

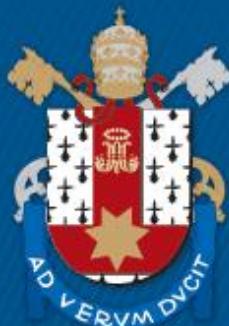
ESCOLA DE CIÊNCIAS DA SAÚDE E DA VIDA  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO DA BIODIVERSIDADE  
MESTRADO EM ECOLOGIA E EVOLUÇÃO DA BIODIVERSIDADE

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**FILOGENIA DE ACENTROSCELUS SIMON, 1886 (ARANEAE: THOMISIDAE) E A  
EVOLUÇÃO DO NANISMO NAS ARANHAS CARANGUEJO**

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**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**

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**DISSERTAÇÃO DE MESTRADO**

**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**

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**Orientador: Renato A. Teixeira**

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**PORTO ALEGRE – RS – BRAZIL**

**2020**

“Dejemos por lo tanto de divagar y continuemos tejiendo,  
como una araña laboriosa que trabaja desde la mañana hasta el atardecer  
y que no cesa en su empeño de concluir su telaraña fina y casi imperceptible,  
el hilo de nuestro relato”

Mario Mendoza

A todos aqueles loucos que agora  
começam a incursionar neste  
surpreendente e magnífico universo da  
aracnologia. Bem-vindos a uma vida de  
confusão, infortúnios, choros, raiva,  
interrogantes, mas sobretudo assombro,  
conhecimento, alegria e êxtase.

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## RESUMO

*Acentroscelus* é um gênero de aranhas neotropicais pertencentes à tribo Tmarini, caracterizadas principalmente por seu pequeno porte. Atualmente o conhecimento do gênero encontra-se limitado às descrições taxonômicas originais das onze espécies descritas. A fim de testar as relações evolutivas do gênero e destrinchar a classificação taxonômica das suas espécies, realizamos uma análise filogenética, a revisão taxonômica do grupo, e mediante o uso de ferramentas morfométricas fizemos aNoteções integrativas sobre duas espécies de *Acentroscelus*. Para isto, nosso trabalho foi dividido em três fases principais. A primeira fase corresponde à validação taxonômica de *Acentroscelus ramboi* e *Acentroscelus versicolor*, cujas descrições foram feitas originalmente em base à morfologia das fêmeas e seus machos eram desconhecidos. Por esta razão, quisemos avaliar a disparidade dos machos, que apresentam uma alta semelhança morfológica. Com os resultados do teste feito a partir do uso de marcos anatômicos na carapaça e no pedipalpo dos machos destas duas espécies, ratificamos a validade taxonômica, encontrando que além da clara diferença das fêmeas, os machos de *A. ramboi* possuem o prossoma mais largo e achatado do que os machos de *A. versicolor*; e apresentam a apófises ventral da tibia (VTA) mais fina na base e seu ramo ectal mais curvo. A segunda fase corresponde à análise filogenética feita em base a caracteres morfológicos. Neste teste confirmamos a monofilia do grupo avaliado, porém, encontramos o clado subdividido em três grupos. Baseados nestes clados, propusemos a subdivisão de *Acentroscelus latu sensu* em três gêneros diferentes: *Maeanderion*, *Whittickius* e *Acentroscelus*. Além de brindar a primeira aproximação sistemática do grupo, avaliamos o tamanho corporal nas espécies da tribo Tmarini inclusas na análise, descrevendo o clado *Acentroscelus latu sensu* como aranhas em condição de miniaturização. Por último, a terceira fase esteve constituída pela revisão taxonômica de *Acentroscelus latu sensu*. Diagnosticamos e descrevemos *Maeanderion*, com *Maeanderion peruvianus* (Keyserling, 1880) como única espécie do gênero. Além disso, revalidamos o gênero amazônico *Whittickius* Mello-Leitão, 1940 com *W. singularis* Mello-Leitão, 1940 como espécie tipo; redescrivemos dentro deste gênero *W. granulosus* e *W. guianensis*, cujo macho foi descrito pela primeira vez; e descrevemos duas espécies novas: *W. caxiuana* e *W. echinithorax*. *Acentroscelus stricto sensu* foi redescrito junto com suas cinco espécies, distribuídas na Mata Atlântica: *Acentroscelus albipes*, *Acentroscelus versicolor*, *Acentroscelus ramboi* e duas espécies novas. *Acentroscelus muricatus* foi considerado sinônimo junior da espécie tipo *A. albipes*.

**Palavras chave:** Neotrópico; miniaturização; macroevolução

## ABSTRACT

*Acentroscelus* is a genus of neotropical spiders belonging to the Tmarini tribe and characterized by its small size. Currently, knowledge of this genus is limited to the original taxonomic descriptions of its species. In order to test the evolutionary relations of the genus and to unravel the taxonomic classification of its species, we performed a phylogenetic analysis, the taxonomic revision of the group, and through the use of morphometric tools we made integrative notes on two species of *Acentroscelus*. For this, our work has been divided into three main phases. The first phase corresponds to the taxonomic validation of *Acentroscelus ramboi* and *Acentroscelus versicolor*, whose descriptions were originally made based on the morphology of females and their males present a high morphological similarity. Assessing the carapace and pedipalp of males of these two species, we obtained a clear disparity. With the results of the test made from the use of anatomical landmarks we ratified the taxonomic validity, finding that besides the clear difference of the females, the males of *A. ramboi* have the prosoma wider and flatter than the males of *A. versicolor*; besides presenting the ventral apophysis of the tibia (VTA) thinner at the base and its ectal branch more curved. The second phase corresponds to the phylogenetic analysis based on morphological characters. In this test we confirmed the monophily of the evaluated group, but we found the clade subdivided into three groups. Based on these clades, we proposed the subdivision of *Acentroscelus* latu sensu into three different genera: *Maeanderion*, *Whittickius* and *Acentroscelus*. In addition to the first systematic approach of the group, we evaluated the body size in the Tmarini species included in the analysis, describing the clado *Acentroscelus* latu sensu as spiders in miniaturization condition. Finally, the third phase was the taxonomic revision of *Acentroscelus* latu sensu. We diagnosed and described *Maeanderion*, with *Maeanderion peruvianus* (Keyserling, 1880) as the only species of the genus. Besides, we revalidated the Amazonian genus *Whittickius* (Mello-Leitão, 1940) with *W. singularis* (Mello-Leitão, 1940) as a type species; we re-described inside this genus *W. granulosus* and *W. guianensis*, whose male was described for the first time; and we described two new species: *W. caxiuana* and *W. echinithorax*. *Acentroscelus* stricto sensu was re-described together with its five species, distributed in the Atlantic Forest: *Acentroscelus albipes*, *Acentroscelus versicolor*, *Acentroscelus ramboi* and two new species. *Acentroscelus muricatus* has been considered as junior synonym of the species type *A. albipes*.

**Key words:** Neotropic, miniaturization; macroevolution

## INTRODUÇÃO GERAL

### Introdução

#### *Estado taxonômico e sistemático do grupo*

As aranhas pertencentes à família Thomisidae são comumente conhecidas como aranhas-caranguejo devido a seu aspecto geral, atribuído a possuir as pernas I e II maiores e mais robustas que as pernas III e IV. Caracterizam-se também por apresentar os olhos sobre tubérculos, presença de uma apófise retrolateral e ventral na tíbia do palpo do macho e tégulo em forma de disco (Ono 1988).

Na atualidade, Thomisidae encontra-se classificada em seis subfamílias: Aphantochilinae, Bominae, Dietinae, Stephanopinae, Stiphropodinae e Thomisinae (Ono 1988; Teixeira et al. 2014). A distribuição geográfica desta família é cosmopolita, porém, a maior diversidade encontrasse na região tropical e subtropical. No Neotrópico encontram-se representantes de quatro das seis subfamílias, sendo Thomisinae a maior do grupo.

Apesar de ser a sétima maior família de aranhas, 2148 espécies descritas em 170 gêneros (WSC 2019), o conhecimento sistemático e filogenético de Thomisidae ainda é precário. Existem apenas quatro trabalhos filogenéticos focados na família, sendo dois testando a monofilia da família e algumas relações supragênericas (Benjamin et al. 2008 e 2011) e outros dois centrados em testar a monofilia de gêneros e seus grupos irmãos (Teixeira et al. 2014 e Machado et al. 2017).

Uma das tribos que compõem esta subfamília Thomisinae é Tmarini (Ono 1988). Embora não se tenha realizado nenhuma análise cladística da tribo, a filogenia de Araneae — apresentada por Wheeler e colaboradores (2017) — recuperou o grupo como monofilético no “Clado Thomisus”; composto por *Acentroscelus*, *Titidius*, *Monaeses* e *Tmarus*.

*Acentroscelus* Simon, 1886 caracterizado principalmente por seu pequeno porte, céfalon-tórax alto, mais longo que largo, com clípeo vertical, e margem posterior inclinada e com cerdas na borda (Keyserling 1880). Também apresenta tegumento coriáceo e granuloso, pernas delgadas e míticas, e um abdômen ovalado (Mello-Leitão 1929). As fêmeas apresentam duas espermatecas reniformes e, os machos, tibias do palpo com apófises retrolaterais tangentes à apófise ventral (Rinaldi 1984).

O gênero é atualmente composto por 11 espécies neotropicais com uma distribuição geográfica desde Guiana Francesa à Argentina (WSC 2019). A espécie-tipo de *Acentroscelus* (*A. albipes* Simon, 1886) foi descrito originalmente da Serra do Caraça em Minas Gerais, e neste mesmo trabalho *Acanthonotus peruvianus* Keyserling, 1880 e *Acanthonotus guianensis* Taczanowski, 1872 foram combinadas à *Acentroscelus*. As demais espécies foram descritas ao longo da primeira metade do século XX. Mello-Leitão (1929) descreveu *Acentrocelus granulosus*, *A. nigrianus* e *A. secundus* a partir de espécimes da Bahia, Amazonas e Rio de Janeiro, respectivamente. Depois, Soares (1942) descreveu *Acentroscelus versicolor* de um espécime de São Paulo. E na sequência, *Acentroscelus ramboi* é descrito do Rio Grande do Sul (Mello-Leitão 1943a), *Acentroscelus gallinii* de Cóboda (Mello-Leitão 1943b) e *Acentroscelus muricatus* de Minas Gerais (Mello-Leitão 1947). A última espécie assignada à *Acentroscelus* foi combinada a partir de *Whittickius singularis* Mello-Leitão, 1940 (Rinaldi 1984). Como *Whittickius* era um gênero monotípico, ele foi considerado sinônimo júnior de *Acentroscelus*. Segundo Rinaldi (1984), a presença de tubérculos na margem posterior do cefalotórax e as espermatecas reniformes eram características que sustentavam a sinonímia de *Whittickius*.

### *Miniataturização*

O tamanho corporal é uma característica evidente dos organismos, que está ligada a diferentes fatores intrínsecos e extrínsecos, como a nutrição, pressões ambientais, e inclusive tendências evolutivas (Goulde e MacFadden 2004). Um dos casos mais conhecidos na evolução do tamanho corporal é o fenômeno conhecido como nanismo ou “miniaturização”, representado pela redução no tamanho corporal em um grupo taxonômico, que pode incluir redução e simplificação estrutural (Hanken 1993). Este fenômeno por sua vez tem importantes impactos na maioria das características principais da história da vida das espécies, incluindo o crescimento, o cuidado maternal, o intervalo de dispersão e o grau de especificidade do habitat (Rainford 2016). Da mesma maneira o nanismo pode determinar a diversificação filogenética de um grupo supraespecífico, tanto que Gould e MacFadden (2004) sugerem que estudos de evolução do tamanho corporal devem estar intimamente ligados a uma filogenia antes de ser capaz de distinguir se o tamanho realmente está relacionado à história evolutiva do táxon ou a outros fatores ambientais, genéticos ou individuais da população.

Em aranhas, o estudo do nanismo tem sido tratado principalmente como parte do dimorfismo sexual exibido em algumas espécies ou grupos de espécies. Esta característica é mais comumente vista em aranhas orbiculares (e.g. Araneidae e Tetragnathidae) e aranhas caranguejo (e.g. Thomisidae) (Hormiga 2000); porém, o nanismo também ocorre quando representantes dos dois sexos são anões e sua evolução não é necessariamente regida por mecanismos de seleção sexual (Wildish 2016).

Apesar de haver casos de nanismo em espécies de Thomisidae — como mostra Dodson (2015) em *Misumenoides formosipes* —, isso só foi estudado como característica típica dos machos, por causa do dimorfismo sexual existente no grupo. Até o momento, não há trabalhos que estudem a evolução deste caractere em grupos onde machos e fêmeas apresentam um tamanho corporal reduzido. Entretanto, existem descrições de aranhas caranguejo que são particularmente pequenos, como os organismos da subfamília Bominae e Stiphropodinae, e as aranhas do gênero *Acentroscelus* (e.g., Lawrence, 1952; Rinaldi, 1984; Dippenaar-Schoeman, 1986; 1989; Ono, 1988; Szymkowiak & Królikowska, 2017; Benjamin & Ranasinghe, 2019).

Embora este gênero nunca tenha sido assignado como anão, suas espécies são descritas como pequenas e pouco dimórficas. Além disso, comparando o tamanho corporal das espécies de *Acentroscelus* com as dos demais gêneros da tribo Tmarini, podemos ratificar o tamanho minúsculo que seus indivíduos possuem. O que torna estes organismos um bom modelo para avaliar a condição de miniaturização em aranhas.

## Objetivos

- Testar a monofilia de *Acentroscelus*
- Testar, a partir de uma abordagem morfométrica, a validade de duas espécies de *Acentroscelus* com machos crípticos.
- Revisar a taxonomia do gênero, atualizando as descrições das espécies e descrevendo possíveis novas espécies.
- Testar se a miniaturização de *Acentroscelus* representa uma condição plesiomórfica ou derivada na tribo Tmarini

## Estrutura da dissertação

A fim de desenvolver os objetivos planteados, o corpo do trabalho encontra-se distribuído em três capítulos redigidos em inglês e formatados para submissão à diferentes revistas. Os capítulos ainda não foram enviados à revisão linguística e, portanto, podem conter pequenos erros gramaticais. Os capítulos estão organizados em

ordem de prioridade para publicação; portanto, os capítulos posteriores podem citar os anteriores. Uma vez que os capítulos ainda não foram publicados, eles são citados como “und. sub.” (=*undergoing submission*).

O capítulo 1, intitulado **“Who is more taxonomically informative, males or females of tiny crab spiders? The use of geometric morphometric for testing the validation of two species of the genus *Acentroscelus* (Araneae: Thomisidae)”**, está formatado para ser submetido na revista *Zoologischer Anzeiger*. Aqui descrevemos pela primeira vez os machos de *Acentroscelus ramboi* e *A. versicolor*, partindo da incerteza deles representarem as referidas espécies, devido à grande semelhança da morfologia entre eles. Mediante o uso da morfometria geométrica encontramos evidências que mostram a diferença dos indivíduos pertencentes às duas entidades, atualizamos a taxonomia destas espécies e discutimos a importância da utilização de outras ferramentas e evidências que contribuem ao conhecimento taxonômico das aranhas.

O capítulo 2, intitulado **“Phylogenetic analysis of tiny crab-spiders of *Acentroscelus* (Araneae: Thomisidae) and a small foray into their miniaturized world.”**, está formatado para ser submetido na revista *Organism Diversity and Evolution*. Neste capítulo avaliamos a monofilia de *Acentroscelus* através de uma análise filogenética, baseada em caracteres morfológicos. Usando duas abordagens foram resgatados três clados independentes, que forneceram evidências para propor mudanças taxonômicas no grupo. Assim, aqui propomos a criação de um novo gênero e a revalidação de *Whittickius*. Adicionalmente, usando a topologia mais congruente, avaliamos o tamanho corporal em função de comprimento da carapaça

O capítulo 3, intitulado **“Neotropical tiny crab–spiders of the tribe Tmarini: a revision of *Acentroscelus*, *Whittickius* and *Maeanderion*.”**, está formatado para ser submetido na revista *Zootaxa*. Aqui realizamos a descrição taxonômica dos três gêneros propostos na análise filogenética: *Maeanderion*, *Whittickius* e *Acentroscelus*. Redescrevemos e fizemos as diagnoses de cada uma das espécies que compõem estes três grupos e descrevemos quatro novas entidades. Adicionalmente, com a comparação dos tipos nomeamos *Acentroscelus muricatus* como sinônimo júnior de *Acentroscelus albipes*, e atribuímos a categoria de *species inquirenda* a três das espécies de *Acentroscelus* descritas em base de material juvenil. Por último foi realizada uma atualização dos registros geográficos das espécies dos três gêneros.

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**<sup>1</sup>CHAPTER 1: Are *Acentroscelus* males informative to define species? Case study of two species of tiny crab spiders with cryptic males.**

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**Abstract**

The shape of copulatory structures in spiders (i.e., epigyne and palps) is essential to recognize the different species. However, species with a wide geographical distribution may have variations in copulatory structures in one or both sexes. In Thomisidae the species *Acentroscelus ramboi* and *Acentroscelus versicolor* are described for females, whose epigyne are markedly distinct. However, the males found with the females of both species have very similar copulatory structures. It is doubtful if these species are a single species in which the females have variable epigyne, or two species with males with very similar male palps. These two species present a sympatric distribution just in the end of Atlantic forest, in the limit between Paraguay, Argentina and Brazil. In order to test these hypotheses, we use geometric morphometric tools, evaluating the disparity of the cephalothorax and the male palpus. A sample of 46 male individuals deposited in biological collections was used. Their identification was made based on the females with which they were collected. With the data analyzed we found a distinction in the shape of the cephalothorax and both in the size and shape of the male palpus. For this reason, here we decided treat these two entities like different species and we present a diagnosis of these two species, including for the first-time characteristics of the males.

**Keywords.** Integrative taxonomy, Neotropic, crab-spider

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<sup>1</sup> Este capítulo está redigido em inglês e formatado para submissão na revista Zoologischer Anzeiger.

## 1. Introduction

Since the creation of the Linnean system of classification, morphological variations have been used by taxonomists to describe and discriminate species. However, some animal groups have few morphological variations and the apparition of cryptic species are more common in the last few years (Struck and Cerca, 2019). Owing to these problems, “integrative taxonomy” appeared as a discipline that integrates different kinds of information for delimiting species (Dayrat, 2005; Pante et al., 2015). Geometric morphometrics has become a commonly tool in different animal groups to study morphologically stable genus (Hulme-Beaman et al., 2018; Karanovic et al., 2016; Zúñiga-Reinoso and Benítez, 2015). This methodology had been used in spiders to answer questions related to sexual dimorphism (Fernández-Montraveta and Marugán-Lobón, 2017), variation of somatic (Bond and Beamer, 2006) and sexual characteristics (Crews, 2009), and as a resource of information to differentiate between species (Spasojevic et al., 2016).

In the last decade, efforts to study Neotropical tomisids have been focused mainly on groups belonging to the Stephanopinae subfamily (Do Prado et al., 2018; Machado et al., 2019a, 2019b, 2017b, 2017a; Machado and Teixeira, 2015). However, the greater diversity of the family is represented by the Thomisinae subfamily (World Spider Catalog, 2019). A genus of this group is *Acentroscelus* Simon, 1895, composed of eleven valid species, distributed from the French Guiana to Argentina (World Spider Catalog, 2019). This group of tiny spiders are characterized by its small size, modification in the posterior zone of the cephalothorax as, inclined margin and projections on the edge (Keyserling, 1880), and punctured surface and thin and mutic legs (Mello-Leitão, 1929). Nevertheless, the somatic characteristics do not represent enough evidence to diagnose or differentiate between species of this group, due to their

great morphological similarity. The species differentiation has been based mainly on sexual females features. In general, females of this genus have reniform spermathecae (Rinaldi, 1984), males palp with a retrolateral tibial apophysis (RTA) reduced and ventral tibial apophysis (VTA) branched.

In the current work, two species of *Acentroscelus* are studied: *Acentroscelus ramboi* Mello-Leitao, 1943 and *Acentroscelus versicolor* Soares, 1942; both only described based of female specimens. The known geographical distribution is limited to the type locality, with the state of Rio Grande do Sul for *A. ramboi*, and the city of Osasco, in the state of São Paulo for *A. versicolor*. The species are discriminated by reproductive structures, mainly in the excavation of the atrium and the length of the copulatory ducts. Reviewing the biological material available in the collections of these two species, we wanted to describe the male specimens. However, due to the morphological similarity and small size of these spiders, its taxonomic determination was complicated. For this reason, we wanted to evaluate the taxonomic validity of the two species whose males present an intrinsic similarity or crypsis, when the specific unit is based on two easily distinguishable females (Fig.1). Taxonomic decisions were made using geometric morphometric tools, where we evaluated the existence of a morphological distinction in the males found with the females of *A. ramboi* and *A. versicolor*. In addition, the geographical information was used for complementing the results obtained with statistical analysis.

## 2. Materials and methods

### 2.1. Revision of collections

We examined 125 specimens fixed in ethanol 70%, deposited in seven biological collections (abbreviation and curator): Instituto Butantan, São Paulo (IBSP, A. Brescovit); Muséum National d'Histoire Naturelle, Paris (MNHN, C. Rollard); Museo

Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN, M. Ramírez); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCTP, R. A. Teixeira); 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 (MZSP, R. Pinto-da-Rocha); Museu Nacional do Rio de Janeiro (MNRJ, A. Kury).

## **2.2. Taxonomic treatment**

Specimens were classified according to female reproductive characteristics, size and locality, comparing with the type material and the original descriptions of the species. The taxonomic determination of the males depended on the female with which they were deposited. The males collected alone were specifically selected according to the geographic area where they were found and those who were collected alone and in the sympatry area are not used in this study. Only males in good condition (specimens with complete male palps and spiders do not dehydrated or dry) were used to evaluate morphometrically the disparity of these two groups. In total, were photographed 46 males; previously identified (Appendix S1).

## **2.3. Geometric morphometric analyses**

### **2.3.1. Structures analyzed**

We utilized somatic characteristics, assessing the carapace form in dorsal view (Fig.2A). This structure was used for evaluating the body form and size, but we do not used all body, because the opisthosoma is a structure very variable and dependent from a lot of environment, age and sexual state (Foelix, 1996). Additionally, the sexual characteristics of the males belonging to the two study entities were evaluated. We

analyzed the form of pedipalp tibia with its apophysis in ventral view (Fig.2B). The difficulty in evaluating the complete male palp is due to the mobility of multiple parts such as the embolous or the same tegulum and cymbium; for this reason, we used the tibiae and its apophysis like reproductive features evaluated. These tibial processes are used to fix the male pedipalp to the female's epigynum, guaranteeing the subsequent intrusion of the embolus for the transfer of sperm (Huber, 1995).

The structures were photographed using a L Multipurpose Zoom Microscope Leica M205A with a Leica DMC2900 camera and made multifocus images with Leica application suite 4.12.0 version.

Configuration of cartesian points of both structures were recorded from the photographs using tpsDig 2.12 (Rohlf, 2005), using equidistant points for each curve by the tool “draw background curve”. Curves were converted as points, using “append tps curves to landmark” in TPSUtil 32 (Rohlf, 2015), and using the tool “Make sliders file” we create a file with the definition of landmarks and semilandmarks. For the cephalothorax, 8 landmarks were set to each eye border (Fig 2A-blue points) and two curves consisting of 6 and 18 points, the first in the front and the former in the back contour of carapace (Fig.2A-red points). In the case of male palp, the configuration of points consisted of three curves, the first and last points of each curve were landmarks and the other semilandmarks; the first curve had 15 points, the second 15 points and the third 10 points points (Fig.2B). The semi-landmarks adjustment was made using a sliding method of bending energy. (Bookstein, 1996). Configuration of landmarks and semilandmarks were adjusted with a generalized Procrustes analysis using ‘gagen’ function in ‘GEOMORPH’ package (Adams et al., 2019). This type of superimposition is achieved by translating, rotating and scaling all configurations on a common reference system or the mean (Adams et al., 2019). For the cephalothorax we performed

the Procrustes superimposition using an analysis of bilateral symmetry with the ‘bilat.symmetry’ function of the same package. Subsequently, we performed a Principal Component Analysis (PCA) to graphically observe the variation of the main components that explain the variation of the shape of the analyzed structures.

### 2.3.2. Statistical analyses

We carry out an analysis using the ‘procD.lm’ function of ‘geomorph’ package to assess the existence of allometry between the size and shape of each structure. In the case of pedipalps, with positive allometry, we worked excluding the effects of said phenomenon to run the analysis of difference in the shape of the structure. The centroid size (CS), which corresponds to the square root of the sum of the square distances from each reference point to the centroid (Bookstein, 1991), resulting from the Procrustes analysis was used to evaluate the difference in size of the structures analyzed for both species. For this, we conducted a Student's t-Test with the ‘t.test’ function of ‘STATS’ package. That test was performed to evaluate both structures shape. The disparity of the *A. ramboi* and *A. versicolor* was evaluated through the shape of the palp and cephalothorax, performing a Procrustes multivariate ANOVA, using the ‘procD.lm’ function of ‘GEOMORPH’ package (Adams et al., 2019). A discriminant analysis was performed to evaluate how well the two study species could be discriminated according to palp and cephalothorax forms. This analysis was performed with “lda” function of ‘MASS’ package (Linear Discriminant Analysis; Venables and Ripley, 2002). We also carried out a Canonical Variates Analysis (CVA) to simplify graphically the description of the difference among groups, through the ‘CVA’ function of ‘MORPHO’ package. All these analyses were performed using the programming language R (Ihaka and Gentleman, 1996; R Core Team, 2018) for subsequent statistical analyses.

### 2.3.3. Mapping

The elaboration of the map was done using Qgis (QGIS Development Team, 2019), with the coordinates reported on the labels of the analyzed specimens (Appendix S1). When they did not present, these were generated using Geonames Gazetteer (Wick, 2019) or Google Earth (GlobeDigital, 2019).

## 3. Results

We found that male palp shape is significantly correlated with its size, represented by the CS, although in the case of cephalothorax, no evidence of correlation was found.

