs. 16E, 16F). This character was proposed by Simon (1895) to diagnose the genus and distinguish it from *Onocolus* species. However, based on this character, the comparison with *Epicadus* was just recently been made by Machado *et al.* (2015). Machado *et al*. (2015) also highlighted the striking resemblance between these two genera by the shape and disposition of the abdominal projections. In a recent taxonomic review of the genus *Epicadus*, Silva-Moreira & Machado (2016) corroborates the assumptions made by Machado *et al.* (2015) mentioning that *Tobias* is the genus whose boundaries with *Epicadus* are most undefined, pointing the similarities between the descriptions of *T. albicans, T. paraguayensis* and *T. trituberculatus* with *E. planus*. Silva-Moreira & Machado (2016) also present the median spire on the thoracic region (char. 22; Fig. 17F) as part of the diagnosis for *Epicadus*, however, in the present analysys this character was coded as absent in some *Epicadus* species and appears independently in other branches, being a homoplasy shared with *Stephanopis* species.

The ingroup showed a basal dichotomy for *Epicadus*. Several morphological features related to genitalia, morphology of legs, setae shape and its microstructures, number and disposition of the abdominal tubercles and presence/absence of polychromatism (Fig. 3), give us evidence to suppose that some *Epicadus* species are adapted to be cryptic on tree barks and branches (Fig. 4A). On the other hand, some species are specialized to hunt on flowers (Fig. 4B), being capable to change their body coloration according to the substrate. The group formed by *E. caudatus* comb. nov., *E.*

pustulosus comb. nov. and *E. granulatus* is called here as the "*pustulosus* clade". This group of species present a granulated tegument (char. 2) usually with organic particles attached (char. 3) and essentially brown (char. 1; Fig. 3B, 4A), squared patellae, tibiae and metatarsi (char. 46; Fig. 18C) and vestigial abdominal tubercles (*E. granulatus*), or when conspicuous, disposed laterally, giving a flat and quadratic aspect to these spiders (*E. caudatus* and *E. pustulosus*). The strong branch support for the relation between *E. caudatus* comb. nov. and *E. pustulosus* comb. nov. shows that the diagnostic character proposed by Machado el al. (2015), as the presence of ventral blister-shaped tubercles on anterior femora (char. 42; Fig. 18D) is in fact a synapomorphy to this particular clade, while the quadratic aspect of legs appeared as a homoplasy shared by these two species with *E. granulatus* and the *Stephanopis* genus. These set of features may be related to the habit of these spiders at living camouflaged on dark subtrates like barks or tree branches (Fig. 4A). According to Lawton (1978), the surface of tree trunks exhibit a high structural complexity composed by depressions and irregularities formed by the presence of lichens and mosses. This wide variety of microhabitats provide a stable food source for many predator arthropods (such as spiders) that we can call "bark-dwellings", as studied and characterized by Wunderlich (1982). Szinetár & Horváth (2005) corroborated this results stating that the diverse bark structure provides a more balanced microclimate and a high number of hiding places, and especially for spiders, may be a landing strip for the ballooning species that use aerial dispersion. In the case of the species of the *pustulosus* clade, more than adapted to hunt on tree trunks, we can presume that the presence of yellow or orange blister-shaped tubercles on their anterior femora may be related to some type of camouflage between lichens and fungi, once these pustules resemble fruiting structures as a perithecium. Although these are for now mere speculative observations, we highlight that more records on the natural history and behavior of these spiders are needed to improve our knowledge about the group.

The other clade, here called "*heterogaster* clade", include species with lighter body coloration that, according to photographic records of specimens *in vivo*, seem to be capable to change its color or at least present a wide range of polichromatism (Fig. 3). These two different sets of characteristics and behaviors are widely documented for thomisids and may be related to two different strategies to prey on insects (Bhaskara *et al*. 2009). According to Théry & Casas (2002) and Théry *et al*. (2005) for exemple, *Thomisus onustus* Walckenaer, 1805 is capable to be cryptic to their prey and predators by merging with the background. However, some species like *Misumena vatia* (Clerck,

1757) attract their prey by high chromatic and UV contrast (Greco & Kevan, 1994). Therefore, both the *pustulosus* and *heterogaster* clades seems to adopt the first strategy, while the second strategy is probably adopted just by the *heterogaster* clade (Fig. 4).

The "*heterogaster* clade" is supported by three unambiguous synapomorphies: presence of a reverse V-shaped mark on the clypeus (char. 16; Fig.15B) and presence of a tibial gutter on legs I and II (char. 48; 21E). The third synapomorphy is the presence of an incomplete median septum on the epigynal plate (char. 66), a character proposed by Silva-Moreira & Machado (2016) to diagnose the genitalia of all females of *Epicadus*. However, in the present study this character was scored as absent for all *pustulosus* clade and *E. pulcher*. From *E. taczanowskii* to *E. heterogaster,* also can observed a gradual increase in the number of abdominal projections (chars. 58, 60 and 61), as well its disposition, which become more vertical from the basal species to the more derivate ones. Once many crab spiders are ambush predators on flowers (Lovell, 1915; Chittka, 2001; Bhaskara *et al*. 2009; Peixoto *et al*. 2012), such modifications on the opisthosoma may possibly be related to some extreme type of mimicry of floral parts as stamens, carpels or petals.

The lack of resolution for some clades in the equally weighted analysis may be influenced by a set of missing characters, which emerges as homoplasies, therefore we chose to perform the implied weighting method in order to allow that other characters explain the relations between taxa. The relatively weak branch supports should be related to the constant state reversals and shared characters, even so, our cladistic analysis allied to all taxonomic data, corroborate classical inferences about the proximity of *Onocolus* and *Epicadus* and provides evidence that justify a new synonymy for the genus *Tobias*. Although the existence of remarkable morphological differences between *E. caudatus* comb. nov. and *E. pustulosus* comb. nov. in relation to the other *Epicadus* species, such as the quadratic aspect of legs, presence of pustular setiferous tubercles on femora I and II, dark body coloration, shape and disposition of the abdominal projections, the males of these species present the same palpi characteristics found in another males of the genus (discoid tegulum, embolus filiform and elongated and canoe-shaped RTA fused to DTA). The external genitalia of females of *E. caudatus* comb. nov. and *E. pustulosus* comb. nov. differs a little from the standard pattern found in epigynum of other species of the genus, which presents elevated lateral folds forming an incomplete median septum on a downgraded median filed, however, in dorsal view, the CD conformation and shape of spermatechae shows the close relation between all those species. The internal genitalia of

E. pustulosus comb. nov., for example, is very similar to those of *E. heterogaster*, however, when we look the position of the secondary spermatecae, it seems to be suffered a twist on the upper curve of the CD (Fig. 22F); the dorsal view of the epigynum of *E. granulatus* resemble those of *E. camelinus* comb. nov., with reduced secondary spermatechae (Fig. 6B). To avoid a splitting taxonomic act that would be based simply on the body coloration pattern and shape of the opisthosoma, we decided to keep *E. granulatus*, *E. caudatus* comb. nov. and *E. pustulosus* comb. nov. in *Epicadus* based on the conformation of the prosoma of the individuals, with thoracic portion higher than cephalic area (char. 21) and by the similarities found in male and female genitalia.

Figure 3. *Epicadus trituberculatus* (A), *Epicadus rubripes* (B, C) and *Epicadus taczanowskii* (D, E), representing the polychromatism observed in females of the genus. Photo credit: Edelcio Muscat (A), Enio Branco (B), Almir Cândido de Almeida (C), César Favacho (D) and Nicky Bay (E).

Figure 4. *Epicadus caudatus* (A) and *Epicadus heterogaster* (B) representing the behavior and characteristic hunting sites of the representatives of the *pustulosus* and *heterogaster* clades. Photo credit: Alfredo Colón Archilla (A) and Maxwel Rocha (B).

TAXONOMY

GENUS EPICADUS SIMON, 1895

Epicadus Simon, 1895: 1052, figure 1085; *Epicadus* O. Pickard-Cambridge, 1900: 160, figure 34; *Epicadus* Vellard, 1924: 9, figure 4; *Epicadus* Mello-Leitão, 1929: 94; *Epicadus* Silva-Moreira & Machado (2016); *Tobias* Simon, 1895: 105; *Tobias* Simon, 1895: 1053; *Tobias* O. Pickard-Cambridge, 1900: 161, figures 37, 38; *Tobias* Mello-Leitão, 1929: 80-93, figures 183-195; *Tobias* Mello-Leitão, 1944: 11; *Tobias* Roewer, 1951: 448; *Tobias* Birabén, 1955: 73-75, figures 1-8; *Tobias* Machado, Teixeira & Lise, 2015: 566-573, figures 1-24 syn. nov.

Type species: *Epicadus heterogaster* (Guérin-Méneville, 1829)

Updated diagnosis: Epicadus is related to *Onocolus* and *Epicadinus* by the shape of male genitalia but differs from these genera and from other Neotropical Stephanopinae by the prosoma elevated on the thoracic portion, presence of dorsal depressions on tibiae that are connected to sensorial pits formed by a group of thricobothria surrounded by many duster-shaped setae and by the epigynal plate with concave posterior edges, forming a pair of "C-shaped" structures that join in the middle to form a remarkable median septum.

Diagnosis and description: Silva-Moreira & Machado, 2016
Distribution: Silva-Moreira & Machado, 2016

EPICADUS CAMELINUS SIMON, 1895 COMB. NOV.

(FIGS 5 – 6)

Stephanopis camelina O. Pickard-Cambridge, 1869: 64, figures 44, 45, 46, 47, 48, 49; (female holotype designated by monotypy, Amazonas, Brazil, deposited in OUMNH labelled "Amazon; Bates 1861", presumed lost);
Tobias camelinus: Simon, 1895: 1053 comb. nov.;
Tobias martinezi Birabén, 1955: 74, figures 1, 2, 3, 4 (female holotype by monotypy, Buena Vista, Santa Cruz, Bolivia, A. Martínez leg., deposited on MLP 0400, examined) syn. nov.

Material examined: BOLIVIA, *Santa Cruz* (Buenavista), 1 f, II.1950, A. Martínez leg., [-17.4588, -63.6591], (MLP 0400); BRAZIL, *Amazonas*, 4 m, 5 f, [-3.4168, -65.8560], (MNHN 2617); *Acre* (Senador Guiomard), 1 f, XI.2010, G.H.F. Azevedo & A.J. Santos leg., [-10.0718, -67.6238], (UFMG 11007); *Paraná* (Santa Helena, Refúgio Biológico Bela Vista), 1 f, 12-16.XI.1991, A.B. Bonaldo leg., [-25.4509, -54.5541], (MCN 21767).

Diagnosis: Females of *E. camelinus* comb. nov. resemble those of *E. trituberculatus* comb. nov. by the shape and disposition of abdominal projections, but can be distinguished by large brown stains on prosoma and femora I and by the V-shaped mark on patellae I (Figs 5A, 5E, 6E). The epigynum in ventral view is also very similar to other species of the genera (especially with *E. trituberculatus* comb. nov. and *E. taczanowskii* comb. nov.) but differs by the straight lateral folds delimiting a deeper median field and by the reduced secondary spermatecae (Fig. 6A, 6B). Males of *E. camelinus* comb. nov. are very similar to those of *E. taczanowskii* comb. nov., with even the tegular furrow laying at the same position (ten o'clock) (Fig. 6C), however, it can be distinguished by the dark pigmentation on the sides of prosoma and clypeus, shorter RTA and curved DTA.

Description: Female. Anterior eye row strongly recurved, posterior slightly procurve, almost straight. Prosoma as long as wide, MS and TWS present, LBL extends longitudinally till the PME (Fig. 5A, 5C, 5E). Clypeus wide, with a black upside down V-shaped mark and lateral margins projected forward (Fig. 5B). Chelicerae, sternum, endites, and labium yellow. Opisthosoma brown with black knobs and five projections faced backward (Fig. 5A, 5E). MPP larger than lateral ones, distally enlarged, ending in two roundish tips. In posterior view, between the dorsolateral and ventrolateral projections, there is a black triangular taint. Anterior border of opisthosoma strongly concave. Femora II have black spots on prolateral surface, one on median and other on distal region. Legs I and II with a median keel extending through the entire patella till the tarsal joint; anterior tibiae present a dorsal naked gutter connected to the sensorial pit. Femora I and II present two ventral lines of setiferous tubercles. Tarsal claws curved and pectinated with teeth restricted to basal portion. Epigynum presents an incomplete median septum, secondary spermatechae reduced, primary spermatechae dark-brown, globular (Fig. 6B). Posterior handles of copulatory ducts long (exceeding the length of primary spermatechae).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.14, PME 0.10, PLE 0.08, AME-AME 0.26, AME-ALE 0.12, PME-PME 0.36, PME-PLE 0.18; MOQ length 0.58, MOQ posterior width 0.58, MOQ anterior width 0.56; leg formula: 1-2-4-3: leg I – femur 3.50/ patella 2.00/ tibiae 2.35/ metatarsus 1.75/ tarsus 1.40/ total 11.00; II –

3.50/ 2.00/ 2.30/ 1.60/ 1.40/ 10.80; III – 1.70/ 1.15/ 1.20/ 1.40/ 0.60/ 6.05; IV – 1.90/ 1.05/ 1.50/ 1.35/ 0.60/6.40. Total body length 7.75; prosoma 3.75 length, 3.75 wide; opisthosoma length 4.00; clypeus 0.50 height; sternum 1.68 length, 1.16 width; endites 1.08 length, 0.50 width; labium 0.66 length, 0.60 width.

Male. Eye arrangement as in females, ALE on discrete ocular mounds, prosoma granulated, orange with a longitudinal brown line on the thoracic region and darker taints on the sides (Fig. 5C). Sternum orange with brown borders, labium and endites dark-brown. Clypeus differing from the rest of Prosoma in color (Fig. 5D). Opisthosoma yellow with tiny darker scales. Legs coloration: femora yellow with brown stains, patellae yellow, tibiae, metatarsi and tarsi brown. Palpi with discoid tegulum, RTA elongated and canoe-shaped. DTA acute, very curved, pointing backward and fused to RTA (Fig. 6D).

Measurements: eyes diameters and eyes interdistances: AME 0.07, ALE 0.09, PME 0.06, PLE 0.06, AME-AME 0.12, AME-ALE 0.10, PME-PME 0.22, PME-PLE 0.10; MOQ length 0.34, MOQ posterior width 0.28, MOQ anterior width 0.27; leg formula: 1-2-4-3: leg I – femur 1.40/ patella 0,.60/ tibiae 0.86/ metatarsus 0.68/ tarsus 0.48/ total 4.02; II – 1.34/ 0.66/ 0.82/ 0.64/ 0.50/ 3.96; III – 0.82/ 0.40/ 0.52/ 0.40/ 0.28/ 2.42; IV – 0.70/ 0.38/ 0.58/ 0.52/ 0.34/2.52. Total body length 3.22; prosoma 1.59 length, 1.47 wide; opisthosoma length 1.63; clypeus 0.28 height; sternum 0.72 length, 0.70 width; endites 0.34 length, 0.20 width; labium 0.22 length, 0.28 width.

Distribution: Bolivia (Santa Cruz) and Brazil (Acre, Amazonas and Paraná) (Fig. 13).

Variation: Females may present the dorsal area of the opisthosoma predominantly yellow with black triangular spots only between the upper and lower lateral projections (Fig. 5A) or entirely dark-brown (Fig. 5E).

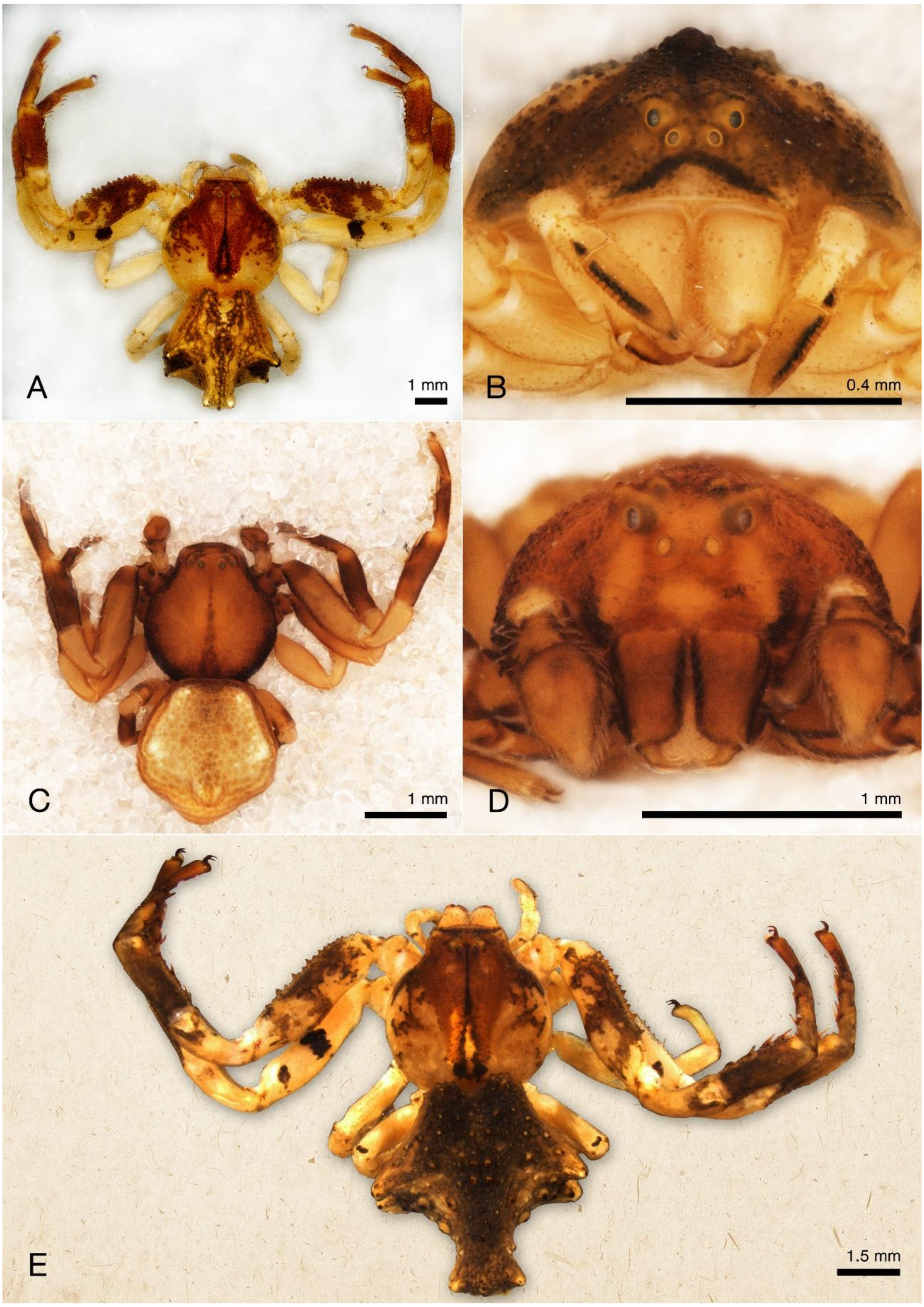

Figure 5. *Epicadus camelinus* comb. nov.: female habitus (A) and front (B) (UFMG 11007); male habitus (C) and front (D) (MNHN 2617); female variation (E) (MLP 400).

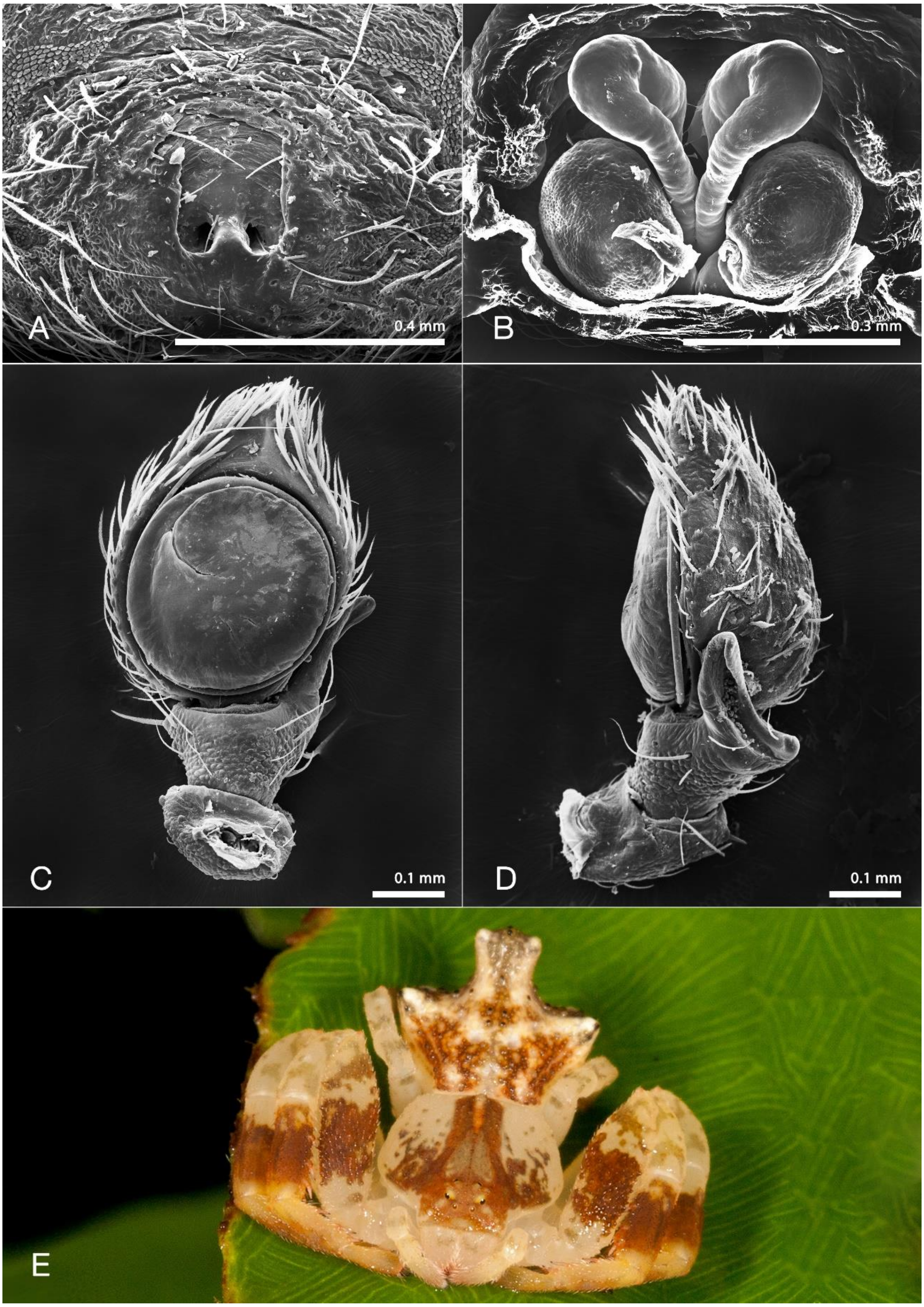

Figure 6. *Epicadus camelinus* comb. nov.: ventral view of epigynum (A) (UFMG 11007); dorsal view of epigynum (B) (UFMG 11007); ventral view of male palpus (C) (MNHN 2617); retrolateral view of the male palpus (D) (MNHN 2617); female *in vivo* (E). Photo credit: Karl Kroeker (E).

EPICADUS CAUDATUS MELLO-LEITÃO, 1929 COMB. NOV

Diagnosis and description: See Machado *et al.* (2015)

Distribution: See Machado *et al.* (2015)

Variation: See Machado *et al.* (2015)

EPICADUS GRANULATUS BANKS, 1909

(FIG 7)

Epicadus granulatus Banks, 1909: 214, figure 25, (female holotype designated by monotypy, Surubres, Costa Rica, [9.5987, -84.3020], N. Banks leg., deposited in MCZ 21488, examined);

Tobias inermis Mello-Leitão, 1929: 84, figures 177, 178, (6 female syntypes from Içá, Amazonas; Pará, Brazil; Tarapoto, Peru, deposited in MNHN 3403, examined) syn. nov.

Material examined: Only the type material.

Diagnosis: Females of *E. granulatus* are related to those of *E. caudatus* comb. nov. and *E. pustulosus* comb. nov. by the straight anterior border of opisthosoma and quadratic aspect of legs, and to *E. camelinus* comb. nov. by the curvature of copulatory ducts, shape and size of the spermatecae. However it can be easily recognized by lighter body coloration, round opisthosoma and by the transversal stains on femora I and II with leg segments getting gradually darker from the patellae to tarsi. The epigynum is also distinguished from those of other species by the elevated median field and large septum, resembling a shape of a pig snout in ventral view (Fig. 7C).