Analyzing the body size, in this case through cephalothorax size, shows no difference between *A. ramboi* and *A. versicolor* (T-student  $t = 1.6774$ ,  $p\text{-value} = 0.0973$ ). Nonetheless, we did find a significant difference in the size of the VTA of male palp (T-student  $t = 3.2078$ ,  $p\text{-value} = 0.0019$ ). Analyzing the averages, *A. ramboi* ( $X = 1315.950$ ) presents a larger size than *A. versicolor* ( $X = 1255.692$ ; Fig. 3).

The PCA explains 75.4% of the variation in the first two components in the cephalothorax case (Fig. 4A) and 66.5% in the palp case (Fig. 4B). According to the Procrustes multivariate ANOVA results, the males of the two species show a significant difference in both the shape of the cephalothorax (ANOVA  $F_{1,86} = 15.979$ ,  $P < 0.001$ ) and the shape of the palpus (ANOVA  $F_{1,86} = 26.487$ ,  $P < 0.001$ ). Similarly, the CVA represents a clear difference between the males of the two species evaluated both for cephalothorax ( $p < 0.001$ ) and palp ( $p < 0.001$ ) (Appendix S2). Our confusion matrix (cross-validation) obtained 93% (male palps) and 89% (cephalothorax) accuracy in the adequate identification of individuals of two species.

In addition, the geographical distribution of the two species (Appendix S4) varies latitudinally, where records found for *A. versicolor* are restricted to a north-central

region of the current Atlantic forest (diamonds, Appendix S4); while records reported for *A. ramboi* are restricted to the southern limits of the Atlantic forest, mainly over Ombrophyle mixed formation, and in part of the Pampas (circles, Appendix S4).

## 4. Discussion

### 4.1. Validation of two species

With our data and the analyzed structures, we found a clear distinction between the males of *A. ramboi* and *A. versicolor*. We evaluate body size based on the size of the cephalothorax, since as argued by Foelix (1996), this structure only expands in the molt because it is covered by two firm plates; unlike the opisthosoma, which is softer and its size depends on food intake or the development of structures associated with reproduction, unlike the opisthosoma, which varies considerably due to factors such as feeding, reproductive status and even the preservation status of the specimen. With the analysis of the cephalothorax we found that, although its shape differs from species to species, the body size is relatively similar in the males of the two entities. The cephalothorax or prosoma is a very important part of spiders, because its structures are related to vital functions such as locomotion, ingestion, and integrative nerve functions; therefore, probably the larger the cephalothorax, the better the resource retention, trophic efficiency and mobility of the individual (Fernandez, 2017). In addition to its functionality, morphologically it is a useful structure for determining entities, as demonstrated by our data, and previous works that ratify the shape of the cephalothorax as a useful character in phylogenetic studies (Bond and Beamer, 2006).

On the other hand, both the size and shape of the sexual structures, analyzed on the basis of the VTA of the male palpus, are distinctively different, where *A. ramboi* presents a larger, thinner and more elongated pedipalp than *A. versicolor* (Appendix S3

A, D). Although this apophysis does not intervene directly in spermatic transfer, this is the first male structure that establishes a well-defined contact with the female. This process has been reported in the case of spiders that have a well-developed RTA (Huber, 1995; Eberhard, 2004); nevertheless, since *A. ramboi* and *A. versicolor* have a reduced RTA and due to the ventrolateral shape and position of their VTA, this structure may be performing the function described for RTA at the time of copulation in these two species. Furthermore, due to the division of the VTA, the mesial branch of this process may be developing the function described for *Misumenops tricuspidatus*, where this structure guides the rotation of the tegulum produced by hematodocal expansion (Huber, 1995). Due to the high specificity of these tibial processes, which Huber (1995) himself describes, and their important intervention during the copulation process, the difference found both in shape and in size of the *A. ramboi* and *A. versicolor* VTA is a strong test and justification to define these males as different. Notwithstanding, these physiological hypotheses of the tibial processes must be tested in subsequent studies.

With these distinctive characteristics, we propose the first diagnosis of these two species, based on the characteristics of the two sexes (see Taxonomy). This, added to the clear differentiation between the females, justifies the status of the *A. ramboi* and *A. versicolor* species.

Since all eleven species of the genus *Acentroscelus* are described on the basis of female morphology (World Spider Catalog, 2019), it is not surprising that the morphological difference between *A. ramboi* and *A. versicolor* females is evident, mainly regarding the conformation of its genital structure (Appendix S3 B-C, E-F). For the most part, the main morphological differentiation is evidenced in males of spider species; however, in the case of *Acentroscelus*, it is the females that show the greatest

morphological variation. This phenomenon can be explained by a reversal of sexual roles, where perhaps men are the scarce resource that women select; and male mating preferences may be generating sexual selection in female phenotypes, expressed in this observed differentiation (Bonduriansky, 2001). Said role reversal has been evaluated in some wolf spiders, where males have the power to select females to copulate (Aisenberg et. al, 2010). However, these are conjectures that must be thoroughly evaluated.

It is relevant to discuss about the known geographical distribution of the species. These two species are relatively distant latitudinally, where *A. versicolor* is predominantly distributed in Ombrophyle mixed formation (diamonds, Appendix S4) and *A. ramboi* in part of the Pampas (circles, Appendix S4). However, there is an area of sympatry for these two species in the semi-deciduous seasonal forest reserves of the Atlantic Forest located in the Paraná river basin. These reports correspond to some females collected in these surroundings. Nevertheless, the material found in this transition zone is not very representative in order to carry out an adequate statistical analysis that assesses the morphology of the populations of these two species when they coexist in the same geographic space.

### **Taxonomy.**

Here we propose the diagnosis of each species. The proper description will be provided in a revision under preparation.

Thomisidae Sundevall, 1833

*Acentroscelus* Simon, 1886

### **1.1.1. *Acentroscelus ramboi* Mello-Leitão, 1943 (Appendix 3A-C)**

**Type material. Holotype.** 1 female, **BRAZIL**, Rio Grande do Sul (MNRJ-42524, examined).

**Diagnosis.** Males of this species is characterized by present a VTA divided in two branches, but it differs of *A. versicolor* by possess the more elongated and acuminate lateral projection (Appendix 3A). Females of *A. ramboi* have a great depression in the atrium, a character shared with *A. versicolor*, which differs from the smallest circular shape and for presenting a transverse fold at the base of the atrium (Appendix 3B). Unlike *Acenstroscelus albipes* and *A. versicolor* copulatory ducts longer than the dorsal projection of the atrium (Appendix 3C).

### **1.1.2. *Acentroscelus versicolor* Soares, 1942 (Appendix 3D-F)**

**Type material. Holotype.** 1 female, **BRAZIL**, São Paulo, Osasco, [23°33'07.0"S 46°51'59.6"W], 26 October 1941, Lane and Soares (MZSP-45, examined).

**Examined material.** See appendix S1.

**Diagnosis.** In the same way as to *A. ramboi*, males of *A. versicolor* possess a palp with a VTA divided in two branches, but these exhibit lateral projection shorter and larger than males of *A. ramboi* (Appendix 3D). The females of *A. versicolor* are very similar to the ones of *A. ramboi* by the general shape of the epigynum but can be distinguished by posses a greater deep atrium (Appendix 3E). The copulatory openings are disposed more laterally and are shorter than *A. ramboi*. Its copulatory ducts are shorter than the dorsal projection of the atrium like *A. albipes* (Appendix 3F).

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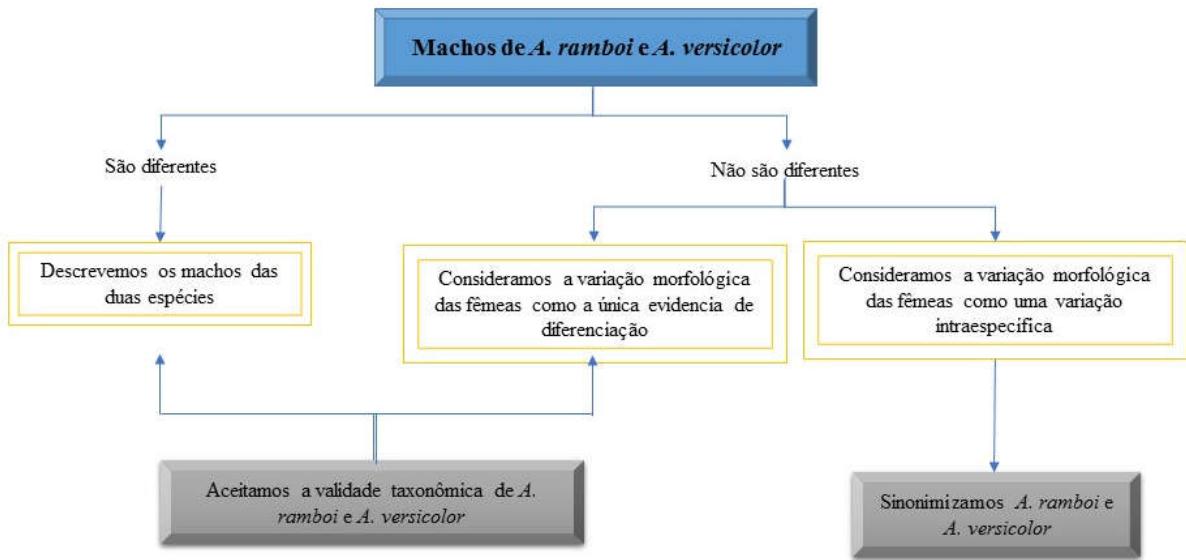
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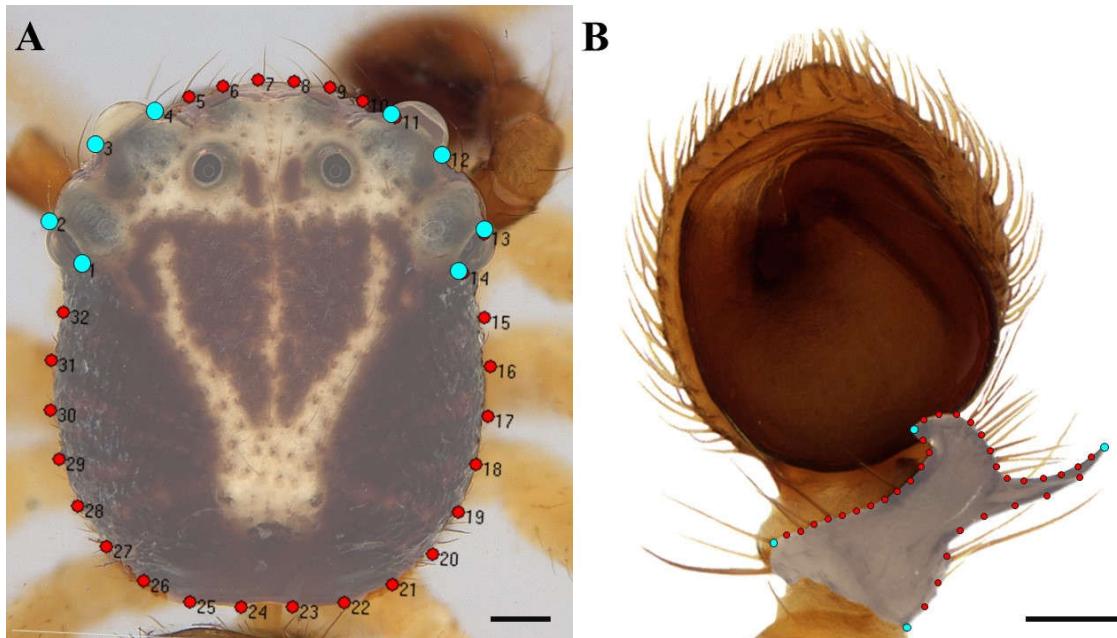
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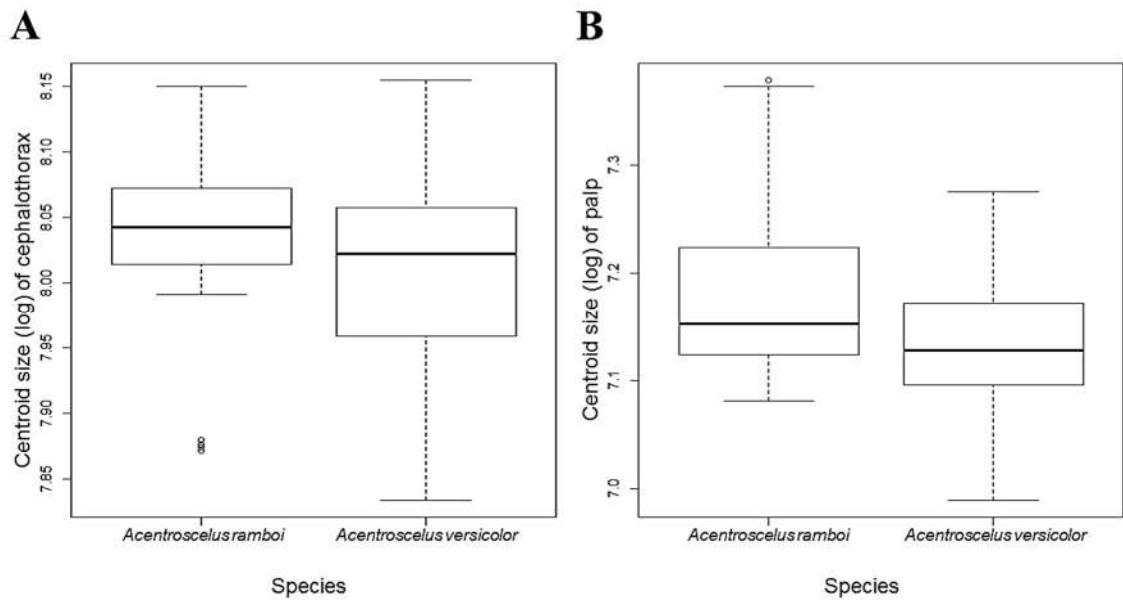
## Figures



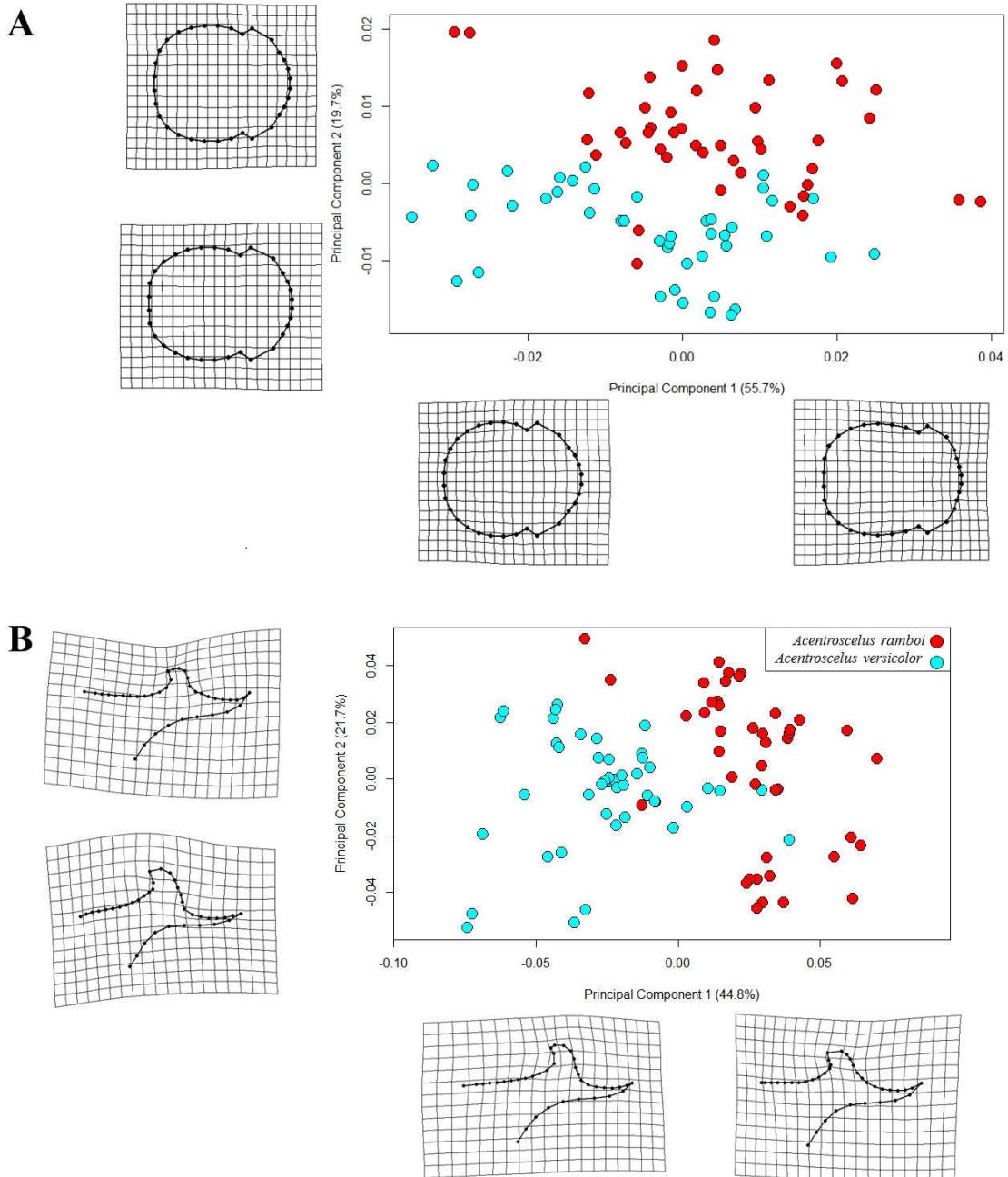
**Figure 1:** Diagram of taxonomic solutions, according to the possible results. Starting in blue box and ending in one of the gray boxes.



**Figure 2:** Male structures analyzed. **A.** Male cephalothorax dorsal view, with configuration of points. **B.** male palp ventral view, with configuration of points. Blue points (landmarks) and red points (semilandmarks). Scale bar: 0.1 mm.



**Figure 3:** Comparison between centroid sizes (log) of male's structures. **A.** Cephalothorax and **B.** palp. Boxplot: Box - first and third quartiles; whiskers - minimum and maximum ranges of variation; median (black line) - second quartile; points - outliers.



**Figure 4:** Principal Component Analysis of shape variation. **A.** cephalothorax shapes and **B.** palp. Extreme shapes are represented at the axis.

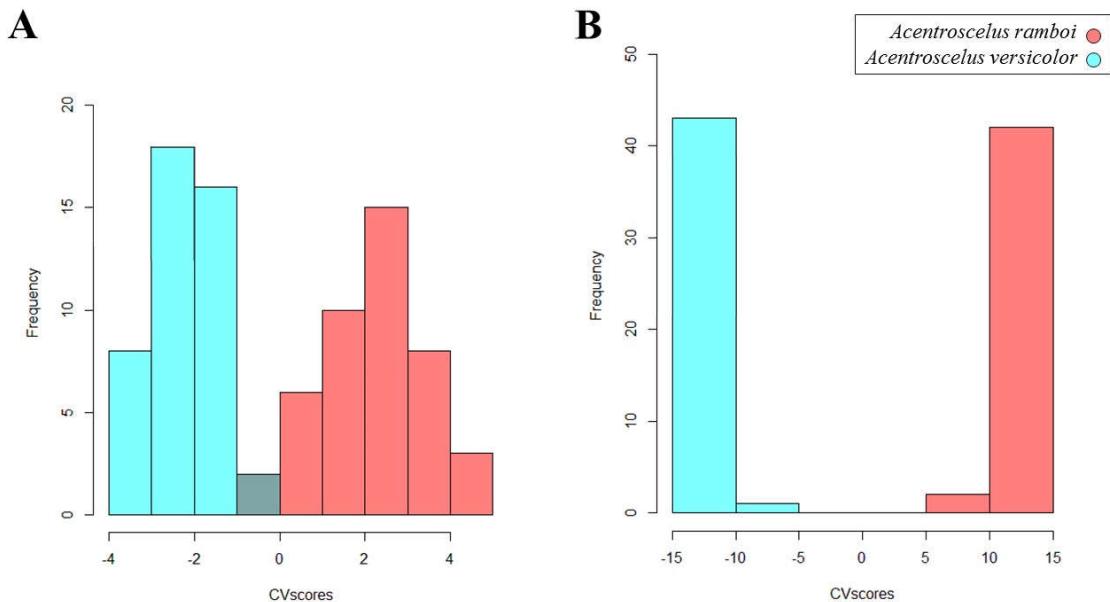
**Appendix S1.** List of material analyzed. Exemplar taxa, voucher specimens and photographed males. Codes marked with asterisk (\*) were photographed specimens for the morphometric analysis (described in Material and Methods).

SPECIES	CODE	♂	♀	LOCALITY	DATE	COLETOR
<i>A. versicolor</i>	IBSP-120943*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120718*	1	-	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120921*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120691*	1	-	Brasil, São Paulo, São Paulo, Parque Estadual do Jaraguá	14-23 October 2002	Equipe Biota
<i>A. versicolor</i>	IBSP-120712*	1	-	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-27259*	1	-	Brasil, São Paulo, São Paulo, Reserva Florestal CUASO, Campus USP	July 1985	S.A. Vanin
<i>A. versicolor</i>	IBSP-120692*	1	-	Brasil, São Paulo, São Paulo, Parque Estadual do Jaraguá	14-23 October 2002	Equipe Biota
<i>A. versicolor</i>	IBSP-120719*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120719*	1	-	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120918*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120941*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120924*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120913*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120942*	1	-	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-121983*	1	-	Brasil, São Paulo, Itapevi	I-December 1999	C. Bertim
<i>A. versicolor</i>	IBSP-120693	-	1	Brasil, São Paulo, São Paulo, Parque Estadual do Jaraguá	14-23 October 2002	Equipe Biota
<i>A. versicolor</i>	IBSP-120933	-	1	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120909	-	1	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120919	-	1	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120949	-	1	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-120929	-	1	Brasil, São Paulo, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>A. versicolor</i>	IBSP-32802	-	1	Brasil, São Paulo, São Paulo, Reserva Florestal CUASO, Campus USP	29 October 1999	D.F. Candiani
<i>A. versicolor</i>	IBSP-120690	-	1	Brasil, São Paulo, São Paulo, Parque Estadual do Jaraguá	14-23 October 2002	Equipe Biota
<i>A. versicolor</i>	IBSP-120709	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120714	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120715	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120717	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120907	-	1	Brasil, São Paulo, Iporanga, Parque Estadual Turístico do Alto do Ribeira	12-18 October 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120908	-	1	Brasil, São Paulo, Iporanga, Parque Estadual Turístico do Alto do Ribeira	12-18 October 2001	Equipe Biota
<i>A. ramboi</i>	IBSP-120998	-	1	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota
<i>A. versicolor</i>	IBSP-120711	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. versicolor</i>	IBSP-120716	-	1	Brasil, São Paulo, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16-22 July 2001	Equipe Biota
<i>A. ramboi</i>	IBSP-120999*	1	-	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota
<i>A. ramboi</i>	IBSP-121004*	1	-	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota

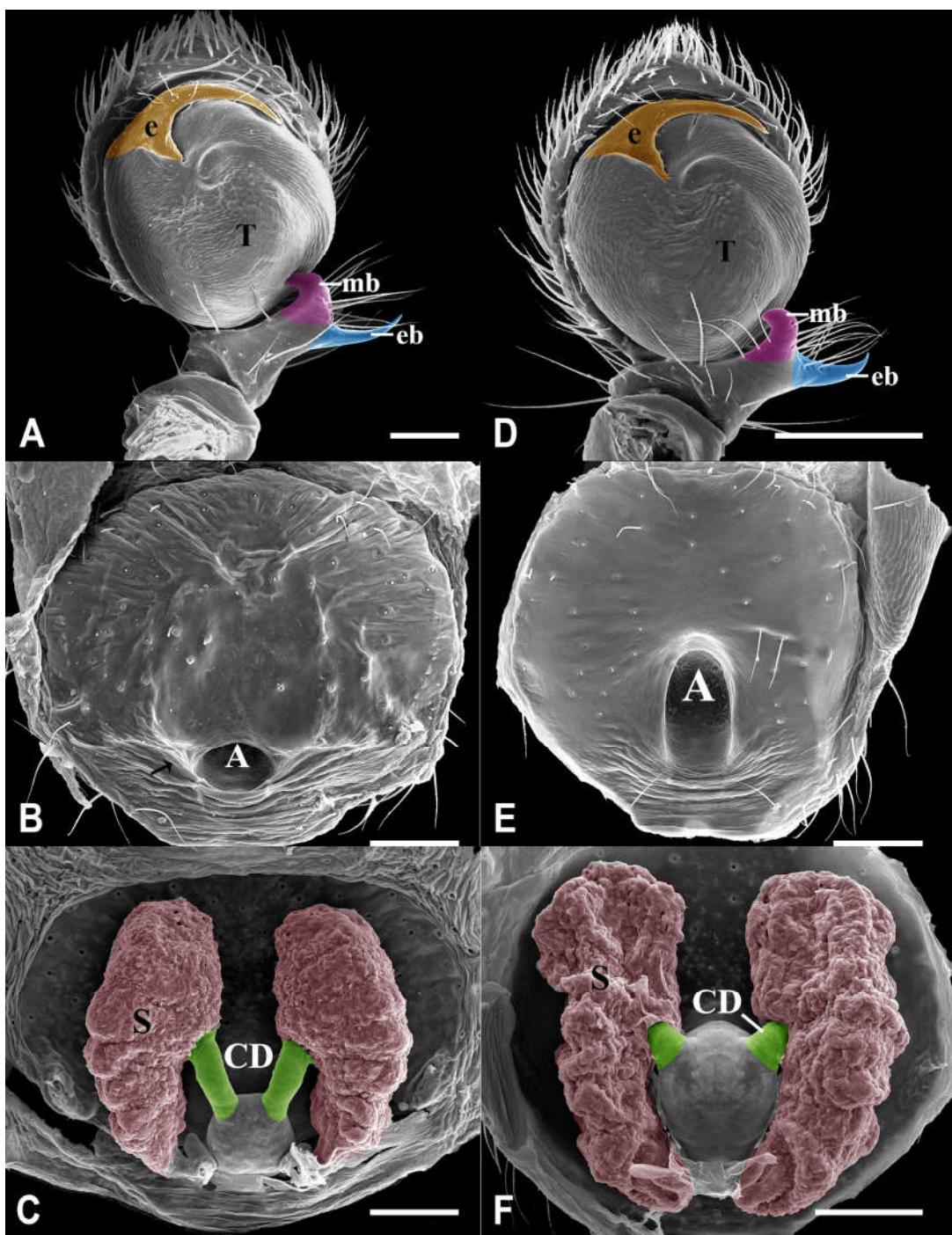
<i>A. ramboi</i>	IBSP-121003*	1	-	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota
<i>A. ramboi</i>	IBSP-121001	-	1	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota
<i>A. ramboi</i>	IBSP-121000	-	1	Brasil, Rio Grande do Sul, Derrubadas, Parque Estadual do Turvo	11-18 January 2002	Equipe Biota
<i>A. versicolor</i>	MACN--	1	-	Argentina, Provincia Buenos Aires, Dep. San Antonio, Arrollo El Central	Novembro	M.E. Galiano
<i>A. versicolor</i>	MACN--	1	-	Argentina, Provincia Misiones, Parque Nacional Iguazú, Sendero Macuco	08-15 February 1995	M.J. Ramírez
<i>A. ramboi</i>	MACN-10781	1	-	Argentina, Provincia Misiones, Parque Nacional Iguazú	22-30/VIII-1986	M.J. Ramírez
<i>A. versicolor</i>	MACN-10780	1	-	Argentina, Provincia Misiones, Parque Nacional Iguazú	October 1978	Galiano
<i>A. ramboi</i>	MACN-1970	1	-	Argentina, Provincia Misiones, Cerca de Puerto Rico, Gruta India, Ruta 12	Outubro 1977	M.E. Galiano
<i>A. ramboi</i>	MCNZ-8031*	2	1	Brasil, Rio Grande do Sul, Itaúba/Arroio do Tigre	22 April 1978	Arno A. Lise
<i>A. ramboi</i>	MCNZ-21912*	1	-	Brasil, Rio Grande do Sul, Guaíba	29 December 1991	A.B. Bonaldo
<i>A. ramboi</i>	MCNZ-15076*	1	-	Brasil, Rio Grande do Sul, Campo Bom	19-20 May 1986	C.J. Becker
<i>A. ramboi</i>	MCNZ-33180*	1	-	Brasil, Rio Grande do Sul, Viamão, Arroio Pesqueiro	36676	A.B. Bonaldo
<i>A. ramboi</i>	MCNZ-18448*	1	-	Brasil, Rio Grande do Sul, Bom Jesus, Fazenda Aver	24 March 1989	A.B. Bonaldo
<i>A. ramboi</i>	MCNZ-10920	-	1	Brasil, Rio Grande do Sul, General Câmara	17 Setember 1982	V. Pitoni
<i>A. ramboi</i>	MCNZ-13469	-	1	Brasil, Rio Grande do Sul, Campo Bom	30 Setember 1995	C.J. Becker
<i>A. ramboi</i>	MCNZ-18505	-	2	Brasil, Rio Grande do Sul, Guaíba	12 January 1989	A.D. Brescovit et al.
<i>A. ramboi</i>	MCNZ-33088	-	5	Brasil, Rio Grande do Sul, Gravataí, Morro do Tigre	15 July 2000	A.B. Bonaldo
<i>A. ramboi</i>	MCNZ-11087	-	1	Brasil, Rio Grande do Sul, Cambará do Sul, General Câmara	14 Outubro 1982	C.J. Becker
<i>A. ramboi</i>	MCNZ-11093	-	1	Brasil, Rio Grande do Sul, General Câmara	14 October 1982	M. Rosenau
<i>A. ramboi</i>	MCNZ-15173	-	1	Brasil, Rio Grande do Sul, Novo Hamburgo	17 June 1986	C.J. Becker
<i>A. ramboi</i>	MCTP-34758	-	1	Brasil, Rio Grande do Sul, São Borja, São Donato, Reserva Biológica	28 January 2012	Miguel Machado
<i>A. versicolor</i>	MCTP-42255	1	-	Brasil, Paraná, Ponta Grossa	02/02/1987	Profaupar
<i>A. ramboi</i>	MCTP-10474*	1	-	Brasil, Rio Grande do Sul, São Sepé	December 1994	R.C. Costa
<i>A. ramboi</i>	MCTP-40120*	1	-	Brasil, Rio Grande do Sul, Santa Maria	28 July 1998	Indrusiak, L.
<i>A. ramboi</i>	MCTP-1126*	1	-	Brasil, Rio Grande do Sul, Campo Bom	25 July 1986	C.J. Becker
<i>A. ramboi</i>	MCTP-10343*	1	-	Brasil, Rio Grande do Sul, Santa Maria Cidade dos Meninos	03 July 1998	Indrusiak, L.
<i>A. ramboi</i>	MCTP-19480*	1	-	Brasil, Rio Grande do Sul, Terra de Areia	28 June 2002	Estevam L.C. da Silva leg
<i>A. ramboi</i>	MCTP-10244*	1	-	Brasil, Rio Grande do Sul, São Sepé	03 June 1994	E.C. Costa
<i>A. ramboi</i>	MCTP-6714*	2	-	Brasil, Rio Grande do Sul, Guaíba	02 July 1995	Arno A. Lise
<i>A. ramboi</i>	MCTP-8780*	2	-	Brasil, Rio Grande do Sul, Guaíba	02 June 1995	Arno A. Lise
<i>A. ramboi</i>	MCTP-8245*	1	-	Brasil, Rio Grande do Sul, Guaíba Fazenda São Maximiano, Guaíba	09 January 1996	Arno A. Lise
<i>A. ramboi</i>	MCTP-7543*	1	-	Brasil, Rio Grande do Sul, Guaíba	28 April 1995	Arno A. Lise
<i>A. ramboi</i>	MCTP-3534*	1	-	Brasil, Rio Grande do Sul, Cachoeira do Sul, Porteira Sete	12 Setember 1992	Regina G. Buss
<i>A. ramboi</i>	MCTP-8781*	1	-	Brasil, Rio Grande do Sul, São Sepé	03 June 1994	Isabel Junqueira
<i>A. ramboi</i>	MCTP-4010*6	1	1	Brasil, Rio Grande do Sul, Santa Maria	August 1995	Kotzian, C.B.
<i>A. ramboi</i>	MCTP-40110*	2	4	Brasil, Rio Grande do Sul, Santa Maria	21 May 2000	Kotzian, C.B.
<i>A. ramboi</i>	MCTP-140	-	1	Brasil, Rio Grande do Sul, Campo Bom	17 December 1986	C.J. Becker
<i>A. ramboi</i>	MCTP-4829	-	1	Brasil, Rio Grande do Sul, Guaíba	03 June 1994	Arno A. Lise
<i>A. ramboi</i>	MCTP-10240	-	1	Brasil, Rio Grande do Sul, São Sepé	06 March 1994	E.C. Costa
<i>A. ramboi</i>	MCTP-10252	-	1	Brasil, Rio Grande do Sul, São Sepé	20 February 1994	E.C. Costa
<i>A. ramboi</i>	MCTP-10473	-	1	Brasil, Rio Grande do Sul, São Sepé	01 October 1994	E.C. Costa
<i>A. ramboi</i>	MCTP-19506	-	1	Brasil, Rio Grande do Sul, São Francisco de Paula	31 July 2003	L.C. da Silva

<i>A. ramboi</i>	MCTP-27129	-	1	Brasil, Rio Grande do Sul, Augusto Pestana	11 January 2009	Lígia V. Silva et. al.
<i>A. ramboi</i>	MCTP-37558	-	1	Brasil, Rio Grande do Sul, São Borja, São Donato, Reserva Biológica	22 November 2012	Miguel Machado
<i>A. ramboi</i>	MCTP-40108	-	1	Brasil, Rio Grande do Sul, Santa Maria	09 July 2000	Indrusiak, L.
<i>A. ramboi</i>	MCTP-40111	-	1	Brasil, Rio Grande do Sul, Santa Maria	27 May 2000	Indrusiak, L.
<i>A. ramboi</i>	MCTP-41406*	1	1	Brasil, Rio Grande do Sul, Santa Maria	21 December 1993	Indrusiak, L.
<i>A. ramboi</i>	MCTP-41407	-	1	Brasil, Rio Grande do Sul, Santa Maria	29 June 2005	Indrusiak, L.
<i>A. versicolor</i>	MHNCL-4554	1	-	Brasil, Paraná, Curitiba, Burigui	28 April 1961	R. Lange
<i>A. versicolor</i>	MHNCL-4561	-	1	Brasil, Paraná, Curitiba, Barigui	20 Setember 1960	R. Large
<i>A. versicolor</i>	MHNCL-	-	1	Brasil, Paraná, Curitiba, Barigui	10 February 1959	R. Lanpe
<i>A. ramboi</i>	MNRJ-42524	-	1	Brasil, Rio Grande do Sul	-	-
<i>A. versicolor</i>	MZSP-9777	2	-	Brasil, São Paulo, São Roque	16199	F. Lane
<i>A. versicolor</i>	MZSP-45	-	1	Brasil, São Paulo, Osasco	26 October 1941	Lane
<i>A. versicolor</i>	MZSP-143	1	-	Brasil, São Paulo, Guarulhos, Carvalho Araujo	15462	A. Zoppei
<i>A. versicolor</i>	MZSP-27976*	1	-	Brasil, São Paulo, São Paulo	10 November 2000	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-12833*	1	-	Brasil, São Paulo, República Nova, Cocaia	25 January 1948	H. Urbam
<i>A. versicolor</i>	MZSP-27994*	1	-	Brasil, São Paulo, São Paulo	2 March 2001	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-27985*	2	-	Brasil, São Paulo, Guarulhos	22 December 2000	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-27995*	1	-	Brasil, São Paulo, São Paulo	2 March 2000	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-9776*	1	-	Brasil, São Paulo, São Paulo, Vila Água Funda	07 June 1962	Biasi
<i>A. versicolor</i>	MZSP-27982*	1	-	Brasil, São Paulo, São Paulo	9 August 2000	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-12835*	2	1	Brasil, São Paulo, São Roque	16206	F. Lane
<i>A. versicolor</i>	MZSP-27984	-	1	Brasil, São Paulo, Guarulhos	28 October 2000	R. Pinto Da Rocha et. Al.
<i>A. versicolor</i>	MZSP-3542	-	1	Brasil, São Paulo, Guarulhos, Carvalho Araujo	15462	A. Zoppei
<i>A. versicolor</i>	MZSP-5952	-	1	Brasil, São Paulo, -, Bosque Clande	9 Setember 1944	F. Lane
<i>A. versicolor</i>	MZSP-12829	-	1	Brasil, São Paulo, Itapecerica, Embú	2 October 1949	F. Lane
<i>A. versicolor</i>	MZSP-13765	-	1	Brasil, São Paulo, São Paulo, Cidade Universitária,IBUSP	13 March 1992	T.P. Amarante
<i>A. versicolor</i>	MZSP-12832	1	-	Brasil, São Paulo, São Paulo, Vila Água Funda	28 March 1952	F. Lane
<i>A. versicolor</i>	MZSP-3543	1	-	Brasil, São Paulo, Guarulhos, Carvalho Araujo	15464	A. Zoppei

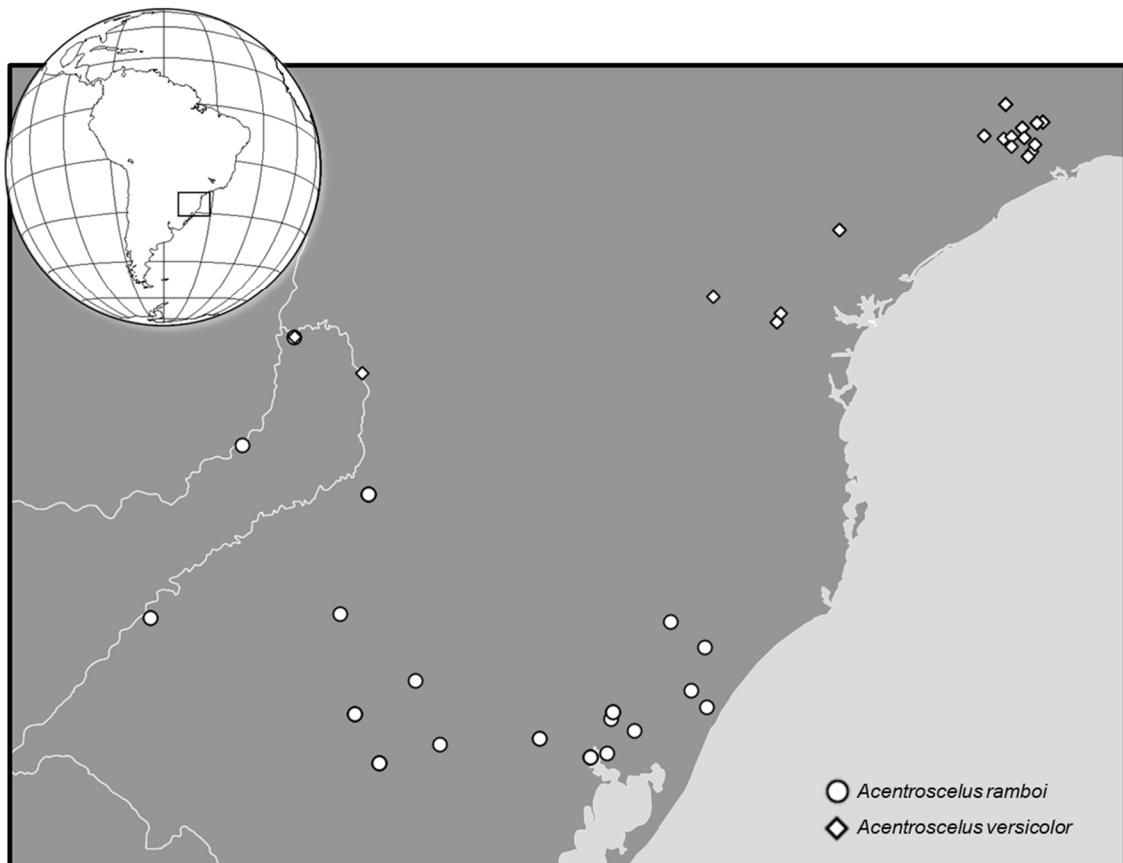
**Appendix S2.** Canonical Variate Analysis graphic shape. **A.** Male cephalothorax, **B.** Male palp.



**Appendix S3.** Principal morphological characteristics of studied species. Scanning electron images. *A. ramboi*: **A.** Male palp ventral view, embolous (e; orange), tegulum (T), mesial branch (mb; magenta) and ectal branch (eb; blue). Epyginum **B.** Ventral view, atrium (A) and horizontal fold at the anterior margin of atrium (arrow) **C.** Dorsal view, spermathecae (S) and copulatory ducts (CD). *A. versicolor*: **D.** Male palp ventral view, embolous (e; orange), tegulum (T), mesial branch (mb; magenta) and ectal branch (eb; blue). Epyginum **E.** Ventral view, atrium (A). **F.** Dorsal view, spermathecae (S) and copulatory ducts (CD). Scale bar: 0.1 mm.



**Appendix S4.** Geographic distribution of *Acentroscelus ramboi* and *Acentroscelus versicolor*.



**<sup>2</sup>CHAPTER 2: Phylogenetic analysis of tiny crab-spiders of *Acentroscelus* (Araneae: Thomisidae) and a small foray into their miniaturized world.**

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**Abstract**

In this study we tested the monophyly of tiny-crab spiders of the *Acentroscelus* genus, through a phylogenetic analysis; and we made a first analysis of the miniaturization state of the group based on the evaluation of body size. Phylogenetic analyses were based on a matrix with 27 taxa and 113 morphological characters. The search was performed through the use of two sub-matrices: one based on discrete characters only; and the other using continuous and discrete characters, after the elimination of dependent characters. Through the two approaches, three independent clades were recovered, providing evidence to propose taxonomic changes in the group. Thus, here we propose the creation of a new genus and the revalidation of *Whittickius*. Based on the measurement of the length of the cephalothorax, we evaluated the body size within the recovered clade with the species of the Tmarini tribe, measuring the phylogenetic signal and reconstructing the ancestral state of the character in the most congruent topology. The condition of miniaturization emerged in the entire clade of *Acentroscelus* *latu sensu*, although the tendency to miniaturization is clearer in females.

**Key words:** macroevolution, Neotropic, systematic, Tmarini.

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<sup>2</sup> O capítulo está redigido em inglês e formatado nas regras da revista *Organism Diversity and Evolution*

## 1. Introduction

Thomisidae, spiders commonly known as crab-spiders, are the seventh largest family of spiders in the world, with 2148 species distributed in 170 genera (World Spider Catalog 2019). Despite advances in the field, knowledge of the evolutionary history of the family is currently poor and confusing (Benjamin 2011; Teixeira et al. 2014). Two approaches focused on family knowledge were made by Benjamin et al. (2008) and Benjamin (2011) based in molecular and morphological approach, respectively. These works, together with that carried out by Wheeler et al. (2017), represent the most complete and up-to-date information on the evolutionary relationships of the family. Nevertheless, these proposals do not support the taxonomic subdivision described by Ono (1988), which defines seven subfamilies and that are still frequently used (i.e. Aphantochilinae, Bominae, Dietinae, Stephanopiinae, Stiphropodinae, Strophiinae and Thomisinae). Although recent efforts have focused on the systematic study of the relationships of some groups in this family (Teixeira et al. 2014; Machado et al. 2017), few have been focused on Thomisinae genera (Benjamin and Clayton 2016; Ileperuma et al. 2019).

One of the tribes belonging to Thomisinae is Tmarini, and according to the proposal made by Ono (1988) it include eleven genera: *Monaeses* Thorell, 1869, *Tmarus* Simon, 1875, *Pherecydes* O. P.-Cambridge, 1883, *Acentroscelus* Simon, 1886, *Philodamia* Thorell, 1894, *Titidius* Simon, 1895, *Gnoericha* Dahl, 1907, *Haplotmarus* Simon, 1909, *Latifrons* Kulczyn'ski, 1911 and *Titidiops* Mello-Leitão, 1929. Although the relationships of this tribe have not been the focus of any phylogenetic study, in the latest proposal on the spider tree of life (Wheeler et al. 2017), Tmarini recovered as a monophyletic clade.

*Acentroscelus* Simon (1886), is one of the four genera of Tmarini distributed in the Neotropics, as such *Titidiops*, *Titidius* and *Tmarus*. Currently, *Acentroscelus* is composed by 11 species, whose distribution is spread from the French Guiana to the north of Argentina (World Spider Catalog 2019). This genus is characterized by having high cephalothorax, longer than wide, tall at the top and tilted behind; also it has a row of spines on the upper edge and has a vertical clip, longer than wide (Keyserling 1880). Also, for its coriaceous and granular tegument; thin and mutual legs; and oval abdomen, longer than wide (Mello-Leitão 1929).

The taxonomic history of *Acentroscelus* includes several events that complicate the clear recognition of the species that make up this group. Initially, Taczanowski (1972) described a genus called ‘*Acanthonotus*’ with ‘*Acanthonotus guianensis*’ as type-species; and Keyserling (1880) redescribed ‘*A. guianensis*’ and described ‘*Acanthonotus peruvianus*’. A few years later, Simon (1886) proposed the genus *Acentroscelus* with *Acentroscelus albipes* as type-species, and later himself assigned the two species of ‘*Acanthonotus*’ as *Acentroscelus* (Simon 1895). The remain species of *Acentroscelus* were described over the first half of the century XX in many different papers (Mello-Leitão, 1929; 1943a; 1943b; 1947; Soares, 1942). This last species currently assigned to *Acentroscelus* had been originally described as *Whittickius singularis* by Mello-Leitão (1940). The last species currently assigned to *Acentroscelus*, originally described as *Whittickius singularis* by Mello-Leitão (1940), was combined to the genus because its tubercles on cephalothorax and the general shape of genitalia look like with ones of the *Acentroscelus granulosus* (Rinaldi 1984). Although these eleven species are described under the same taxonomic group, the lack of systematic evidence and the marked morphological variation shown by some species cast doubt about its relationship.

Furthermore, body size is one of the most relevant features in these spiders. Although never considered dwarfs, spiders belonging to *Acentroscelus* are characterized by having a tiny size, compared to the other genera of the Tmarini tribe. A phenomenon related to the evolution of body size is "dwarfism" or "miniaturization", which denotes a tiny body size in a specific taxonomic group and may include structural reduction and simplification (Hanken and Wake 1993). In general, this characteristic may be due to different intrinsic and extrinsic factors, such as nutrition, environmental pressures, or even evolutionary trends (Gould and MacFadden 2004). At the same time, miniaturization influences many of the features related to the life history of the species, as such: growth, parental care, dispersal range and degree of habitat specificity (Rainford et al. 2016). Likewise, this phenomenon can determine the phylogenetic diversification of a group above the species level, the reason why suggest that studies of body size evolution should be closely linked to a phylogeny (Gould and MacFadden 2004). This phenomenon has been present throughout the evolutionary history of panarthropoda (Polilov and Beutel 2019), finding it for example in crustaceans such as copepods; basal insects such as collombolous and psocopters to derivate insects such as strepsipters, thysanopters, hymenopters and coleopters; even chelicerates such as mites and spiders of the family Symphytognathidae (Menelli and Giuseppe 2019). The great variety of sizes, shapes, bauplanes and niches that the Chelicerata occupy make this group an ideal model for evaluating the phenomenon of miniaturization (Dunlop, 2019). In this way, we can discern if the size is really related to the evolutionary history of the taxon or other environmental, genetic or individual factors of the population. For all of the above reasons, the objective here is to recover the *Acentroscelus* phylogeny, both for systematic purposes and to understand the influence of evolutionary history on *Acentroscelus* body size.

## **2. Materials and methods**

The analyzed material (**Appendix S1**) belongs to the following biological collections (museum acronym, curator of the collection): American Museum of Natural History, New York (AMNH, L. Prendini); British Entomological and Natural History Society, London (BENH); California Academy of Science, San Francisco (CAS, C. Griswold); Field Museum of Natural History, Chicago (FMNH, P. Sierwald); Instituto Butantan, São Paulo (IBSP, A. Brescovit); Instituto de Ciencias Naturales de la Universidad Nacional, Bogotá (ICN, E. Flórez); Instituto Nacional de Pesquisas da Amazônia, Coleção Sistemática da Entomologia, Manaus (INPA, C. Magalhães); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN, M. Ramírez); Museu de Ciências e Tecnologia da PUCRS, Porto Alegre (MCTP, R. A. Teixeira); Museu de Ciencias Naturais da Fundação Zoológica do Rio Grande do Sul, Porto Alegre (MCNZ, R. Ott); Museu de Historia Natural Capão da Imbuia, Curitiba (MNHCl, M. Zamoner); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto-da-Rocha); Museu Paraense Emílio Goeldi, Belém (MPEG, A. B. Bonaldo); Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe (SMNK, H. Höfer); Universidad Nacional Mayor de San Marcos, Museo de Historia Natural, Lima (MUSM, D. Silva); Universidade do Rio Janeiro, Museu Nacional, Rio de Janeiro (MNRJ, A. B. Kury); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG, A. J. Santos); Universidade Federal do Rio de Janeiro, (UFRJ, R. Baptista).

The observations were made directly from the collection material and with the help of photographs and scanning electron microscopy images. To analyze the genitalia of the females, we dissected and submerged the epigynum in pancreatin about six hours for to remove soft tissues, follows Álvarez-Padilla and Hormiga (2007) and then dried for 24 h at room temperature. The photographs were taken using a Leica M205A Multipurpose

Zoom Microscope at the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), with a Leica DMC2900 camera and made multifocus images with Leica application suite 4.12.0 version. Additionally, some images were obtained using Scanning electron microscopy conducted in a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (LabCEMM) at PUCRS.

## 2.1 Cladistics analysis

### 2.1.1 Taxon sampling

The analyzed data matrix present 27 terminal taxa, 16 of which are the out-group and 11 of which are the in-group (**Appendix S2**). As taxonomic knowledge of *Acentroscelus* is limited to the original descriptions of the species and there is no taxonomic review of the genus, only the species that when reviewing the type material and the description could be considered valid were used in this study. The taxonomic treatment of the group will be evaluated extensively in another study (Molina–Gomez and Teixeira, und. sub. [chapter 3]). Thereby, the ingroup in this analysis comprises eleven species, seven valid species and four new morphospecies: *Acentroscelus albipes* Simon, 1886; *A. granulosus* Mello–Leitão, 1929; *A. guianensis* (Taczanowski, 1872); *A. peruvianus* (Keyserling, 1880); *A. ramboi* Mello–Leitão, 1943; *A. singularis* Mello–Leitão, 1943; *A. versicolor* Soares, 1942; *A. sp. 1*, *A. sp. 2*, *A. sp. 3* and *A. sp. 4*.

The outgroup selection was based on the *Thomisus* group proposed by Wheeler et al. (2017), considering both the Tmarini clade and the other clades close related. Representing the Tmarini outgroup were added three species of *Titidius*, four of *Tmarus*, one morphospecies of *Monaeses* and the unique species of *Titidiops* (*T.*

*melanosternum*). In order to include species of the other clades, even other subfamilies, it was decided to add *Boliscus tuberculatus*, *Bomis larvata*, *Cymbacha festiva*, *Heterogriffus berlandi* and *Stiphropus gruberi*. Some of these species are also tiny spiders, it was added to increase the explanatory power at any body size optimization and evolutionary tests. *Epicadus heterogaster* were used to root trees because any Stephanopinae is clearly basal to the Tmarini (Wheeler et al. 2017).

### 2.1.2 Character sampling

Some characters used in the last systematic works done with Thomisidae by Benjamin (2011), Teixeira et. al (2014) and Machado et. al (2017) were reinterpreted, but most of the characters are proposed in this study (**Appendix S3**). Both discrete and continuous characters were used in this study. Some potentially continuous characters were codified as discrete only when contrastanting and unequivocal gaps were recognized between character states. The other characters codified as continuous were obtained from measurements made on photographs. Six individuals of each of the species included in the analysis were photographed, three males and three females. This process was performed with three replicas, using the same equipment and the same position of specimens in order to reduce measurement errors Seifert (2002).