Description: Female. Anterior eye row recurved and posterior procurve. Prosoma totally orange, without dark stripes or whitish stains, furnished with several granules distributed randomly. Thoracic medial spire discrete, sometimes absent. Chelicerae with needle-shaped setae, orange. Sternum, endites and labium orange. Opisthosoma with gnarled surface, predominantly yellow with dorsal black streaks (7A, 7E); three abdominal projections, median posterior bigger than lateral ones, rounded and lateral ones very reduced. Femora I and II present same kind of granules present on prosoma, tibiae I and II with two naked gutters connected to sensorial pits. Tarsal claws curved, pectinated and unequals (mesial claw presents more than twice the number of teeth than the ectal claw).

Measurements: eyes diameters and eyes interdistances: AME 0.13, ALE 0.16, PME 0.13, PLE 0.10, AME-AME 0.54, AME-ALE 0.20, PME-PME 0.72, PME-PLE 0.18; MOQ length 0.75, MOQ posterior width 0.76, MOQ anterior width 0.74; leg formula: 1-2-4-3: leg I – femur 5.67/ patella 3.08/ tibiae 3.50/ metatarsus 2.42/ tarsus 1.67/ total 16.34; II – 4.84/ 2.91/ 3.50/ 2.25/ 1.25/ 14.75; III – 2.75/ 1.75/ 1.75/ 1.42/ 0.84/ 8.51; IV – 3.00/ 1.58/ 2.08/ 1.67/ 0.84/ 9.17. Total body length 10.34; prosoma 5.75 length, 5.62 wide; opisthosoma length 4.58; clypeus 0.88 height; sternum 2.62 length, 2.00 width; endites 1.10 length, 0.70 width; labium 0.82 length, 0.90 width.

Distribution: Brazil (Amazonas) and Costa Rica (Surubres) (Fig. 13).

Variation: Females of *E. granulatus* may present the opisthosoma light-yellow (Figs. 7A, 7F) or light-yellow with dorsolateral black taints (Fig. 7E). The anterior femora (I and II) may be totally uniform in coloration or present three large transversal black stripes (Figs. 7A, 7E).

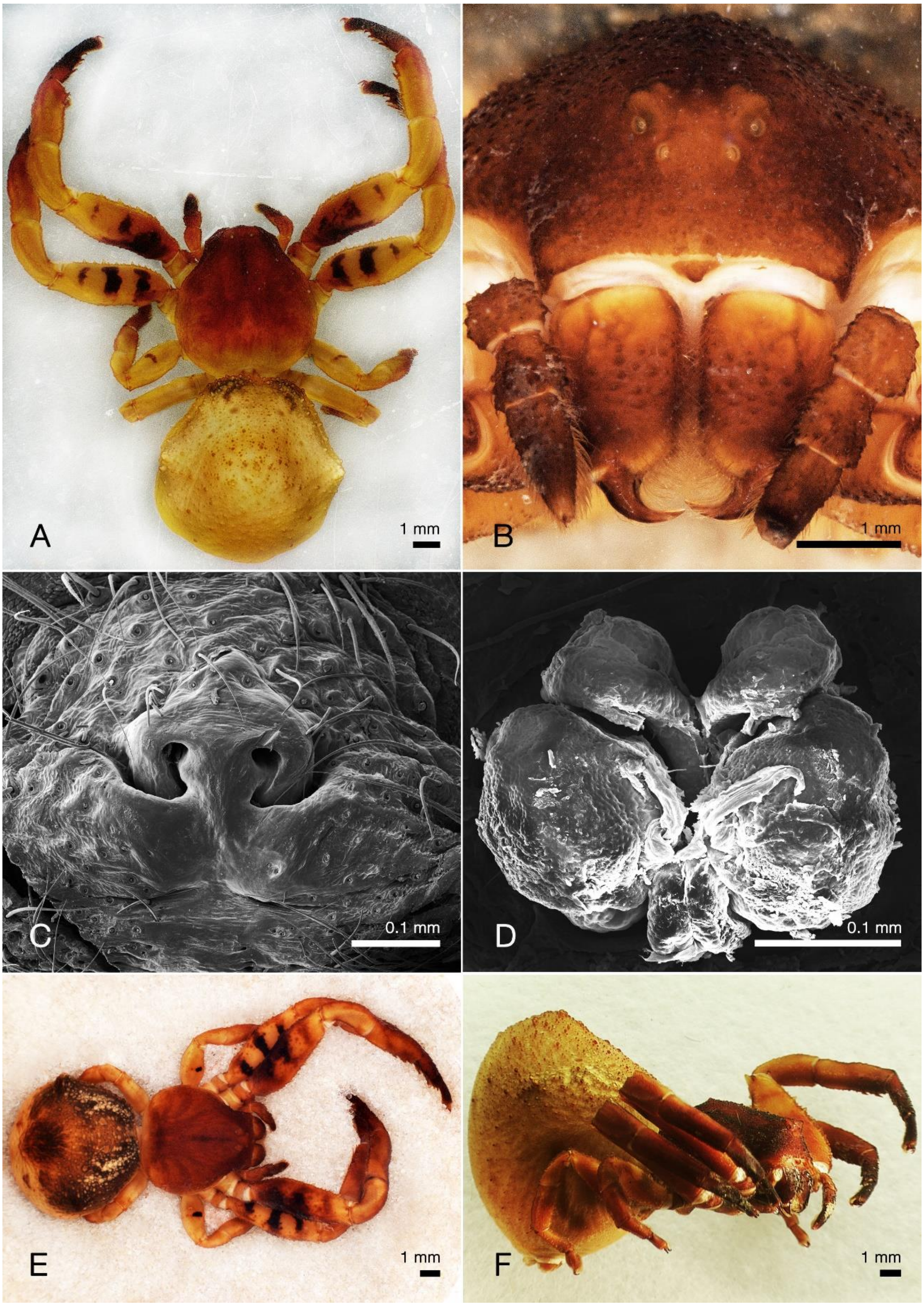

Figure 7. *Epicadus granulatus*: female habitus (A) and front (B) (MNHN 3403); ventral (C); dorsal view of epigynum (MNHN 3403); female variations (E) MNHN 3403, (F) (MCZ 21488).

EPICADUS PULCHER MELLO-LEITÃO, 1929 COMB. NOV.

(FIG 8)

Tobias pulcher Mello-Leitão, 1929: 90, figures 189, 190, (2 female syntypes from São Paulo de Olivença, Brazil [-3.6499, -69.0969], (MNHN 137, examined);

Tobias epicadoides Mello-Leitão, 1944: 11, (female holotype by monotypy, Igarapé Aurá, Pará, Brazil, deposited on MNRJ, examined) syn nov.;

Tobias regius Birabén, 1955: 74, figures 5, 6, 7, 8, (female holotype by monotypy, Buena Vista, Santa Cruz, Bolivia, deposited on MLP 0405, examined) syn. nov.

Material examined: BRAZIL: *Pará* (Belém), 1 f, C. F. Mello-leitão, [-1.4557, -48.4901], (MNRJ 0082); *Bahia* (Governador Lomanto Júnior)**,** 1 f, 28.VI.1968, CEPLAC, [-14.8101, -39.4717], (MNRJ 06861).

Diagnosis: Females of *E. pulcher* comb. nov. resemble those of *E. trituberculatus* and *E. camelinus* by the five abdominal projections, however, the median posterior projection is single tiped. *E. pulcher* also can be distinguished from other *Epicadus* species by the well-developed TWS surrounded by a dual LBL, presence of transversal black stains on anterior femora and tibiae, whitish and flat opisthosoma with strongly concave anterior border and by the five short and pointed abdominal projections, which the lower lateral pair is bigger than the upper one (Fig. 8A, 8E).

Description: Female. Anterior eye row recurved and posterior procurve. Prosoma yellow with black stains at cephalic region, TWS well developed, with three anterior tips and surrounded by a dual LBL (8A); MS absent. Chelicerae yellow with proximal black stains. Sternum, endites and labium uniformly yellow. Opisthosoma with five projections faced backward; LLP longer than others, tail-like; whitish-yellow with a median longitudinal black line and some dark punctuations randomly distributed. Clypeus projected as in *E. camelinus* comb. nov., upside down V-shaped black mark incomplete (Fig. 8B). Leg characters as in *E. camelinus* comb. nov.. Epigynum presents the simplest external design of all *Epicadus* species, with no septum, elevated lateral folds or differentiation between the median field and the rest of the epigynal plate. The copulatory ducts are short when compared to those of other representatives of the genus and the secondary pair of spermatechae is as big as the primary. The primary spermatechae are dark-brown and spherical (8D). Posterior handles of copulatory ducts short (ending at the limit of primary spermatechae length).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.14, PME 0.08, PLE 0.06, AME-AME 0.36, AME-ALE 0.20, PME-PME 0.44, PME-PLE 0.22; MOQ length 0.72, MOQ posterior width 0.68, MOQ anterior width 0.66; leg formula: 1-2-4-3: leg I – femur 4.92/ patella 2.58/ tibiae 3.05/ metatarsus 2.10/ tarsus 1.40/ total 14.05; II – 4.50/ 2.45/ 3.15/ 2.00/ 1.65/ 13.75; III – 2.25/ 1.50/ 1.50/ 1.35/ 0.65/ 7.25; IV – 2.75/ 1.44/ 1.79/ 1.75/ 0.65/ 8.38. Total body length 9.70; prosoma 4.75 length, 4.55 wide; opisthosoma length 4.95; clypeus 0.50 height; sternum 2.10 length, 1.60 width; endites 1.20 length, 0.66 width; labium 0.76 length, 0.78 width.

Distribution: Bolivia (Santa Cruz) and Brazil (Pará, Amazonas and Bahia) (Fig. 13).

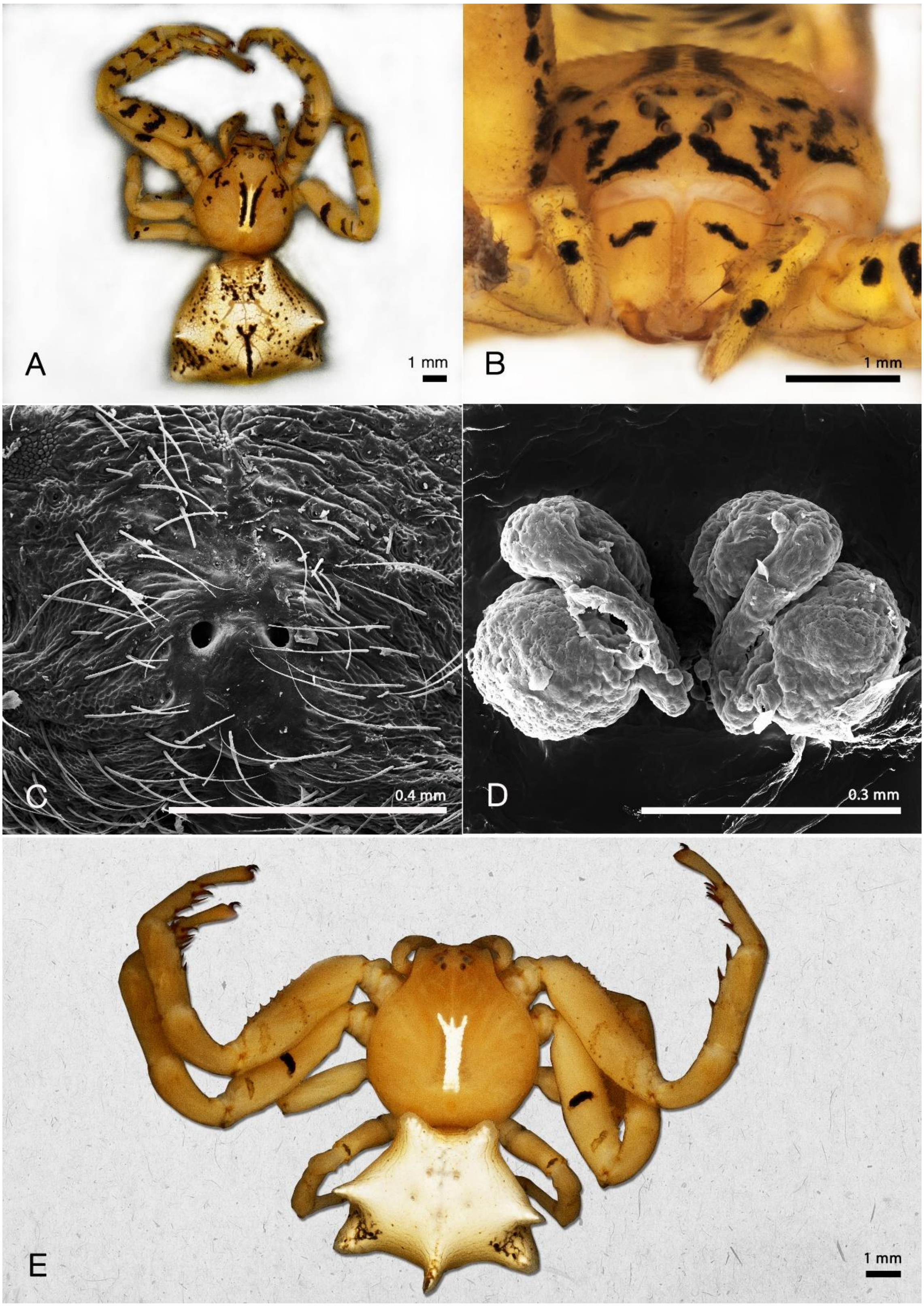

Figure 8. *Epicadus pulcher* (MNHN 137): female habitus (A) and front (B); ventral view of epigynum (C); dorsal view of epigynum (D); female variation (E).

EPICADUS PUSTULOSUS MELLO-LEITÃO, 1929 COMB. NOV.

Diagnosis and description: See Machado *et al.* (2015)

Distribution: See Machado *et al.* (2015)

Variation: See Machado *et al.* (2015)

EPICADUS TACZANOWSKII (ROEWER, 1951) COMB. NOV.

(FIGS 9 – 10)

Thomisus rugosus Taczanowskii, 1872: 95, (male holotype and four female paratypes from Cayenne, French Guiana, deposited in MZPW, presumed lost);
Stephanopis rugosa: Keyserling, 1880: 177, figure 97 comb. nov.;
Tobias rugosus: Simon, 1895: 1051 comb. nov.;
Tobias rugosus: O. Pickard-Cambridge, 1900: 161, figures 37, 38;
Tobias taczanowskii Roewer, 1951: 448 (replaced name).

Material examined: PANAMA: *Colón* (Portobelo), 3 m, 12.VIII.1936, A.M. Chickering, [9.5500, -79.6500], (MCZ); *Canal Zone* (Barro Colorado Island), 4 m, VII.1936, A.M. Chickering, [9.1521, -79.8464], (MCZ); 1 m, VI.1939, A.M. Chickering, (MCZ); 5 m, VII.1939, A.M. Chickering, (MCZ); 2 m, 1–4.VII.1950, A.M. Chickering (MCZ); 4 m, 2 f, 11.VII.1950, A.M. Chickering, (MCZ); 5 m, 1 f, 16–20.VII.1950, A.M. Chickering, (MCZ); 2 m, 23.VII.1950, A.M. Chickering, (MCZ); 1 m, 02.VII.1954, A.M. Chickering, (MCZ); 1 m, 02.VIII.1954, A.M. Chickering, (MCZ); 2 m, 15.VIII.1954, A.M. Chickering, (MCZ); 2m, 04.II.1958, A.M. Chickering, (MCZ); 1 m, 20.II.1958, A.M. Chickering, (MCZ); 1 m, 19.VII.1958, A.M. Chickering, (MCZ); BRAZIL: *Amazonas*, 2 m, 29 f, C. F. Mello-leitão, (MNHN ex. 2617); *Bahia*, 1 m, [-12.5797, -41.7007], (MNHN 18452); *Mato Grosso* (Barra do Tapirape), 1 f, 1–23.XII.1961, B. Malkin, [-10.4291, -51.2813], (AMNH); (Canarana), 1 m, 10.VI.2006, G. Dall'osto, [-13.0736, -52.3819], (MPEG 022624); 1 m, 10.VI.2006, D. F. Candiani, (MPEG 022626); 1 m, 16.VI.2006, N. F. Lo-Man-Hung, [-12.8297, -52.4577], (MPEG 022628); 1 m, 17.VI.2006, D. F. Candiani, [-12.0740, -52.3891], (MPEG 022629); *Minas Gerais* (Belo Horizonte), 1 f, 25.X.2008, I. L. F. Magalhães, [-19.8744, -43.9727], (UFMG 5852).

Diagnosis: The females of *E. taczanowskii* comb. nov. are related to those of *E. camelinus* comb. nov. and *E. trituberculatus* comb. nov. by the knobby opisthosoma and presence of a LBL on prosoma, but can be recognized by the opisthosoma with only three projections and MPP rounded and single tipped. Males of *E. taczanowskii* comb. nov. are very similar to those of *E. camelinus* comb. nov., with even the TTF emerging at the same position (ten o'clock), however can be distinguished by the serrated anterior border of opisthosoma (Fig. 9C) higher clypeus (Fig. 9D) and straight and longer DTA and RTA (10D).

Female. Anterior eye row recurved and posterior slightly procurve, almost straight. Prosoma pale yellow with dark granules aggregate on the median region; TWS and LBL extending till the PME. Thoracic medial spire absent, chelicerae pale yellow with a diagonal dark stripe. Sternum, endites and labium with same color of prosoma. Opisthosoma pale yellow with dark granules outlining its dorsal edges, an anterior pair of black stains, three abdominal projections faced backward and concave anterior border. Legs coloration resembles those of *E. pulcher* comb. nov., although, the stripes and taints are lighter. Epigynum with CO opening sideways, separated by a large and flattened median septum; median field delimited by curved lateral folds that resemble upside-down commas (10A). Secondary spermatechae very enlarged, almost the same size of primary ones (10B). Primary spermatechae dark-brown and spherical, posterior handles of copulatory ducts short.

Measurements: eyes diameters and eyes interdistances: AME 0.12, ALE 0.20, PME 0.16, PLE 0.12, AME-AME 0.29, AME-ALE 0.18, PME-PME 0.42, PME-PLE 0.17; MOQ length 0.60, MOQ posterior width 0.54, MOQ anterior width 0.52; leg formula: 1-2-4-3: leg I – femur 4.20/ patella 2.40/ tibiae 2.75/ metatarsus 1.95/ tarsus 1.40/ total 12.70; II – 3.34/ 2.25/ 2.60/ 1.95/ 1.25/ 11.39; III – 2.08/ 1.42/ 1.34/ 1.00/ 0.67/ 6.51; IV – 2.50/ 1.20/ 1.60/ 1.40/ 0.65/ 7.35. Total body length 10.67; prosoma 4.75 length, 4.50 wide; opisthosoma length 5.92; clypeus 0.50 height; sternum 2.12 length, 1.55 width; endites 1.03 length, 0.53 width; labium 0.68 length, 0.75 width.

Male. Eye arrangement as is female, ALE on discrete ocular mounds. Prosoma granulated, predominantly orange, darker at sides and median region (Fig. 20C). Thoracic medial spire and TWS absent. Sternum orange with darker borders, labium endites and chelicerae reddish-brown. Clypeus orange with two diagonal darker taints (Fig. 20D). Opisthosoma characteristics as in males of *E. camelinus* comb. nov. Legs present orange femora, tibiae, tarsi and metatarsi, while patellae are yellow. General palpi characteristics as in males of *E. camelinus* comb. nov.

Measurements: eyes diameters and eyes interdistances: AME 0.06, ALE 0.08, PME 0.07, PLE 0.04, AME-AME 0.12, AME-ALE 0.08, PME-PME 0.21, PME-PLE 0.10; MOQ length 0.28, MOQ posterior width 0.20, MOQ anterior width 0.19; leg formula: 1-2-4-3: leg I – femur 1.09/ patella 0.50/ tibiae 0.70/ metatarsus 0.50/ tarsus 0.40/ total 3.19; II – 0.92/ 0.50/ 0.68/ 0.50/ 0.40/ 3.00; III – 0.72/ 0.36/ 0.44/ 0.33/ 0.22/ 2.07; IV – 0.70/ 0.32/ 0.50/ 0.39/ 0.24/ 2.15. Total body length 2.56; prosoma 1.30 length, 1.24 wide; opisthosoma length 1.26; clypeus 0.22 height; sternum 0.63 length, 0.60 width; endites 0.32 length, 0.16 width; labium 0.18 length, 0.24 width.

Distribution: Panama (Colón) and Brazil (Amazonas, Mato Grosso and Minas Gerais) (Fig. 13).

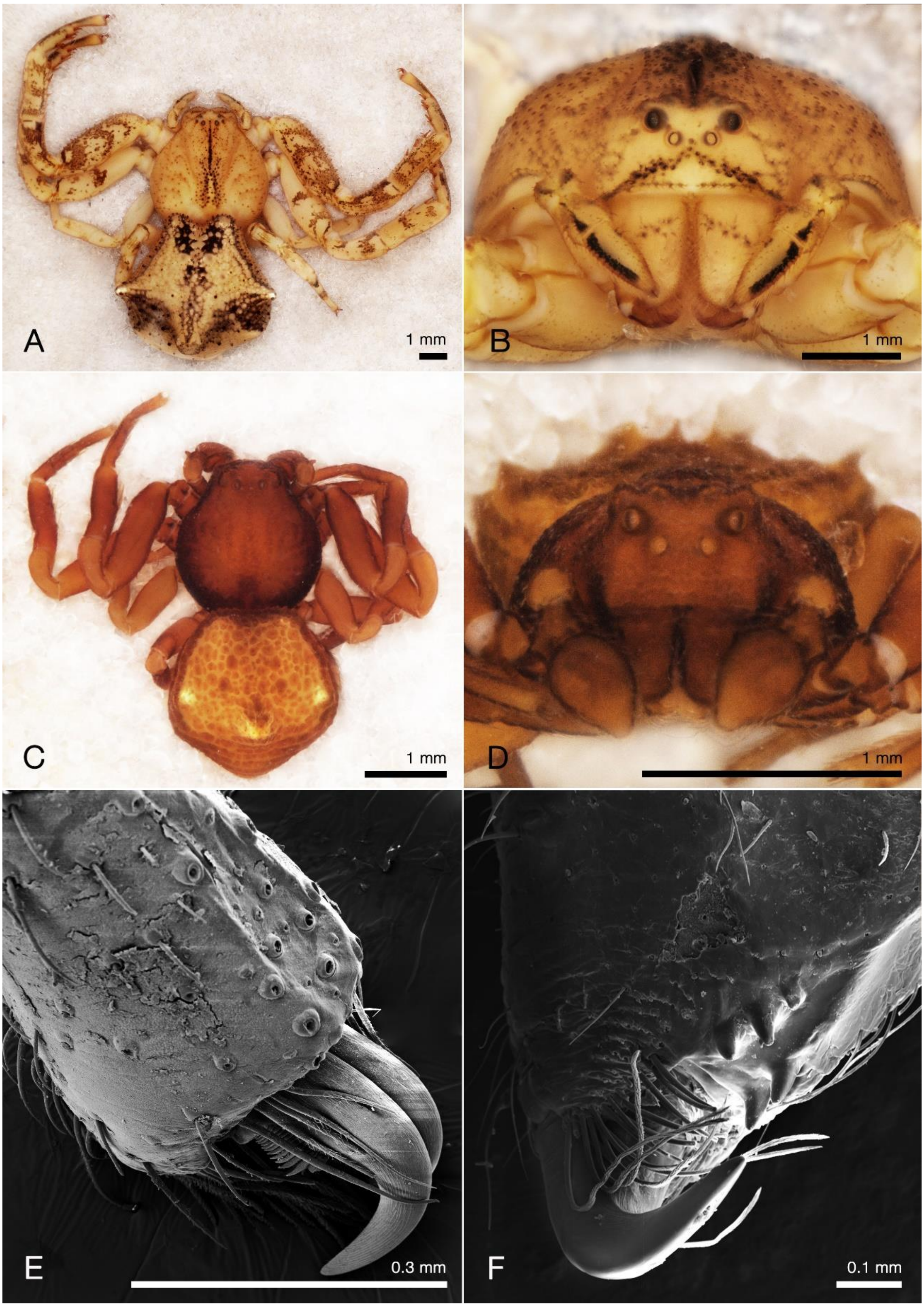

Figure 9. *Epicadus taczanowskii*: female habitus (A) and front (B) (MNHN 2617); male habitus (C) and front (D) (MPEG 22624); detail of female tarsal claws (E) and cheliceral teeth (F) (MCZ).

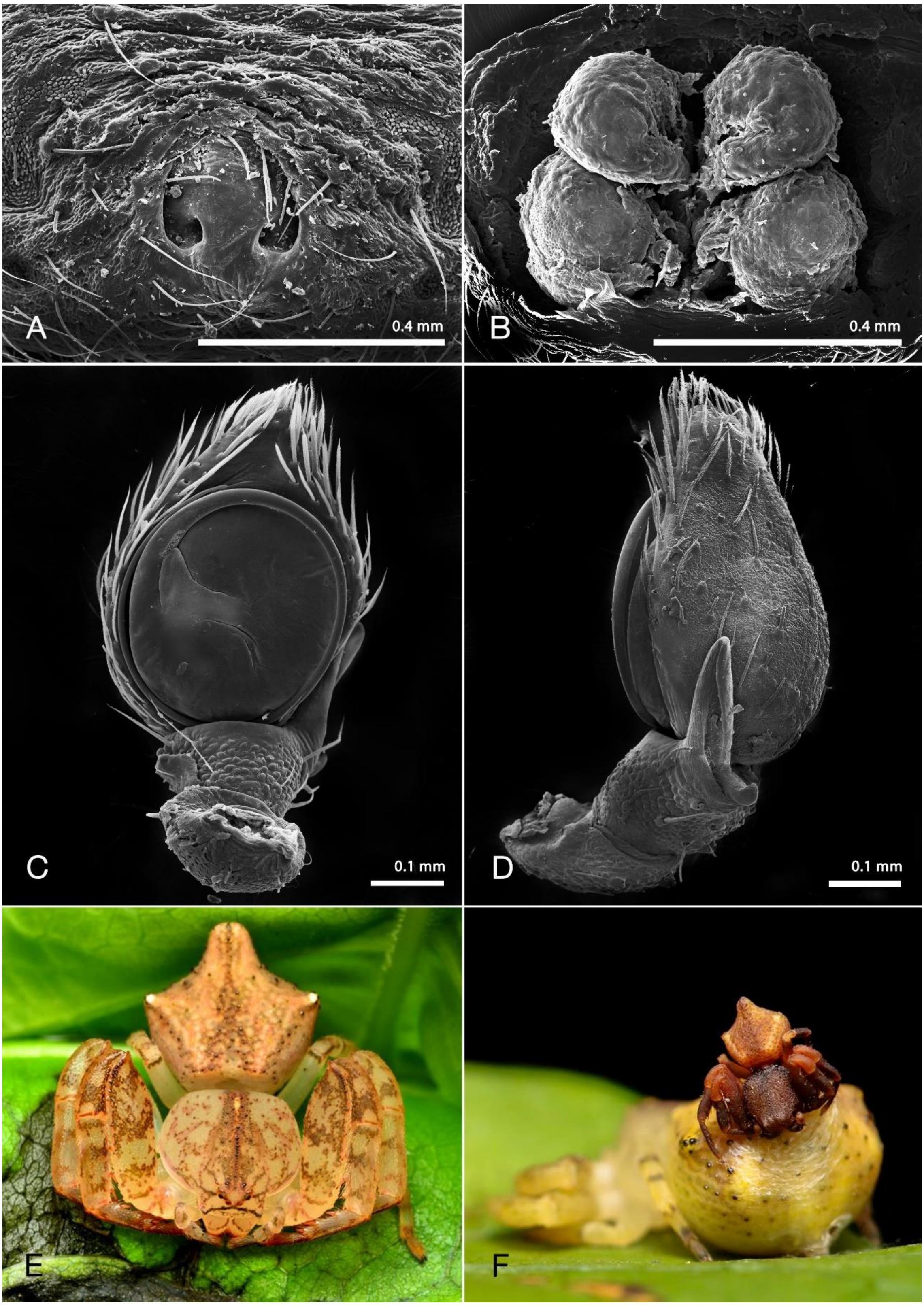

Figure 10. *Epicadus taczanowskii*: ventral (A) and dorsal view of epigynum (B) (MNHN 2617); ventral(C) and retrolateral view of the male palpus (D) (MPEG 22268); female (E) and couple (F) *in vivo*. Photo credit: Cesar Favacho (E, F).

EPICADUS TRITUBERCULATUS (TACZANOWSKII, 1872) COMB. NOV.

(FIGS 11 – 12)

Thomisus trituberculatus Taczanowski, 1872: 92, figure 7, (males and females syntypes from Cayenne, Iles du Salut, Saint Laurent du Maroni and Uassa, French Guiana, deposited on MZPW, presumed lost).

Tobias trituberculatus: Simon, 1895: 1047, figure 1029 comb. nov.;

Tobias paraguayensis Mello-Leitão, 1929: 91, figures 191, 192, 193, 194, 195 (female and 2 males, Paraguay, deposited on MNHN 8790, examined) syn. nov.

Epicadus planus Mello-Leitão, 1932: 73 (female holotype by monotypy, Ilhéus, Bahia, Brazil, deposited on MNRJ 14205, examined) syn. nov.

Material examined: BRAZIL: *Amapá* (Ilha de Maracá), 1 m, 1–14.II.1992, A. A. Lise, [3.4166, -61.6666], (MCTP 1943); *Pará* (Santarém), 1 f, 25.X.1969, EPA, [-2.4520, -54.6926], (MZUSP 11605); *Amazonas* (Manaus), 1 m, 08.I.1992, A. A. Lise, [-3.1189, -60.0215], (MCTP 2001); (Coari), 1 f, 26.IX.2004, A. B. Bonaldo, [-4.0945, -63.1446], (MPEG 022672); *Mato Grosso*, 8 m, 4 f, C. F. Mello-Leitão, (MNHN 10358); (Canarana), 1 m, 27.V.2006, D. F. Candiani, [-13.0736, -52.3819], (MPEG 022621); 1 m, 28.VIII.2006, D. F. Candiani, (MPEG 022622); 1 m, 08.VI.2006, D. F. Candiani, (MPEG 022623); 1 m, 11.VI.2006, D. F. Candiani, (MPEG 022625); 1 m, 15.VI.2006, N. F. Lo-Man-Hung, (MPEG 022627); (Chapada dos Guimarães), 4 m, 15–26.VII.1992, A. A. Lise, [-15.3582, -55.8979], (MCTP 2192); (Poconé), 1 m, 01.III.1992, A. Braul, [-16.2664, -56.6266], (MCTP 2482); *Goiás* (Goiânia), 1 m, 18.VI.1942, F. Jaime, [-16.6868, -49.2647], (MZUSP 386); Minas Gerais (Marliéria, Parque Estadual do Rio Doce), 1 f, 25.VII.2011, G.H.F. Azevedo, [-19.7162, -42.7338], (UFMG 10873); *Espirito Santo* (Linhares), 1 m, 21.IX.1942, Svans, [-19.3158, -40.1202], (MZUSP 8594); 1 m, 22.IX.1942, Svans, (MZUSP 7654); *Paraná* (Jundiaí do Sul), 1 f, 23.XII.1987, A. D. Brescovit, [-23.4703, -50.2244], (MCTP 38706); (Foz do Iguaçu), 2 m, 29.III.1993, A. B. Bonaldo, [-25.4605, -53.8177], (MCTP 4322); *Santa Catarina* (Mondaí), 1 m, 08.VIII.1998, P. P. Marques, [-27.1039, -53.4446], (MCTP 10313); *Rio Grande do Sul* (Pirapó), 1 m, 24.IV.1994, Projeto Garabi, [-28.0443, -55.2006], (MCTP 055); (São Borja), 1 f, 31.I.2012, M. Machado, [-29.0466, -56.0837], (MCTP 34653); PARAGUAY: 2 m, 1 f, C. F. Mello-Leitão, (MNHN 8790); ARGENTINA: *Misiones* (San Javier), 1 m, 22–30.X.1998, Projeto Garabi, [-27.8719, -55.1389], (MCTP 1661); 1 m, 21–30.VI.1998, Projeto Garabi, (MCTP 0567).

Diagnosis: Females of *E. trituberculatus* comb. nov. are related to those of *E. camelinus* comb. nov. by the presence of LBL on prosoma, shape and disposition of abdominal projections and three-pointed MPP, however, can be differentiated from the later by the totally yellow prosoma (with no brown stains on cephalic region) (Fig 11A, 11E, 11F). Males of *E. trituberculatus* comb. nov. also present several similarities with *E. camelinus* comb. nov. males, such as the orange prosoma as same legs coloration pattern, however, the most reliable diagnostic characteristic is the position of the TTF, which in the case of *E. trituberculatus* comb. nov. is at eight o'clock (Fig. 12C).

Description: Female. Anterior eye row strongly recurved and posterior slightly procurve. Prosoma yellow, dome-shaped, with a MS, TWS and LBL disposed exactly as in females of *E. camelinus* comb. nov. Clypeus present the upside-down V-shaped mark as in *E. camelinus* comb. nov. and irregular dark stains running through the lateral of prosoma till the ALE. Femora I yellow with large dark spots; tarsi of all legs are reddish-brown. Chelicerae yellow with discrete dark stripes, sternum, endites and labium totally yellow. Opisthosoma predominantly yellow with black knobs and a longitudinal median dark taint. Other opisthosoma and leg characteristics as in *E. camelinus* comb. nov. epigynum presents a short median septum, CO are not visible in ventral view, covered by the posterior folds of epigynal plate (Fig. 12A). Secondary spermatechae very enlarged (almost the size of primary ones) dark-brown, globular (Fig. 12B).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.12, PME 0.10, PLE 0.07, AME-AME 0.26, AME-ALE 0.16, PME-PME 0.34, PME-PLE 0.14; MOQ length 0.50, MOQ posterior width 0.42, MOQ anterior width 0.39; leg formula: 1-2-4-3: leg I – femur 3.75/ patella 1.84/ tibiae 2.70/ metatarsus 1.84/ tarsus 1.67/ total 11.80; II – 3.70/ 1.75/ 2.67/ 1.75/ 1.42/ 11.29; III – 1.84/ 1.25/ 1.34/ 1.25/ 0.75/ 6.46; IV – 2.17/ 1.21/ 1.58/ 1.34/ 0.62/ 6.92. Total body length 8.28; prosoma 4.20 length, 4.00 wide; opisthosoma length 4.08; clypeus 0.48 height; sternum 1.98 length, 1.58 width; endites 1.00 length, 0.52 width; labium 0.68 length, 0.68 width.

Male. Eye arrangement as in females, ALE on discrete ocular mounds, prosoma granulated, orange with a rectangular TWS on the thoracic region (Fig. 11C). Sternum, labium and endites characteristics as in males of *E. camelinus* comb. nov. Clypeus have the same color of the entire prosoma, with no marked taints (Fig. 11D). Opisthosoma characteristics as in males of *E. camelinus* comb. nov. Femora and patellae yellow, tibiae, metatarsi and tarsi brown. Palpi simple, with discoid tegulum, RTA very elongated and canoe-shaped. DTA acute, curved, fused and forming almost a right angle with RTA. *Measurements:* eyes diameters and eyes interdistances: AME 0.07, ALE 0.08, PME 0.06, PLE 0.04, AME-AME 0.16, AME-ALE 0.10, PME-PME 0.22, PME-PLE 0.12; MOQ length 0.30, MOQ posterior width 0.25, MOQ anterior width 0.23; leg formula: 1-2-4-3: leg I – femur 1.30/ patella 0.70/ tibiae 0.88/ metatarsus 0.64/ tarsus 0.56/ total 4.08; II – 1.28/ 0.70/ 0.88/ 0.63/ 0.58/ 4.07; III – 0.65/ 0.40/ 0.52/ 0.44/ 0.29/ 2.30; IV – 0.90/ 0.40/ 0.58/ 0.49/ 0.30/ 2.67. Total body length 3.11; prosoma 1.58 length, 1.56 wide; opisthosoma length 1.53; clypeus 0.28 height; sternum 0.63 length, 0.70 width; endites 0.40 length, 0.22 width; labium 0.24 length, 0.28 width.

Distribution: Argentina (Misiones), Brazil (Amapá, Pará, Amazonas, Mato Grosso, Goiás, Espírito Santo, Paraná, Santa Catarina e Rio Grande do Sul) and Paraguay (Fig. 13). (See also data about *E. planus* in Silva-Moreira & Machado, 2016).

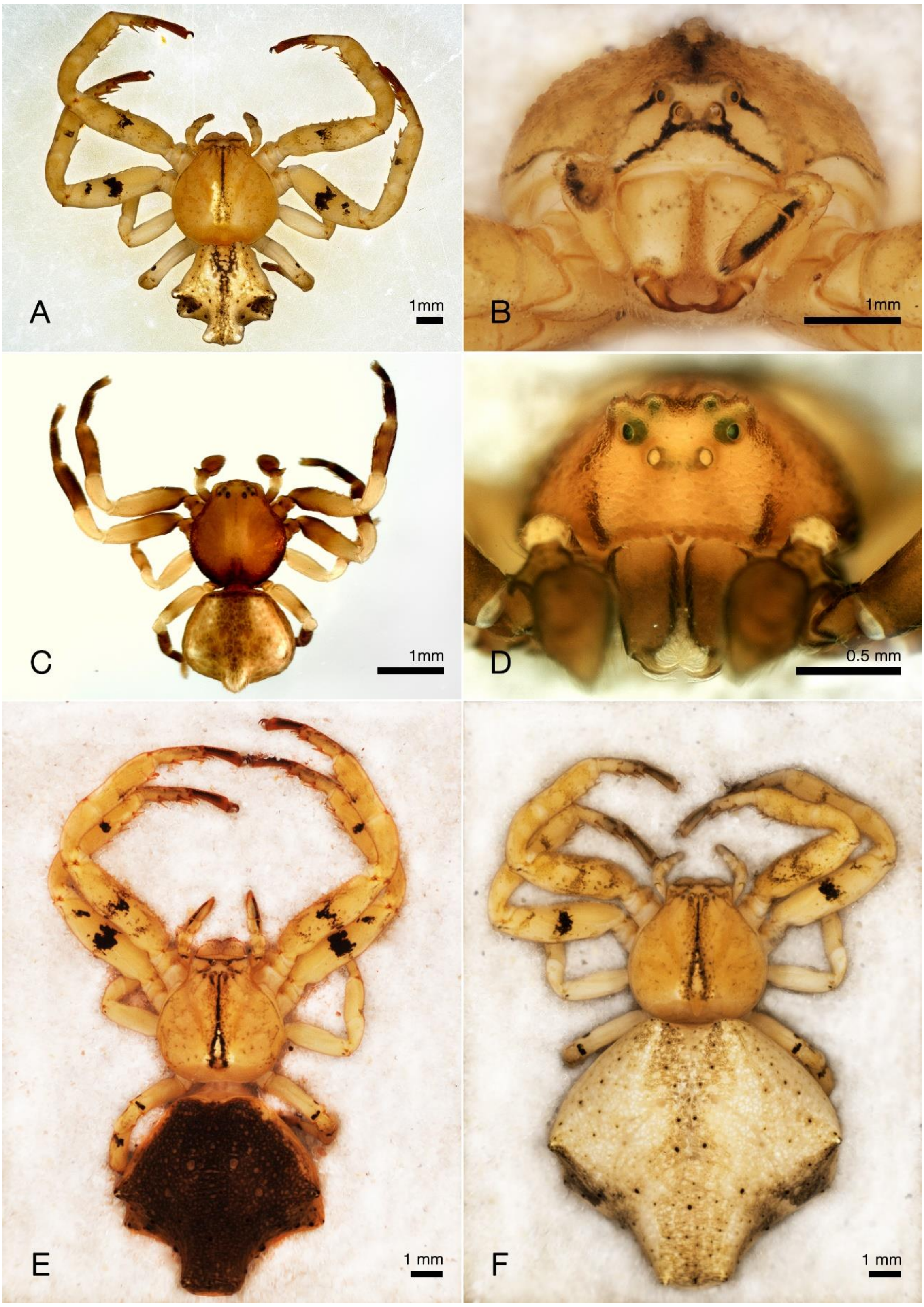

Figure 11. *Epicadus trituberculatus*: female habitus (A) and front (B) (MPEG 22662); male habitus (C) and front (MPEG 22623); female variations (E) (MCTP 34653); (F) (MCTP 38706).

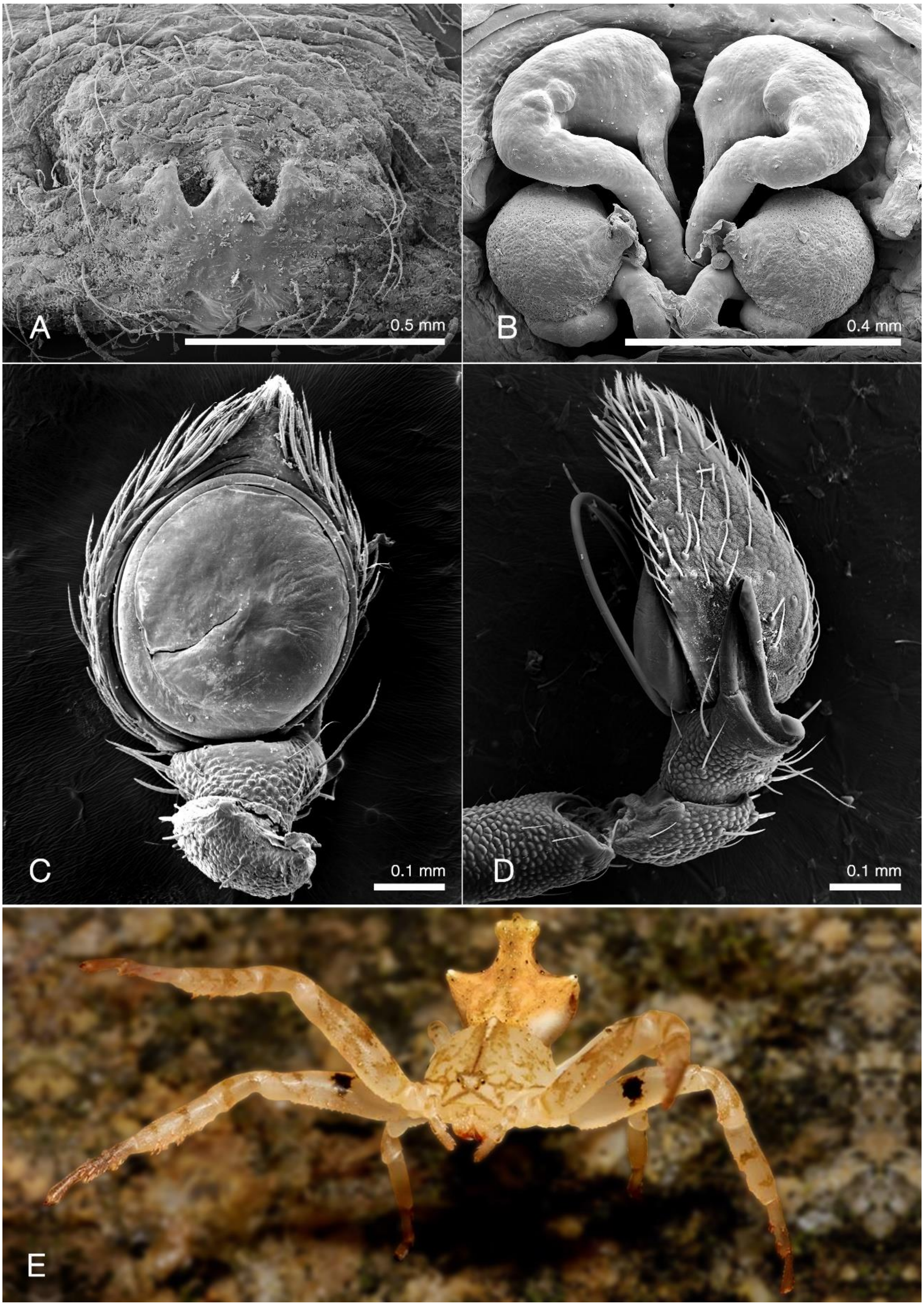

Figure 12. *Epicadus trituberculatus*: ventral (A) and dorsal view of epigynum (B) (MCTP 34653); ventral (C) and retrolateral view of the male palpus (D) (MCTP 567); female *in vivo* (E). Photo credit: Edelcio Muscat (E).

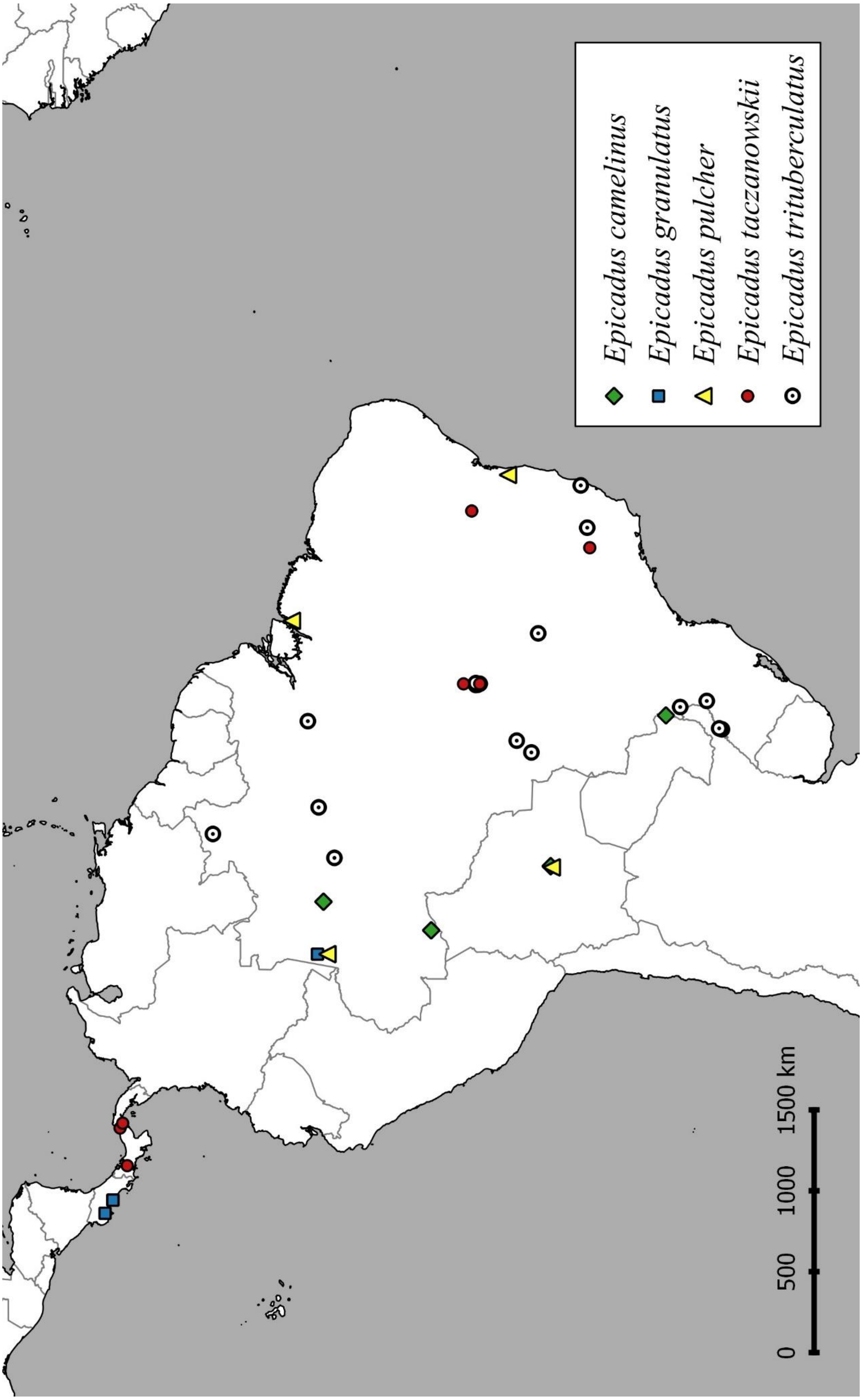

Figure 13. Geographic distribution records of the *Epicadus* species.

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APPENDIX 1: MORPHOLOGICAL CHARACTERS

Prosoma

1. Prosoma, coloration: (0) brownish red (Figs. 14B, 15D, 15E, 15F 16E, 17D); (1) yellow (Figs. 14A, 15B, 16A, 17C)

2. Prosoma, surface , texture (adapted from Benjamin, 2011: char. 63): (0) smooth (Fig. 14C); (1) granulated (Figs. 14D, 16B)

3. Prosoma, organic particles (adapted from Wunderlich, 2004): (0) absent (Fig. 14C, 14D); (1) present (Fig. 17E) – when present, the spider tegument is impregnated with soil particles or lichen, sometimes even covering some setae.