The complete matrix was composed by 113 characters, of which 57 were continuous characters and 56 discretes. Amongst of the 27 species, 24 were scored for both males and females, and three species were scored only for females. The continuous ones were usually treated as ratios, following the recommendations of Mongiardino et al. (2015), i.e., numerator and denominator were carefully ordered. Additionally, these ratios were rescaled according to Goloboff et al. (2008), in order to make them comparable with

discrete characters. Due to the artificial inflation of consistency index generated by the autapomorphies (Bryant 1995), these were excluded from the matrix.

Material review and photo capture was performed using a Leica M205A Multipurpose Zoom Microscope at the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS); using a Leica DMC2900 camera and made multifocus images with Leica application suite 4.12.0 version. The scanning electron micrographs (SEM) was conducted in a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (CEMM) at PUCRS. The terminology used was adapted from Benjamin (2011), Teixeira et al. (2014) and Machado et al. (2017).

### **2.1.3 Parsimony analysis**

The construction and editing of the matrices were carried out in Mesquite 3.2 (Maddison and Maddison 2017). A matrix with all characters was constructed, including discrete and continuous characters. However, features with the same ontological origin (eyes) or structures that arose by serial homology (legs) could have an undesirable dependence to the phylogenetic analysis. Thus, it was used the same procedures of Mongiardino et al. (2014), who made linear regression between pairs of similar features to search outliers that can show any species not predicted thought the multiple regression model. These outliers were, therefore, evidence that such pair of similar features have some degree of independence along the phylogeny. The lack of correlation or variations upper to 50% of Y-predicted were considered evidence to keep the characters as independent (Fig. 1).

To evaluate the phylogenetic relationships of *Acentroscelus*, two submatrices were created: (1) including only the discrete characters matrix (aka. “DC Matrix”); (2)

including discrete characters and only the continuous ones whose had the independency shown after regression tests (aka. “ICC Matrix”).

Both matrices were analyzed under maximum parsimony criteria, which were carried out in TNT 1.5 (Goloboff and Catalano 2016). The continuous characters in ICC matrix were standardized [nstates stand] before the heuristic search start. The searches used three algorithms implemented in TNT: (1) ratchet [rat:equal upfac5 downfac5 autoconst10]; (2) sectorial search [css rss]; and (3) tree fusing [tfuse:default]. The implemented routine included maintaining of 500k trees in memory [hold 500000], start search from random seed [rseed \*], and ten replicates of the algorithms until to reach the lesser, and probably the best, tree 2 times [xmult:hit2 rep10 ras css rss rat100 fuse2]. We calculated the relative Bremer support after assign the suboptimal parameters [sub 10x0.6] and performing a similar search routine than described above. The symmetric resampling was accessed in 1000 replications of the default TBR search, in which matrix was modified up to 33%.

## 2.2 *Macroevolutionary analysis*

In order to evaluate the miniaturized condition of the genus *Acentroscelus*, we evaluate the body size in relation to the phylogenetic reconstruction. The macroevolutionary analysis was performed using the clade shown only Tmarini species in the strict consensus tree recovered using the ICC matrix. We use this topology due to its higher resolution. Cephalothorax length was used as a measure of body size and was taked for males and females; this employing the same methods and parameters utilized for take the measures used in phylogenetic reconstruction. According to Munkemuller et. al (2012), phylogenetic signal is the tendency of related species to resemble each other more than species drawn at random from the same tree; or according to Revell et. al

(2008), the statistical dependence among observations for species related by a phylogenetic tree. For this reason, this signal was calculated, using a Blomberg's K parameter (Blomberg et al. 2003), that is estimated denoted from 0 to  $\infty$ , where  $K < 1$  corresponds to a low phylogenetic signal and evidences an evolution of the studied trait due to different pressures than its evolutionary history;  $K = 0$  corresponds to the evolution of the attribute under the Brownian motion model; and  $K > 1$  like high phylogenetic signal and corresponds to a greater similarity of the phylogenetically related species than to the other species. Although this parameter was designed under the Brownian motion model, Münkemüller et al (2012) identified this like a great qualifier of phylogenetic signal and they ratified that it can even show an efficient result without following the Brownian evolution model. This process was estimated in R study environment, using the packages ‘APE’ (Analyses of Phylogenetics and Evolution — Paradis et al. 2004), ‘GEIGER’ (Harmon et al. 2008) and ‘phytools’ (Phylogenetic Tools for comparative biology — Revell 2012). Previously, the tree branches length was assigned as equal to 1, based on the assumption of that the effect of branch length information is low (Münkemüller et al. 2012). For a better understanding, exploration and complement of the data, according to Ollier et al (2006), the body size was mapped in the phylogeny proposal. This process was built with command ‘contMap’ of ‘phytools’ package, which plots a tree with a mapped continuous character, and generates a reconstruction of the ancestral states of the evaluated character. This process was estimated after generated an Ultrametric tree, with the APE package.

### 3. Results

#### 3.1 Cladistic analysis

We obtained a matrix of 113 characters, 57 continuous and 56 discrete (**Appendix S2**).

The continuous characters were scores around 51% to females and 49% to males. Regression analysis applied to continuous characters showed a correlation of at least 21 characters, which were excluded because of its dependence on other characters (**Appendix S3**).

The analysis done with the DC matrix resulted in six most parsimonious trees with 178 steps (CI=34; RI=62). In this analysis *Acentroscelus* was recover in monophyly but with many internal nodes in polytomy after strict consensus and branch support usually low (**Fig. 2**). In other hand, the ICC Matrix recovered only one most parsimonious tree with 284.79 best score, which also recover *Acentroscelus* in monophyly (**Fig. 3**). However, this analysis also recovered three lineages representing the classical groups assigned to *Acentroscelus* species, originally proposed as genus by Keyserling (1880), Simon (1886) and Mello-Leitão (1940). Despite the relationship itself has seemed to support the *Acentroscelus* as a single valid genus, the low branch support both in DC and ICC matrix led us to draw conclusions from the synapomorphies in each lineage. The clade comprising all lineages was referred as *Acentroscelus lato sensu* clade or, hereinafter, just ‘ALS clade’.

One of the lineages was evinced by *Acentroscelus peruvianus*, which split of other *Acentroscelus* by having two unambiguous and homoplastic synapomorphies (Char. 30:1 and Char. 43:1, in DC matrix). Besides, it can be considered an independent lineage due to characters uncoded here to be autapomorphic (e.g. folds in the distal portion of the spermatic duct on the male palp; tegulum with a distal projection; copulatory ducts reaching the anterior margin of the epigynal plate). Every one of the

evidences above led us to propose this lineage as a new genus (see taxonomy to details), and hereinafter referred as '*Maeanderion* clade'.

The remaining species of *Acentroscelus* were recovered into two lineages. One composed mainly by species with Amazonian distribution (*A. granulatus*, *A. guianensis*, *A. singularis* and two new morphospecies, *Acentroscelus* sp. 1 and *Acentroscelus* sp. 2) and other with species distributed around Atlantic forest (*A. albipes*, *A. ramboi*, *A. versicolor* and two new morphospecies, *Acentroscelus* sp. 3 and *Acentroscelus* sp. 4). Once the clade with Amazonian species of *Acentroscelus* includes the species previously assigned to *Whittichius* (i.e., *A. singularis*), we proposed to treat this clade as *Whittichius* genus revalidated. The ‘*Whittichius* clade’ (hereinafter) was supported two unambiguous synapomorphies (Char. 12:1/2 and Char. 40:1). Otherwise, the clade with species distributed over Atlantic forest and surroundings (hereinafter, ‘*Acentroscelus* clade’) has no unambiguous synapomorphy to the discrete matrix, being supported solely for transformations in the continuous characters (**Fig. 3**).

### 3.2 Macroevolutionary analysis

The body size was analyzed for males and females using the tree full resolved of the ICC matrix. Both females and males reported low phylogenetic signal and it was not significant (Female’s  $K = 0.6113$   $P = 0.0708$ , Male’s  $K = 0.4106$   $P = 0.471$ ) under Blomberg’s K parameter. After mapping the body size, in general, we notice a tendency to decrease in body size in each of the branches of the ‘ALS clade’, remarking the notable reduction suffered by *A. versicolor* and *A. ramboi*. However, there is no evidence of an extreme or differentiated body size between the clade and the other species of the Tmarini tribe (**Fig. 4**). Despite this, and although the pattern is not repeated in males, it is possible to observe a difference between the size of the females

of the 'ALS clade' (yellow to red, **Fig. 4A**), with that of the other females of the other species of the Tmarini tribe (blue to green, **Fig. 4A**). Despite the species of *Acenstroscelus* small-sized, its change isn't abrupt when compared to the remaining Tmarini species. So much, that size estimated to ancestors of all remaining Tmarini is very similar to ancestor's size of the *Acentroscelus* lineages.

## 4. Discussion

### 4.1 Systematic consideration over the phylogeny

The monophyly of Tmarini was recovered only in the analysis with ICC matrix, which also suggests 'ALS clade' as a sister-group of the other Tmarini species (Fig. 2). Sure, some similarities with *Tmarus* and *Titidius* have already been reported. Like Simon (1886) reporting the general shape of the body and eyes in *Acentroscelus* similar to *Tmarus*; or as Simon (1895) describing the high cephalothorax of *Acentroscelus* as such indication of its similarity with *Titidius*. However, few considerations can be made regarding the external group, since of the around 300 species of the tribe (WSC 2020) were included only 17 species, besides four new morphospecies.

Also were the similarities in carapace features that led Simon (1895) and Rinaldi (1984) to consider, respectively, '*Acanthonothus*' and *Whittickius* as junior synonymy for *Acentroscelus*. Something reflected in amounts of discrete and continuous characters supporting the 'ALS clade' (see transformations in **Fig. 3**). While some characters - such as spineless legs (Char. 21:0 and Char. 26:0) and the tubercles over the posterior slope margin (Char. 13:1) - has reflected the first diagnostic features of the genus (Simon 1886; Mello-Leitão 1929; Rinaldi 1984). Others have reflected common features of the species of Tmarini, like the spotting patterns on the cephalothorax and legs (Char. 6:1;

Char. 8:1; Char. 23:0) and the size of atrium over epigynal plate (Char. 35:0; Char. 38:1). Every issue above possibly contributed to the low branch support values (**Fig. 2**).

If, on the one hand, both analyzes support the monophyly of *Acentroscelus*, on the other hand, there is low branch support and the set of synapomorphies is highly homoplastic. This leads us to observe the internal strains of the 'ALS clade' with more attention. Once the features of the carapace and abdomen are often homoplastic, the strategy for assigning more stable genera has been to recognize lineages with a set of copulatory characteristics conspicuous and quite distinct from other groups (e.g., Benjamin and Clayton 2016; Machado et al. 2017).

The '*Maeanderion* clade' includes only *A. peruvianus*, and it is distinguished from the others *Acentroscelus*, both for some homoplasies recovered and additional autapomorphic characters not included in the analysis. These characters are mainly copulatory features, such as the sinuous course of the spermatic duct, the distal projection on the tegulum and the microstructuration of the embolus apex. This clade also shares several plesiomorphies with the remaining Tmarini, as the presence of median anal tubercle on abdomen and male palp with paracymbium (Char. 30:1; Char. 42:1). Although this species was originally described as *Acanthonotus* by Taczanowski (1872), this is a preoccupied name in fish (Bloch, 1797) and, therefore, it is necessary to describe a new genus to allocate this species (see Taxonomy section below). The examination of other specimens during this work suggests there are species to be described in this clade, which were not included here because there were few samples of them and usually the SEM (useful for coding) damages the specimens.

The '*Whittickius* clade' is represented by the Amazonian species currently allocated in *Acentroscelus*. Once this clade includes *A. singularis*, which was originally described by Mello-Leitão (1940) in the genus *Whittickius*, we propose to revalidate this genus to

include: *A. granulatus*; *A. guianensis*; *A. singuari*s; and two new species, represented here by *Acentroscelus* sp. 1 and *Acentroscelus* sp. 2. We can argue little about the original diagnosis since Mello–Leitão (1940) generally did not use copulatory features in diagnosis of genus, still '*Whittickius* clade' is recovered due to the presence of large projections in the dorsal and lateral region of the carapace (Char. 12:1), median septum on epigynum (Char. 40:1), and excavation on ectal branch of VTA (Char. 54:1).

Finally, the '*Acentroscelus* clade' is proposed to maintain the species from the Atlantic rain forest and its surroundings, i.e., pampa and cerrado. Although this clade be supported only by ambiguous characteristics - e.g., median depression over posterior slope (Char. 11:1), presence of numerous punctures next to the bristle socket in the carapace (Char. 14:1); small copulatory ducts (Char. 31:0) and large spermatheca (Char. 34:0), there are several continuous transformations reported as synapomorphy of this clade (Fig. 2). Once the classical diagnoses (Simon 1886, Mello–Leitão 1929) describe only general features of the carapace and abdomen, the only feature in common with the current clade is the presence of punctures on the carapace.

#### 4.2 Miniaturization

Although characterizing and quantifying miniaturization is problematic, its definition itself is arbitrary. While this is a general corporal state, the most obvious way to evaluate miniaturization is through body size (Hanken and Wake 1993) and as any evaluation of a feature associated with organisms, it must be made against their evolutionary history (Gould and MacFadden 2004; Hanken and Wake 1993; Pérez-Ben et al. 2018). However, evaluating the body size throughout the topology obtained, there is no evidence of an extreme reduction. This decrease in size throughout the phylogeny occurs gradually, evident mainly in the case of females. The notable reduction of body

size was reported only in few stems of the ‘ALS clade’, mainly in species of the ‘*Acentroscelus* clade’ (Fig. 3). Following the concept proposed by Hanken and Wake (1993), where the miniaturization condition is characterized by an extreme reduction in body size and must be evaluated under phylogenetic criteria. However, it is pertinent to evaluate this condition from other characteristics that are not limited to body size, in future research. Furthermore, the evaluation of a characteristic also depends on the phylogenetic scale at which a characteristic is being analyzed; for this reason, it would be interesting to use a topology that includes more species from the tribe and from Thomisidae.

One important issue observed was that male and female body size seems to evolve independently across ALS clades, just like Nephilidae (Kuntner et al. 2019). The state of miniaturization in males can be a condition associated with sexual dimorphism (Blanckenhorn 2005), so their evolution is driven by factors other than evolutionary history.

Once size reduction in *Acentroscelus* was not abrupt and extreme, as initially inferred, it is possible to hypothesize that: or (1) miniaturization can derive from less severe cases of size reduction, such as continuous reductions along the phylogeny; or (2) this state had been driven by a different pressure (maybe related to dwelling or foraging). The next steps should be to evaluate other features related to miniaturization, as the simplification of the Bauplan (Hanken and Wake 1993; Diakova et al. 2018), reduction in the number and size of cells (Minelli and Fusco 2019), and the shortening of legs and eyes (Dunlop 2019).

## 5. Taxonomy

THOMISIDAE Sundevall

Genus *Maeanderion* gen. nov.

*Acentroscelus* Simon, 1886: 185.

*Updated diagnosis*

Unlike *Acentroscelus* and *Whittickius* species, *Maeanderion* does not own punctuated carapace and its micro bristles arising from conical soquets like in the most genera of Tmarini. Also, the species of this genus present a transverse line of small setiferous tubercles on the posterior margin of the carapace declivity. However, the tubercles are very small comparing with another species. Male palps like in some species of *Titidius* and that difference from *Acenstroscelus* and *Whittickius*, present paracimbium, distal projection on the tegulum and the VTA is reduced and not divided. The RTA is larger than VTA, conical and is not reduced. Unlike *Acentroscelus* and *Whittickius*, the embolous is small and presents microsculpture in the apex, with a straight direction. Females with copulatory copulatory ducts short and a single pair of reniform-shape spermathecae, unlike *Acentroscelus* and *Whittickius* because its spermathecae do not have differently divided chambers.

*Distribution*

Species of *Maeanderion* occur from Colombia to Brazil.

*Composition*

The genus is monotypic: *Maeanderion peruvianus* (Keyserling, 1880), **comb. nov.**

Genus ***Acentroscelus*** Simon

*Updated diagnosis*

*Acentroscelus* species are different from all other Neotropical Tmarini by present all punctuated carapace with micro bristles arising from the punctures and a transverse line of small setiferous tubercles on the posterior margin of the carapace declivity. Male palpus like those of *Titidius* with discoid tegulum and reduced RTA, but with a forked ventral tibial apophysis (VTA), with the most shorted and ventral branch curved mesially, and the other branch strongly pointed laterally. Females with a single pair of reniform–shape spermathecae clearly divided in chambers. The genus is related to *Tmarus* but differs markedly by presenting muticus legs.

*Distribution*

Species of *Acentroscelus* occur from Brazil to Argentina.

*Composition*

The genus contains three valid species: *Acentroscelus albipes* Simon, 1886; *Acentroscelus ramboi* Mello–Leitão, 1943; *Acentroscelus versicolor* Soares, 1942.

Genus ***Whittickius*** Mello–Leitão

*Acentroscelus* Simon, 1886: 185 (Rinaldi, 1984: 109).

*Updated diagnosis*

The species of this genus are differed of other Tmarini by present lateral puncturated soquets and a transverse line of great setiferous tubercles on the posterior margin of the carapace declivity, excepting *W. echinithorax* sp. nov. Male palp like *Acentroscelus* with discoid tegulum and reduced RTA and with a forked VTA, but this last ribbed. Females differs in the epigynum with medial septum and two copulatory ventrally

visible openings. The genus is related to *Acentroscelus* but differs markedly by epyginum form and body size.

*Distribution*

Species of *Whittickius* occur from Colombia to Brazil.

*Composition*

The genus contains three valid species and two to be described: *Whittickius singularis* (Mello-Leitão, 1940), **comb. nov.**, *Whittickius guianensis* (Taczanowski, 1872), **comb. nov.** and *Whittickius granulosus* (Mello-Leitão, 1929), **comb. nov.**

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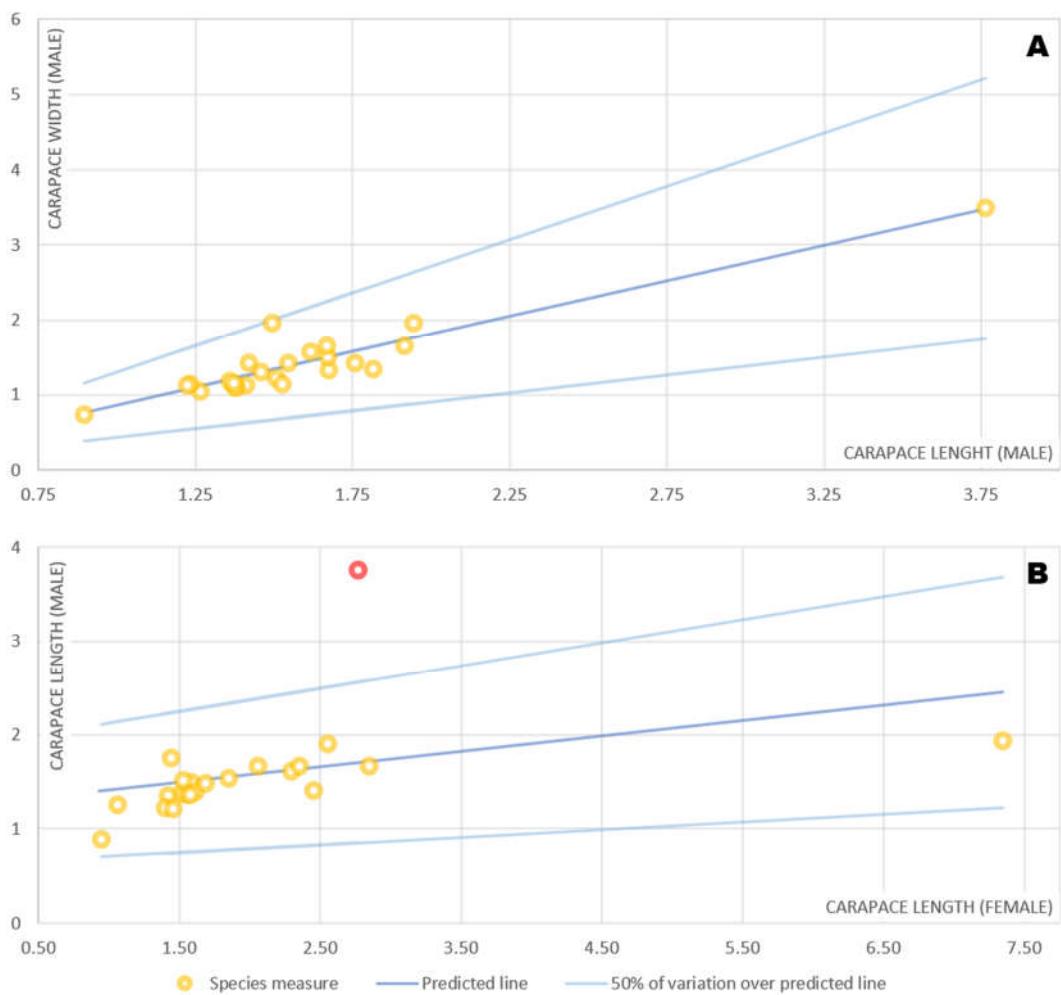
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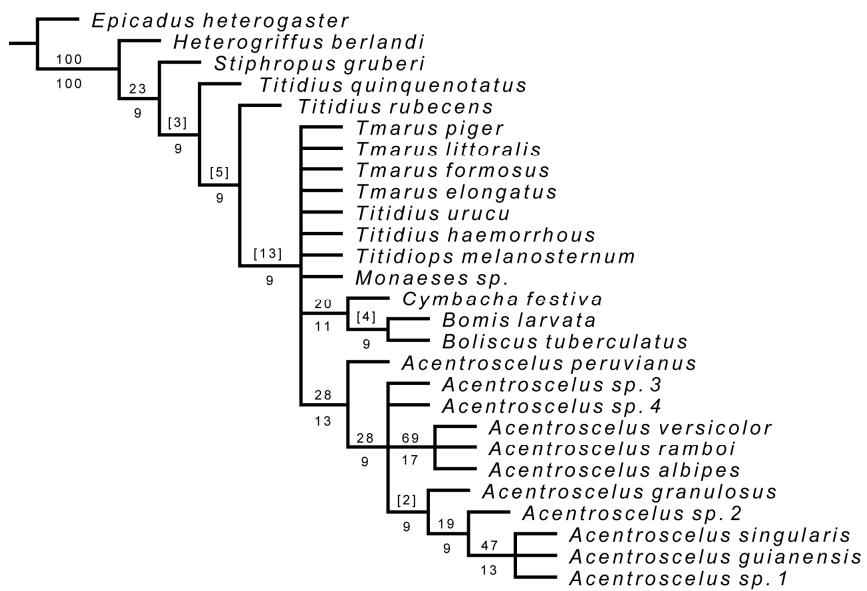
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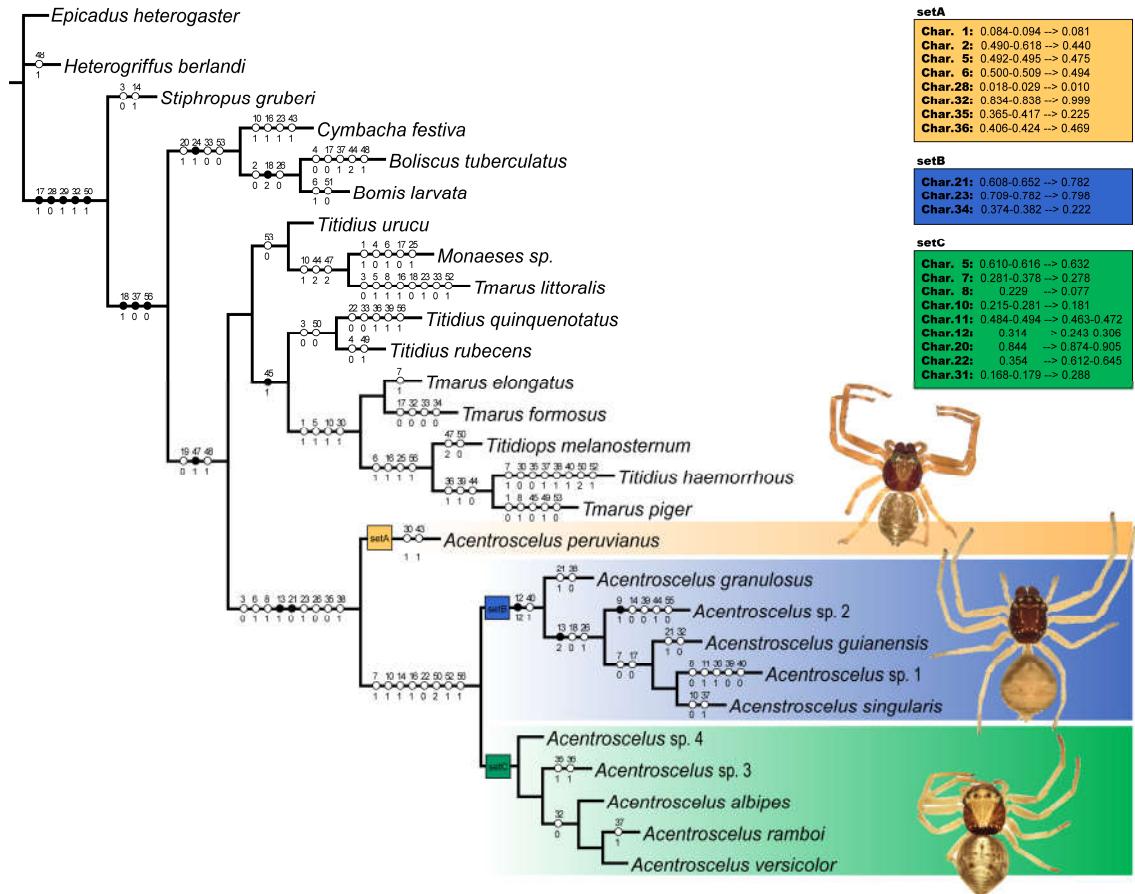
## Figures



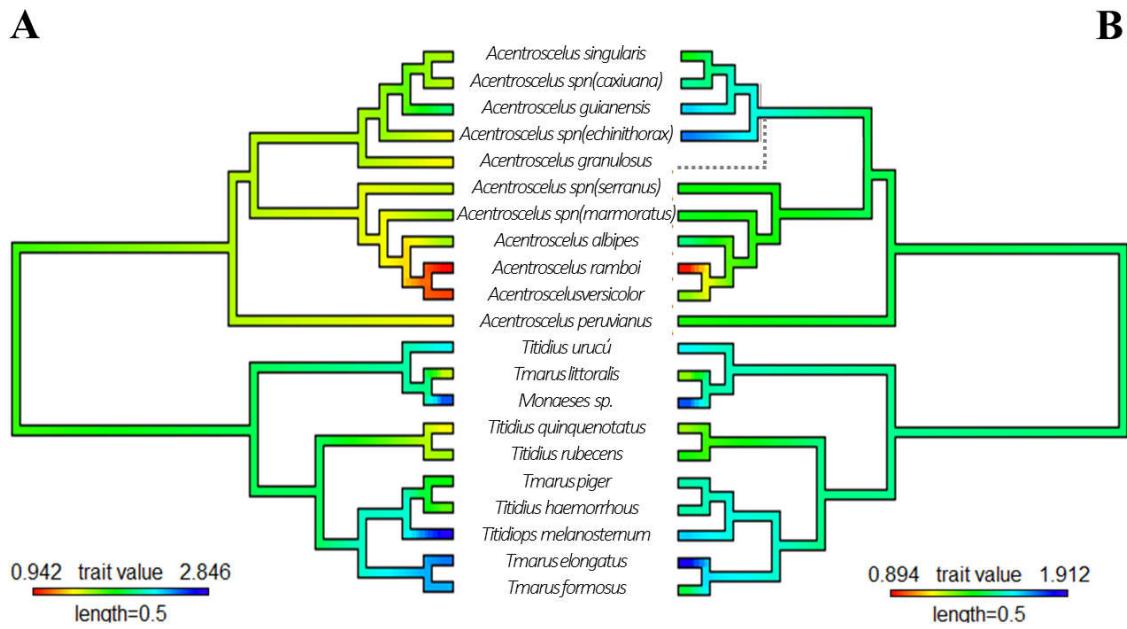
**Figure 1:** Regression analysis for independence of continuous characteristics. (A) Graphic performance of characters considered to be dependent, with variations lower to 50% of Y-predicted. (B) Conduct of the of the treated characters as independent, with variations of more than 50% of the Y-predicted.