4. Prosoma, sternum, coloration: (0) uniform (Fig. 14E); (1) stained/bicolor (Fig. 14F)

5. Prosoma, sternum, setae, general shape: (0) pointed (Figs. 20A, 20C, 20D, 20F); (1) clavated (Figs. 20B, 20E)

6. Prosoma, sternum, setae, scales shape: (0) smooth (Fig. 20A); (1) plumose (Fig. 20B); (2) serrated (Fig. 20C)

7. Prosoma, sternum, surface, texture (adapted from Benjamin, 2011: char. 65): (0) smooth (Fig. 20C); (1) granulated (Fig. 20D) (bristles with conical sockets– similar to tiny tubercles or tegument papules)

8. Prosoma, sternum, anterior curvature: (0) straight; (1) concave (Fig. 15A)

9. Prosoma, sternum, posterior border, emargination between coxae IV: (0) absent (Figs. 14E, 14F); (1) present (Fig. 15A)

10. Prosoma, carapace setae, general shape: (0) pointed (Fig. 20F); (1) clavated (Fig. 20E)

11. Prosoma, carapace, setae, scales, shape: (0) smooth (Fig. 14C); (1) plumose (Fig. 16B);

12. Prosoma, carapace, setae, scales, density: (0) sparce; (1) agglomerated

13. Prosoma, dorsal view, median longitudinal band (MLB): (0) absent (Fig. 14B, 17D); (1) present (Fig. 14A, 15C, 15D)

14. Prosoma, dorsal view, MLB color: (0) black (Fig. 15C); (1) yellow (Fig. 15D)

15. Prosoma, dorsal view, thoracic portion, guanine white spot: (0) absent (Figs. 14B, 15D, 17C, 17D); (1) present (Figs. 14A, 15C)

16. Prosoma, frontal view, clypeus, reverse V-shaped mark (RVM): (0) absent (Fig. 16A); (1) present (Fig. 15B)

17. Prosoma, lateral view, clypeus slope: (0) vertical (90 degrees to the longitudinal body axis); (1) proclive (projected beyond the ocular area, in lateral view ,< 60 degrees to the longitudinal body axis)

18. Prosoma, chelicerae, frontal view, chilum (Ramírez, 2014: char. 30): (0) absent (Fig. 16A); (1) present (Fig. 15E, 15F)

19. Prosoma, frontal view, clypeus, median pair of macrosetae: (0) absent (Fig. 16A); (1) present (Fig. 16B) – Considered present when this pair of setae are bigger and stouter than the other carapace setae and located on clearly distinct sockets. Bristles that have the same length and thickness of the others carapace bristles were not considered macrosetae

20. Prosoma, clypeus, lateral margin profile: (0) not projected (Figs. 17C, 17D); (1) projected (Figs. 14A, 15C)

21. Prosoma, thoracic portion, height in relation to cephalic portion: (0) same height/ ”flat” (Fig. 16E); (1) elevated (Fig. 16F)

22. Prosoma, thoracic portion, lateral view, median spire: (0) absent (Fig. 16E); (1) present (Fig. 16F)

23. Prosoma, thoracic portion, lateral view, median spire, type (0) vertical (Fig. 16F); (1) backward tilted (Fig. 16E)

24. Prosoma, chelicerae, frontal view, papules: (0) absent; (1) present

25. Prosoma, chelicerae, coloration: (0) uniform (Fig. 16A); (1) stained/bicolor (Fig. 16C)

26. Prosoma, chelicerae, promarginal teeth line (PTL), teeth number: (0) zero; (1) two (Fig. 18B); (2) three (Fig. 17F)

27. Prosoma, chelicerae, retromarginal teeth line (RTL), teeth number: (0) zero; (1) one (Fig. 18B); (2) two (Fig. 17F); (3) three

28. Prosoma, chelicerae, teeth, size proportion: (0) sub equal (Figs. 17F, 18B); (1) unequal (Fig. 18A) (when unequal, the second retromarginal tooth, from proximal to distal portion of chelicerae, is bigger than other teeth)

29. Prosoma, labium, apex, macrosetae: (0) absent; (1) present

30. Prosoma, labium, general shape: (0) truncated (Fig. 17A); (1) trapezoidal (Fig. 17B); (2) rounded

31. Prosoma, endite, general shape: (0) truncated (Fig 17A).; (1) semicircular (Fig. 17B) (cambered retromargin) – considered truncated when there is just one curve/angle between the ectal and mesial distal borders of the endite. Semicircular when there is a gradual bending between the distal borders

Eyes

32. Eyes, relative size of ALE and AME (see Benjamin, 2011: char.48): (0) sub equal (Figs. 14C, 14D, 15B, 15F, 16B, 17E); (1) ALE 2x AME (Figs. 15E, 16A)

33. Eyes, ocular mound (adapted from Benjamin, 2011: char. 55): (0) absent (Figs. 14D, 15B, 15E, 15F, 16A, 16C, 17E); (1) present (Figs. 14C, 16B, 16E, 16F) (ALE + PLE + PME grouped)

34. Eyes, ocular mound, type: (0) spiniform (Fig. 14C) ; (1) rounded (Fig. 16B)

35. Eyes, anterior eye row (AER) curvature: (0) straight (Fig. 17E); (1) recurve (Fig. 14C, 14D, 15B, 15E, 15F, 16A, 16B, 16C)

36. Eyes, posterior eye row (PER) curvature: (0) straight (Fig. 6D); (1) procurve (Figs. 14A, 14B, 15C, 15D); (2) recurve (Fig. 17C)

37. Eyes, ocular tubercles, color (Adapted from Benjamin, 2011: char. 58): (0) same color of prosoma (Fig. 16A); (1) yellowish-white (Figs. 15E, 16E)

Legs

38. Legs, anterior femora (I and II), apical region, prolateral apophysis: (0) absent (Fig. 18E); (1) present (Fig. 18F)

39. Legs, anterior femora (I and II), apical region, retrolateral apophysis: (0) absent (Fig. 18E); (1) present (Fig. 18F)

40. Legs, anterior femora (I and II); dorsolateral setiferous tubercles: (0) absent (Fig. 18F); (1) present (Fig. 18E)

41. Legs, anterior femora (I and II); ventral setiferous tubercles: (0) absent (Fig. 18F); (1) present (Fig. 18C, 18D)

42. Legs, anterior femora (I and II); ventral setiferous tubercles, socket type: (0) conical (Fig. 18E); (1) blister-shaped (Fig. 18C, 18D)

43. Legs, anterior femora (I and II), coloration: (0) uniform; (1) striped

44. Legs, anterior patellae (I and II), ventral macrosetae: (0) absent; (1) present

45. Legs, anterior patellae (I and II), median keel: (0) absent; (1) present

46. Legs, patellae, transversal section, shape (See diagnosis for *Rejanellus venustus* in Lise, 2005; pg. 153): (0) circular (ordinary); (1) rectangular (Fig. 18C)

47. Legs, anterior tibiae (I and II), lateral view, dorsal depression: (0) absent (Fig. 18F); (1) present (Fig. 18E)

48. Legs, anterior tibiae (I and II), lateral view, dorsal depression, anterior gutter (0) absent (Fig. 21A); (1) present (Fig. 21E) – the gutters are naked and depressed areas that are longitudinal extensions of the sensorial pits

49. Legs, anterior tibiae (I and II), lateral view, shape: (0) straight (Fig. 21A); (1) curve (Fig. 21B)

50. Legs, anterior metatarsi (I and II), dorsal view, median line of plumose setae: (0) absent; (1) present

51. Legs, anterior tibiae (I and II), dorsal view, tibial depression: (0) absent; (1) present

52. Legs, anterior tibiae (I and II), dorsal view, tibial depression, length: (0) short (Fig. 18E); (1) long – considered short when concentrated at the proximal region of tibiae (Fig. 21E) and long when projected almost till the metatarsal joint

53. Legs, anterior tibiae (I and II), ventral macrosetae: (0) three pairs (Fig. 21E); (1) four pairs (Fig. 18E); (2) five pairs; (3) more than 5 pairs (Fig. 21A)

54. Legs, anterior metatarsi (I and II), ventral macrosetae: (0) three pairs; (1) more than three pairs

55. Legs, tarsi, claw tuft, density: (0) scarce (confined below the claws) (Fig. 21D); (1) dense (covering the claws) (Fig. 21C)

56. Legs, tarsi, claws teeth, disposition: (0) restricted to the basal portion of the claw (Fig. 21D); (1) exceeding half of the claw length (Fig. 21C)

57. Legs, tarsi, claws teeth, number of teeth: (0) both claws similarly toothed (Fig. 21C); (1) ectal claw with more teeth than mesial claw (Fig. 21D)

Opisthosoma

58. Opisthosoma, median posterior projection: (0) absent (Fig. 19B); (1) present (Figs. 19A, 19C) – when absent, the opisthosoma is considered ordinarily ovoid/sac-like)

59. Opisthosoma, median posterior projection, apex: (0) single-tip (Fig. 19C); (1) trifid (Fig. 19A) – even for females with trifid posterior abdominal projection, co-specific males do not present this characteristic conspicuously

60. Opisthosoma, dorsolateral projection: (0) absent (Fig. 19B); (1) present (Fig. 19A, 8C) – reduced in males

61. Opisthosoma, ventrolateral projection: (0) absent (Fig. 19C); (1) present (Fig. 19A) – absent in males

62. Opisthosoma, ventral surface, guanine stain: (0) absent; (1) present (Fig. 19D)

63. Opisthosoma, anterior border: (0) rounded (Fig. 19B); (1) straight (Fig. 19C); (2) concave (Fig. 14A, 19A) – in *E. heterogaster*, the anterior border of the opisthosoma is strongly recurved, forming a pair of anterior projections

Female genitalia

64. Epigynum, ventral view, copulatory openings, position in epigynal plate: (0) anterior (Fig. 19F); (1) median; (2) posterior (Fig. 19E)

65. Epigynum, ventral view, median septum: (0) absent (Fig. 22B); (1) present (Fig. 22A)

66. Epigynum, ventral view, median septum, type: (0) complete (Fig. 22A); (1) incomplete (Figs. 5A, 12A) – considered complete when the anterior border of epyginal plate is on the same height of the posterior border and connected by a elevated septum

67. Epigynum, dorsal view, copulatory ducts, entry: (0) directed anteriorly; (1) directed posteriorly

68. Epigynum, dorsal view, secondary spermatechae: (0) absent (Fig. 22C); (1) present (Fig. 22D, 22F)

69. Epigynum, dorsal view, size of secondary spermatechae in relation to primary spermatechae: (0) subequal (Fig. 22D, 22E); (1) smaller (Fig. 22F)

70. Epigynum, dorsal view, proximity between spermatechae chambers: (0) separated by a ductus (Fig. 22D, 22F); (1) fused (Fig. 22E)

71. Epigynum, dorsal view, position of the upper curve of secondary spermatechae: (0) mesial (Fig. 22F); (1) ectal (Fig. 22D)

72. Epigynum, dorsal view, shape of primary spermatechae: (0) rounded (Fig. 22D); (1) elongated (Figs. 22C, 22E, 22F)

73. Epigynum, dorsal view, copulatory duct conformation: (0) straight to spermatechae (Figs. 22C, 22E); (1) helicoid (Figs. 22D, 22F)

Male genitalia

74. Palpi, tibiae, macrosetae (see Benjamin, 2011: char. 2): (0) absent; (1) present (Fig. 23A)

75. Palpi, patellae, macrosetae: (0) absent (Fig. 23A); (1) present (Fig. 23B)

76. Palpi, tibiae, macro-trichobothrium (see Benjamin, 2011: char. 3): (0) absent; (1) present (Fig. 23F)

77. Palpi, retrolateral tibial apophysis (RTA), shape: (0) canoe (Fig. 23C); (1) digitiform (Fig. 23D); (2) roundish (Fig. 23A) – when canoe-shaped, the RTA is fused to DTA

78. Palpi, distal tibial apophysis (DTA): (0) absent (Fig. 12D); (1) present (Fig. 23C)

79. Palpi, distal tibial apophysis (DTA), type: (0) smooth ordinary (Fig. 23C); (1) grooved (Fig. 23E)

80. Palpi, tegulum, shape (adapted from Benjamin, 2011: char. 11): (0) disk-shaped (Fig. 24B); (1) oval-shaped (Fig. 24A, 24C, 24D)

81. Palpi, tegulum, tegular ridge: (0) absent (Figs. 24A, 24B); (1) present (Figs. 24C, 24D)

82. Palpi, conductor: (0) absent (Figs. 24B, 24C)); (1) present (Figs. 24A, 24D)

83. Palpi, tegulum, median apophysis (see Benjamin, 2011: char. 16): (0) absent (Figs. 24B, 24C); (1) present (Figs. 24A, 24D)

84. Palpi, embolus, resting position (adapted from Benjamin, 2011: char. 20): (0) encircling the tegulum (Fig. 24B); (1) on tegulum (Fig. 24A, 24C, 24D)

85. Palpi, embolus, shape: (0) filiform (Fig. 24B); (1) laminar (Figs. 24A, 24C, 24D)

86. Palpi, embolus, length: (0) half turn around the tegulum; (1) one turn around the tegulum; (2) one turn and a half around the tegulum

87. Palpi, embolus, pars pendula: (0) absent (Figs. 24B, 24C); (1) present (Figs. 24A, 24D)

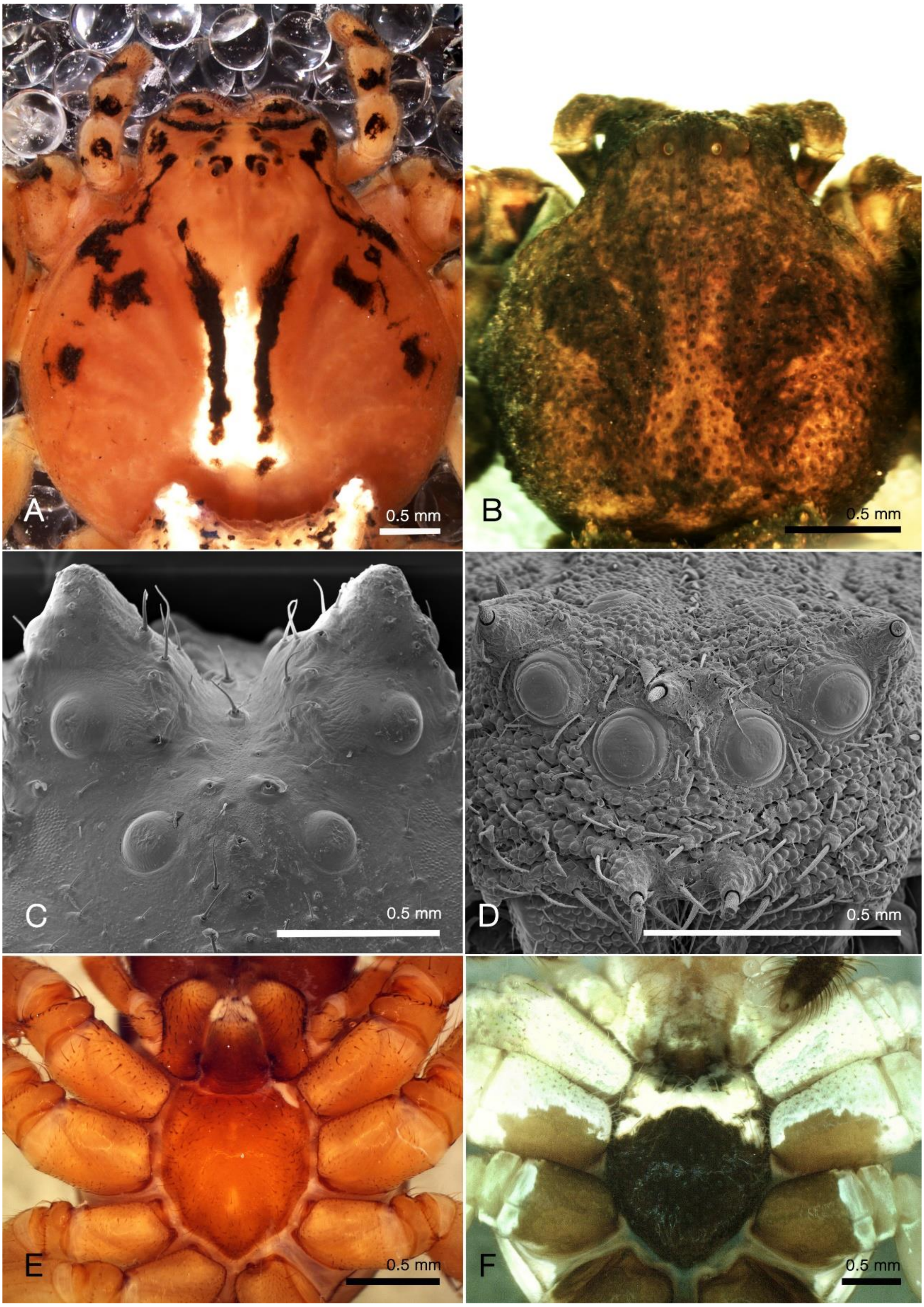

Figure 14. Dorsal view of the prosoma of *Epicadus pulcher* (A), *Epicadus caudatus* (B); frontal view of the prosoma of *Epicadus heterogaster* (C) and *Onocolus infelix* (D); sternum of *Stephanopoides sexmaculata* (E) and *Phrynarachne ceylonica* (F).

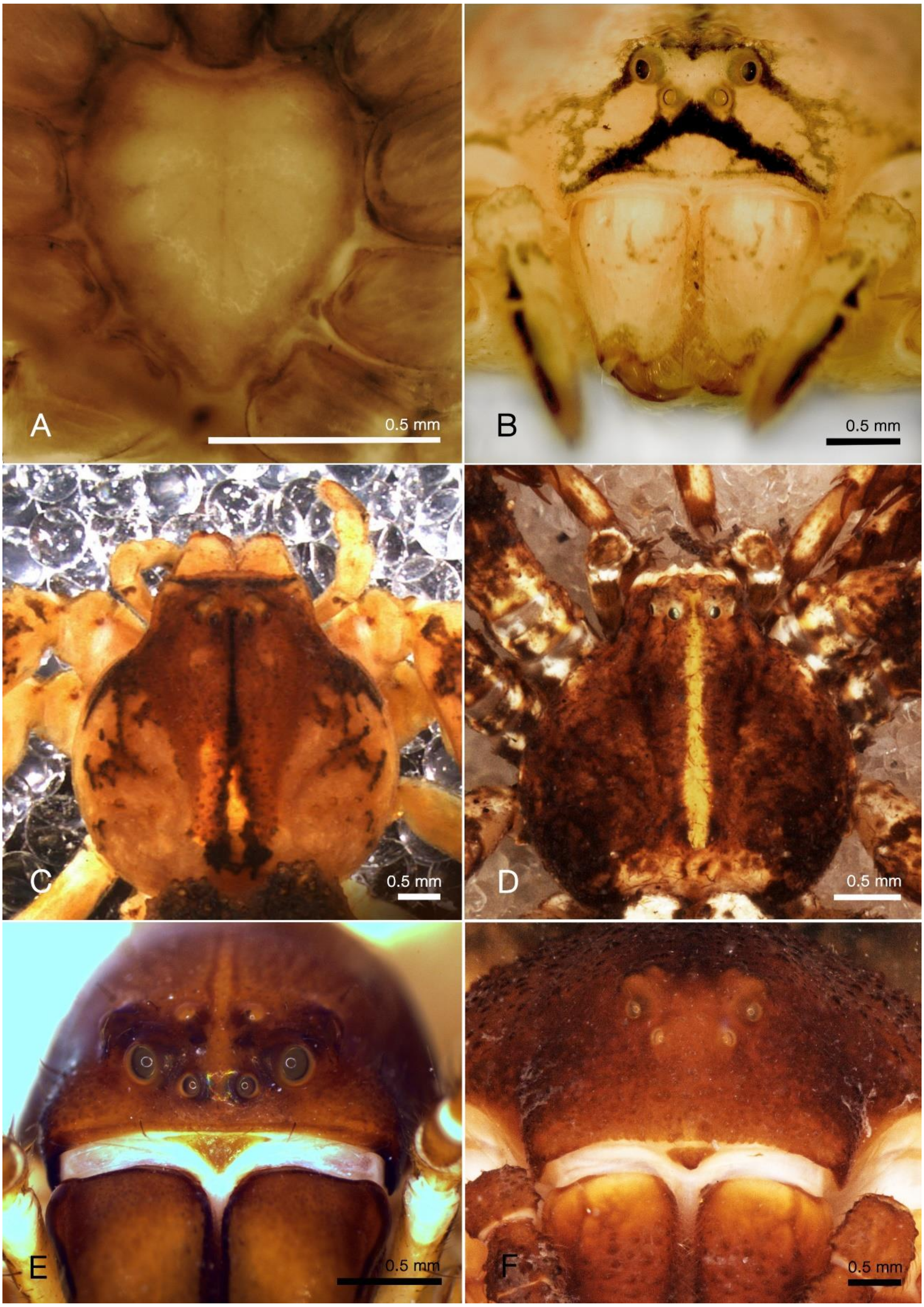

Figure 15. Sternum of *Hedana ocellata* (A); frontal view of the prosoma of *Epicadus trituberculatus* (B); dorsal view of the prosoma of *Epicadus camelinus* (C) and *Stephanopis quinquetuberculata* (D); frontal view of the prosoma of *Stephanopoides sexmaculata* (E) and *Epicadus granulosus* (F).

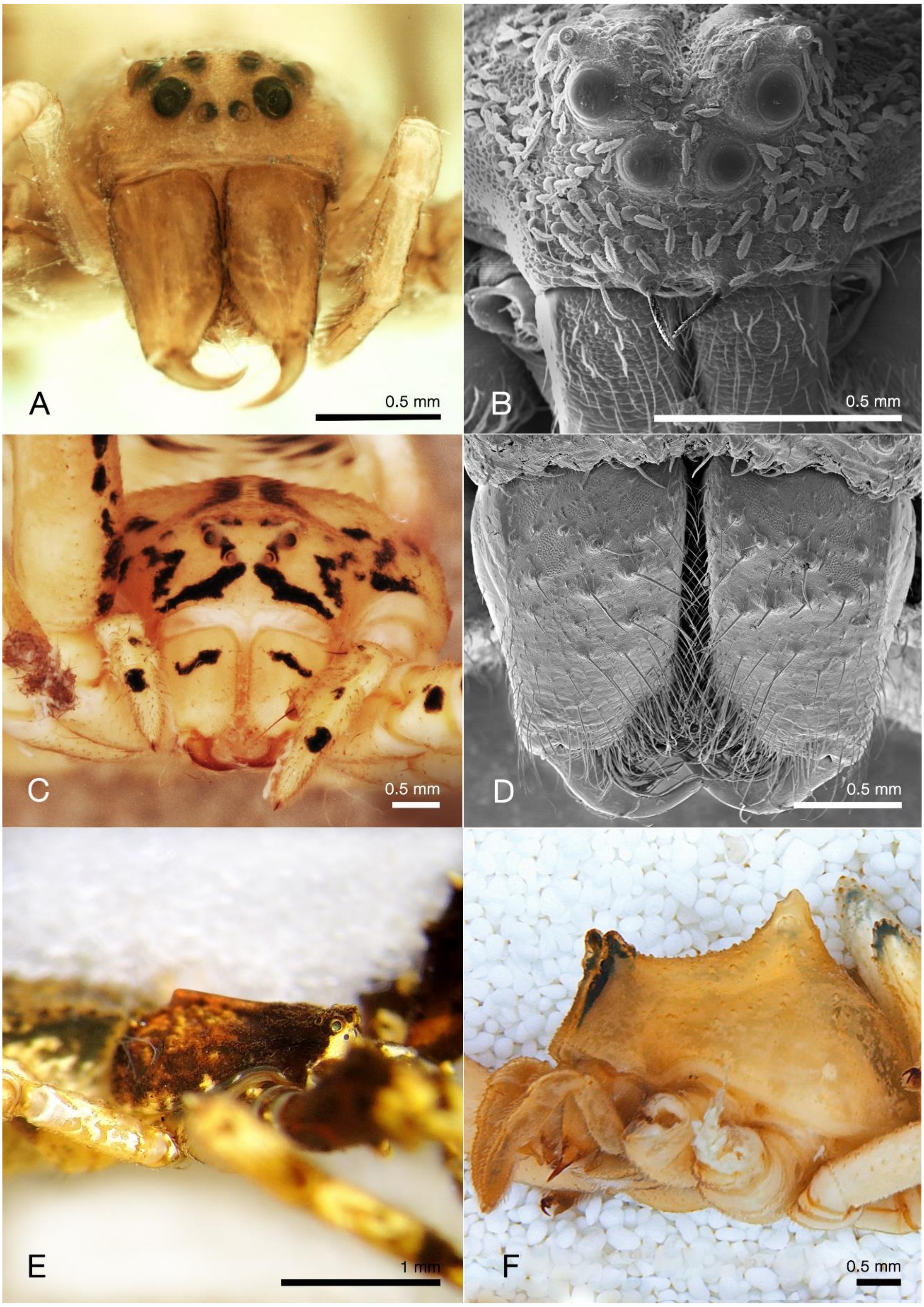

Figure 16. Frontal view of the prosoma of *Epidius pallidus* (A), *Stephanopis quinquetuberculata* (B) and *Epicadus pulcher* (C); frontal view of the chelicerae of *Epicadus caudatus* (D); lateral view of the prosoma of *Stephanopis* sp.(E) and *Epicadus heterogaster* (F).

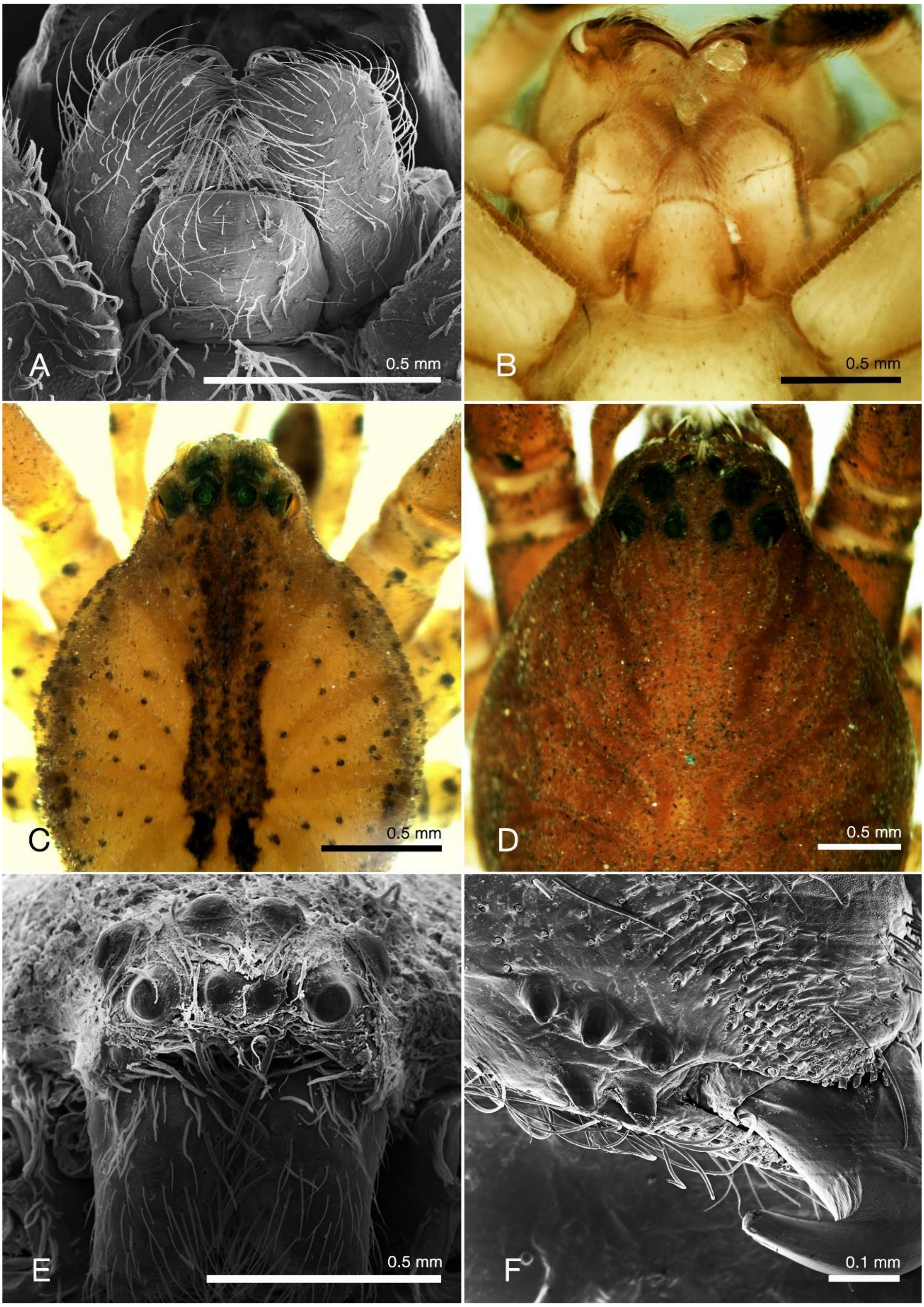

Figure 17. Endites and labium of *Stephanopis* sp. (A) and *Epicadus camelinus* (B); dorsal view of the prosoma of *Isala punctata* (C) and *Synalus angustus* (D); frontal view of the prosoma of *Borboropactus* sp. (E); cheliceral teeth of *Epicadus caudatus* (F).

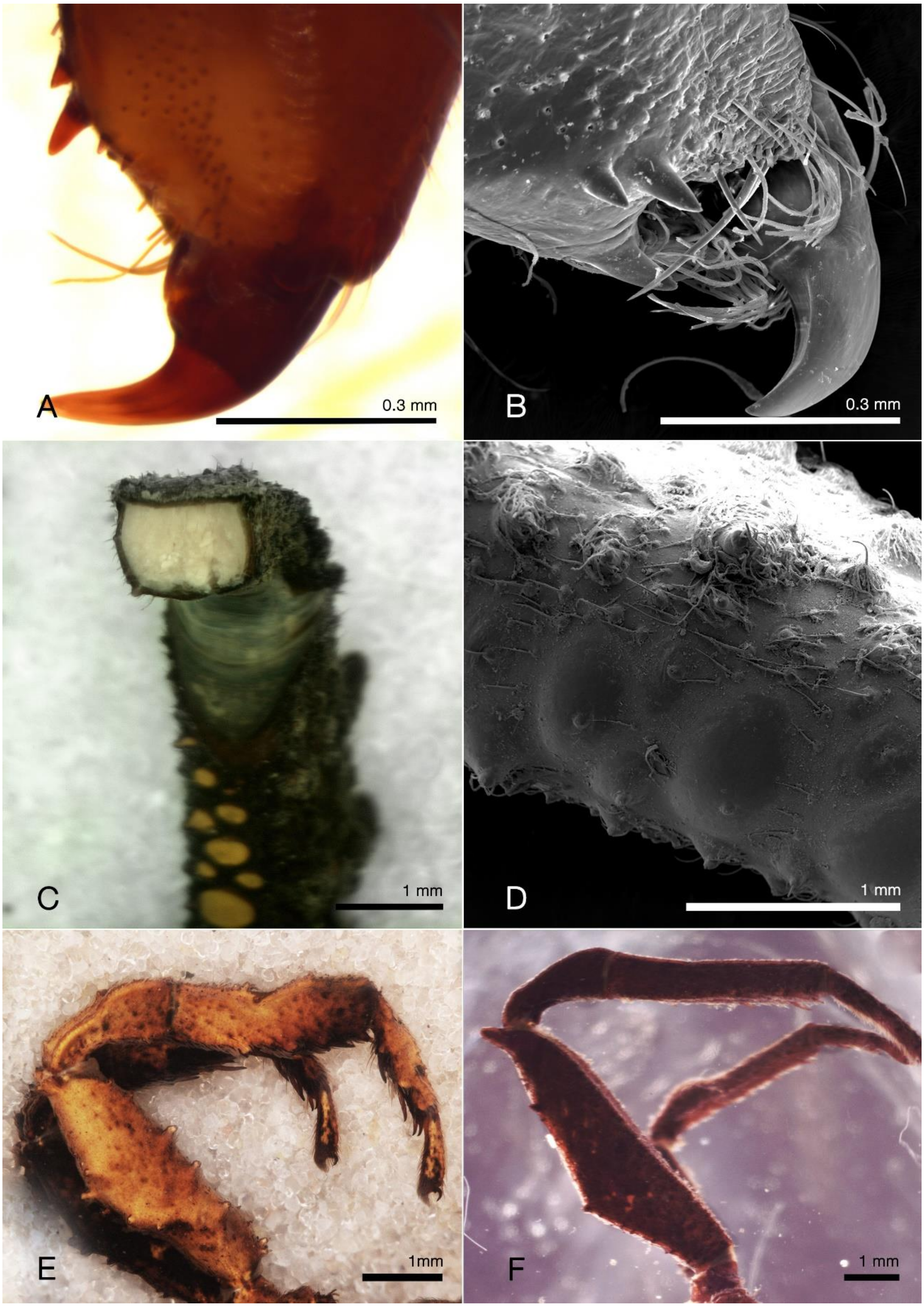

Figure 18. Photographs of the cheliceral teeth of *Stephanopoides sexmaculata* (A) and *Phrynarachne ceylonica* (B); transversal section of the patellae I (C) and ventral view of setae sockets on femur I of *Epicadus pustulosus* (D); anterior legs of *Stephanopis quinquetuberculata* (E) and *Coenypha edwardsi* (F).

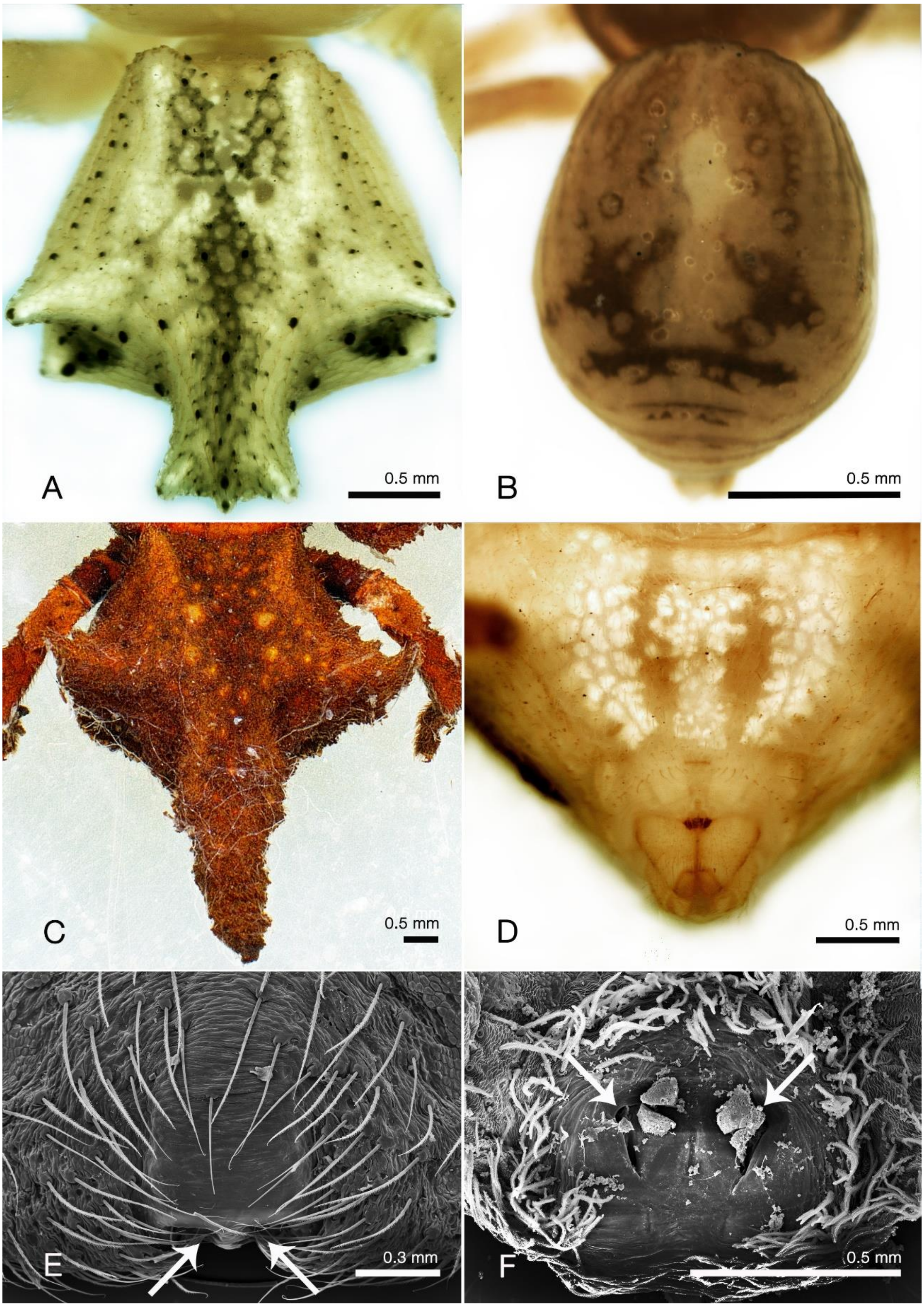

Figure 19. Dorsal view of the opisthosoma of *Epicadus trituberculatus* (A), *Hedana ocellata* (B) and *Epicadus caudatus* (C); guanine stain on ventral surface of the opisthosoma of *Epicadus trituberculatus* (D); ventral view of the epigynum of *Onocolus infelix* (E) and *Stephanopis altifrons* (F) (arrows indicate the position of copulatory openings).

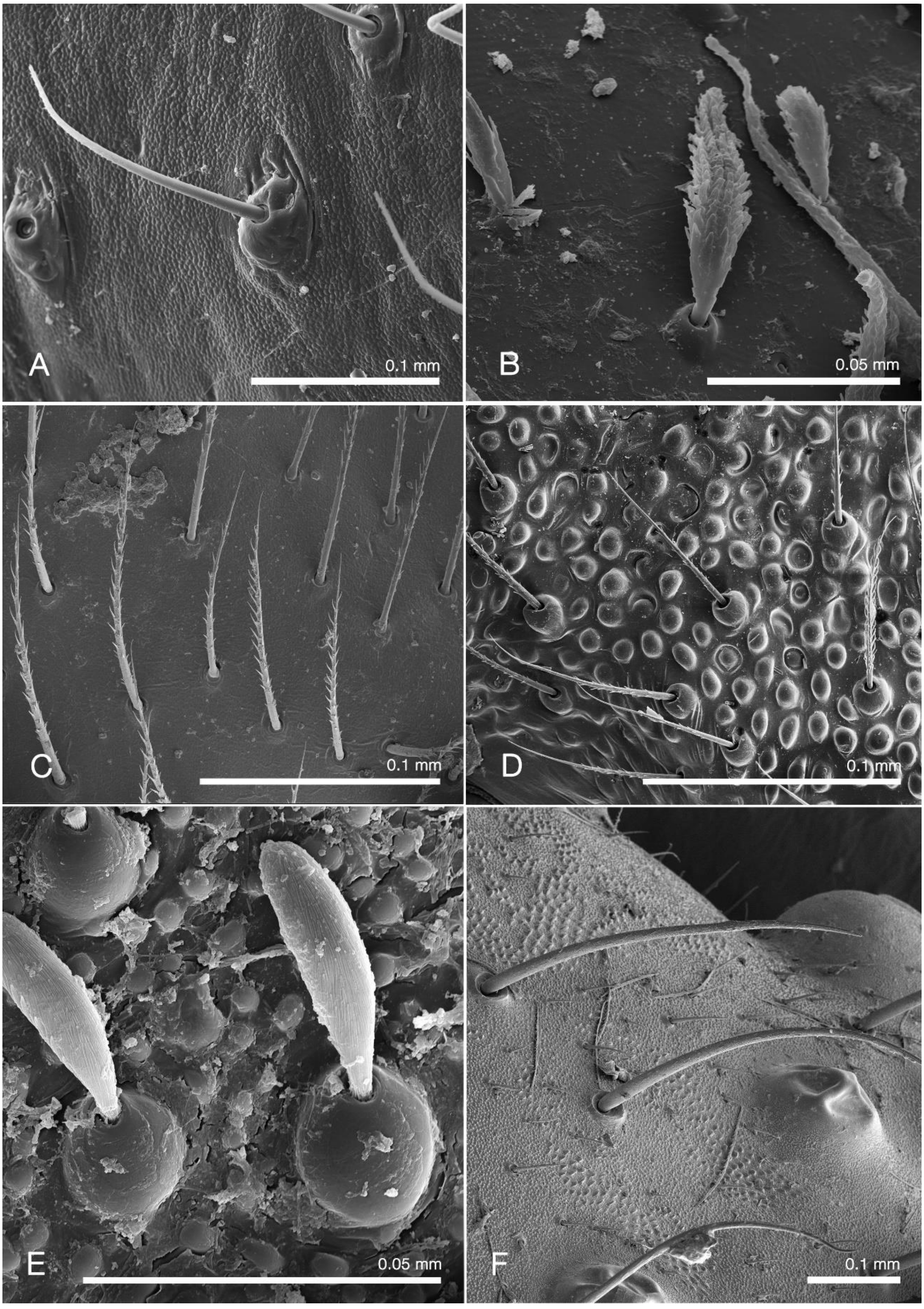

Figure 20. Sternum setae of *Epicadus trituberculatus* (A), *Borboropactus* sp. (B), *Tmarus polyandrus* (C) and *Onocolus intermedius* (D); prosoma setae of *Isala punctata* (E) and *Tmarus polyandrus* (F).

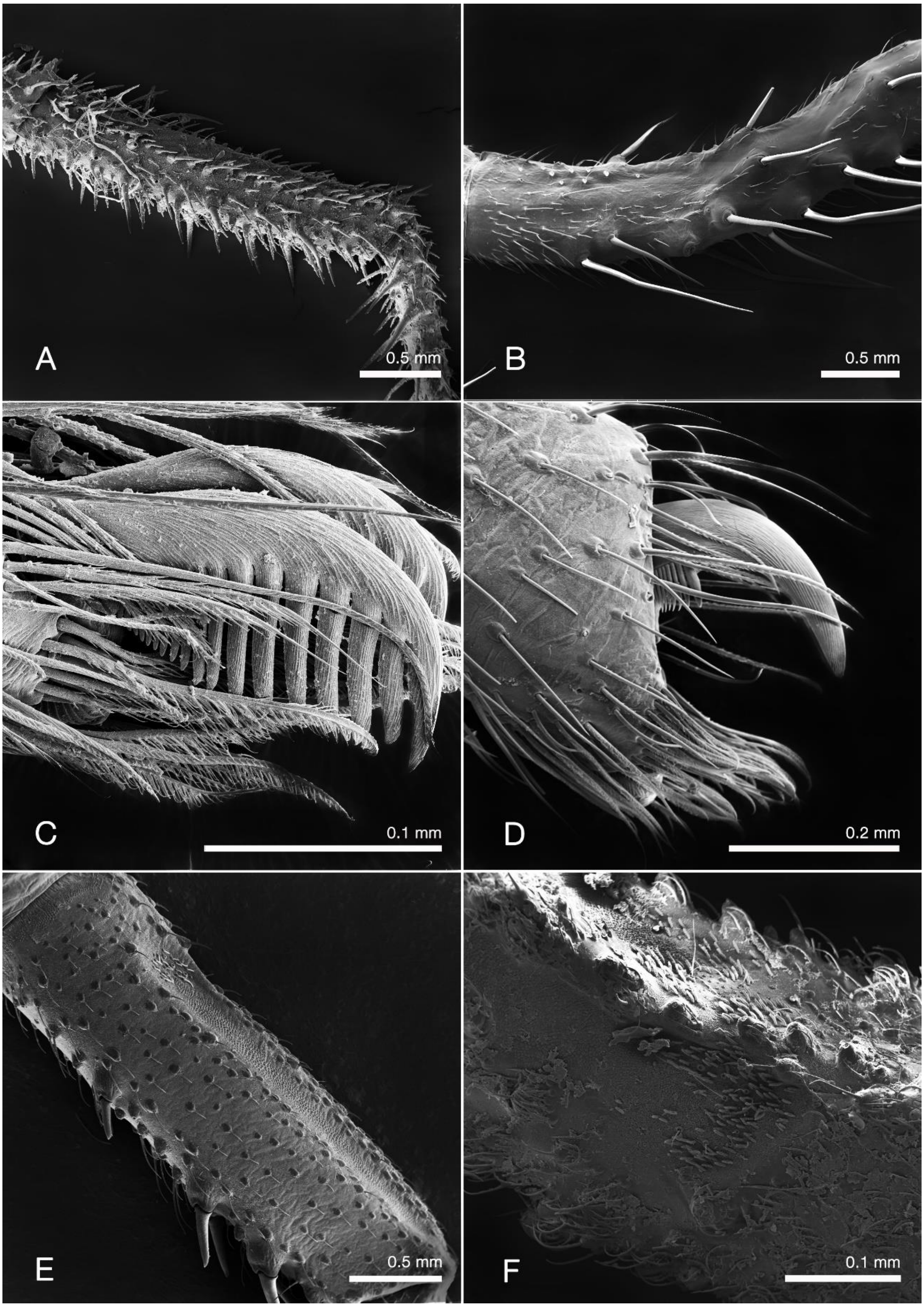

Figure 21. Tibia I of *Epicadinus trispinosus* (A) and *Phrynarachne ceylonica* (B); tarsal claws of *Tmarus polyandrus* (C) and *Epicadus trituberculatus* (D); tibial gutters and sensory pits of *Epicadus trituberculatus* (E) and *Epicadus pustulosus* (F).

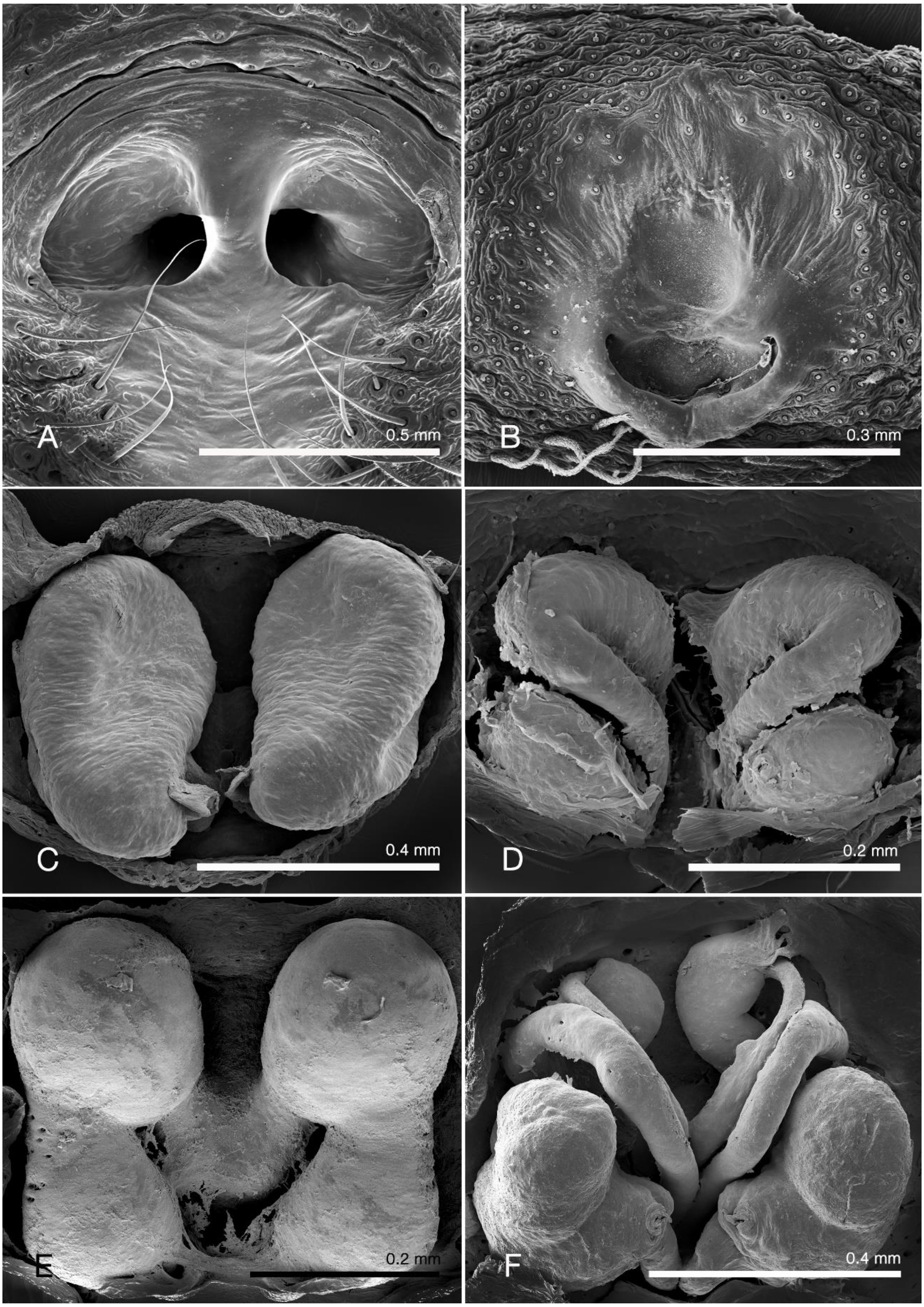

Figure 22. Epyginum of *Epicadus caudatus* (A); ventral view of the epyginum of *Stephanopis* sp. (B); dorsal view of spermatechae of *Stephanopis quinquetuberculata* (C), *Epicadinus trispinosus* (D), *Tmarus polyandrus* (E) and *Epicadus caudatus* (F).