**Figure 2:** Strict consensus of the six most parsimonious trees using discrete characters (length: 178 steps). Relative Bremer support value are indicated on branches and frequency of CG groups (calculated using Symmetric Resampling) are represented below branches.



**Figure 3:** Consensus of the most stable tree after removing the continuous characters that showed dependence. Synapomorphies are represented by black circles and homoplastic characters by white circles. The three squares at the base of the clades formed in the internal group reference three sets of transformations of the continuous characters.



**Figure 4:** Evolution of body size in *Acentroscelus* latu sensu. A) Female body length, B), male body length. An ultrametric tree was pruned to contain the 21 Tmarini taxa with known size variation in females and 20 in males (*Acentroscelus granulosus* male lack of known male specimens). Phylogenetic signal: Female's  $K = 0.6113$   $P = 0.0708$ ; Male's  $K = 0.4106$   $P = 0.471$ .

**Appendix 1.** List of material analyzed. Exemplar taxa, voucher specimens. All specimens were photographed and measured. The number of specimens in the list corresponds to the number of individuals used to take the measurements, not to the entire lot.

SPECIES	CODE	♂	♀	LOCALITY	DATE	COLETOR
<i>Bomis larvata</i>	MAS-15271	-	1	Australia, Australia, Sidney, Royal National Park	07/08/1969	R. Mascoro
<i>Boliscus sp.</i>	ZMBH-48566	-	1	South Africa, South Africa, -, Lekgalameetse Nature Reserve	18/12/1995	F. Koch
<i>Tmarus piger</i>	SMF-26364	1	-	Germany, Germany, Frankfurt am Main, -	06/05/1952	R. Braun
<i>Tmarus piger</i>	SMF-26416	1	1	Germany, Germany, Frankfurt am Main, Zoology	03/05/1966	LC
<i>Tmarus piger</i>	SMF-15355	1	1	Germany, Germany, Frankfurt am Main, -	06/05/1905	R. Braun
<i>Heterogriffus berlandi</i>	CAS-9046678	1	1	Democratic Republic of the Congo, Democratic Republic of the Congo, Tshikapa, 17 miles west	09/08/1957	R.E. Leech
<i>Cymbacha festiva</i>	CAS-77330	1	-	Australia, Australia, Sidney, Royal National Park	15/12/166	R. Mascoro
<i>Cymbacha festiva</i>	CAS-77329	-	2	Australia, Australia, Sidney, Royal National Park	20/05/1967	R. Mascoro
<i>Titidiops melanosternum</i>	MCN-30813	1	-	Brasil, Brasil, São Francisco de Paula, Barragem dos Burgueses	23- 25/11/1988	L.A. Moura
<i>Titidiops melanosternum</i>	MCN-36517	1	1	Brasil, Brasil, Triunfo, Parque Copesul de Proteção Ambiental	21/10/2003	A. Barcellos and L. Smichdt
<i>Titidiops melanosternum</i>	MCN-30096	1	-	Brasil, Brasil, Salto de Jacuí, Morto CEEE	19/10/1998	A.B. Bonaldo
<i>Epicadus heterogaster</i>	MCTP-7101	-	1	Brasil, Brasil, Morretes, Serra da Graciosa	09- 20/01/1995	A. Braul
<i>Epicadus heterogaster</i>	MCTP-41197	-	1	Brasil, Brasil, Imbituba, -	30/02/2013	F.M. Bianchi Flavio
<i>Epicadus heterogaster</i>	MCTP-11446	-	1	Brasil, Brasil, Chapecó, -	14/12/2000	García Mello
<i>Epicadus heterogaster</i>	MCTP-1722	1	-	Brasil, Brasil, Uraricoera, Ilha de Maracá	31/01/2014	A.B. Bonaldo
<i>Epicadus heterogaster</i>	MCTP-32096	1	-	Brasil, Brasil, Varginha, -	09/05/2011	R.C. Francisco
<i>Titidius rubecens</i>	MCTP-1130	-	1	Brasil, Brasil, Manaus, Reserva Ducke	12/03/1987	L. S. de Aquino
<i>Tmarus formosus</i>	MCTP-3529	-	1	Brasil, Brasil, Cachoeira do Sul, Alto dos casemiros	14/11/1992	Reina G. Buss
<i>Tmarus formosus</i>	MCTP-3627	1	-	Brasil, Brasil, Cachoeira do Sul, Capanezinho	12/05/1993	Reina G. Buss
<i>Tmarus formosus</i>	MCTP-4081	-	1	Brasil, Brasil, Florianópolis, Ilha do Arvoredo	15/10/1993	Arno A. Lise D.R.
<i>Titidius quinquenotatus</i>	MPEG-5324	-	1	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	09/09/2003	Santos—So uza
<i>Titidius rubecens</i>	MCTP-5335	-	1	Brasil, Brasil, Pantano Grande, Fazenda Souza Cruz	08/12/2007	G. Depra
<i>Titidius quinquenotatus</i>	MPEG-5340	-	1	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	12/09/2003	A.B. Bonaldo
<i>Titidius rubecens</i>	MPEG-5404	1	-	Brasil, Brasil, Pantano Grande, Fazenda Souza Cruz	08/12/2007	G. Depra
<i>Titidius quinquenotatus</i>	MPEG-5446	1	-	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	16/09/2003	A.B. Bonaldo

<i>Titidius quinquevittatus</i>	MPEG-5447	1	-	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	16/03/2004	D.D. Guimarães
<i>Tmarus formosus</i>	MCTP-6869	-	1	Brasil, Brasil, Cachoeira do Sul, -	20/10/1994	Reina G. Buss
<i>Tmarus formosus</i>	MCTP-8164	1	-	Brasil, Brasil, Viamão, Instituto Educacional Nossa Senhora das Graças	17/10/1995	Arno A. Lise
<i>Titidius rubecens</i>	MCTP-9507	1	-	Brasil, Brasil, Melgaço, Caxiuana	11/08/1996	Arno A. Lise
<i>Titidius rubecens</i>	MCTP-9508	1	-	Brasil, Brasil, Melgaço, Caxiuana	11/08/1996	Arno A. Lise
<i>Titidius rubecens</i>	MCTP-9653	-	1	Brasil, Brasil, Manaus, Reserva Ducke	12/03/1987	L. S. de Aquino
<i>Titidius urucu</i>	MPEG-13292	1	-	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	16/03/2004	D.D. Guimarães
<i>Titidius urucu</i>	MPEG-13347	-	1	Brasil, Brasil, Novo Progresso, Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	16/03/2004	D.D. Guimarães
<i>Titidius quinquevittatus</i>	MPEG-15567	-	1	Brasil, Brasil, Carana/Querencia, Fazenda Tanguru, antiga Fazenda Morro Azul	28/05/2006	D.F. Candiani
<i>Titidius quinquevittatus</i>	MPEG-15569	1	-	Brasil, Brasil, Carana/Querencia, Fazenda Tanguru, antiga Fazenda Morro Azul	17/06/2006	N.F. LoManHun g
<i>Tmarus littoralis</i>	MCTP-32014	1	1	French Guiana, French Guiana, Inselberg, -	05/09/2010	V. Vedel
<i>Tmarus littoralis</i>	MCTP-32018	1	1	French Guiana, French Guiana, Inselberg, -	09/09/2010	V. Vedel
<i>Tmarus littoralis</i>	MCTP-32016	1	1	French Guiana, French Guiana, Baggot Cacao, -	01/02/2010	V. Vedel
<i>Tmarus elongatus</i>	MCTP-39987	1	-	Brasil, Brasil, Pantano Grande, Fazenda Souza Cruz	08/12/2007	G. Depra
<i>Tmarus elongatus</i>	MCTP-39992	-	1	Brasil, Brasil, São Borja, Campus URCAMP	11/10/2008	R.A. Boelter
<i>Tmarus elongatus</i>	MCTP-39994	1	-	Brasil, Brasil, Santa Maria, Cidade dos Meninos	18/02/1999	L. Industriak
<i>Tmarus elongatus</i>	MCTP-40000	-	1	Brasil, Brasil, Cachoeira do Sul, -	25/05/1993	Reina G. Buss
<i>Tmarus elongatus</i>	MCTP-40143	1	-	Brasil, Brasil, Santa Maria, São Marcos	25/02/1999	L. Industriak
<i>Titidius urucu</i>	MCTP-40716	1	-	French Guiana, French Guiana, -, -	09/11/2014	V. Vedel
<i>Titidius urucu</i>	MPEG-40717	-	1	French Guiana, French Guiana, -, -	12/11/2014	V. Vedel
<i>Tmarus elongatus</i>	MCTP-41397	-	1	Brasil, Brasil, Santa Maria, -	02/12/1998	Arno A. Lise
<i>Tmarus formosus</i>	MCTP-42030	1	-	Argentina, Argentina, Cordoba, -	07/03/2014	C.I. Argañaraz
<i>Stiphropus gruberi</i>	SMF-30404	1	1	Indonesia, Indonesia, -, Fort de Kock	01/06/1905	Jacorson
<i>Monaeses sp.</i>	ZMBH-48568	1	-	South Africa, South Africa, -,	-	F. Kodh
<i>Acentroscelus albipes</i>	IBSP-120882	-	1	Brasil, Brasil, Barra Mansa, Floresta da Cicuta, Volta Redonda	11—18/06/2001	Equipe Biota A.D.
<i>Acentroscelus albipes</i>	IBSP-120859	-	1	Brasil, Brasil, Barra Mansa, Floresta da Cicuta, Volta Redonda	5—11/12/1999	Brescovit et. al.
<i>Acentroscelus albipes</i>	MZSP-27983	-	1	Brasil, Brasil, Guarulhos, P.E. Serra da Canteira	9/08/2000	R. Pinto Da Rocha
<i>Acentroscelus albipes</i>	UFMG-3166	1	-	Brasil, Brasil, Nova Lima, RPPN Mata Samuel de Paula	30/04/2001	J.P.P Pena
<i>Acentroscelus albipes</i>	UFMG-2749	1	-	Brasil, Brasil, Nova Lima, RPPN Mata Samuel de Paula	01/05/2007	J.P.P Pena
<i>Acentroscelus albipes</i>	LACB-1068	1	-	Brasil, Brasil, Santana do Rioachão, PARNA, Serra do Cipó, Portaria Palácio	16/07/01	E.S.S. Álvarez

<i>Acentroscelus peruvianus</i>	MUSM -	2	1	Perú, Perú, Puerto Maldonado, MD. KM 15	3 VI—24 VII 1989	Silva
<i>Acentroscelus peruvianus</i>	MPEG-13237	-	1	Brasil, Brasil, Coari, Porto Urucu, Base de Operações Geólogo Pedro de Moura	x 2006	LO Man Hung
<i>Acentroscelus peruvianus</i>	ICN-AR-10238	-	1	Colombia, Colombia, San José del Guaviare, Vereda Playa Güío, Sector Iracas, finca Galicua	16/04/2013	E.Flórez et al.
<i>Acentroscelus peruvianus</i>	ICN-AR-7615	1	-	Colombia, Colombia, San José del Guaviare, -	09/10/2013	E.Flórez et al.
<i>Acentroscelus ramboi</i>	MCTP-40111	-	1	Brasil, Brasil, Santa Maria, -	27/05/2000	Indrusiak, L.
<i>Acentroscelus ramboi</i>	MCTP-41406	-	1	Brasil, Brasil, Santa Maria, -	21/12/1993	Indrusiak, L.
<i>Acentroscelus ramboi</i>	MCTP-41407	-	1	Brasil, Brasil, Santa Maria, -	29/06/2005	Indrusiak, L.
<i>Acentroscelus ramboi</i>	MCTP-10474	1	-	Brasil, Brasil, São Sepé, -	December 1994	R.C. Costa
<i>Acentroscelus ramboi</i>	MCTP-40120	1	-	Brasil, Brasil, Santa Maria, -	28 July 1998	Indrusiak, L.
<i>Acentroscelus ramboi</i>	MCTP-1126	1	-	Brasil, Brasil, Campo Bom, -	25 July 1986	C.J. Becker
<i>Acentroscelus</i> sp. 4	MCN Z-33020	1	-	Brasil, Brasil, Viamão, Três Figueiras Arraio	13 July 2000	A.B. Bonaldo
<i>Acentroscelus</i> sp. 4	MCTP-17195	1	-	Brasil, Brasil, São Francisco de Paula, Potreiro Velho	-	-
<i>Acentroscelus</i> sp. 4	MCTP-6265	1	-	Brasil, Brasil, Caxias do Sul, -	November 1993	A.A. Lise
<i>Acentroscelus</i> sp. 4	MCN Z-25487	-	1	Brasil, Brasil, Cambará do Sul, -	11—15 April 1994	M.A.L. Marques
<i>Acentroscelus</i> sp. 4	MCTP-17200	-	1	Brasil, Brasil, São Francisco de Paula, Potreiro Velho	23 July 1998	A.A. Lise
<i>Acentroscelus</i> sp. 4	MCTP-17197	-	1	Brasil, Brasil, São Francisco de Paula, Potreiro Velho	August 2002	L.A. Bentocello
<i>Acentroscelus versicolor</i>	IBSP-120913	1	-	Brasil, Brasil, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>Acentroscelus versicolor</i>	IBSP-120942	1	-	Brasil, Brasil, Jundiaí, Serra do Japi	15-19 July 2002	Equipe Curso USP
<i>Acentroscelus versicolor</i>	IBSP-121983	1	-	Brasil, Brasil, Itapevi, -	I-December 1999	C. Bertim
<i>Acentroscelus versicolor</i>	MZSP-27976	-	1	Brasil, Brasil, São Paulo, -	10 November 2000	R. Pinto Da Rocha
<i>Acentroscelus versicolor</i>	MZSP-12833	-	1	Brasil, Brasil, Repúblia Nova, Cocaia	25 January 1948	H. Urbam
<i>Acentroscelus versicolor</i>	MZSP-27994	-	1	Brasil, Brasil, São Paulo, -	2 March 2001	R. Pinto Da Rocha
<i>Acentroscelus granulosus</i>	UFMG-16082	-	1	Brasil, Brasil, Guarulhos, -	IX—October 2014	P.H. Martins
<i>Acentroscelus</i> sp. 3	IBSP-120970	1	-	Brasil, Brasil, Catas Altas, RPPN Serra da Caraça	24/IV—May 2002	Equipe Biota
<i>Acentroscelus versicolor</i>	IBSP-120710	1	-	Brasil, Brasil, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu	16—22 July 2001	Equipe Biota
<i>Acentroscelus</i> sp. 3	MZSP-27978	1	-	Brasil, Brasil, Mairiporã, P.E. Serra da Cantareira Pinheirinho	29 October 2000	R. Pinto Da Rocha
<i>Acentroscelus</i> sp. 3	MZSP-27992	-	1	Brasil, Brasil, Mairiporã, P.E. Serra da Cantareira Pinheirinho	29 October 2000	R. Pinto Da Rocha
<i>Acentroscelus</i> sp. 3	MZSP-27986	-	1	Brasil, Brasil, Mairiporã, P.E. da Cantareira Pinheirinho	29 April 2001	R. Pinto Da Rocha
<i>Acentroscelus</i> sp. 3	MZSP-27991	-	1	Brasil, Brasil, Mairiporã, P.E. da Cantareira Pinheirinho	23 June 2001	R. Pinto Da Rocha
<i>Acentroscelus</i> sp. 1	ICN-AR-10236	1	-	Colombia, Colombia, Valle Del Guamuez, Territorio Kofan	20/09/1998	A. Rodríguez
<i>Acentroscelus</i> sp. 1	MPEG-15563	1	-	Brasil, Brasil, Belém, Reserva	11 December	S.C. Dias

				Mocambo	2007	
<i>Acentroscelus</i> sp. 1	MPEG-4326	1	-	Brasil, Brasil, Altamira, Castelo dos Sonhos	10 November 2005	D.R. Santos
<i>Acentroscelus</i> sp. 1	MACN-10781	-	1	Brasil, Brasil, Belém, Utinga	August 1970	C.M. Galiano
				Brasil, Brasil, Canarana/Querência,		N.F.
<i>Acentroscelus</i> sp. 1	MPEG-15559	-	1	Fazenda Tangueo, antiga Fazenda Morro Azul	09 June 2006	LoManHun g
					15—28	A.D.
<i>Acentroscelus</i> sp. 1	IBSP-47142	-	1	Brasil, Brasil, Una , Reserva Biológica de Una	November 2000	Brescovit et. al.
					14—23	
<i>Acentroscelus</i> sp. 2	IBSP-120677	1	-	Brasil, Brasil, Bonito, —	October 2002	Equipe Biota
				Brasil, Brasil, Alto Alegre, Ilha de		
<i>Acentroscelus</i> sp. 2	MCTP-7550	1	-	maracá, Estação Ecológica de Maracá	31/I—14 February 1992	Arno A. Lise
				Brasil, Brasil, Novo Progresso,		
<i>Acentroscelus</i> sp. 2	MPEG-5405	1	-	Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	15 October 2003	D.R. Santos
				Brasil, Brasil, Alto Alegre, Ilha de		
<i>Acentroscelus</i> sp. 2	MCTP-1769	-	1	maracá, Estação Ecológica de Maracá	31/I—14 February 1992	Arno A. Lise
				Brasil, Brasil, Novo Progresso,		
<i>Acentroscelus</i> sp. 2	MPEG-5328	-	1	Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	15 October 2003	D.R. Santos
				Brasil, Brasil, Novo Progresso,		
<i>Acentroscelus</i> sp. 2	MPEG-5406	-	1	Serra do Cachimbo, Campo de Provas Brigadeiro Velloso	15 October 2003	D.R. Santos
<i>Acenstroscelus guianensis</i>	IBSP-17306	-	1	Brasil, Brasil, Iranduba, Ilha de Curará, Paraná	3 VIII 1979	J. Adis et al.
<i>Acenstroscelus guianensis</i>	IBSP-120676	-	1	Brasil, Brasil, Bonito, -	14—23 October 2002	Equipe Biota
<i>Acenstroscelus guianensis</i>	IBSP-120674	-	1	Brasil, Brasil, Bonito, -	14—23 October 2002	Equipe Biota
<i>Acenstroscelus guianensis</i>	MCTP-1959	1	-	Brasil, Brasil, Alto Alegre, Ilha de maracá, Estação Ecológica de Maracá	01/05/1952	Marcelo N.
<i>Acenstroscelus guianensis</i>	MCTP-2177	1	-	Brasil, Brasil, —, Chapada do Guimarães	15—26/07/1992	A.A. Lise
<i>Acenstroscelus guianensis</i>	IBSP-120702	1	-	Brasil, Brasil, Itabaiana, Estação Ecológica da Serra de Itabaiana	14—20/09/1999	A.D. Brescovit
<i>Acenstroscelus singularis</i>	MACN-19120	1	1	Brasil, Brasil, Manaus, Reserva Ducke	01/08/2004	M.E. Galiano
<i>Acenstroscelus singularis</i>	MPEG-8768	1	-	Brasil, Brasil, Juruti, Vale do Igapá Mutum, Platô do Rio Juruti	04/08/2004	D.F. Candiani P.
<i>Acenstroscelus singularis</i>	INPA-22682	-	1	Brasil, Brasil, Manaus, Reserva Ducke	09/04/1973	Alboquerque P.
<i>Acenstroscelus singularis</i>	INPA-22683	-	1	Brasil, Brasil, Manaus, Reserva Ducke	10/04/1973	Alboquerque P.
<i>Acenstroscelus singularis</i>	INPA-22684	1	-	Brasil, Brasil, Manaus, Reserva Ducke	11/04/1973	Alboquerque P.

## Appendix 2

**Table S1:** List of continuous characters and its numeration in the nexus matrix. Characters marked with asterisk (\*) were excluded of the analysis after the regression test (described in Material and Methods).

Character n°		
Female	Male	Description
1	2	Carapace length
3	4	Carapace, ratio width:length
5	6	Carapace, ratio lateral width:total width
7	8	Carapace, ratio height:length
9	10	Legs, Femur I, ratio, femur:caparace length
11	12	*Legs, Femur II, ratio, femur:caparace length
13	14	Legs, Femur III, ratio, femur:caparace length
15	16	*Legs, Femur IV, ratio, femur:caparace length
17	18	*Legs, ratio, femur I:II
19	20	*Legs, ratio, femur I:III
21	22	*Legs, ratio, femur I:IV
23	24	Sternum, ratio, width:length
25	26	Endites, ratio, width:length
27	28	Labium, ratio, width:length
29	30	Abdomen, ratio, width:length
31	32	Carapace, Clypeus, angle
33	34	Carapace, Eyes, ratio, AME:caparace length
35	36	Carapace, Eyes, ratio, ALE:caparace length
37	38	*Carapace, Eyes, ratio, PME:caparace length
39	40	Carapace, Eyes, ratio, PLE:caparace length
41	42	Carapace, Eyes, ratio, AME:ALE
43	44	*Carapace, Eyes, ratio, PME:PLE
45	46	*Carapace, Eyes, ratio, AME:PME
47	48	Carapace, Eyes, ratio, ALE:PLE
49	50	*Carapace, Eyes, ratio, PME:ALE
51	52	*Carapace, Eyes, ratio, AME:PLE
	53	Male palp, size, ratio, tegulum length:palp length
	54	Male palp, tegulum, size, ratio, width:length
55		Epigynum, epigynal plate, ratio, width:length
56		Epigynum, copulatory openings, transversal position in relation to epigynal plate width
57		Epigynum, copulatory openings, longitudinal position in relation to epigynal plate length

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**Table S2:** List of discrete characters, its states and some additional.

- (1) *Carapace, background coloration* (Same as char. 2. from Machado et al. 2017): (0) Brownish red (Figs S#1A); (1) yellow.
- (2) *Carapace, clypeus, macrosetae* (Same as char. 13. from Teixeira et al. 2015): (0) absent; (1) present (S#1B-E).
- (3) *Carapace, dorsal surface, microstructure of tegument, papule* (Same as char. 5. from Teixeira et al. 2015): (0) absent (S#1B-C, F); (1) present (S#1C, G).
- (4) *Carapace, dorsal view, coloration pattern, longitudinal line* (It is inconspicuous in some males): (0) absent; (1) present (S#1A).
- (5) *Carapace, dorsal view, coloration pattern, radial stripes on the lateral region* (Usually visible on the female but inconspicuous on the male): (0) absent; (1) present.
- (6) *Carapace, dorsal view, coloration pattern, transversal stripe behind the PLE*: (0) absent; (1) present (S#1A).
- (7) *Carapace, dorsal view, coloration pattern, transversal stripe over the clypeus*: (0) absent; (1) present (S#1A).
- (8) *Carapace, dorsal view, coloration pattern, V-like bounding the dorsal region* (Should be conspicuous to be considered as "Present"): (0) absent; (1) present (S#1A).
- (9) *Carapace, laterals, two pairs of depression*: (0) absent (S#1A, C, E); (1) present (S#1D).
- (10) *Carapace, lateral view, coloration pattern, longitudinal strip in the margin of carapace*: (0) absent (S#2B); (1) present (S#2A).
- (11) *Carapace, posterior slope, median depression* (Same as char. 6. Teixeira et al. 2015): (0) absent (S#1D-E); (1) present (S#1C).
- (12) *Carapace, tegument, dorsal and lateral region, tubercles*: (0) absent (S#1E); (1) present, few (S#1C); (2) present, many (S#1D).
- (13) *Carapace, tegument, posterior slope, marginal tubercles*: (0) absent (S#1E); (1) present, small (S#1C); (2) present, big (S#1D).
- (14) *Carapace, tegument, shape of the setae sockets* (Same as char. 15. from Teixeira et al. 2015): (0) conical (S#1G); (1) punctured (S#1F).
- (15) *Chelicerae, anterior surface, apex, setae, shape* (Same as char. 36. from Benjamin 2011; Same as char. 36. from Teixeira et al. 2015): (0) pointed; (1) peg-like.
- (16) *Sternum, coloration, in relation with color pattern of the coxae*: (0) same color (with same color pattern of the coxae — S#2E, F); (1) darker (S#2D); (2) lighter (S#2E).
- (17) *Sternum, posterior border, emargination between coxae IV* (Same as char. 09. from Machado et al. 2017): (0) absent (S#2C, E); (1) present (S#2D, F).
- (18) *Sternum, posterior end, emargination, general shape* (Same as char. 9. from Machado et al. 2017): (0) rhombus (ângulo obtuso — S#2G); (1) pointed (ângulo reto para agudo — S#2H); (2) retangular.
- (19) *Legs, anterior metatarsi (I and II), dorsal macrosetae* (Modified of the char. 53 from Machado et al. 2017): (0) absent (S#2G, H); (1) present.
- (20) *Legs, anterior patella I, medial keel* (Same as char. 46. from Machado et al. 2017): (0)
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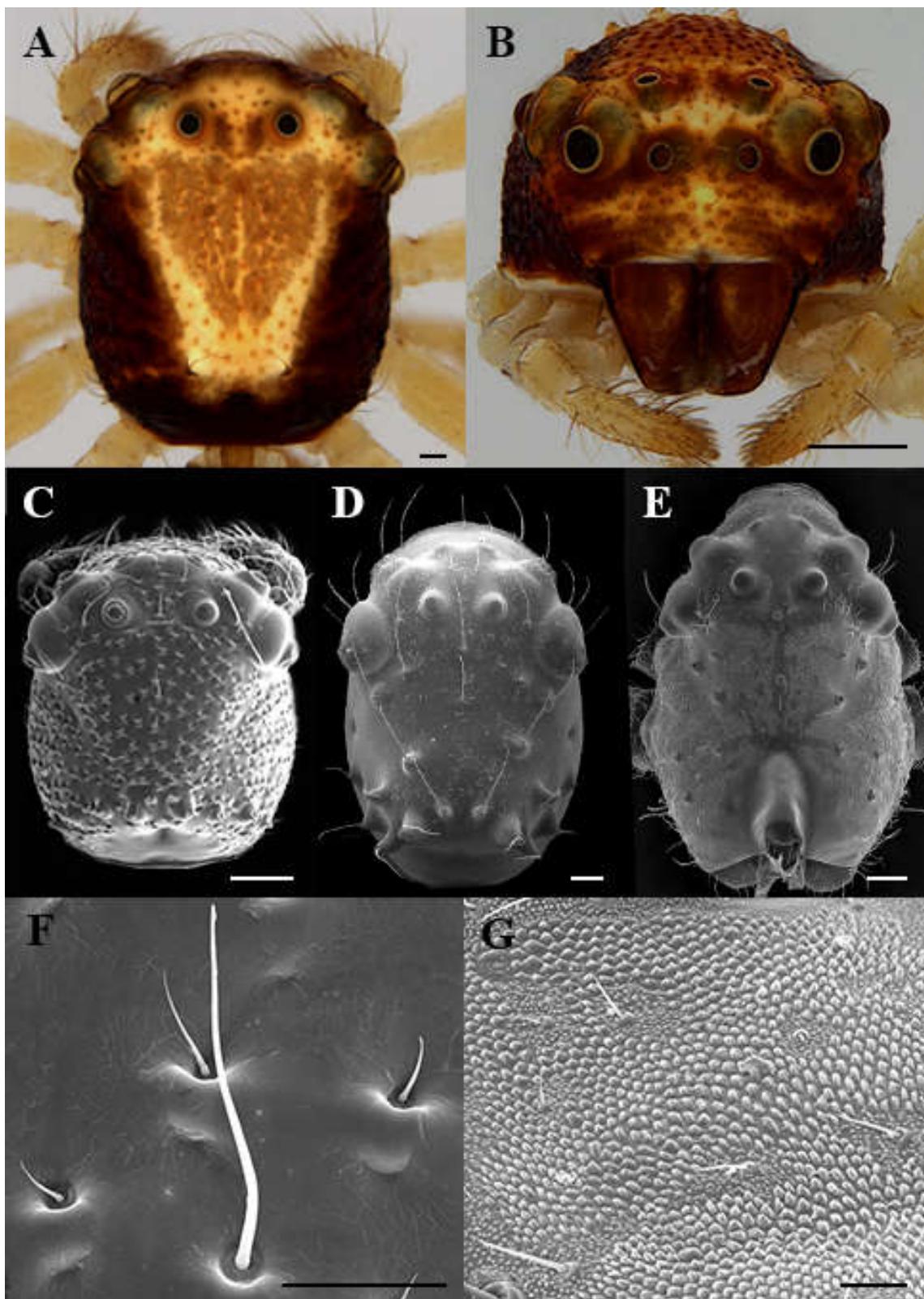
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absent (S#2H); (1) present (S#2G).

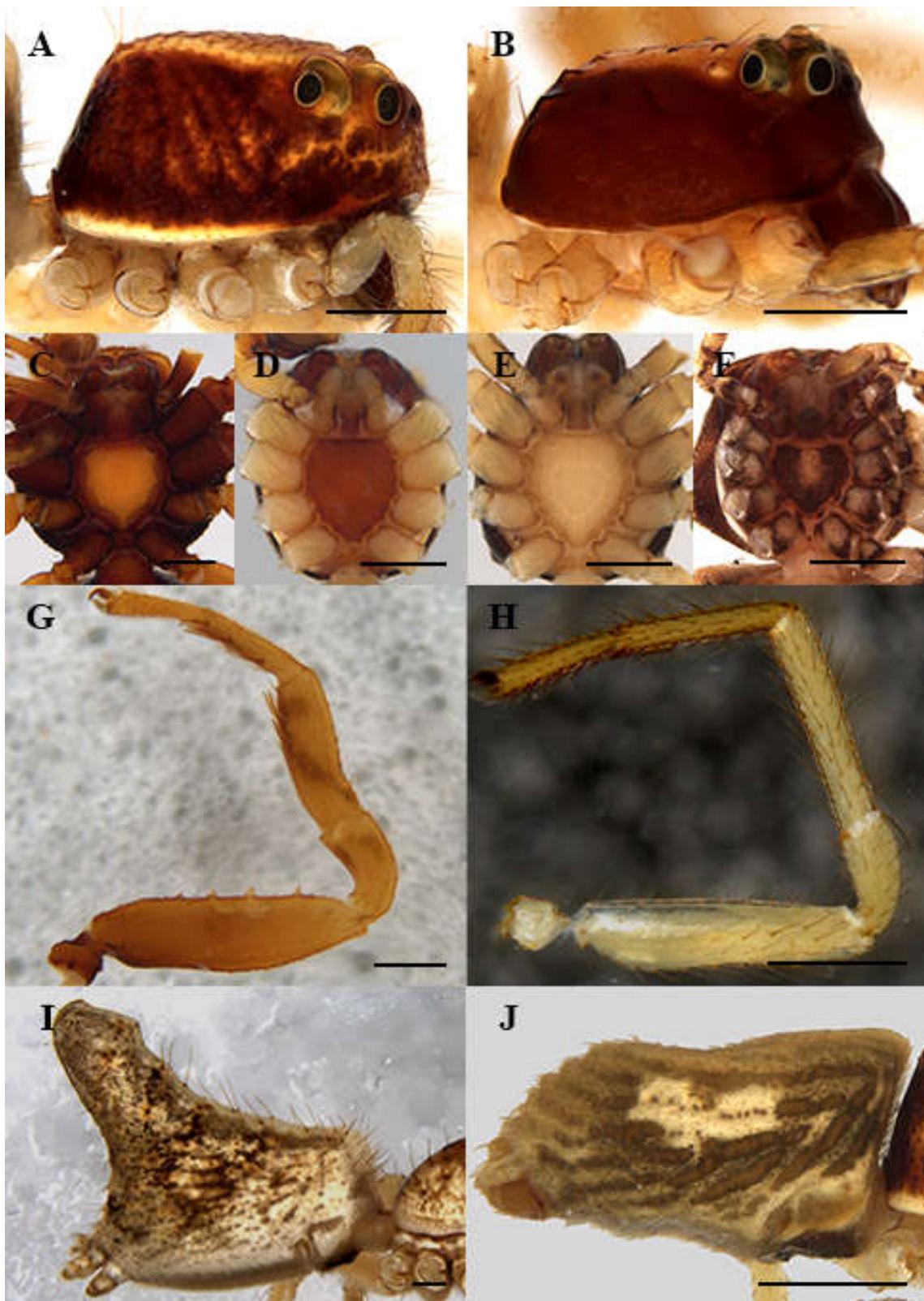
- (21) *Legs, anterior tibiae I, dorsal macrosetae*: (0) absent (S#2H); (1) present (S#2G).
  - (22) *Legs, anterior tibiae I, ventral macrosetae* (usually the same pattern is preset in the matatarsus): (0) absent (S#2H); (1) present (S#2G).
  - (23) *Legs, background coloration, femur I, in relation to carapace coloration*: (0) absent (S#2G); (1) present (S#2H).
  - (24) *Legs, coloration pattern, femur with base lighter than apex*: (0) absent (S#2G, H); (1) present.
  - (25) *Legs, coloration pattern, scattered small black spots*: (0) absent (S#2G, H); (1) present.
  - (26) *Legs, femur I, dorsal macrosetae*: (0) absent (S#2H); (1) present (S#2G).
  - (27) *Legs, femur I, ventral macrosetae*: (0) absent (S#2H); (1) present (S#2G).
  - (28) *Legs, femur I, ventral tubercles*: (0) absent (S#2H); (1) present (S#2G).
  - (29) *Legs, tarsi, claw teeth (pro or retro), disposition* (Same as char. 55. from Machado et al. 2017): (0) restricted to the basal portion of the claw (S#2G); (1) exceeding half of the claw length (S#2H).
  - (30) *Opisthosoma, dorsal, posterior region, anal median tubercle*: (0) absent (S#2G-H); (1) present.
  - (31) *Epigynum, copulatory duct, lenght, in relation to spermatheca lenght* (Same as char. 76. modified from Teixeira et al. 2015): (0) longer or equal (S#3A); (1) smaller (S#3B).
  - (32) *Epigynum, dorsal view, copulatory ducts, entry direction* (Same as char. 66. from Machado et al. 2017): (0) ascendant (S#3B); (1) descendent (S#3A).
  - (33) *Epigynum, dorsal view, of primary spermatheca, shape* (Same as char. 75. from Teixeira et al. 2015; adapted from Benjamin 2011 char32): (0) rounded; (1) reniform to elongated (S#3A-B).
  - (34) *Epigynum, dorsal view, of primary spermatheca, size*: (0) as large as the EP (S#3B); (1) smaller than EP (Should be half-sized or less than this (S#3A).
  - (35) *Epigynum, epigynal plate, atrium, depth* (Same as char. 71. from Teixeira et al. 2015): (0) deep (S#3C); (1) shallow (S#3D).
  - (36) *Epigynum, epigynal plate, atrium, margin delimiting atrium, anterior outline* (Same as char. 73. from Teixeira et al. 2015): (0) absent (S#3C); (1) present (S#3D, E).
  - (37) *Epigynum, epigynal plate, atrium, margin delimiting atrium, posterior outline* (Same as char. 74. from Teixeira et al. 2015): (0) absent (S#3C-E); (1) present.
  - (38) *Epigynum, epigynal plate, atrium, size*: (0) as large as the EP (S#3C); (1) smaller than EP (S#3D).
  - (39) *Epigynum, epigynal plate, atrium* (Same as char. 70. from Teixeira et al. 2015): (0) absent (S#3A, E); (1) present (S#3B-D).
  - (40) *Epigynum, epigynal plate, median field, median ridge* (Same as char. 65. from Teixeira et al. 2015): (0) absent (S#3C); (1) present (S#4D, E).
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- (41) *Male palp, conductor*: (0) absent (S#4A); (1) present (S#4B-F).
- (42) *Male palp, cymbium, paracymbium* (Same as char. 94. from Teixeira et al. 2015): (0) absent (S#4A-C); (1) present (S#4D-F).
- (43) *Male palp, embolus, apex, microstructuring, denticules*: (0) absent (S#4B, C, E); (1) present (S#4A, D).
- (44) *Male palp, embolus, length* (Same as char. 113. from Teixeira et al. 2015), *comparing with the tegulum circumference*: (0) less than  $\frac{1}{4}$  (S#4A-D); (1) about  $\frac{1}{2}$  (S#4F); (2) about 1 time or more (S#4E).
- (45) *Male palp, tegulum, tegular apophysis*: (0) absent (S#4A-E); (1) present (S#4F).
- (46) *Male palp, tegulum, tegular apophysis, position*: (0) basal; (1) apical (S#4F).
- (47) *Male palp, tegulum, tegular ridge, direction* (Same as char. 102. from Teixeira et al. 2015): (0) apical-prolateral; (1) apical-retrolateral (See Benjamin 2011 — S#4B, C, D, F); (2) basal-retrolateral (S#4E).
- (48) *Male palp, tegulum, tegular ridge (tr)* (Same as char. 101. from Teixeira et al. 2015): (0) absent (S#4B-F); (1) present (S#4A).
- (49) *Male palp, tibia, RTA, apex, direction* (Same as char. 89. from Teixeira et al. 2015): (0) upper (S#4A-E); (1) retrolateral (S#4F).
- (50) *Male palp, tibia, RTA, length, relative to tibia length* (Modified 83. from Teixeira et al. 2015): (0) longer (S#4F); (1) about equal (S#4A, D, E); (2) thin, similar to a conical tooth (S#4B, C).
- (51) *Male palp, tibia, ventral tibial apophysis (VTA)* (Same as char. 79. from Teixeira et al. 2015): (0) absent; (1) present (S#4A-F).
- (52) *Male palp, tibia, VTA, branched*: (0) absent (S#4A, D-F); (1) present (S#4B, C).
- (53) *Male palp, tibia, VTA, direction*: (0) absent (S#4A, E); (1) present (S#4B-D, F).
- (54) *Male palp, tibia, VTA, ectal branch, excavated*: (0) absent (S#4B); (1) present (S#4D).
- (55) *Male palp, tibia, VTA, ectal branch, size comparing with the mesial branch*: (0) smaller (1) longer (S#4B, D).
- (56) *Male palp, tibia, VTA, length relative to tibia length* (Same as char. 81. from Teixeira et al. 2015): (0) smaller (S#4A, C, E, F); (1) longer than tibia (S#4B, D).
-

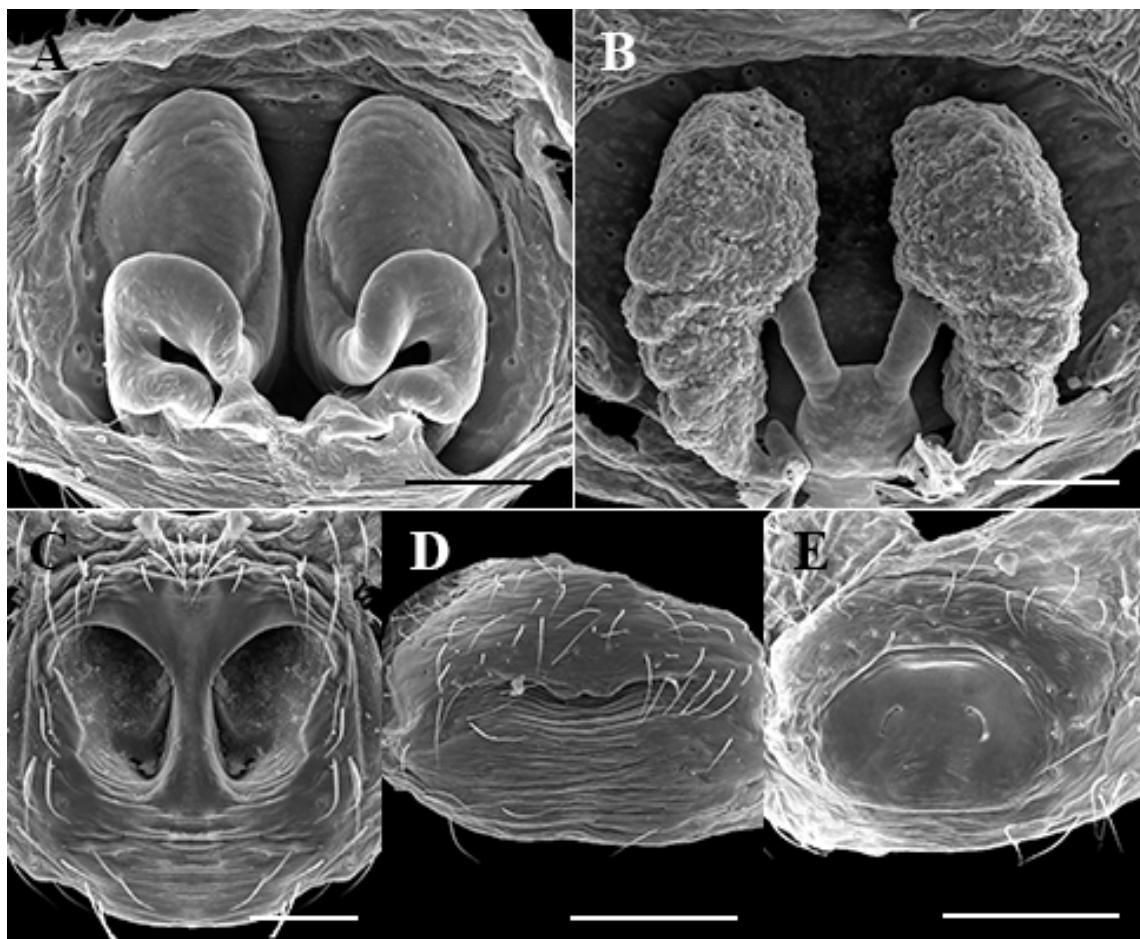
## Supplementary figures



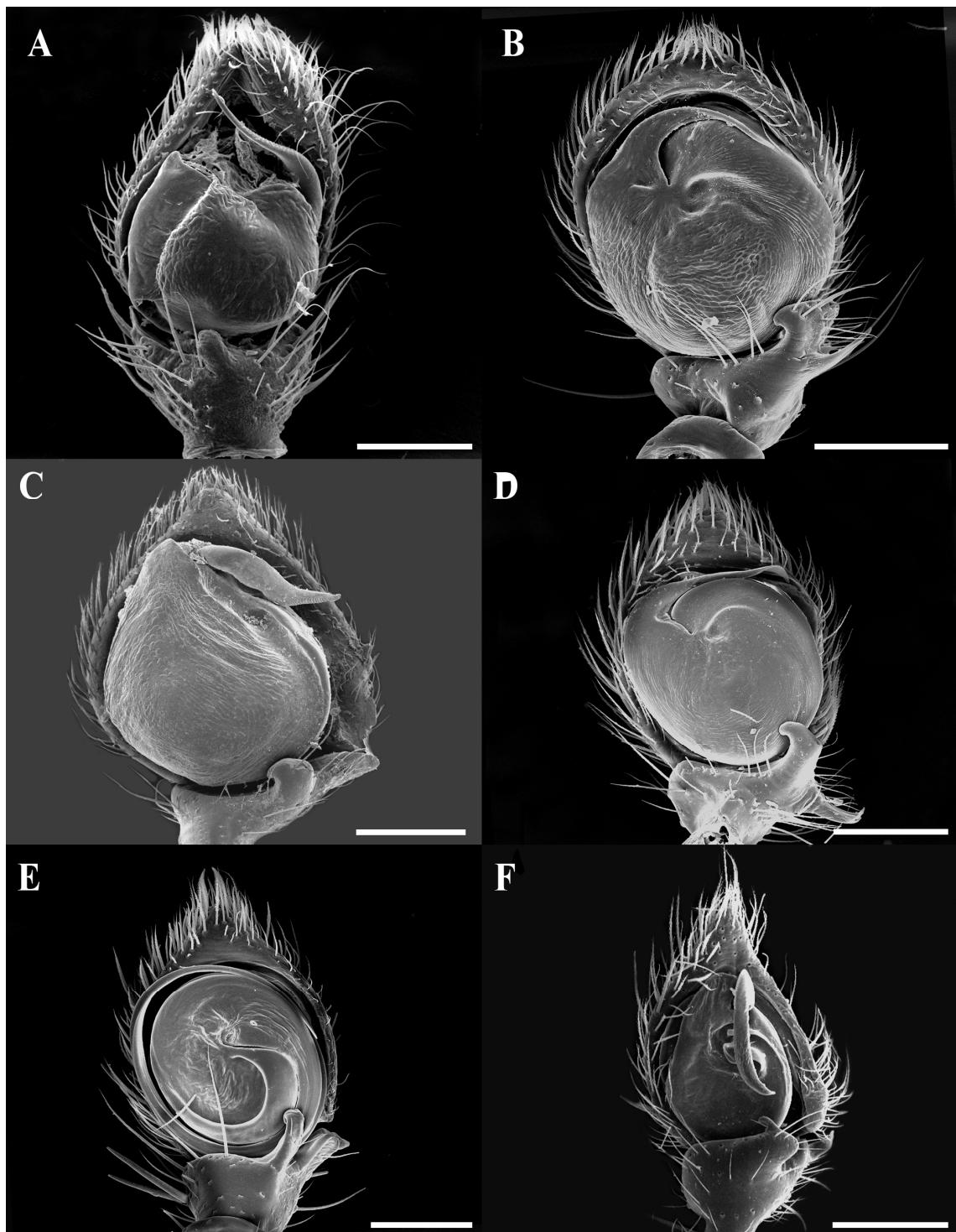
**Figure S#1:** *Acentroscelus albipes*. **A** habitus dorsal (female—MACN19120); **B** habitus frontal (female—INPA22682); **C** habitus dorsal (female—IBSP120875). **D** *Whittickius singularis* habitus dorsal (female—MCTP42630); **E** *Tmarus piger* habitus dorsal. **F** *A. albipes* dorsal tegument of carapace (MCTP). **F** *T. piger* dorsal tegument of carapace (SMF). Scale bars: 0.2 mm (A–E); 0.5 mm (F–G).



**Figure S#2:** Lateral of cephalothorax. **A** *Acentroscelus marmoratus* (female—MZSP27992); **B** *Maeanderion peruvianus* (male—MUSM). Sternum. **C** *Epicadus heterogaster* (male—MCTP1772); **D** *Acentroscelus albipes* (male—MZSP27978); **E** *Maeanderion peruvianus* (female—ICN-AR7615); **F** *Boliscus tuberculatus* (female—ZMBH48566). Leg I. **G** *Epicadus heterogaster* (male—MCTP1772); **H** *Acentroscelus albipes* (female—IBSP120882). Lateral of abdomen. **I** *Titidiops melanosternum* (female—MCN36517); **J** *Acentroscelus ramboi* (female—MCTP40111). Scale bars: 0.5 mm (A–F).



**Figure S#3:** Epyginum dorsal view. **A** *Whittickius granulosus* (female–UFMG16082); **B** *Acentroscelus ramboi* (female– IBSP121002). Epyginum ventral view. **C** *Whittickius granulosus* (female–UFMG16082); **D** *Acentroscelus marmoratus* (female– MZSP27978); **E** *Whittickius caxiuana* (female– ICN-AR10236). Scale bars: 0.1 mm (A–E).



**Figure S#4:** Male palp ventral view. **A** *Cymbacha festiva* (CAS 77330); **B** *Acentroscelus marmoratus* (MZSP-27978); **C** *Maeanderion peruvianus* (MUSM); **D** *Whittickius singularis* (MCTP42634); **E** *Monaeses* sp. (ZMBH48569); **F** *Titidius rubecens* (MCTP). Scale bars: 0.2 mm (A–E).

### Appendix 3.

Character matrix presented in two parts: discrete and continuous data matrix. The numbering corresponding to the characters described in the appendix 2.

#### Discrete data matrix

The first state is '0', followed by '1', '2', etc., '?' denotes missing data, '-' is inapplicable and 'A' represents polymorphic character states (0/1)

Taxa		0000000001 1234567890	111111112 1234567890	222222223 1234567890	3333333334 1234567890	4444444445 1234567890	555555 123456
<i>Epicadus heterogaster</i>	[01]	011000000	0000020001	1100011100	0001101011	00020--000	0----
<i>Boliscus tuberculatus</i>		0010000000	0000100211	1101000010	?002-01-01	00?20-0101	100--0
<i>Bomis larvata</i>		0011010000	0000101211	1101000010	??0?-00-00	10000--0--	0----
<i>Cymbacha festiva</i>		0111000001	0000111111	1111010010	?101-00-01	10100--001	100--0
<i>Heterogriffus berlandi</i>		01?0000000	0000000010	1100011100	0011111011	00010-0100	101--1
<i>Monaeses sp.</i>		1110010001	0000000100	1100110010	?111-00-00	01020-2101	100--0
<i>Stiphropus gruberi</i>		01000000000	0001101010	11000?2010	?111111010	11010--001	101--1
<i>Titidiops melanosternum</i>		1111110001	0000011100	1100110011	?1??-00-00	01?1102100	101--1
<i>Titidius haemorrhous</i>		1111111001	0000011100	1100110010	?111011111	00?0101102	111011
<i>Titidius quinquenotatus</i>		01010000000	0000001100	1000010010	?101110010	00?1111100	101--1
<i>Titidius rubecens</i>		01000000000	0000001100	1100010010	?111-00-00	01?1111110	101--0
<i>Titidius urucu</i>		01110000000	0000001100	1100010010	?111-00-00	01000-1101	100--0
<i>Tmarus elongatus</i>		1111101001	0000001100	1100010011	?111-00-00	00?1101101	101--0
<i>Tmarus formosus</i>		1111100001	0000000100	1100010011	?000-00-00	00?1101101	101--0
<i>Tmarus littoralis</i>		0101100101	0000011000	1110010010	?101-00-00	00?20-2101	110000
<i>Tmarus piger</i>		0111110101	0000011100	11[01]0110011	?1?1110010	01?00-1111	100--1
<i>Acentroscelus albipes</i>		0101011101	1011011100	0010000010	1010000110	00000-1102	111011
<i>Acentroscelus peruvianus</i>		0101010100	0010001100	0110000011	1110000110	01100-1101	101--0
<i>Acentroscelus ramboi</i>		0101011101	1011011100	0010000010	1010001110	00000-1102	111011
<i>Acentroscelus spn(serranus)</i>		0101011101	1011011100	0010000010	1110000110	00000-1102	111011
<i>Acentroscelus versicolor</i>		0101011101	1011011100	0010000010	1010000110	00000-1102	111011
<i>Acentroscelus granulosus</i>		0101011101	1211011100	1010000010	0111000011	???????????	??????
<i>Acentroscelus spn(marmoratus)</i>		0101011101	1011011100	0010000010	1110110110	00000-1102	111011
<i>Acentroscelus spn(caxiuana)</i>		0101010001	1121010000	0010010010	1110-10-00	00000-1102	111111
<i>Acentroscelus spn(echinithorax)</i>		0101011111	0220011000	0010010010	0111-00-01	00010-1102	111101
<i>Acenstroscelus guianensis</i>		0101010101	0121010000	1010010010	1010000111	00000-1102	111111
<i>Acenstroscelus singularis</i>		0101010100	0121010000	0010010010	1110001111	00000-1102	111111

### Continuous data matrix

Characters marked with asterisk (\*) were excluded of the analysis after the regression test (described in Material and Methods).