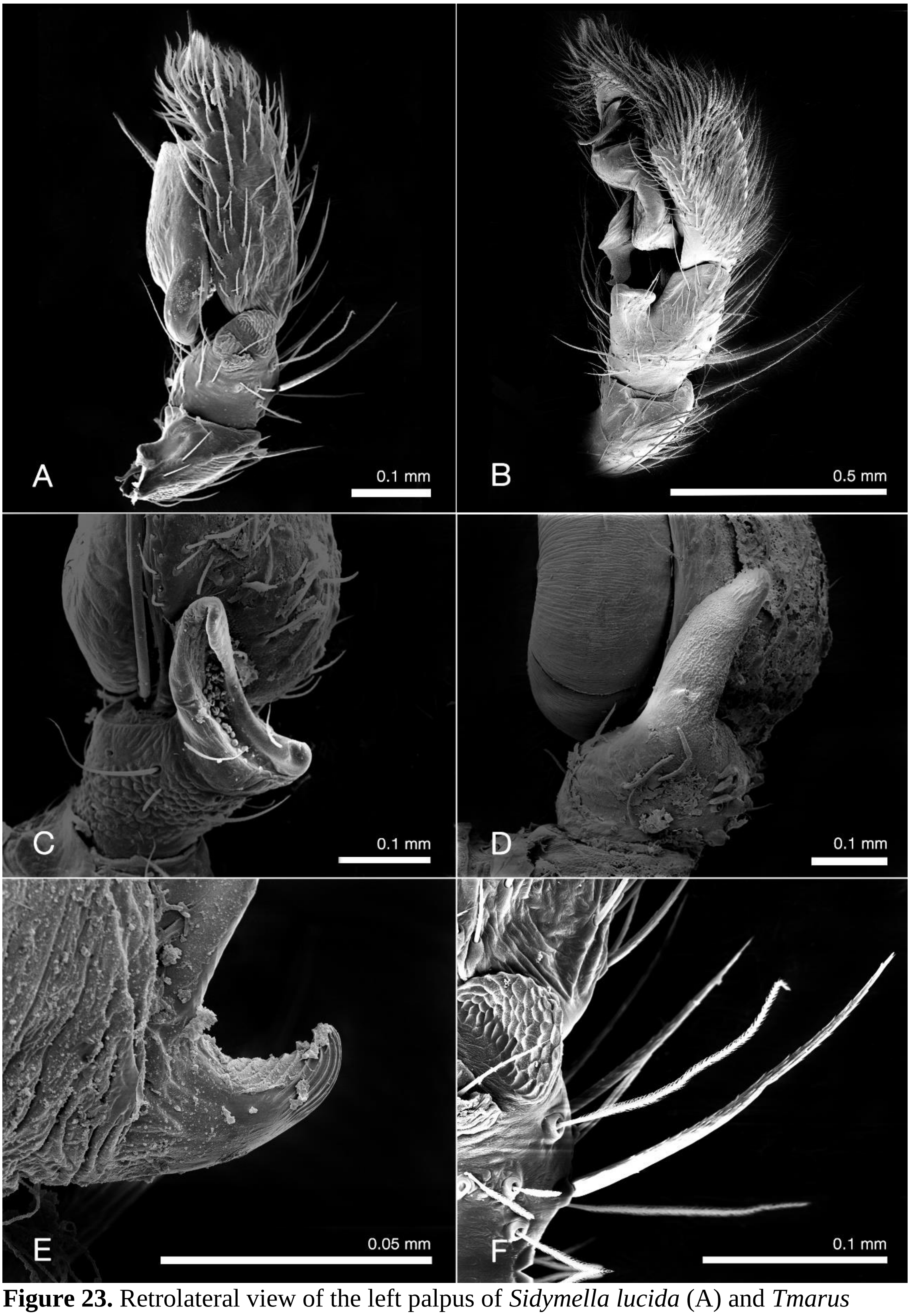

Figure 23. Retrolateral view of the left palpus of *Sidymella lucida* (A) and *Tmarus polyandrus* (B); detail of the RTA+DTA of *Epicadus taczanowskii* and RTA of *Stephanopis quinquetuberculata* (D); grooved DTA of *Onocolus infelix* (E); tibial macro-trichobothrium and macrosetae on male palpus of *Sidymella lucida* (F).

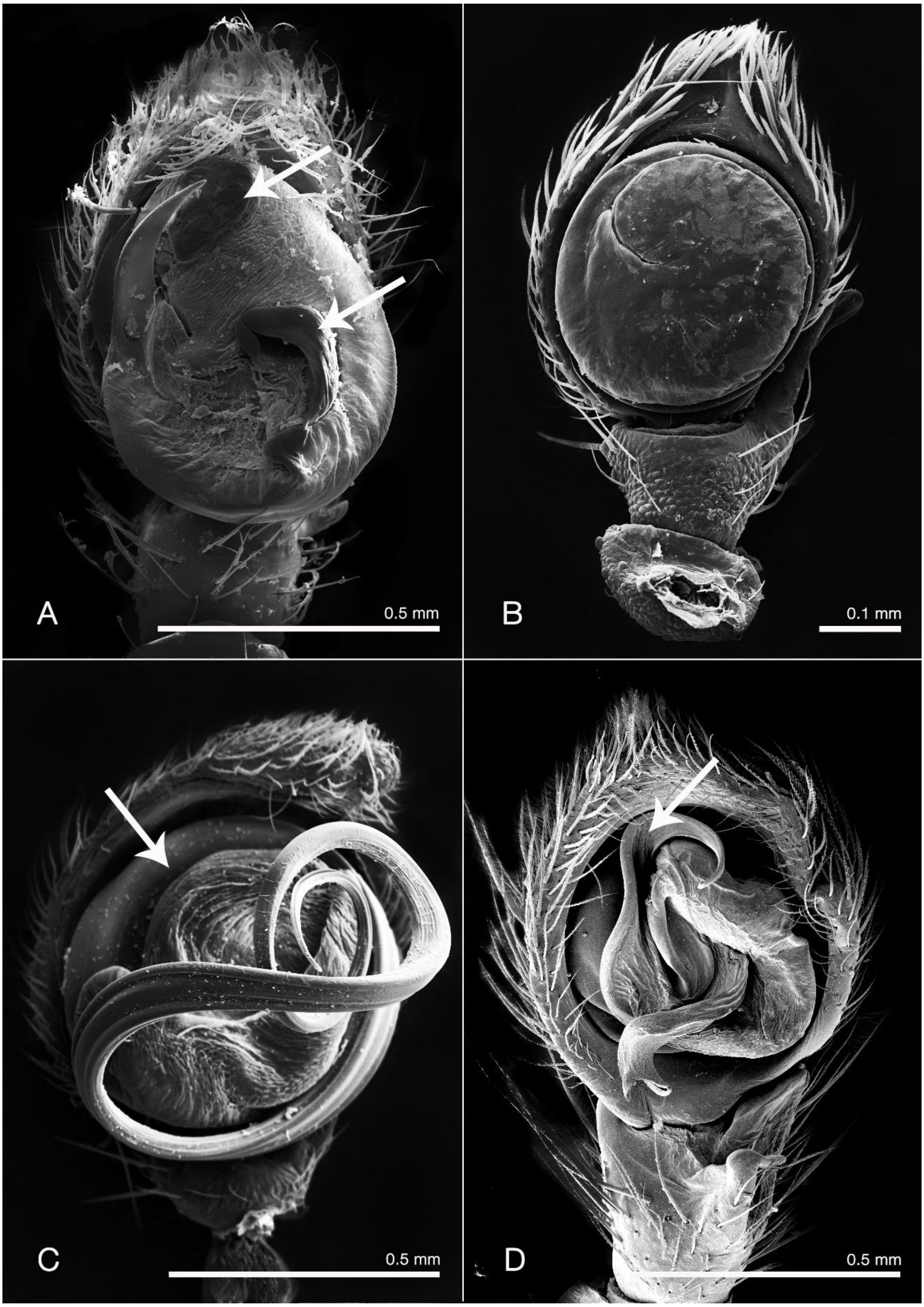

Figure 24. Ventral view of male palp of *Borboropactus* sp. (A) (upper arrow indicates the conductor and bottom arrow indicates the median apophysis); *Epicadus camelinus* (B); *Stephanopis ditissima* (C) (arrow indicates the tegular ridge); *Tmarus polyandrus* (arrow indicates the pars pendula) (D).

APPENDIX 2: CHARACTER MATRIX

Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Tmarus polyandrus	1	0	0	0	0	2	0	0	0	0	0	0	0	-	0	0	1	1	0	0
Stephanopoides sexmaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	1	0	0
Synalus angustus	0	0	0	0	0	?	0	0	0	?	?	0	0	-	0	0	0	1	0	0
Stephanopis ditissima	1	1	1	0	1	2	0	1	0	1	0	0	0	-	1	0	0	0	1	0
Sidymella lucida	1	0	0	0	0	2	0	1	0	0	0	0	0	-	0	0	0	0	0	0
Rejanellus pallescens	1	1	0	0	0	2	0	1	0	0	1	0	0	-	0	0	1	0	1	0
Rejanellus mutchleri	1	1	0	0	0	2	0	1	0	0	1	0	0	-	0	0	1	0	1	0
Phrynarachne ceylonica	0	1	0	1	0	2	0	1	0	0	1	0	0	-	0	0	0	0	0	0
Onocolus infelix	1	1	0	0	0	2	0	1	0	0	0	0	0	-	0	0	0	1	1	0
Onocolus intermedius	1	1	0	0	0	2	1	1	0	0	0	0	0	-	0	0	0	0	1	0
Isala punctata	1	1	1	1	0	2	0	0	1	1	0	0	1	0	0	0	0	0	1	0
Hedana ocellata	1	0	0	0	0	?	0	1	1	0	?	0	0	-	0	0	0	0	0	0
Epidius pallidus	1	0	0	0	0	?	0	1	1	0	?	0	0	-	0	0	0	0	0	0
Epicadus heterogaster	1	0	0	0	0	0	0	1	0	0	0	0	0	-	1	0	0	1	0	1
Epicadus rubripes	1	0	0	1	0	0	0	1	0	0	0	0	0	-	1	1	0	1	0	1
Epicadinus trispinosus	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0
Epicadinus spinipes	0	1	1	1	0	1	0	1	0	0	0	0	0	-	0	0	0	1	0	0
Coenypha edwardsi	0	1	1	0	1	2	0	1	0	1	0	0	0	-	0	0	0	0	1	0
Borboropactus nyerere	0	0	1	0	1	1	0	0	0	1	0	0	0	-	0	0	0	0	1	0
Tobias caudatus	0	1	1	0	0	0&1	1	1	0	0	0&1	1	0	-	0	0	0	1	1	0
Tobias inermis	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Tobias camelinus	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1
Tobias pustulosus	0	1	1	0	0	0&1	1	1	0	0	0&1	1	0	-	0	0	0	1	1	0
Tobias pulcher	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1
Tobias taczanowskii	1	1	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1
Tobias trituberculatus	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1
Stephanopis sp.	0	1	1	1	0	2	0	1	0	1	1	1	0	-	0	0	0	0	1	0
Stephanopis quinquetuberculata	0	1	1	1	0	2	0	1	0	1	1	1	0&1	1	0	0	0	0	1	0
Stephanopis altifrons	0	1	1	0	0	0	0	1	0	0	1	1	0	-	0	0	0	0	0	0

Taxa	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
T. polyandrus	0	0	-	1	0	0	0	-	0	1	0	1	0	-	0	0	1	0	0	0
S. sexmaculata	0	0	-	0	0	1	3	1	1	0	1	1	0	-	1	1	0	0	0	0
S. angustus	0	0	-	0	0	2	2	1	0	2	1	0	0	-	1	0	0	0	0	0
S. ditissima	0	1	1	0	0	1	2	0	0	0	0	0	0	-	1	1	0	1	1	1
S. lucida	0	0	-	1	0	2	2	0	1	2	0	1	0	-	1	0	0	0	0	0
R. pallescens	0	0	-	1	0	2	2	0	0	1	1	1	0	-	1	0	0	0	0	1
R. mutchleri	0	0	-	1	0	2	2	0	0	1	1	1	0	-	1	0	0	0	0	1
P. ceylonica	0	0	-	1	0	1	1	0	0	1	1	0	0	-	1	0	1	0	0	0
O. infelix	0	0	-	1	0	2	2	0	0	1	1	0	0	-	1	0	0	0	0	0
O. intermedius	0	0	-	1	0	2	2	0	0	1	1	0	0	-	1	0	0	0	0	0
I. punctata	0	0	-	0	1	2	2	0	0	0	0	1	0	-	1	1	0	0	0	0
H. ocellata	0	0	-	?	0	1	1	0	0	1	1	1	0	-	0	1	0	0	0	0
E. pallidus	0	0	-	?	0	2	2	1	0	2	1	0	0	-	1	1	0	0	0	0
E. heterogaster	1	1	0	1	0	2	2	0	0	1	1	0	1	0	1	1	0	0	0	0
E. rubripes	1	1	0	1	1	2	2	0	0	1	1	0	1	0	1	1	0	0	0	0
E. trispinosus	0	0	-	1	0	2	2	0	0	2	0	0	1	0	1	1	0	0	0	0
E. spinipes	0	0	-	1	0	2	2	0	0	2	0	0	1	0	1	1	0	0	0	1
C. edwardsi	0	0	-	0	0	1	2	0	0	0	1	0	0	-	1	0	0	1	1	1
B. nyerere	0	0	-	0	0	2	3	0	1	0	0	1	0	-	0	0	0	0	0	1
T. caudatus	1	0	-	1	0	2	2	0	0	1	1	0	0	-	1	1	0	1	1	1
T. inermis	1	0	-	1	0	2	2	0	0	1	1	0	0	-	1	1	0	0	0	0
T. camelinus	1	1	1	1	0	2	2	0	0	1	1	0	0	-	1	1	1	0	0	0
T. pustulosus	1	0	-	1	1	2	2	0	0	1	1	0	0	-	1	1	0	1	1	1
T. pulcher	1	0	-	1	1	2	2	0	0	1	1	0	0	-	1	1	0	0	0	0
T. taczanowskii	1	0	-	1	1	2	2	0	0	1	1	0	0	-	1	1	0	0	0	0
T. trituberculatus	1	1	1	1	1	2	2	0	0	1	1	0	0	-	1	1	0	0	0	0
Stephanopis sp.	0	1	1	1	1	2	2	0	0	0	0	0	1	1	1	1	1	1	0	1
S. quinquetuberculata	0	1	1	1	1	2	2	0	0	0	0	0	1	1	1	1	1	1	0	1
S. altifrons	0	0	-	1	1	2	2	0	0	2	1	1	1	0	1	1	1	0	0	1

Taxa	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
T. polyandrus	0	-	0	0	0	0	0	-	0	0	0	-	0	1	1	1	0	0	-	0
S. sexmaculata	0	-	0	0	0	0	0	-	0	0	0	-	2	0	1	1	0	0	-	0
S. angustus	0	-	0	0	0	0	0	-	0	0	0	-	2	1	1	1	0	0	-	0
S. ditissima	0	-	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	-	1
S. lucida	0	-	0	0	0	0	0	-	0	0	0	-	2	1	0	1	1	0	-	1
R. pallescens	1	0	0	0	0	1	0	-	0	0	1	0	0	0	0	0	1	1	0	1
R. mutchleri	1	0	0	0	0	1	0	-	0	0	1	0	0	0	0	0	1	1	0	1
P. ceylonica	1	0	1	0	0	0	0	-	1	0	0	-	2	1	0	1	0	0	-	1
O. infelix	1	0	0	0	0	0	0	-	0	0	0	-	0	0	0	0	1	1	0	1
O. intermedius	1	0	0	0	0	0	0	-	0	0	0	-	0	0	0	0	1	1	0	1
I. punctata	0	-	1	0	1	0	0	-	0	0	1	1	2	0	0	1	0	0	-	0
H. ocellata	0	-	0	0	0	0	0	-	0	0	0	-	1	0	-	1	-	0	-	0
E. pallidus	0	-	0	0	0	?	0	-	0	0	0	-	1	0	0	1	0	0	-	0
E. heterogaster	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	0	1
E. rubripes	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	0	1
E. trispinosus	0	-	0	0	0	0	0	-	0	0	1	1	0	0	0	0	0	1	0	1
E. spinipes	0	-	1	0	0	0	0	-	1	0	1	1	3	1	0	0	0	1	0	1
C. edwardsi	0	-	0	0	0	0	1	0	0	0	1	0	2	1	1	0	1	0	-	1
B. nyerere	0	-	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	0	-	0
T. caudatus	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1
T. inermis	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	1	1	0	1
T. camelinus	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1
T. pustulosus	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1
T. pulcher	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	1
T. taczanowskii	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	0	1
T. trituberculatus	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1
Stephanopis sp.	1	0	1	1	1	1	1	0	1	1	1	0	3	0	1	0	1	1	0	1
S. quinquetuberculata	1	0	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	0	1
S. altifrons	1	0	0	0	1	1	0	-	0	1	1	0	1	0	0	0	1	0	-	0

Taxa	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**
T. polyandrus	0	0	0	0	0	-	0	1	0	1	-	0	0	1	1	1	2	0	-	?	1	1	1	1	1	0	1
S. sexmaculata	0	1	0	2	1	0	0	0	-	-	-	1	0	1	0	0	-	0	-	0	1	0	0	0	0	2	0
S. angustus	0	0	1	0	0	-	1	0	-	-	-	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. ditissima	1	1	2	1	1	0	0	0	-	-	-	1	0	1	1	1	1	0	-	1	1	0	0	0	1	1	0
S. lucida	0	1	1	1	0	-	0	1	0	1	-	0	1	1	1	1	2	0	-	1	0	0	0	1	0	0	0
R. pallescens	0	0	1	0	0	-	1	1	0	0	0	0	0	1	1	0	1	0	-	1	0	0	0	1	0	0	0
R. mutchleri	0	0	1	0	0	-	1	1	0	1	-	0	0	0	0	0	1	0	-	1	0	0	0	1	0	0	0
P. ceylonica	0	0	1	1	0	-	0	0	-	-	-	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
O. infelix	0	1	1	2	1	0	0	1	1	0	1	0	1	1	1	1	0	1	1	0	0	0	0	0	0	2	0
O. intermedius	0	1	1	2	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	2	0
I. punctata	0	0	1	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0	-	1	0	1	0	2	1	0	1
H. ocellata	0	0	0	1	1	0	1	0	-	-	-	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. pallidus	0	0	1	0	0	-	1	0	-	-	-	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. heterogaster	1	1	1	2	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0
E. rubripes	1	1	2	1	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0
E. trispinosus	0	1	1	1	1	0	0	0	-	-	-	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
E. spinipes	0	0	1	1	0	-	0	0	-	-	-	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0
C. edwardsi	0	0	2	1	1	-	0	0	-	-	-	1	0	1	1	0	1	0	-	1	1	0	0	0	1	1	0
B. nyerere	0	0	2	2	0	-	0	1	0	1	-	1	0	0	0	0	1	0	-	1	0	1	1	1	1	0	1
T. caudatus	0	0	1	1	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	2	0
T. inermis	0	0	1	1	1	0	0	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. camelinus	1	1	2	1	1	1	0	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0
T. pustulosus	0	0	1	1	1	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	2	0
T. pulcher	1	1	2	1	1	1	0	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. taczanowskii	0	1	2	1	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0
T. trituberculatus	1	1	2	1	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0
Stephanopis sp.	1	0	2	2	0	-	0	0	-	-	-	1	0	0	1	0	1	0	-	1	0	0	0	1	0	0	0
S. quinquetuberculata	1	0	2	2	0	-	0	0	-	-	-	1	0	1	0	0	1	0	-	1	0	0	0	1	0	0	0
S. altifrons	0	0	1	0	0	-	1	0	-	-	-	0	1	1	1	0	1	0	-	1	0	0	0	1	0	0	0

APPENDIX 3: LIST OF EXAMINED MATERIAL

Outgroup

Borboropactus nyerere Benjamin, 2011. TANZANIA: *Usambara Mountains* (Mazumbai forest), 1m and 3 f, 12-20.XI.1995, C. Griswold, N. Scharff & D. Ubick leg., [-4.8166, 38.4916], (CAS 9046658).

Coenypha edwardsii (Nicolet, 1849). CHILE: *Talca*, 1 m, 19.VI.1981, (CAS 9046659); *Angol*, 1 f, 20.V.1986, H. Levi leg., (CAS9046660).

Epicadinus spinipes (Blackwall, 1862). BRAZIL: *Rio Grande do Sul* (Viamão), 1 m, IV.2002, L.E. Costa leg., [-30.0814, -51.0260], (MCTP 15331); (Augusto Pestana), 1 f, 06.IX.2009, L.V. Silva & L.B. Medeiros leg., (MCTP 30592).

Epicadinus trispinosus (Taczanowski, 1872). PANAMA: *Arraiján*, 1 m and 1 f, 07.VI.1950, A.M. Chickering leg., (MCZ).

Epicadus heterogaster (Guérin, 1829). BRAZIL: *Roraima* (Reserva Biológica Ilha de Maracá), 1 m, 14.II.1992, A.B. Bonaldo leg., (MCTP 1772); *Paraná* (Morretes), 1 f, 09-20.I.1995, Arachnology lab staff leg., (MCTP 7101).

Epicadus rubripes (Mello-Leitão, 1924). BRAZIL: *Rio Grande do Sul* (Guaíba, Fazenda Matzenbacker), 2 m, 26.VIII.1994, A.A. Lise et al. leg., (MCTP 5432); (Viamão), 1 f, 20.XII.2000, P.P. Júnior leg., (MCTP 21868).

Epidius pallidus (Thorell, 1890). INDONESIA: *Sumatra*, holotype female, T. Thorell leg., (OUMNH 1233).

Isala punctata L. Koch, 1876. AUSTRALIA: *Tasmania* (Trevallyn), 1m and 2 j, 11.VII.1939, V.V. Hickman leg., [-41.4354, 147.1191], (AMS ks 31520).

Hedana ocellata Thorell, 1890. SRI LANKA: 1 f, 20.XI.1960, R. Sherriffs leg., (ZMUC298).

Onocolus infelix Mello-Leitão, 1941. BRAZIL: *Rio Grande do Sul* (Viamão), 1 m and 1 f, 17.X.1995, A.A. Lise et al. leg., (MCTP 8098).

Onocolus intermedius (Mello-Leitão, 1929). BRAZIL: *Rio Grande do Sul* (Viamão), 2m and 1 f, 7.X.1994, A.A. Lise et al. leg., (MCTP 5628).

Phrynarachne ceylonica (O. Pickard-Cambridge, 1884). SRI LANKA: 1 m and 1 f, 01.XI.1912, O. Pickard-Cambridge leg., (OUMNH 1268).

Rejanellus mutchleri (Petrunkevich, 1930). PUERTO RICO: *Adjuntas* (Jayua road), male holotype and female paratype, 02.VI.1915, Mutchleri leg., (AMNH 49681).

Rejanellus pallescens (Bryant, 1940). CUBA: *Pico Turquino,* female holotype, VI.1936, P.J. Darlington leg., (MCZ); HAITI: Pourt-au-Prince, male alotype, 02.X.1934, P.J. Darlington leg., (MCZ).

Sidymella lucida (Keyserling, 1880). BRAZIL: *Rio Grande do Sul* (Cachoeira do Sul), 1 m and 3 f, 31.X.1992, R.G. Buss leg., [-30.0336, -52.8932], (MCTP 3485).

Stephanopis altifrons O. Pickard-Cambridge, 1869. AUSTRALIA: *Queensland* (Edmonton), 1 m and 1 f, 15.V.1972, E. Coleman & R. Mascord leg., [-17.0193, 145.7434], (AMS ks 108666).

Stephanopis ditissima (Nicolet 1849). CHILE: *Cautín* (Villarrica), 1 m and 1 f, 16-31.XII.1964, Lapeña leg., (MCZ).

Stephanopis quinquetuberculata (Taczanowski, 1872). BRAZIL: *Paraná* (Morretes, Serra da Farinha Seca), 1 m and 1 f, 15-20.IX.1995, Arachnology lab staff leg., (MCTP 7665).

Stephanopis sp. BRAZIL: *Amazonas* (Coari, Porto Urucu), 2 m, VII.2006, S.C. Dias leg., [-4.8125, -65.0327], (MPEG 13329); 2 f, 13.VII.2003, D. Guimarães leg., [-4.8686, -65.2647], (MPEG 22795).