Continuous character number	Female	Male												
	1	2	3	4	5	6	7	8	9	*10	*11	12	13	14
<i>Epicadus heterogaster</i>	7.342	1.942	0.993	1.015	0.362	0.295	0.646	0.665	0.772	1.007	0.735	0.956	0.391	0.533
<i>Boliscus tuberculatus</i>	1.720	?	1.094	?	0.181	?	0.712	?	0.547	?	0.604	?	0.467	?
<i>Bomis larvata</i>	0.895	?	1.059	?	0.211	?	0.694	?	0.531	?	0.606	?	0.428	?
<i>Cymbacha festiva</i>	2.346	1.667	1.067	0.993	0.215	0.190	0.546	0.495	0.963	0.804	0.995	0.909	0.734	0.632
<i>Heterogriffus berlandi</i>	1.681	1.491	1.338	1.321	0.301	0.324	0.119	0.073	0.888	0.981	1.199	1.248	0.960	0.963
<i>Monaeses sp.</i>	2.660	1.815	0.753	0.745	0.209	0.197	?	0.417	?	1.662	?	1.626	?	0.674
<i>Stiphropus gruberi</i>	1.610	1.456	0.968	0.899	0.197	0.161	0.455	0.405	0.571	?	0.621	?	0.596	0.495
<i>Titidiops melanosternum</i>	2.846	1.67	0.987	0.902	0.188	0.223	0.553	0.420	1.070	1.326	1.093	1.284	0.706	0.840
<i>Titidius haemorrhous</i>	1.680	1.53	1.119	1.144	0.097	?	?	?	1.071	1.431	1.095	1.471	0.738	0.712
<i>Titidius quinquenotatus</i>	1.393	1.233	0.971	0.932	0.142	0.169	0.468	0.468	1.279	1.453	1.258	1.470	0.640	0.664
<i>Titidius rubecens</i>	1.572	1.371	0.873	0.850	0.190	0.200	0.554	0.462	1.148	1.474	1.087	1.378	0.602	0.683
<i>Titidius urucu</i>	2.289	1.615	0.918	0.981	0.227	0.271	0.490	0.484	1.349	1.627	1.349	1.614	0.739	0.799
<i>Tmarus elongatus</i>	2.551	1.912	0.907	0.866	0.194	0.260	0.424	0.376	1.044	1.737	1.307	1.708	0.821	0.770
<i>Tmarus formosus</i>	2.447	1.418	0.893	1.013	0.218	0.243	0.488	0.382	1.353	1.463	1.350	1.468	0.740	0.773
<i>Tmarus littoralis</i>	1.450	1.223	0.921	0.928	0.265	0.269	0.405	0.455	1.302	1.654	1.368	1.741	0.776	0.899
<i>Tmarus piger</i>	1.842	1.542	0.926	0.929	0.210	0.227	0.512	0.409	1.067	1.307	1.083	1.306	0.579	0.770
<i>Acentroscelus albipes</i>	1.578	1.505	0.783	0.814	0.075	0.085	0.553	0.567	0.696	0.759	0.689	0.746	0.486	0.494
<i>Acentroscelus peruvianus</i>	1.418	1.356	0.936	0.879	0.185	0.210	0.475	0.450	1.006	1.010	0.992	0.690	0.646	0.595
<i>Acentroscelus ramboi</i>	0.942	0.894	0.822	0.838	0.105	0.164	0.868	0.836	1.162	1.150	1.105	1.123	0.794	0.786
<i>Acentroscelus spn(serranus)</i>	1.507	1.381	0.849	0.804	0.144	0.151	0.593	0.597	0.679	0.681	0.698	0.720	0.563	0.579
<i>Acentroscelus versicolor</i>	1.056	1.263	0.822	0.831	0.098	0.113	0.762	0.556	0.961	0.832	0.947	0.811	0.684	0.573
<i>Acentroscelus granulosus</i>	1.405	?	0.838	?	0.076	?	0.576	?	0.762	?	0.737	?	0.527	?
<i>Acentroscelus spn(marmoratus)</i>	1.610	1.408	0.827	0.809	0.070	0.084	0.614	0.589	0.760	0.763	0.757	0.800	0.534	0.557
<i>Acentroscelus spn(caxiuana)</i>	1.526	1.525	0.752	0.749	0.105	0.106	0.591	0.562	0.805	0.966	0.883	0.977	0.596	0.601
<i>Acentroscelus spn(echinithorax)</i>	1.437	1.755	0.888	0.813	0.115	0.109	0.635	0.612	0.842	0.923	0.815	0.902	0.560	0.626
<i>Acenstroscelus guianensis</i>	2.051	1.671	0.793	0.801	0.138	0.140	0.581	0.667	0.874	0.919	0.826	0.902	0.600	0.634
<i>Acenstroscelus singularis</i>	1.553	1.374	0.808	0.801	0.137	0.113	0.574	0.655	0.992	1.144	0.968	1.143	0.641	0.671

	Female	Male	Female	Male												
Continuous character number	*15	*16	*17	*18	19	20	*21	*22	23	24	25	26	27	28		
<i>Epicadus heterogaster</i>	0.500	0.627	1.050	1.053	1.976	1.890	1.545	1.607	0.713	1.032	0.628	0.517	0.956	1.216		
<i>Boliscus tuberculatus</i>	0.536	?	0.905	?	1.171	?	1.020	?	1.046	?	0.497	?	1.141	?		
<i>Bomis larvata</i>	0.493	?	0.876	?	1.240	?	1.077	?	0.951	?	0.434	?	1.169	?		
<i>Cymbacha festiva</i>	0.795	0.687	0.968	0.885	1.312	1.272	1.212	1.171	0.774	0.856	0.359	0.288	0.496	0.558		
<i>Heterogriffus berlandi</i>	0.930	1.056	0.740	0.786	0.925	1.019	0.954	0.929	1.147	1.234	0.214	0.207	0.525	0.586		
<i>Monaeses sp.</i>	?	0.993	?	1.022	?	2.467	?	1.673	?	0.505	?	0.418	?	0.285		
<i>Stiphropus gruberi</i>	0.621	0.501	0.920	?	0.958	?	0.920	?	0.881	0.862	0.362	0.680	0.645	0.387		
<i>Titidiops melanosternum</i>	0.814	1.317	0.979	1.033	1.515	1.580	1.314	1.007	0.844	0.910	0.333	0.349	0.392	0.536		
<i>Titidius haemorrhous</i>	0.833	0.941	0.978	0.973	1.452	2.009	1.286	1.521	0.840	1.025	0.611	0.633	0.577	0.532		
<i>Titidius quinquenotatus</i>	0.783	0.644	1.017	0.988	2.000	2.188	1.633	2.257	0.916	0.991	0.410	0.410	0.642	0.683		
<i>Titidius rubecens</i>	0.777	0.847	1.056	1.070	1.907	2.157	1.476	1.741	0.852	0.949	0.414	0.331	0.523	0.576		
<i>Titidius urucu</i>	0.781	0.887	1.000	1.008	1.826	2.037	1.727	1.834	0.719	0.886	0.384	0.341	0.478	0.567		
<i>Tmarus elongatus</i>	0.855	0.906	0.799	1.017	1.272	2.256	1.221	1.916	0.797	0.675	0.365	0.307	0.460	0.404		
<i>Tmarus formosus</i>	0.873	0.906	1.002	0.996	1.830	1.892	1.550	1.614	0.703	0.876	0.309	0.490	0.440	0.373		
<i>Tmarus littoralis</i>	0.933	0.989	0.952	0.950	1.678	1.841	1.395	1.672	0.871	0.949	0.410	0.352	0.580	0.562		
<i>Tmarus piger</i>	0.688	0.830	0.986	1.001	1.844	1.698	1.550	1.575	0.705	0.866	0.365	0.280	0.548	0.620		
<i>Acentroscelus albipes</i>	0.606	0.571	1.010	1.019	1.433	1.536	1.150	1.331	0.787	0.832	0.417	0.365	0.591	0.554		
<i>Acentroscelus peruvianus</i>	0.703	0.690	1.014	1.464	1.557	1.698	1.430	1.464	0.843	0.915	0.417	0.405	0.534	0.463		
<i>Acentroscelus ramboi</i>	0.799	0.878	1.052	1.024	1.464	1.462	1.454	1.310	0.796	0.783	0.353	0.350	0.681	0.487		
<i>Acentroscelus spn(serranus)</i>	0.623	0.647	0.972	0.947	1.206	1.178	1.089	1.054	0.920	0.908	0.486	0.445	0.474	0.444		
<i>Acentroscelus versicolor</i>	0.811	0.652	1.015	1.026	1.406	1.452	1.186	1.277	0.842	0.888	0.416	0.386	0.528	0.533		
<i>Acentroscelus granulosus</i>	0.631	?	1.033	?	1.446	?	1.208	?	0.851	?	0.408	?	0.507	?		
<i>Acentroscelus spn(marmoratus)</i>	0.647	0.626	1.004	0.955	1.423	1.371	1.176	1.220	0.890	0.876	0.437	0.349	0.610	0.587		
<i>Acentroscelus spn(caxiuana)</i>	0.687	0.694	0.911	0.989	1.351	1.606	1.172	1.392	0.772	0.877	0.452	0.322	0.604	0.598		
<i>Acentroscelus spn(echinithorax)</i>	0.649	0.681	1.033	1.023	1.503	1.473	1.298	1.354	0.786	0.853	0.379	0.426	0.534	0.412		
<i>Acenstroscelus guianensis</i>	0.685	0.688	1.058	1.019	1.457	1.448	1.276	1.336	0.824	0.798	0.382	0.350	0.502	0.446		
<i>Acenstroscelus singularis</i>	0.732	0.805	1.025	1.001	1.546	1.705	1.354	1.421	0.824	0.976	0.397	0.376	0.388	0.563		

	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Continuous character number	29	30	31	32	33	34	35	36	*37	*38	39	40	41	42		
<i>Epicadus heterogaster</i>	1.349	0.877	81.390	86.747	0.025	0.038	0.018	0.044	0.025	0.042	0.029	0.046	1.364	0.859		
<i>Boliscus tuberculatus</i>	1.432	?	106.280	?	0.035	?	0.044	?	0.040	?	0.038	?	0.789	?		
<i>Bomis larvata</i>	1.225	?	46.920	?	0.053	?	0.066	?	0.048	?	?	?	0.797	0.934		
<i>Cymbacha festiva</i>	0.943	0.897	70.264	77.698	0.045	0.041	0.077	0.050	0.056	0.054	0.058	0.073	0.583	0.819		
<i>Heterogriffus berlandi</i>	0.705	0.672	90.000	90.000	0.041	0.041	0.076	0.074	0.033	0.038	0.045	0.033	0.543	0.555		
<i>Monaeses sp.</i>	0.309	0.247	?	62.589	0.030	0.035	0.056	0.067	0.037	0.041	0.067	0.058	0.534	0.521		
<i>Stiphropus gruberi</i>	1.054	0.917	96.249	99.512	0.057	0.042	0.074	0.062	0.030	0.029	0.048	0.043	0.765	0.678		
<i>Titidiops melanosternum</i>	0.550	0.648	73.198	82.077	0.066	0.048	0.065	0.104	0.051	0.059	0.076	0.090	1.016	0.460		
<i>Titidius haemorrhous</i>	0.804	0.684	?	?	0.060	0.039	0.131	0.013	0.071	0.065	0.119	0.105	0.455	3.000		
<i>Titidius quinquenotatus</i>	0.598	0.439	77.281	86.156	0.056	0.051	0.121	0.108	0.066	0.071	0.091	0.104	0.464	0.474		
<i>Titidius rubecens</i>	0.562	0.456	97.834	101.400	0.050	0.048	0.103	0.109	0.064	0.066	0.095	0.095	0.481	0.443		
<i>Titidius urucu</i>	0.648	0.503	75.391	87.313	0.043	0.053	0.093	0.121	0.046	0.059	0.076	0.100	0.467	0.439		
<i>Tmarus elongatus</i>	0.643	0.393	67.952	70.093	0.034	0.039	0.088	0.075	0.050	0.044	0.068	0.074	0.382	0.521		
<i>Tmarus formosus</i>	0.538	0.556	68.276	69.723	0.037	0.044	0.080	0.106	0.046	0.063	0.061	0.113	0.459	0.420		
<i>Tmarus littoralis</i>	0.687	0.511	77.698	87.044	0.046	0.061	0.090	0.120	0.041	0.048	0.079	0.086	0.508	0.510		
<i>Tmarus piger</i>	0.707	0.673	71.710	75.033	0.048	0.051	0.093	0.071	0.055	0.054	0.061	0.071	0.512	0.709		
<i>Acentroscelus albipes</i>	1.185	0.663	92.603	96.903	0.049	0.054	0.115	0.098	0.054	0.056	0.095	0.083	0.431	0.551		
<i>Acentroscelus peruvianus</i>	0.768	0.539	96.142	94.415	0.051	0.044	0.106	0.103	0.066	0.063	0.087	0.083	0.487	0.424		
<i>Acentroscelus ramboi</i>	0.801	0.695	99.720	99.871	0.058	0.049	0.118	0.106	0.059	0.056	0.091	0.089	0.495	0.463		
<i>Acentroscelus spn(serranus)</i>	0.754	0.688	102.540	104.741	0.055	0.059	0.088	0.100	0.052	0.058	0.074	0.080	0.624	0.594		
<i>Acentroscelus versicolor</i>	0.732	0.660	103.225	101.247	0.049	0.050	0.095	0.101	0.058	0.060	0.076	0.089	0.514	0.492		
<i>Acentroscelus granulosus</i>	0.848	?	93.212	?	0.065	?	0.117	?	0.069	?	0.083	?	0.555	?		
<i>Acentroscelus spn(marmoratus)</i>	0.789	0.687	102.673	101.186	0.053	0.055	0.119	0.120	0.066	0.058	0.091	0.087	0.448	0.456		
<i>Acentroscelus spn(caxiuana)</i>	0.700	0.589	104.864	105.215	0.071	0.066	0.142	0.124	0.075	0.073	0.105	0.100	0.500	0.529		
<i>Acentroscelus spn(echinithorax)</i>	0.749	0.735	99.882	98.603	0.061	0.046	0.127	0.103	0.077	0.055	0.103	0.092	0.484	0.444		
<i>Acenstroscelus guianensis</i>	0.690	0.001	100.194	98.206	0.052	0.043	0.102	0.109	0.050	0.063	0.097	0.087	0.512	0.396		
<i>Acenstroscelus singularis</i>	0.852	0.645	107.852	100.116	0.068	0.058	0.131	0.107	0.057	0.064	0.097	0.074	0.522	0.544		

	Female	Male	Male	Male	Female	Female	Female								
Continuous character number	*43	*44	*45	*46	47	48	*49	*50	*51	52	53	54	55	56	57
<i>Epicadus heterogaster</i>	0.843	0.910	0.989	0.901	0.611	0.955	1.379	0.953	0.833	0.820	0.778	0.871	1.352	0.438	0.499
<i>Boliscus tuberculatus</i>	1.046	?	0.882	?	1.169	?	0.895	?	0.923	?	0.825	1.010	2.087	0.499	0.326
<i>Bomis larvata</i>	?	0.754	1.093	1.239	?	1.000	0.729	0.754	?	0.934	0.637	0.949	1.556	0.468	0.358
<i>Cymbacha festiva</i>	0.956	0.744	0.802	0.756	1.314	0.686	0.728	1.084	0.766	0.562	0.694	0.875	2.248	0.507	1.523
<i>Heterogriffus berlandi</i>	0.724	1.163	1.255	1.070	1.671	2.245	0.433	0.518	0.908	1.245	0.781	0.918	1.365	0.451	0.179
<i>Monaeses sp.</i>	0.559	0.705	0.798	0.851	0.836	1.152	0.669	0.612	0.446	0.600	0.715	0.891	0.786	0.493	0.342
<i>Stiphropus gruberi</i>	0.636	0.667	1.857	1.452	1.545	1.429	0.412	0.467	1.182	0.968	0.732	0.785	1.127	0.537	0.582
<i>Titidiops melanosternum</i>	0.674	0.656	1.297	0.808	0.860	1.152	0.784	0.569	0.874	0.530	0.831	0.778	1.556	0.521	0.764
<i>Titidius haemorrhous</i>	0.600	0.625	0.833	0.600	1.100	0.125	0.545	5.000	0.500	0.375	?	?	1.386	0.465	0.570
<i>Titidius quinquenotatus</i>	0.724	0.688	0.848	0.716	1.323	1.039	0.548	0.662	0.614	0.492	0.712	0.770	1.065	0.474	0.336
<i>Titidius rubecens</i>	0.667	0.700	0.780	0.725	1.080	1.146	0.617	0.611	0.520	0.508	0.684	0.750	1.254	0.338	0.849
<i>Titidius urucu</i>	0.600	0.593	0.943	0.896	1.211	1.210	0.495	0.490	0.566	0.531	0.658	0.803	1.394	0.479	0.749
<i>Tmarus elongatus</i>	0.734	0.603	0.677	0.882	1.301	1.021	0.564	0.590	0.497	0.532	0.753	0.904	1.420	0.503	0.619
<i>Tmarus formosus</i>	0.758	0.556	0.796	0.708	1.315	0.938	0.577	0.593	0.604	0.394	0.773	0.876	1.415	0.599	0.859
<i>Tmarus littoralis</i>	0.513	0.562	1.119	1.271	1.130	1.400	0.454	0.401	0.574	0.714	0.427	1.009	1.251	0.425	0.897
<i>Tmarus piger</i>	0.894	0.761	0.871	0.940	1.522	1.009	0.587	0.755	0.779	0.716	0.761	0.754	1.535	0.432	0.349
<i>Acentroscelus albipes</i>	0.567	0.672	0.918	0.964	1.207	1.176	0.470	0.571	0.520	0.648	0.824	0.953	1.345	0.502	0.625
<i>Acentroscelus peruvianus</i>	0.756	0.761	0.785	0.686	1.220	1.230	0.620	0.619	0.593	0.522	0.903	0.845	1.355	0.425	0.810
<i>Acentroscelus ramboi</i>	0.651	0.625	0.982	0.880	1.291	1.188	0.505	0.526	0.640	0.550	0.854	0.885	1.029	0.440	0.305
<i>Acentroscelus spn(serranus)</i>	0.703	0.727	1.064	1.025	1.198	1.255	0.586	0.580	0.748	0.745	0.852	0.889	1.333	0.504	0.654
<i>Acentroscelus versicolor</i>	0.763	0.673	0.843	0.829	1.250	1.133	0.610	0.594	0.643	0.558	0.854	0.896	1.117	0.467	0.385
<i>Acentroscelus granulosus</i>	0.836	?	0.938	?	1.414	?	0.591	?	0.784	?	?	?	0.910	0.488	0.796
<i>Acentroscelus spn(marmoratus)</i>	0.733	0.659	0.804	0.951	1.315	1.374	0.557	0.479	0.589	0.626	0.768	0.886	1.383	0.581	0.776
<i>Acentroscelus spn(caxiuana)</i>	0.713	0.737	0.947	0.893	1.350	1.243	0.528	0.593	0.675	0.658	0.831	0.892	1.265	0.382	0.480
<i>Acentroscelus spn(echinithorax)</i>	0.743	0.593	0.800	0.833	1.230	1.111	0.604	0.533	0.595	0.494	0.730	1.088	1.111	0.724	0.725
<i>Acenstroscelus guianensis</i>	0.513	0.719	1.049	0.686	1.050	1.247	0.488	0.577	0.538	0.493	0.826	0.913	1.036	0.515	0.452
<i>Acenstroscelus singularis</i>	0.589	0.863	1.191	0.909	1.344	1.441	0.438	0.599	0.702	0.784	0.713	0.889	1.166	0.465	0.537

**<sup>3</sup>CHAPTER 3: Neotropical tiny crab–spiders of the tribe Tmarini: a revision of *Acentroscelus*, *Whittickius* and *Maeanderion*.**

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**Abstract**

Spiders of the genus *Acentroscelus* were classically characterized by having the small body size. Recent studies have evidenced this feature as a state of miniaturization, also recovered for close related genera *Whittickius* and *Maeandriion*. Although this size similarity, these three genera were proposed as independent lineage because each one present a set of unique features (=synapomorphies). After review more than 400 specimens, including type materials, we carry out a first taxonomic review of these three genera. This work includes to redescribe all valid species composing these genera, besides of describe two new species for *Acentroscelus* and two for *Whittickius*. We also describe for the first time the male of *Whittickius singularis* and propose *Acentroscelus muricatus* as junior synonym of *Acentroscelus albipes*. Some species originally described over juveniles (i.e., *Acentroscelus gallinii*, *Acentroscelus nigrianus* and *Acentroscelus secundus*) are assign to *species inquirenda* category. Finally, all species have geographical records updated and are highly illustrated.

**Key words:** Amazonian forest, Atlantic rainforest, Neotropic, taxonomy,

**Thomisidae.**

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<sup>3</sup> O capítulo está redigido em inglês e será submetido à revista *Zootaxa*.

## Introduction

Thomisinae is the most diverse subfamily of Thomisidae (WCS 2019). One of the best represented groups of this subfamily, but poorly known, is Tmarini tribe. This group was characterized by Simon (1895) as spiders with lateral eyes larger than the middle eyes, posterior tubercles larger than the previous, elongated body, slim legs of different length and cylindrical segments covered in seats.

In the Neotropic, *Acentroscelus* latu sensu is a representative group of the tiny spiders of Tmarini tribe. Initially, the species of the *Acentroscelus*, *Whittickius* and *Maeanderion* genera were grouped into *Acentroscelus*, mainly characterized by a small size, and distributed from north of French Guiana to north of Argentina (WSC 2019). Notwithstanding, based on morphological characters, Molina–Gómez and Teixeira (und. sub., see chapter 2) reformulate the relationships of these species. Here, the taxonomic categories proposed initially were revalidated, finding now three different genera: *Acanthonotus* Keyserling, 1880, *Acentroscelus* Simon, 1886 and *Whittickius* Mello–Leitão, 1940.

The taxonomic history of this group can be summarized starting from the idea that the species of this group are sundered into two large groups: amazon species and atlantic forest species. Slight morphological differentiation between these two groups is evident, even the Amazonian species were originally described in different genera. The first one was *Acanthonotus* Keyserling, 1880 compounded by two species: *Acanthonotus peruvianus* and *Acanthonotus guianensis*. Simon (1886) described *Acentroscelus* with *A. albipes* like type species and subsequent, in 1895 he treated *Acanthonotus peruvianus* and *Acanthonotus guianensis* like part of *Acentroscelus*, without performing a formal synonym or appropriate taxonomic treatment. The second one was *Whittickius* Mello–Leitão, 1940, proposed like monotopic genus with *W.*

*singularis* like type species. In this case, *Whittickius* was considered as junior synonym of *Acentroscelus* by Rinaldi (1984), based on the similarity between the tubercles of the cephalothorax and the genitalia of the species *A. granulosus* with the drawings and description made by Mello-Leitão (1940) by *W. singularis*.

Consequently, in this paper we present the first taxonomy review of *Acanthonotus*, *Acentrocelus* and *Whittickius*, describing four new species, one new synonymy, and re-describing all species of these groups and providing new distribution records.

## Materials and methods

We described the entities based in somatic and sexual morphological features. The epigynum was dissected and submerged in pancreatin about six hours for to remove soft tissues, follows Álvarez-Padilla & Hormiga (2007) and then dried for 24 h at room temperature. The features were analyzed used a Leica M205A Multipurpose Zoom Microscope at the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS) and photographed with a Leica DMC2900 camera and made multifocus images with Leica application suite 4.12.0 version. In addition, photos were taken Scanning electron microscopy was conducted in a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (LabCEMM) at PUCRS.

Were examined 449 specimens belongs to the following biological collections (Collection, Curator): American Museum of Natural History, New York (AMNH, L. Prendini); California Academy of Science, San Francisco (CAS, C. Griswold); Field Museum of Natural History, Chicago (FMNH, P. Sierwald); Instituto Butantan, São Paulo (IBSP, A. Brescovit); Instituto de Ciencias Naturales de la Universidad Nacional, Bogotá (ICN, E. Flórez); Instituto Nacional de Pesquisas da Amazônia, Coleção

Sistemática da Entomologia, Manaus (INPA, C. Magalhães); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN, M. Ramírez); Museu de Ciências e Tecnologia da PUCRS, Porto Alegre (MCTP, R. A. Teixeira); Museu de Ciencias Naturais da Fundação Zoo–Botanica do Rio Grande do Sul, Porto Alegre (MCNZ, R. Ott); Museu de Historia Natural Capão da Imbuia, Curitiba (MNHCl, M. Zomoner); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto–da–Rocha); Museu Paraense Emilio Goeldi, Belém (MPEG, A. B. Bonaldo); Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe (SMNK, H. Höfer); Universidad Nacional Mayor de San Marcos, Museo de Historia Natural, Lima (MUSM, D. Silva); Universidade do Rio Janeiro, Museu Nacional, Rio de Janeiro (MNRJ, A. B. Kury); Universidade Federal de Minas Gerais, Museu de Historia Natural, Belo Horizonte (UFMG, A. J. Santos); Universidade Federal do Rio de Janeiro (UFRJ, R. Baptista).