Stephanopoides sexmaculata Mello-Leitão, 1929. BRAZIL: *Pará* (Melgaço, Floresta Nacional de Caxiuanã), 1 m and 1 f, 11.VIII.1996, A.A. Lise et al. leg., [-1.7793, -51.4295], (MCTP 9506).

Synalus angustus (L. Koch, 1876). AUSTRALIA: *Sydney* (Royal National Park), 1 f, 19.XI.1996, B. Speechley & R. Mascord leg., [-34.0751, 151.0558], (AMS ks 108747).

Tmarus polyandrus Mello-Leitão, 1929. BRAZIL: *Rio Grande do Sul* (Nova Santa Rita), 1 m, II.2009, A. Oliveira et al. leg., (MCTP36455); (Novo Cabrais), 1 f, 25.X.2007, R.G. Buss leg., (MCTP 28419).

APPENDIX 4: OUTPUT OF THE IMPLIED WEIGHTING ANALYSIS

Values obtained under the script proposed by Mirande (2009) for implied weighting analysis (in grey are the K values that present a most congruent phylogenetic hypothesis).

archivo	**distref**	**kref**	**length**	**trees**	**fit**	**difspr**	**agree**	**nodcons**
K0	50	1.960	300	1	38.355	0	0	0
K1	52.667	2.180	300	1	36.657	0	29	27
K2	55.333	2.428	300	1	34.941	0	29	27
K3	58	2.706	300	1	33.204	0	29	27
K4	60.667	3.022	300	1	31.444	0	29	27
K5	63.333	3.385	300	1	29.657	0	29	27
K6	66	3.804	294	1	27.839	8	20	18
K7	68.667	4.294	294	1	25.922	0	29	27
K8	71.333	4.876	294	1	23.978	0	29	27
K9	74	5.577	294	1	22.003	0	29	27
K10	76.667	6.439	294	1	19.994	0	29	27
K11	79.333	7.522	294	1	17.945	0	29	27
K12	82	8.927	294	1	15.852	0	29	27
K13	84.667	10.820	294	1	13.707	0	29	27
K14	87.333	13.511	294	1	11.505	0	29	27
K15	90	17.636	293	1	9.231	4	21	22

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Taxonomic notes on the crab spider genus *Tobias* Simon, 1895 (Araneae, Thomisidae, Stephanopinae)

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Abstract

The males of *Tobias caudatus* Mello-Leitão, 1929 and *Tobias pustulosus* Simon, 1929 are described for the first time, females are redescribed and both sexes are illustrated. New distribution records are presented for both species. *Tobias monstruosus* Mello-Leitão, 1929 is considered a junior synonym of *T. pustulosus.* The types of *Tobias albovittatus* Caporiacco, 1954, and *Tobias gradiens* Mello-Leitão, 1929 are lost, and *Tobias albicans* Mello-Leitão, 1929 and *Tobias corticatus* Mello-Leitão, 1917 are known only from poorly preserved specimens, thus they all are considered *nomina dubia.*

Key words: taxonomy, arachnology, Neotropical region, new records

Introduction

The Neotropical crab spider genus *Tobias* was proposed by Simon (1895) to include *Stephanopsis camelina* O. Pickard-Cambridge, 1869 (designated as type-species), *Thomisus cornutus* Taczanowski, 1872, *T. quinquetuberculatus* Taczanowski, 1872 and *T. rugosus* Taczanowski, 1872. Currently there are 16 valid species of *Tobias* listed in the World Spider Catalogue (2015), of which *T. gradiens* Mello-Leitão, 1929 is described only from a male, *T. albovittatus* Caporiacco, 1954 from an immature, four species are described for both sexes (*T. monstrosus* Simon in Mello-leitão, 1929, *T. paraguayensis* Mello-Leitão, 1929, *T. taczanowskii* Roewer, 1951 and *T. trituberculatus* (Taczanowski, 1872)), and the remaining 10 species were described only from females.

Tobias was considered by Simon (1895) as closely related to *Onocolus* Simon, 1895 based on the recurved anterior eye row, median eyes smaller than lateral eyes and by the proximity between these latter ones. However, *Tobias* can be distinguished from *Onocolus* by the prosoma shape, which is slightly longer and higher in the thoracic region, by the higher clypeus (about five times the diameter of AME) and by the opisthosoma with lateral and median projections (Simon 1895; Mello-Leitão 1929). Despite these characteristics, the taxonomic status of *Tobias* remained uncertain due its resemblance with other Stephanopinae genera, such as *Epicadinus* Simon, 1895, *Epicadus* Simon, 1895 and *Stephanopis* O. Pickard-Cambridge, 1869.

In this paper, we describe the males of *T. caudatus* Mello-Leitão, 1929 and *T. pustulosus* Simon, 1929 for the first time, and the females of both species are redescribed. *Tobias monstrosus* Mello-Leitão, 1929 is proposed as a junior synonym of *T. pustulosus*. New distribution records are presented for both species. Based on morphological data, we also provide a brief discussion on the taxonomic status of the genus.

Material and methods

The examined material belongs to the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCTP, A.A. Lise), Museu de Ciências Naturais da Fundação Zoo Botânica do Rio Grande do Sul, Porto Alegre (MCN, R. Ott), Museum of Comparative Zoology of Harvard, Cambridge (MCZ, G.

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Giribet and L. Liebensperger), Muséum National D' Histoire Naturelle, Paris (MNHN, C. Rollard), Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ, A. B. Kury), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha). The terminology used in this study follows Lise (2005) for structures of body, Bonaldo (2000) in using the term "primary spermatecha" to designate the structures where the fertilization ducts are connected and "secondary spermatecha" to structures attached to copulatory ducts, and Teixeira and Lise (2012) for male genitalia wherein the left palp was used as model and the clock hours to express the disposition of some structures. All measurements are in millimeters. The male palp and female epigynum were dissected, submerged in proteolytic enzyme during 48 hours in order to eliminate soft tissues, and subjected to scanning electronic microscopy. Photos were taken by a Multipurpose Zoom Microscope Nikon AZ100M and scanning electron microscopy was conducted with a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (CEMM) of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS).

Morphology abbreviations: ALE—anterior lateral eyes, AME—anterior median eyes, DTA—distal tibial apophysis, MOQ—median ocular quadrangle, PLE—posterior lateral eyes, PME—posterior median eyes, RTA—retrolateral tibial apophysis.

Taxonomy

Thomisidae Sundevall, 1833

Stephanopinae O. Pickard-Cambridge, 1871 (*sensu* Ono 1988)

Tobias Simon, 1895

Tobias Simon, 1895: 1053. Mello-Leitão 1929: 80, pl. 2, figs 183–196.
Type species. *Tobias camelinus* (O. Pickard-Cambridge, 1869) by original designation.

Diagnosis. *Tobias* species resemble those of *Epicadus* in the high thoracic region with a median spire and conical abdominal projections (this latter character is shared with *Epicadinus* as well), and *Stephanopis* in the wood bark-like aspect of body with organic particles attached. However, *Tobias* can be distinguished by the quadratic aspect of legs, with patellae, tibiae, metatarsi and tarsi with truncated corners, ventrally and laterally compressed; conical ventral and dorsolateral tubercles on femora I and II and presence of sensorial pits on tibiae and metatarsi. Females have epigynal plate with sclerotized edges joining on the middle to form a median septum; copulatory ducts long, sclerotized; two pairs of spermatecae. Male palp holds an elongated and canoe-shaped RTA fused at its basis to a short, acute and curved DTA.

Description. Medium size spiders, males about five times smaller than females (total length 2.56–3.22 in males and 8.28–15.42 in females). General body coloration yellow with black stains or stripes on prosoma and legs, or predominantly dark-brown. Prosoma as long as wide, with rough surface and needle-shaped setae on spherical sockets; prosoma may bear a distinct white spot on thoracic region with a longitudinal black line to the middle of PME. Clypeus high (about five times the diameter of AME), eyes subequal in size, arranged in a recurved anterior row and slightly procurved posterior row. Chelicerae armed with three promarginal and two retromarginal teeth; endites longer than wide, rounded on the edge, with a scarce promarginal scopula; labium short, truncated; sternum scutiform with concave anterior border. Opisthosoma with five or three remarkable projections (four or two lateral ones and a single median posterior) and straight to concave anterior border. Legs I, II and III anteriorly oriented and leg IV posteriorly oriented; anterior legs larger and stouter than posterior ones, the dorsal surface of tibiae and tarsi with a proximal and a distal depression with many duster-shaped setae surrounding a group of 5–7 trichobothria (sensorial pit); tibiae and tarsi I and II with three pairs of strong ventral macrosetae. Epigynum shows long copulatory ducts with enlarged upper curve, forming a kidney-shaped secondary spermateca; primary spermateca rounded or kidney-shaped, fertilization ducts thin and laterally curved. Male palp characterized by a peer-shaped cymbium and a filiform embolous encircling the discoid tegulum.

Tobias caudatus **Mello-Leitão, 1929**
Figs 1–11

Tobias caudatus Mello-Leitão, 1929: 88, figs 187–188.

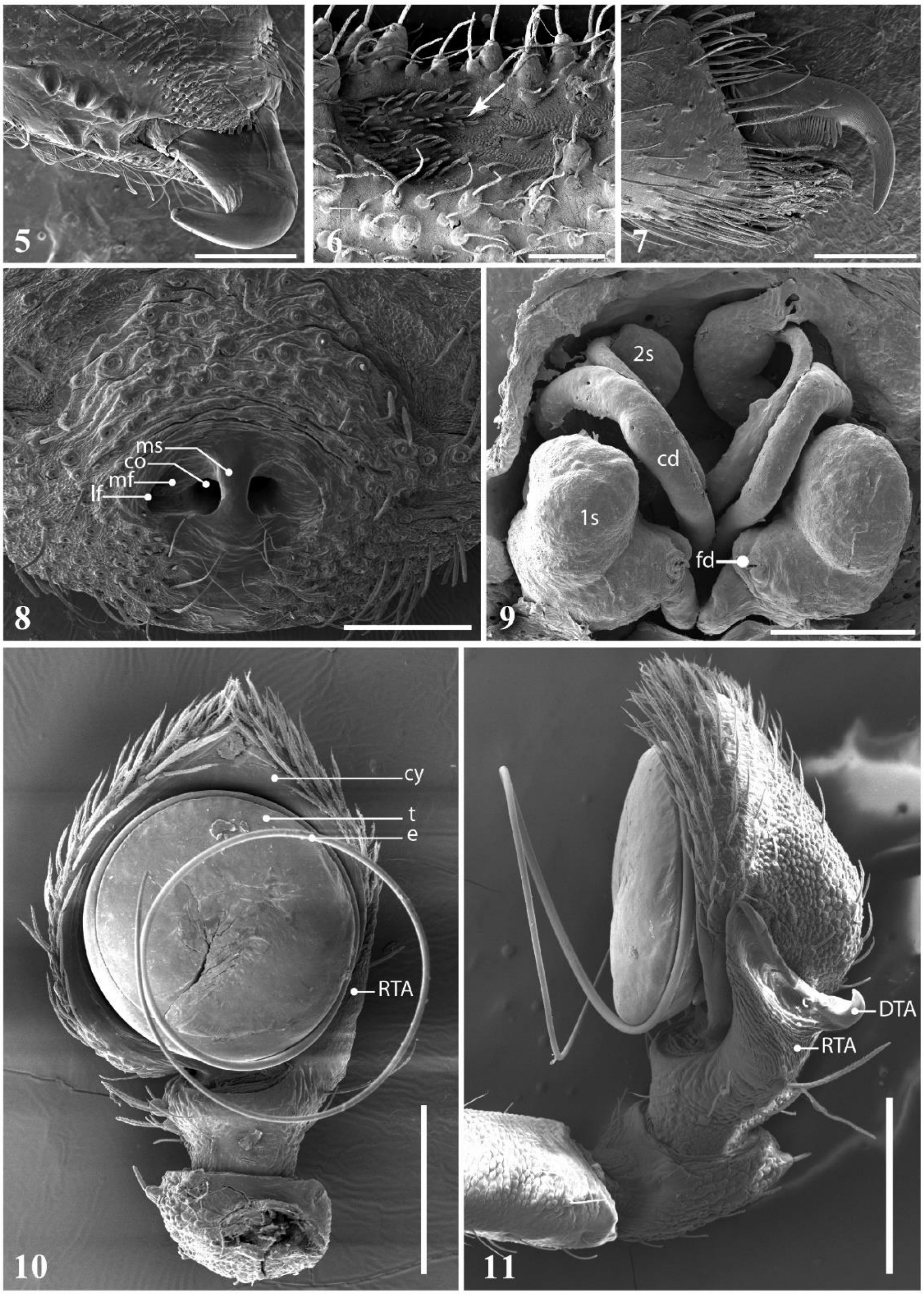
Type material: Holotype (designated by Mello-Leitão, 1929): female, Tijuca [22°57'31.38"S, 43°16'38.56"W, Rio de Janeiro, Rio de Janeiro, Brazil] (MNHN 26036).

FIGURES 1–4. *Tobias caudatus* Mello–Leitão, 1929. 1–3 habitus dorsal; 4 anterior view of the prosoma and ventral region of the left femur I and II (1 and 4 female MCTP 7593, 2 female MCTP 6100, 3 male MCTP 240). Scales: 1mm. White arrow indicates the reddish–brown setiferous tubercles.

Other material examined. PUERTO RICO: ***Mora*****:** 1 female, 18°27'6.76"N, 66°59'15.86"O (A. Schwartz leg., 22 February 1965, MCZ 700). **BRAZIL:** ***Amazonas*****:** 1 female, Benjamin Constant, 4°22'27.79"S, 70° 1'46.99"W (Parko leg., April 1942, MNRJ 2698). ***Bahia:*** 1 female, Itamaraju, 17°2'38.00"S, 39°31'48.00"W (J.S. Santos leg., 7 August 1978, MCN 10690). ***São Paulo*****:** 1 female, Ilha de Búzios, 23°46'35.00"S, 45°21'10.00"W (Zoology department expedition field leg., October 1963, MZSP 11420). ***Paraná:*** 1 male, Morretes, 25°28'31.00"S, 48°49'45.00"W (A. A. Lise leg., 9–20 January 1995, MCTP 7092). ***Santa Catarina*****:** Florianópolis, Reserva Biológica do Arvoredo, 27°17'0.00"S, 48°22'0.00"W, 1 female, 16 October 1993, 1 female, 14 October 1994, 1 female, 6 October 1995, all material leg. A.A. Lise (MCTP 4082, 5120, 7593). ***Rio Grande do Sul*:** 1 female, Derrubadas, Parque Estadual do Turvo, 27°14'60.00"S, 53°52'0.00"W (R. Ott leg, 4–8 May 2004, MCN 38865); 1 female, Iraí, 27°10'60.00"S, 53°15'0.00"W (S. Scherer leg., 19 November 1975, MCN 8130); 1 female, same locality as previous specimen (A. A. Lise leg., 20 November 1975, MCN 8133); 1 female, Nonoai, Parque Estadual de Nonoai, 27°20'48.63"S, 52°45'59.67"W (A. A. Lise leg., 19–24 January 1989, MCN 13075); 1 female, São Borja, 28°11'2.00"S, 55°38'20.00"W (H. Bischoff leg., 10 November 1979, MCN 8670); 1 female, Itaara, 29°34'60.00"S, 53°46'60.00"W (E. L. C. Silva leg., 23 November 2006, MCTP 28508); 1 male, Santa Maria, Cidade dos Meninos, 29°40'41.58"S, 53°43'17.89"W (C. Kotzian & L. F. Indrusiak leg., 7 November 1995, MCTP 10470); 1 female, Novo Hamburgo, 29°41'0.00"S, 51° 7'60.00"W (C. J. Becker leg., 17 June 1986, MCTP 15170); 2 males, same locality as previous specimen (17 June 1988, MCTP 240); 1 female, São Leopoldo, 29°46'0.00"S, 51° 9'0.00"W (C. J. Becker leg., 19–30 July 1982, MCN 10645); 1 female, same locality as previous specimen (A. B. Bonaldo leg., 12 May 1992, MCN 24756); 1 female, Glorinha, 29°52'48.00"S, 50°47'45.00"W (A. B. Bonaldo leg., 14 July 2000, MCN 33052); 1 female, Triunfo, 29°55'60.00"S, 51°42'60.00"W (M. A. L. Marques leg., 28 November 1989, MCN 18999); 1 male, Eldorado do Sul, 30°6'41.38"S, 51°37'50.68"W (A. Braul & C. Aveiróz leg., 18–19 September 1993, MCTP 4133); 1 female, Cachoeira do Sul, 30°1'60.00"S, 52°53'60.00"W (R. G. Buss leg., 27 May 1995, MCTP 6100); 1 female, Porto Alegre, Parque Estadual Delta do Jacuí, 30°1'60.00"S, 51°12'0.00"W (I. Heidrich leg., 26 August 1999, MCN 31483); 1 female (8 July 1999, MCN 31337); 1 male, Viamão, 30° 4'60.00"S, 51° 1'60.00"W (N. J. Ferla leg., 8 December 1992, MCTP 2826); 1 female, same locality as previous specimen (A. Braul leg., 10 October 1993, MCTP 3933); 1 male, same locality as previous specimen (A. A. Lise leg., 17 December 1995, MCTP 8092); 1 male, São Sepé, 30°10'0.00"S, 53°34'0.00"W (E. C. Costa leg., 6 February 1994, MCTP 10246).

Diagnosis. Females of *T. caudatus* resemble those of *T. pustulosus* in the brownish body coloration (Figs 1–2), presence of remarkable setiferous tubercles on femora I and II—the dorsal and lateral tubercles are long and conical, while the ventral tubercles are short and rounded. However, females of *T. caudatus* differ from *T. pustulosus* and other species of *Tobias* by the reddish coloration of the ventral setiferous tubercles of femora I and II (Fig. 4), by the narrow median septum on epigynum, and by the lateral folds delimiting the median field (Fig. 8). Males can be distinguished by yellowish granules on prosoma, yellow half-moon shaped spots on the dorsum of the opisthosoma (Fig. 3), RTA canoe-shaped, deeper, with larger borders than in other species of *Tobias* and by the DTA with curvature directed upwards (Fig. 11).

Description. Female (from Santa Catarina; MCTP 7593): Anterior eye row recurved and posterior row slightly procurve. Prosoma brown with irregular dark-brown spots on the dorsal and lateral regions (Fig. 1). Posterior slope slightly lighter than other regions of the prosoma. Clypeus height 0.65. Chelicerae with three teeth on the promargin and two on the retromargin (Fig. 5). Coloration of chelicera and palp as in prosoma. Sternum, endites and labium reddish-brown. Sternum covered by needle-shaped and feather-shaped setae, scutiform, with anterior margin concave. Endites rounded, with scarce setae on promargin and labium short. Cuneiform opisthosoma with anterior margin slightly concave and three posterior projections, being a pair of lateral projections with the apex directed forward, and a median projection rounded and long (Fig. 1). Abdominal surface rough, granular, dark-brown on the dorsum and light-brown on the anterior lateral margins and along the median projection (Fig. 1). Legs in transverse view square-like, with brown spotted coloration and distinct yellow parts at the distal portion of femur I and proximal portion of tibia I. All femora are covered with setiferous tubercles, with the biggest ones on femora I. The setiferous tubercles on the dorsum and lateral sides of the femora are long and conical, whereas those on the ventral portion of femora I and II are short and rounded and reddish-brown. Tibiae and metatarsi I and II have three pairs of ventral macrosetae. Tibiae, metatarsi and tarsi show a dorsal depression containing a group of trichobothriae and surrounded by many duster-shaped setae (sensorial pit) (Fig. 6). Tarsi ending in scarce scopula. All tarsal claws strongly curved with the first tooth longer and stronger than the remaining teeth (Fig. 7). Epigynum with lateral folds delimiting the median field, copulatory openings separated by a median septum, joined with the lateral folds in the anterior region (Fig. 8). Copulatory ducts long with two pairs of kidney-shaped spermatecae, primary spermatecae are at least two times larger than the secondary pair, with porous surface (Fig. 9). Measurements: eyes diameters and eyes interdistances: AME 0.17, ALE 0.18, PME 0.15, PLE 0.14, AME-AME 0.40, AME-ALE 0.20, PME-PME 0.54, PME-PLE 0.24. MOQ length 0.70, MOQ posterior width 0.65, MOQ anterior width 0.64; leg formula: 1243: leg I—femur 5.92/ patella 3.17/ tibia 3.84/ metatarsus



FIGURES 5–11. *Tobias caudatus* Mello–Leitão, 1929. 5 apex of the left chelicera, anterior and posterior row of teeth and fang; 6 detail of the sensorial pit on tibia I; 7 detail of the tarsus tip and retrolateral claw; 8 epigynum ventral view; 9 epigynum dorsal view; 10 palp ventral view; 11 palp retrolateral view (5–7 female MCTP 813, 8–9 female MCTP 5120, 10–11 male MCTP 1024). Scales: 0.25mm. White arrow indicates the duster-shaped setae. cy—cymbium, DTA—dorsal tibial apophysis, e—embolus, RTA—retrolateral tibial apophysis, t—tegulum, ms—median septum, co—copulatory openings, mf—median field, lf—lateral fold, 1s—primary spermatecae, 2s—secondary spermatecae, cd—copulatory duct, fd—fertilization duct.

2.92/ tarsus 2.00/ total 17.85; II—5.92/ 3.25/ 3.42/ 2.50/ 1.34/ 16.43; III—2.50/ 1.75/ 1.75/ 1.34/ 0.83/ 8.17; IV—2.58/ 1.84/ 2.08/ 1.58/ 1.08/ 9.16. Total length 15.42, prosoma length 5.92, width 5.75, opisthosoma length 9.50, clypeus height 0.78, sternum length 2.35, width 1.95, endites length 1.44, width 0.83, labium length 0.86, width 0.99.

Male (from Eldorado do Sul; MCTP 4133): Anterior and posterior eye rows as in female. Tegument above the ALE presents tiny horns (Fig. 3). Prosoma coloration darker than in the female. Sternum, endites and labium as in female. Patterns of coloration of the opisthosoma as in female, albeit lighter. Lateral projections on the opisthosoma straight and slightly shorter than in females. Legs I and II reddish-brown with some dark spots. Dorsal and lateral setiferous tubercles of legs as in female, ventral tubercles absent. Legs shape and tarsal claw as in females. Palp with discoid tegulum with transversal furrow at seven o'clock position (Fig. 10). Embolus long, filiform, emerging from tegulum at six o'clock position, running two and a half circles around the tegulum. RTA canoe-shaped, joined with DTA, which is hook-like, short, acute and curved upwards (Fig. 11). Measurements: eyes diameters and eyes interdistances: AME 0.06, ALE 0.07, PME 0.08, PLE 0.05, AME-AME 0.12, AME-ALE 0.08, PME-PME 0.20, PME-PLE 0.12. MOQ length 0.26, MOQ posterior width 0.24, MOQ anterior width 0.24; leg formula: 1243: leg I—femur 1.09/ patella 0.72/ tibia 0.80/ metatarsus 0.65/ tarsus 0.47/ total 3.73; II—1.03/ 0.60/ 0.71/ 0.62/ 0.52/ 3.48; III—0.59/ 0.37/ 0.45/ 0.34/ 0.31/ 2.06; IV—0.66/ 0.36/ 0.44/ 0.37/ 0.30/ 2.13; total length 3.28, prosoma length 1.50, width 1.39, opisthosoma length 1.78, clypeus height 0.28, sternum length 0.66, width 0.60, endites length 0.30, width 0.16, labium length 0.18, width 0.30.

Variation. Besides sexual dimorphism in the coloration of the opisthosoma (Fig. 3), the females (e.g. MCTP 6100) might have a darker prosoma and opisthosoma, and no yellow spots on legs. The median projection of the opisthosoma may be longer and acute (Fig. 2).

Distribution. Brazil (Rio Grande do Sul to Amazonas) and Puerto Rico (Mora) (Fig. 23).

Tobias pustulosus **Mello-Leitão, 1929**

Figs 12–22

Tobias pustulosus Mello-Leitão, 1929: 86, figs 183–184
Tobias monstrosus Simon in Mello-Leitão, 1929: 87, figs 185–186; **syn. nov.**

Type material: Holotype (designated by Mello-Leitão, 1929): subadult female, Fonte Boa [2°28'5.16"S, 66° 8'29.49"W, Amazonas, Brazil] (MNHN 4560).

Syntypes of *T. monstrosus*: 5 females from Tefé [3°21'5.31"S, 64°42'53.36"W, Amazonas, Brazil] and Caballococha [3°54'21.00"S, 70°30'59.00"W, Província de Mariscal Ramón Castilla, Loreto, Peru] (MNHN 6981).

Note. The holotype of *T. pustulosus* is a subadult female and presents a pre-epigynum with an initial outgrowth at the median field equivalent to the projection that covers the copulatory openings in adult individuals. Also, the pattern of white punctuations close to the anal tubercle, present in mature individuals, can be observed in this specimen (Figs 12–13).

Other material examined. PANAMA: ***Colón*****:** 1 female, Canal Zone: Fort Sherman, 9°21'50.49"N, 79°57'33.36"W (A. M. Chickering leg., 13 August 1936, MCZ); 1 male, (A. M. Chickering leg., 15 August 1939, MCZ); Barro Colorado Island, 9°9'7.57"N, 79°50'47.33"W, 1 male, 15 July 1934, 1 male, 7–9 July 1936, 1 subadult female, 25 July 1936, 1 male 8–9 August 1936, 1 subadult female, August 1936, 2 males, January 1958, 1 male, June 1950, 1 subadult female, 20 July 1954, 1 male, July 1939, 1 male, August 1939, 2 males, June 1950, 1 subadult female, 23–30 June 1939, 1 subadult female, 04–06 August 1939, 1 subadult female, 23 July 1936, all material leg. A.M. Chickering (MCZ). ***Panama City*****:** 1 male and 1 subadult female, Forest Reserve, 9° 8'32.19"N, 79°43'26.59"W (A. M. Chickering leg., July 1939, MCZ); Summit Park, 9°3'54.80"N, 79°38'43.07"W, 1 male and 1 female, 21–29 July 1950, 2 males and 1 female, 7 July 1950, 1 male, 13 July 1954, 1 male, 16–17 August 1950, 2 subadult males and 1 subadult female, 21–24 July 1930, 2 subadult females, 25 July 1950, 1 male, 25 July 1950, all material leg. A.M. Chickering (MCZ); 1 female, Pedro Miguel, 9° 1'7.06"N, 79°36'44.31"W (A. M. Chickering leg., 7 July 1950, MCZ); 1 male, Exp. Gardens, 9° 1'46.21"N, 79°32'37.11"W (A. M. Chickering leg., 14 July 1954, MCZ); 2 males, same locality (A. M. Chickering leg., 7 November 1954, MCZ); 1 male and 1 female, Mirasflores Locks, 8°59'50.27"N, 79°35'28.33"W (A. M. Chickering leg., 01 March 1958, MCZ); 1 male, Balboa, 8°56'60.00"N, 79°34'0.00"W (A. M. Chickering leg., August 1936, MCZ). **BRAZIL:** ***Roraima*****:** 1 male, Caracaraí

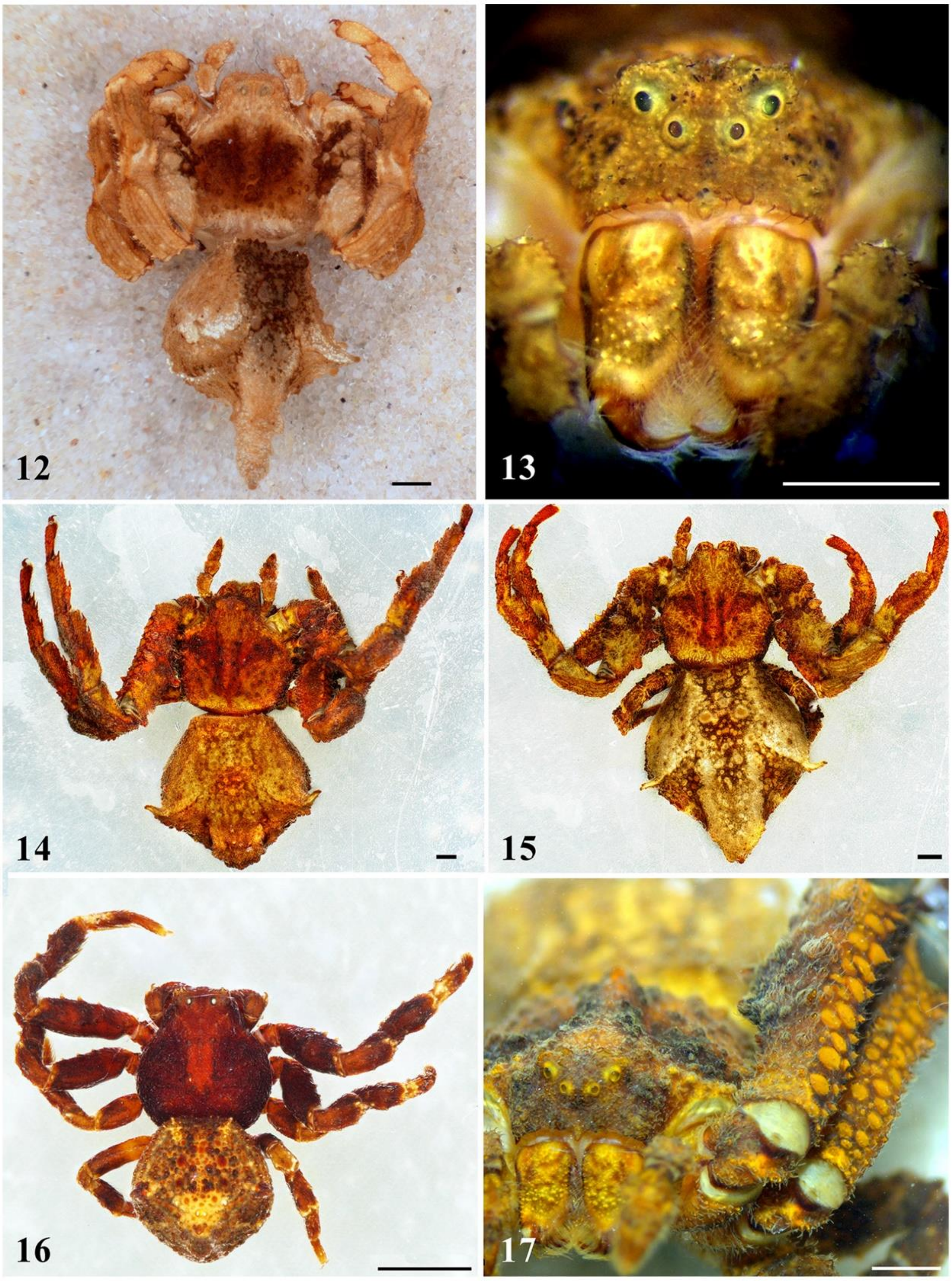
(Parque Nacional do Viruá), 1°42'12.10"N, 61° 8'54.00"W (A. Tourinho leg., 28 May 2006, INPA 1825). ***Rondônia***: 1 subadult female, Ouro Preto do Oeste, 10°36'3.00"S, 62°18'34.50"W (A. Cerruti leg., November 1983, MNRJ 4250). ***Bahia***: 1 female, Camacan, 15°26'52.59"S, 39°31'40.18"W (CEPLAC R2160 leg., 5 November 1968, MNRJ 12690); 1 female, Itamarajó, 17° 2'17.60"S, 39°32'20.31"W (J. S. Santos leg., 7 August 1978, MCN 10690). ***São Paulo***: 1 female, Iporanga, 24°29'8.94"S, 48°38'48.01"W (E. H. Wienkoski leg., October 2001, MNRJ 11520); 1 male, Cananéia, 25° 0'45.16"S, 47°56'6.98"W (E. H. Wienkoski leg., October 2001, MNRJ 11517).

Diagnosis. *Tobias pustulosus* has the same kind of setiferous tubercles on femora I and II as *T. caudatus*, but can be distinguished by the yellow color and high density of the ventral pustular setiferous tubercles (Fig. 17). The epigynum of *T. pustulosus* is distinguished from other species of *Tobias* by the anteriorly wide median septum, like an inversed triangle, and by the copulatory openings hidden by the median septum (Fig. 20). The male palp is similar to that of *T. caudatus* (Figs 10–11), but differs from the latter and other species of the genus by the presence of a basal tooth on the DTA and by its curvature, with the tip stretching to the dorsum of the cymbium (Figs 23–25).

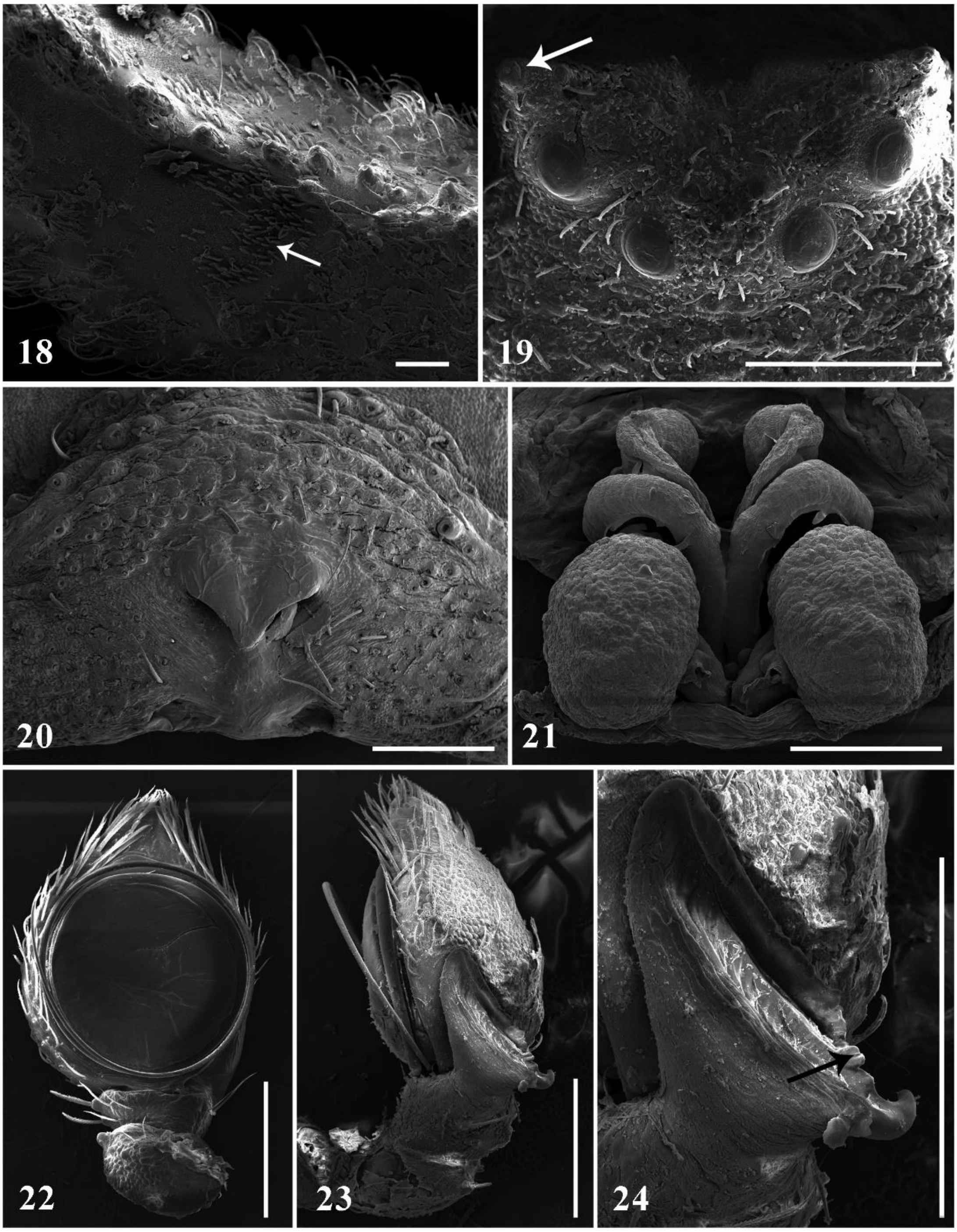
Description. Female (from Tefé; MNHN 6981): Anterior and posterior eye row as in *T. caudatus*. Prosoma light-brown with a brown Y-shaped spot on the dorsum. Chelicerae yellow, sternum brown with reddish-brown spots, endites and labium brown with a yellow apex. Opisthosoma with anterior margin straight and three posterior projections. The pair of lateral projections has the apexes directed forward and the median projection is short and rounded (Fig. 14). Opisthosoma with microstructure and coloration as in females of *T. caudatus*. Legs with shape and coloration as in females of *T. caudatus*. Femora I and II have conical and long setiferous tubercles on the dorsum and lateral regions, while the ventral portion has a high density of short and rounded yellow setae. Tibiae and metatarsi of legs I and II have both three pairs of ventral macrosetae. Sensorial pits on tibiae I and II are divided by a line of setiferous tubercles (Fig. 18). Tarsal setae tuft and claws similar to *T. caudatus*. Median field of the epigynum not delimited by lateral folds. Median septum broad on the anterior portion of the epigynal plate and covering the copulatory openings (Fig. 20). Copulatory ducts are long with two pairs of spermatecae, however the primary spermatecae are at least two times larger than the secondary pair. The primary spermatecae are kidney-shaped and the secondary are ovoid, both with a rough surface (Fig. 21). Measurements: eyes diameters and eyes interdistances: AME 0.14, ALE 0.20, PME 0.14, PLE 0.10, AME-AME 0.41, AME-ALE 0.24, PME-PME 0.60, PME-PLE 0.20. MOQ length 0.76, MOQ posterior width 0.64, MOQ anterior width 0.63; leg formula: 1243: leg I—femur 5.92/ patella 3.34/ tibia 4.08/ metatarsus 3.08/ tarsus 1.75/ total 18.17; II—5.50/ 2.92/ 4.08/ 2.50/ 1.67/ 16.67; III—2.50/ 1.92/ 2.08/ 1.42/ 1.17/ 9.09; IV—3.08/ 1.75/ 2.08/ 1.58/ 1.00/ 9.49. Total length 13.34, prosoma length 5.84 long, width 5.70, opisthosoma length 7.50, clypeus height 0.62, sternum length 2.45, width 1.95, endites length 1.36, width 0.70, labium length 0.90, width 0.94.

Male (from Cananeia; MNRJ 11517): Anterior and posterior eye row as in *T. caudatus*, and ALE with tiny horns (Fig. 19). Prosoma dark-brown with dorsum reddish-brown. Chelicerae and palpi dark-brown ending in a yellow apex. Sternum scutiform, reddish-brown; endites and labium reddish-brown with setae as in *T. caudatus*. Opisthosoma coloration similar to *T. caudatus*, but the tubercles on the surface and the posterior projections are brown (Fig. 16). Legs dark-brown with white spots on the proximal portion of metatarsi I and II and the distal portion of the patellae and tibiae I and II. Other leg characteristics as in female. Palp tegulum is flat and discoid with tranversal furrow at two o'clock. Embolus filiform emerging at twelve o' clock and extending almost two times around in the tegulum (Fig. 22). RTA similar to *T. caudatus*, but with concavity (canoe) less deep than in *T. caudatus* ending in a tooth near to the DTA base (Fig. 23). DTA is hook-like as in *T. caudatus*, but it stretches in a curve towards the back of the cymbium. Measurements: eyes diameters and eyes interdistances: AME 0.06, ALE 0.07, PME 0.06, PLE 0.04, AME-AME 0.14, AME-ALE 0.08, PME-PME 0.20, PME-PLE 0.10. MOQ length 0.24, MOQ posterior width 0.22, MOQ anterior width 0.21; leg formula: 1243: leg I—femur 1.22/ patella 0.60/ tibia 0.78/ metatarsus 0.54/ tarsus 0.42/ total 3.56; II—0.96/ 0.60/ 0.73/ 0.52/ 0.40/ 3.21; III—0.52/ 0.38/ 0.42/ 0.33/ 0.29/1.94; IV—0.70/ 0.38/ 0.50/ 0.38/ 0.34/ 2.30. Total length 2.87, prosoma length 1.42, width 1.36, opisthosoma length 1.45, clypeus height 0.24, sternum length 0.64, width 0.60, endites length 0.30, width 0.16, labium length 0.18, width 0.25.

Variation. Females (e.g. MNRJ 6807) might have a lighter coloration on the prosoma and opisthosoma. The median projection of the opisthosoma may be longer (Figs 12 and 15). This variation in size and shape of the median projection of the opisthosoma, as well as that observed in females of *T. caudatus*, is probably related to the developmental stage and/or the degree of starvation of the spider.



FIGURES 12–17. *Tobias pustulosus* Mello–Leitão, 1929. 12, 14–16 habitus dorsal; 13 anterior view of the prosoma; 17 anterior view of the prosoma and ventral region of the left femur I and II (12, 13 female MNHN 4560, 14, 17 female MNHN 6981, 15 female MNRJ 6807, 16 male MCZ). Scales: 1mm.



FIGURES 18–24. *Tobias pustulosus* Mello–Leitão, 1929. 18 detail of the sensorial pit on tibia I; 19 detail of the horn-like ocular mounds above the ALE; 20 epigynum ventral view; 21 epigynum dorsal view; 22 palp ventral view; 23 palp retrolateral view; 24 details of the canoe–shaped RTA joined with DTA (18, 20 and 21 female MCN 10690, 19 and 22–24 male MCZ). Scales: 0.25mm. White arrow indicates the duster-shaped setae and the ocular mounds; black arrow indicates the teeth at DTA.

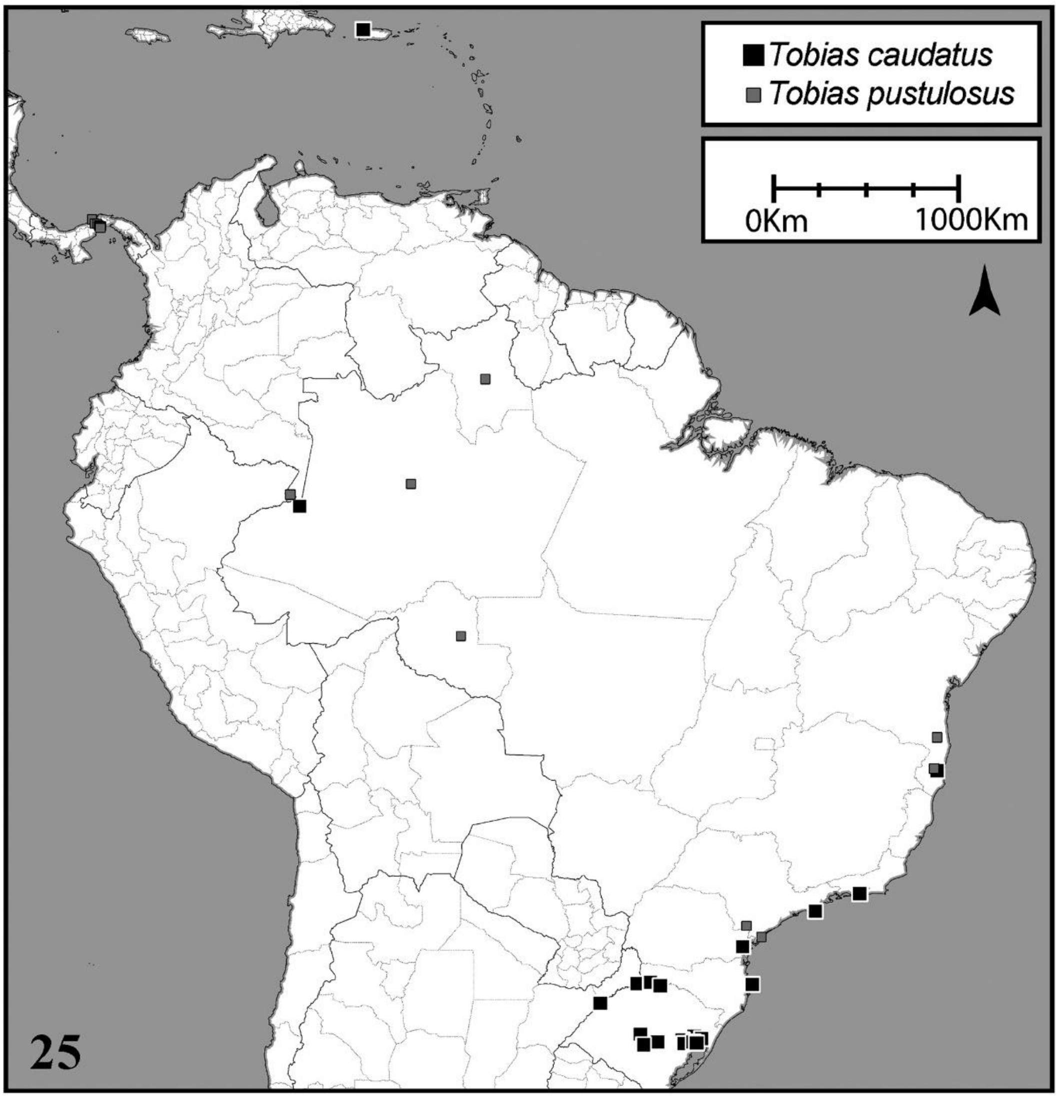


FIGURE 25. Records of *Tobias caudatus* (black square) and *T. postulosus* (grey square) from Central and South America.

Distribution. Distributional range extends from Canal Zone in Panama to the State of São Paulo in Brazil (Fig. 25).

Species inquirenda

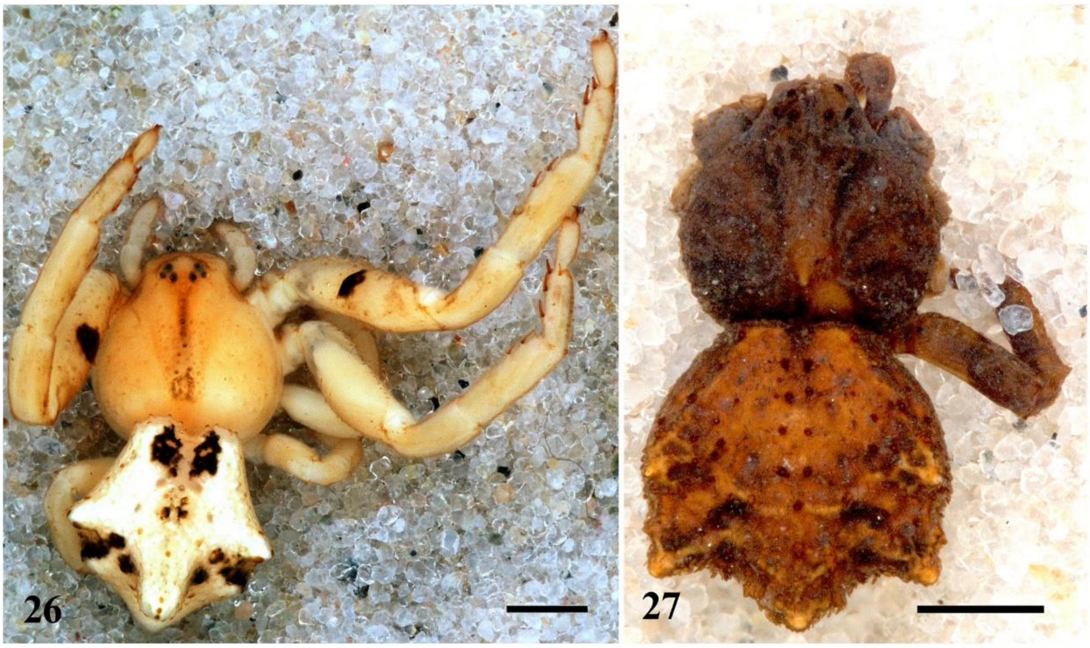
The types of the following nominal species are probably lost or immature, therefore incapable to provide an undoubtful recognition. Since the original descriptions and illustrations also do not allow such identification, these species are here considered as *nomina dubia*.

Tobias albicans Mello-Leitão, 1929
Tobias albicans Mello-Leitão, 1929: 92, fig 196 (Holotype immature from Serra do Communaty, Pernambuco, Brazil, Gounelle leg., deposited in MNHN, examined).

Tobias albovittatus Caporiacco, 1954
Tobias albovittatus Caporiacco, 1954: 131, fig. 35 (Holotype immature from Saint Jean du Maroni and Charvein, French Guiana, Benoit leg., originally deposited in MNHN, presumably lost, not examined).

Tobias corticatus Mello-Leitão, 1917
Tobias corticatus Mello-Leitão, 1917: 123 (Holotype immature from Nova Iguaçu, Rio de Janeiro, Brazil, Henrique Blanc de Freitas leg., deposited in MNRJ 915, poorly conserved, examined). Mello-Leitão, 1929: 88, f.42.

Tobias gradiens Mello-Leitão, 1929
Tobias gradiens Mello-Leitão, 1929: 89, fig. 43 (Holotype male from Petrópolis, Rio de Janeiro, Brazil, Altino de Azevedo Sodré leg., deposited in MNRJ 367, presumably lost, not examined).



FIGURES 26–27. Dorsal habitus of *Tobias* species with immature holotypes. 26 *Tobias albicans* Mello-Leitão, 1929 (Holotype from MNHN); 27 *Tobias corticatus* Mello-Leitão, 1917 (Holotype from MNRJ 915).

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