Morphology abbreviations: ALE—anterior lateral eyes, AME—anterior median eyes, MQO—median ocular quadrangle, PLE—posterior lateral eyes, PME—posterior median eyes, tc—tutaculum, e—embolus, p—paracimbium, RTA—retrolateral tibial apophysis, VTA—ventral tibial apophysis, EB—ectal branch, MB—mesial branch, A—atrium, CD—copulatory duct, CO—copulatory opening, S—spermatheca. The description format follows Machado et. al (2019). All measurements are given in millimeters (mm).

Using Quantum GIS (version 2.14.1), we built the distribution map. Geographical coordinates (expressed between brackets on material examined) were obtained directly from labels of each specimen or by consulting the Geonames Gazetteer (Wick 2019) or Google Earth (GlobeDigital 2019).

## Taxonomy

**Thomisidae Sundevall, 1833**

**Thomisinae Sundevall, 1833**

**Tmarini Simon, 1895**

***Acentroscelus* Simon, 1886**

*Acanthonotus* Taczanowski, 1872: 86, pl. 4, f. 6. *Acanthonotus* Keyserling, 1880: 132, pl. 3, f. 72.

*Acentroscelus* Simon, 1886: 185

*Whittickius* Mello-Leitão, 1940: 183, f. 12–14.

**Type species.** *Acentroscelus albipes* Simon, 1886

**Diagnosis.** See Molina-Gomez and Teixeira, und. sub. [chapter 3]).

**Description.** Dwarf spiders (total length 2.93–3.16 in males, 2.64–3.48 in females) with slight sexual size dimorphism. The coloration-pattern is very similar in all species of the genus, the prosoma ranging from dark to light brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace, and the light-yellow opisthosoma sometimes presents a white paramedian line (Figs 2A-B, 3A-B). Prosoma longer than wide, long and slope in the posterior region with the margin delineated by setiferous tubercles with setae and a posterior median depression (Figs 1A, C). Carapace covered with punctures and setae (Figs 1A-C), the latter larger in the ocular region. Both anterior and posterior eyes disposed in two recurved rows; LE larger than the ME. Vertical clypeus similar or larger than MQO, with setae covered all area (Figs 1D). Fusiform labium reaching half the length of the endites, longer than wide. Sternum cup-shaped with concave anterior edge (Figs 1E).

Opisthosoma longer than wide with setae in the whole area, globose in females and more elongated in males (Figs 2A, 3A). Leg formula: 1–2–4–3; all legs are devoid of thorns, but exhibit setae in all segments.

Male palpus with a filiform to ribbon–shape and short embolus (about a turn around the tegulum), VTA divided and longer than RTA. The latter is reduced and like a conical tooth. Ventral branch of VTA turned formed or not a right angle, and the other branch of VTA shorter or longer than the ventral branch (Figs 2C-E). Epyginal plate septum absent and deep or shallow atrium (Figs 3C, E). Reniphorm spermathecae larger than copulatory ducts (Figs 3D, F).

**Composition.** Five species: *Acentroscelus albipes* Simon, 1886; *A. ramboi* Mello-Leitão, 1943; *A. versicolor* Soares, 1942; *A. marmoratus* sp. nov and *A. serranus* sp. nov.

**Distribution.** BRAZIL: Espírito Santo, Minas Gerais, Rio de Janeiro, Paraná, Rio Grande do Sul, Santa Catarina and São Paulo; ARGENTINA: Misiones.

*Acentroscelus marmoratus* sp. nov.

Figs 2–3.

**Type material: Holotype:** female, Brazil, São Paulo, Mairiporã P.E. da Cantareira Pinheirinho (MZSP-27993). **Paratype:** male, same locality (MZSP-27988).

**Other material examined. BRAZIL: Minas Gerais:** 1 m#, Catas Altas, RPPN Serra da Caraça, [20°05'S 43°29'W], 10 m, 24 April–May 2002, Equipe Biota (IBSP-120970); **São Paulo:** 1 m#, Itú, Faz. Pau de Alho, 23°19'25.9"S 47°15'47.0"W, 17–18 Setember 1960, Biasi (MZSP-12830); 1 m#, Guarulhos, Parque Estadual da Cantareira,

Núcleo Cabuçu, [23°24'15.1"S 46°31'59.7"W], 83 m, 16–22 July 2001, Equipe Biota (IBSP-120710); 1 m#, Mairiporã, P.E. Serra da Cantareira Pinheirinho, 23°25'15.1"S 46°38'38.5"W, 29 October 2000, R. Pinto Da Rocha *et al.* (MZSP-27977); 1 m#, same locality, data and collector (MZSP-27978); 1 m#, same locality, data and collector (MZSP-27979); 1 m#, 4 March 2001, same locality and collector (MZSP-27981); 1 m#, same locality, data and collector (MZSP-27980); 1 m#, 29 April 2001, same locality and collector (MZSP-27987); 1 m#, same locality, data and collector (MZSP-27988); 1 f#, same locality, data and collector (MZSP-27986); 1 f#, 23 June 2001, same locality and collector (MZSP-27991); 1 f#, same locality, data and collector (MZSP-27989); 1 f#, same locality, data and collector (MZSP-27992); 1 f#, same locality, data and collector (MZSP-27993); 1 f#, same locality, data and collector (MZSP-27990); 1 m#, Salesópolis, Estação Biológica de Boracéia, 23°34'38.9"S 45°45'59.0"W, 67 m, 18 May 2001, D.F. Candiani (IBSP-120704); 1 m#, São Paulo, Vila Água Funda, 23°38'14.9"S 46°37'16.9"W, 14 December 1951, Werner (MZSP-12834).

**Diagnosis.** Females of *A. marmoratus* sp. nov. are similar to those of *A. serranus* sp. nov. by spermatheca globose shape, nevertheless, *A. marmoratus* sp. nov. present shallow atrio in the epigynal region (Figs 3C, E). Those females also differ from the other species of the genus by presenting an epigynal plate completely covering the copulatory openings. These openings are disposed in the posterior region of the epigynal plate like in *A. albipes*, *A. ramboi* and *A. versicolor* (Figs 3D, F). Males of *A. marmoratus* sp. nov. assimilate with those of *A. albipes* by VTA of apex curved and disposed toward the tibia forming a right angle; and the lateral branch of VTA pointed; but differs from *A. albipes* owing to ventral branch of VTA is larger than lateral and without curvature in the embolus (Figs 2C-F).

**Description. Female (from Mairiporã; MZSP-27992):** Prosoma dorsally yellowish-white and with two light reddish brown paramedian stripes (Figs 3A-B). Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma light-yellow, globose with a yellowish-white paramedian strip and two white horizontal strips in the posterior dorsal region of abdomen (Fig 3A). Epyginal plate covering copulatory openings, short copulatory ducts and reniform spermathecas (Figs 3D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.11, ALE 0.18, PME 0.10, PLE 0.16, AME-AME 0.25, AME-ALE 0.20, PME-PME 0.30, PME-PLE 0.39, MOQ length 0.28, MOQ width 0.51; leg formula: 1-2-4-3: leg I – femur 1.11/ patella 0.51/ tibiae 0.82/ metatarsus 0.75/ tarsus 0.63/ total 3.81; II – 1.11/ 0.52/ 0.93/ 0.62/ 0.53/ 3.72; III – 0.73/ 0.32/ 0.62/ 0.47/ 0.49/ 2.62; IV – 0.77/ 0.35/ 0.80/ 0.38/ 0.35/ 2.63. Total body length 3.48; prosoma 1.56 length, 1.30 wide; opisthosoma length 1.92; clypeus 0.35 height; sternum 0.71 length, 0.59 width; endites 0.44 length, 0.29 width; labium 0.34 length, 0.21 width.

**Male (from Mairiporã; MZSP-27978):** Prosoma yellowish-white dorsally and with two dark reddish brown paramedian stripes. Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma light-yellow, globose with median strip yellowish-with (Fig 2A). Palp with discoid tegulum, short filiform embolus and lateral branch flimsy and pointed (Figs 2C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.08, ALE 0.19, PME 0.08, PLE 0.15, AME-AME 0.19, AME-ALE 0.15, PME-PME 0.25, PME-PLE 0.36, MOQ length 0.26, MOQ width 0.40; leg formula: 1-2-4-3: leg I – femur 1.07/ patella 0.39/ tibiae 0.79/ metatarsus 0.67/ tarsus 0.56/ total 3.48; II – 1.00/ 0.45/ 0.81/ 0.57/ 0.51/ 3.33; III – 0.62/ 0.33/ 0.42/ 0.30/ 0.30/ 1.97; IV – 0.65/ 0.29/ 0.55/ 0.32/ 0.32/ 2.13. Total body length 3.16; prosoma 1.40 length, 1.14 wide; opisthosoma length 176;

clypeus 0.27 height; sternum 0.63 length, 0.57 width; endites 0.38 length, 0.14 width; labium 0.29 length, 0.10 width.

**Distribution.** BRAZIL: Minas Gerais and São Paulo.

*Acentroscelus serranus* sp. nov.

Figs 4–5.

**Type material:** **Holotype:** female, Brazil, Rio Grande do Sul, São Francisco de Paula, Potreiro Velho (MCTP–17196). **Paratype:** male, same locality (MCTP–17195).

**Other material examined.** BRAZIL: **Paraná:** 1 f#, Rio Negro, 26°05'19.8"S, 49°47'07.5"W (MNRJ 53270); 1 m#, Quatro Barras, Alto da Serra, 25°22'12.1"S, 49°04'42.2"W, 01 December 1987 (MHNCI ); **Rio Grande do Sul:** 1 m#, 1 f#, Cambará do Sul, 28°57'19.6"S 50°06'28.8"W, 25 Novembro 1993, A.B. Bonaldo (MCN Z–24373); 2 m#, 5 f #, Cambará do Sul, 28°57'19.6"S 50°06'28.8"W, 11–15 April 1994, M.A.L. Marques (MCN Z–25487); 1 m#, 1 f #, Viamão, Três Figueiras Arraio, 30°04'48.4"S 51°08'52.7"W, 13 July 2000, A.B. Bonaldo (MCN Z–33020); 1 f#, Rio Negro, 26°05'19.8"S 49°47'07.5"W (MNRJ–53270); 1 m#, Quatro Barras, Alto da Serra, 25°22'12.1"S 49°04'42.2"W, 01 October 1987 (MHNCI); 1 f#, São Francisco de Paula, Potreiro Velho, 29°24'53.6"S 50°15'28.3"W (MCTP–17194); 1 m#, same locality (MCTP–17195); 1 f#, same locality (MCTP–17196); 1 m#, same locality (MCTP–17198); 1 f#, same locality (MCTP–17199); 1 f #, same locality, August 2002, L.A. Bentocello (MCTP–17197); 1 j#, same locality January 1997, A.A. Lise (MCTP–10746); 1 f #, July 1998, same locality and collector (MCTP–17200); 1 m#, Caxias do Sul, 29°13'33.5"S 51°08'54.9"W, 20 November 1993, A.A. Lise (MCTP–6265); 2 m#, Cambará do Sul, 28°57'19.6"S 50°06'28.8"W, 26 October 1993, E.H. Buckup (MCN Z–

24414); 1 f#, Cambará do Sul, Área de Preservação Ambiental Celulose, 28°57'19.6"S 50°06'28.8"W, 19–21 December 1994, A.B. Bonaldo (MCN Z-26025).

**Diagnosis.** Females of *A. serranus* sp. nov. are similar to those of *A. marmoratus* sp. nov. by spermatheca globose shape, nevertheless, *A. serranus* sp. nov. present deep atrium in the epyginal region (Figs 4D, F). Unlike the other species of the *Acentroscelus*, *A. serranus* sp. nov. presents a unique and small copulatory opening in the anterior region of the epiginal plate (Figs 4C, E). Males of *A. serranus* sp. nov. present a short embolus like *A. albipes*; however, can be distinguished by the shorter lateral branch of the VTA and the ventral branch pointing distally.

**Description. Female (from Cambará do Sul; MCNZ-25487):** Prosoma dorsally light brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace (Figs 4A-B). Six dorsal tubercles in the dorsal posterior slope. Legs I–IV light yellow covered with setae from femur to metatarsus. Opisthosoma light-yellow, globose with a yellowish-white paramedian strip and two white horizontal strips in the posterior dorsal region of abdomen (Fig 4A). Posterior region of epyginal plate with deep atrium and copulatory opening, short copulatory ducts and reniform spermathecas (Figs 4C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.09, ALE 0.15, PME 0.79, PLE 0.11, AME–AME 0.20, AME–ALE 0.17, PME–PME 0.26, PME–PLE 0.32, MOQ length 0.30, MOQ width 0.42; leg formula: 1–2–4–3: leg I – femur 0.97/ patella 0.45/ tibiae 0.83/ metatarsus 0.59/ tarsus 0.40/ total 3.23; II – 0.84/ 0.48/ 0.71/ 0.58/ 0.56/ 3.16; III – 0.79/ 0.35/ 0.64/ 0.44/ 0.49/ 2.71; IV – 0.73/ 0.33/ 0.78/ 0.52/ 0.46/ 2.80. Total body length 3.14; prosoma 1.41 length, 1.25 wide; opisthosoma length 173; clypeus 0.34 height; sternum 0.67 length, 0.58 width; endites 0.37 length, 0.16 width; labium 0.27 length, 0.17 width.

**Male (from Cambará do Sul; MCNZ–25487):** Prosoma dorsally dark brown with a light–brown dorsal spot, from the middle posterior eyes to the slope of the carapace. Six dorsal tubercles in the dorsal posterior slope (Figs 5A–B). Legs I–IV light yellow covered with setae from femur to metatarsus. Opisthosoma light–brown, globose with a yellowish–white paramedian strip and two white horizontal strips in the posterior dorsal region of abdomen (Fig 5A). Palp with discoid tegulum, short filiform embolus curved distally and ventral branch of VTA as long as lateral branch (Figs 5C–F).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.16, PME 0.08, PLE 0.11, AME–AME 0.20, AME–ALE 0.14, PME–PME 0.25, PME–PLE 0.31, MOQ length 0.11, MOQ width 0.26; leg formula: 1–2–4–3: leg I – femur 0.80/ patella 0.42/ tibiae 0.79/ metatarsus 0.48/ tarsus 0.44/ total 2.93; II – 0.85/ 0.42/ 0.76/ 0.58/ 0.56/ 3.16; III – 0.68/ 0.38/ 0.54/ 0.40/ 0.41/ 2.40; IV – 0.70/ 0.35/ 0.59/ 0.40/ 0.43/ 2.43. Total body length 2.93; prosoma 1.33 length, 1.22 wide; opisthosoma length 1.60; clypeus 0.30 height; sternum 0.62 length, 0.58 width; endites 0.35 length, 0.14 width; labium 0.27 length, 0.17 width.

**Distribution.** BRAZIL: Paraná and Rio Grande do Sul.

*Acentroscelus albipes* Simon, 1886

Figs 6–7.

*Acentroscelus albipes* Simon, 1886. Rinaldi, 1984: 28, pl. 2, fig. 1–7 & Mello–Leitão, 1929: 31.

*Acentroscelus muricatus* Mello–Leitão, 1947: 14, pl. 4, 6, fig. 32, 47. **New synonym.**

**Type material:** Syntype series of *Acentroscelus albipes*. Male and female, Brazil, Minas Gerais, Serra do Caraça (examined; MNHN-8283).

Holotype of *A. muricatus* (designated by Mello-Leitão, 1947): male, Brazil, Minas Gerais, Carmo do Rio Claro, [21°00'30.1"S, 46°05'55.3"W], 23 September 1965, J.G. Carvalho (MNRJ; examined).

**Other material examined.** BRAZIL: **Minas Gerais:** 1 m#, Santana do Rioachô, Serra do Cipó, Portaria Palácio, 19°15'S, 43°31'W, 16 July 2001, E.S.S. Álvarez and E.O. Machado (LACB-1068); 1 f#, Marliéria, Parque Estadual do Rio Doce, [19°39'30.7"S 42°34'32.2"W], 18–19 October 2003, E.S.S. Álvarez (UFMG-16451); 1 m#, Nova Lima, RPPN Mata Samuel de Paula, [20°0'0"S 43°52'0"W], 30 April 2001, J.P.P Pena-Barbosa (UFMG-3166); 1 f#, 12–14 October 2006, same locality and collector (UFMG-2750); 1 f#, 01 May 2007, same locality and collector (UFMG-2749); **Esírito Santo:** 1 f#, Domingos Martins, São Paulo de Aracé, Parque Estadual Pedra Azul, 20°25'57"S, 41°1'12"W, P.H. Martins and M.T.T. Santos, 12 July 2013 (UFMG-16296); **Rio de Janeiro:** 1 f# Barra Mansa, Floresta da Cicuta, Volta Redonda, 22°33'04.7"S, 44°05'28.4"W, 5–11 December 1999, A.D. Brescovit *et al.* (IBSP-120859); 1 f#, 11–18 June 2001, same locality and collector (IBSP-120875); 1 f#, same locality, data and collector (IBSP-120882); 1 f#, same locality, data and collector (IBSP-120883); **São Paulo:** 1 f#, Barueri, 23°30'09.7"S, 46°56'26.9"W, 5 February 1967, K. Lemko (MZSP-12827); 1 f# Boracéia, 22°11'0.9"S, 48°48'11.1"W, 23 September 1965, P. Briasi, (MZSP-4848); 1 f#, Guarulhos, P.E. Serra da Canteira, 23°24'15.1"S, 46°31'59.7"W, 9 August 2000, R. Pinto Da Rocha *et al.* (MZSP-27983).

**Diagnosis.** Females of *A. albipes* are similar to those of *A. marmoratus* sp. nov. by present shallow atrium, but it differs from the posterior position of the copulatory opening. Additionally, *A. albipes* is different of all species of genus by the copulatory opening present an anterior sclerotized structure with cup-shape (Figs 6C, E). Males are similar to the ones of *A. serranus* sp. nov. by the curved shape of the embolus, but can

be differentiated by the shape of the longer and sturdy lateral branch of the VTA, like in *A. marmoratus* sp. nov., is disposed towards the distal portion of the palp and is larger than the ventral branch of the VTA (Figs 7C-F).

**Description. Female (from Barra Manza; IBSP-120875):** Prosoma dorsally light brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace. Eight dorsal tubercles in the dorsal posterior slope (Figs 6A-B). Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma light-yellow, globose with a yellowish-white paramedian strip and two white horizontal strips in the posterior dorsal region of abdomen (Fig 6A). Anterior region of epiginal plate with shallow atrium and copulatory opening, short copulatory ducts and reniform spermathecas (Figs 6C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.07, ALE 0.13, PME 0.07, PLE 0.11, AME-AME 0.23, AME-ALE 0.16, PME-PME 0.29, PME-PLE 0.31, MOQ length 0.29, MOQ width 0.44; leg formula: 1-2-4-3: leg I – femur 0.92/ patella 0.35/ tibiae 0.74/ metatarsus 0.50/ tarsus 0.41/ total 2.90; II – 0.89/ 0.37/ 0.77/ 0.60/ 0.53/ 3.17; III – 0.60/ 0.27/ 0.47/ 0.34/ 0.40/ 2.09; IV – 0.63/ 0.27/ 0.53/ 0.31/ 0.39/ 2.64. Total body length 2.64; prosoma 1.30 length, 1.05 wide; opisthosoma length 1.34; clypeus 0.27 height; sternum 0.68 length, 0.53 width; endites 0.39 length, 0.16 width; labium 0.25 length, 0.15 width.

**Male (from Carmo do Rio Claro; MNRJ):** Prosoma dorsally dark brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace. Eight dorsal tubercles in the dorsal posterior slope (Figs 7A-B). Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma light-yellow, globose with a yellowish-white paramedian strip and two white horizontal strips in the posterior dorsal

region of abdomen (Fig 7A). Palp with discoid tegulum, short filiform embolus curved distally and ventral branch of VTA shorter than lateral branch (Figs 7C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.08, ALE 0.17, PME 0.08, PLE 0.11, AME-AME 0.21, AME-ALE 0.17, PME-PME 0.26, PME-PLE 0.35, MOQ length 0.29, MOQ width 0.40; leg formula: 1-2-4-3: leg I – femur 0.87/ patella 0.46/ tibiae 0.86/ metatarsus 0.45/ tarsus 0.42/ total 3.06; II – 0.86/ 0.45/ 0.84/ 0.57/ 0.44/ 3.17; III – 0.71/ 0.28/ 0.46/ 0.39/ 0.35/ 2.18; IV – 0.85/ 0.29/ 0.50/ 0.38/ 0.33/ 2.34. Total body length 3.07; prosoma 1.40 length, 1.11 wide; opisthosoma length 1.67; clypeus 0.27 height; sternum 0.62 length, 0.53 width; endites 0.37 length, 0.15 width; labium 0.29 length, 0.15 width.

**Distribution.** BRAZIL: Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo.

**Note.** The original descriptions of *A. albipes* and *A. muricatus* were poor and lack any illustrations and are based on intraspecifically variable characters (such as size and coloration). Rinaldi (1984) realized the redescription of the *A. albipes*, but according to the code of material used to perform said work (MZSP-9776; 9777), the specimens described corresponds to a female of *A. versicolor* and not to the *A. albipes* species. For this reason, the illustrated description made by Rinaldi must be reevaluated.

Concerning to study of the type specimens, *A. albipes* and *A. muricatus* were found great similarity in the sexual and somatic features, for this reason by the principle of priority we propose *A. muricatus* as junior synonym of *A. albipes*, type species.

*Acentroscelus ramboi* Mello-Leitão, 1943

Figs 8–9.

**Type material. Holotype.** 1 ♀, BRAZIL, Rio Grande do Sul (MNRJ-42524, examined).

**Other material examined.** BRAZIL: *Rio Grande do Sul*: 1 f#, Derrubadas, Parque Estadual do Turvo, [27°00'-27°20'S 53°40'54''W], 11-18 January 2002, Equipe Biota (IBSP-120998); 1 m#, same locality, data and collector (IBSP-120999); 1 f#, same locality, data and collector (IBSP-121000); 1 f#, same locality, data and collector (IBSP-121001); 1 m#, same locality, data and collector (IBSP-121003); 1 m#, same locality, data and collector (IBSP-121004); 1 f#, Augusto Pestana, 28°36'35.1"S 53°57'49.2"W, 11 January 2009, Lígia V. Silva *et. al.* (MCTP-27129); 1 f#, São Borja, São Donato, Reserva Biológica, 28°39'01.3"S 55°58'27.9"W, 22 November 2012, Miguel Machado (MCTP-37558); 1 f#, same locality, data and collector (MCTP-34758); 1 m#, Bom Jesus, Fazenda Aver, 28°41'18.9"S 50°28'23.4"W, 24 March 1989, A.B. Bonaldo (MCNZ-18448); 1 f#, Cambará do Sul, General Câmara, 28°57'19.6"S 50°06'28.8"W, 14 Outubro 1982, C.J. Becker (MCNZ-11087); 2 m#, 1 f#, Itaúba, Arroio do Tigre, 29°18'46.1"S 53°10'02.6"W, 22 April 1978, Arno A. Lise (MCNZ-8031); 1 f#, São Francisco de Paula, 29°24'53.6"S 50°15'28.3"W, 31 July 2003, L.C. da Silva (MCTP-19506); 1 m#, Terra de Areia, 29°35'28.1"S 50°05'30.3"W, 28 June 2002, Estevam L.C. da Silva leg. (MCTP-19480); 1 m#, Campo Bom, 29°38'43.6"S 51°05'02.8"W, 19-20 May 1986, C.J. Becker (MCNZ-15076); 1 m#, Campo Bom, 29°38'43.6"S 51°05'02.8"W, 25 July 1986, C.J. Becker (MCTP-1126); 1 f#, Campo Bom, 29°38'43.6"S 51°05'02.8"W, 17 December 1986, C.J. Becker (MCTP-140); 1 f#, Campo Bom, 29°38'43.6"S 51°05'02.8"W, 30 September 1995, C.J. Becker (MCNZ-13469); 1 m#, 1 f#, Santa Maria, 29°39'31.4"S 53°48'50.2"W, August 1995, Kotzian, C.B. (MCTP-40106); 2 m#, 4 f#, May 2000, same locality and collector (MCTP-40110); 1 m#, 1 f#, same locality, 21 December 1993, Indrusiak, L. (MCTP-41406); 1 m#, 28 July 1998, same locality and collector (MCTP-40120); 1 f#, 27 May 2000, same locality and collector (MCTP-40111); 1 f#, 09 July 2000, same locality and collector

(MCTP-40108); 1 f#, 29 June 2005, same locality and collector (MCTP-41407); 1 m#, Santa Maria, Cidade dos Meninos,  $29^{\circ}39'31.4"S$   $53^{\circ}48'50.2"W$ , 03 July 1998, Indrusiak, L. (MCTP-10343); 1 f#, Novo Hamburgo,  $29^{\circ}42'57.8"S$   $51^{\circ}05'48.3"W$ , 17 June 1986, C.J. Becker (MCNZ-15173); 5 f#, Gravataí, Morro do Tigre,  $29^{\circ}50'05.7"S$   $50^{\circ}51'09.6"W$ , 15 July 2000, A.B. Bonaldo (MCNZ-33088); 1 f#, General Câmara,  $29^{\circ}55'09.0"S$   $51^{\circ}51'28.2"W$ , 17 September 1982, V. Pitoni (MCNZ-10920); 1 f#, General Câmara,  $29^{\circ}55'09.0"S$   $51^{\circ}51'28.2"W$ , 14 October 1982, M. Rosenau (MCNZ-11093); 1 m#, Cachoeira do Sul, Porteira Sete,  $29^{\circ}58'54.5"S$   $52^{\circ}54'28.2"W$ , 12 September 1992, Regina G. Buss (MCTP-3534); 1 m#, Viamão, Arroio Pesqueiro,  $30^{\circ}04'48.4"S$   $51^{\circ}08'52.7"W$ , 36676, A.B. Bonaldo (MCNZ-33180); 2 f#, Guaíba,  $30^{\circ}06'53.4"S$   $51^{\circ}19'08.4"W$ , 12 January 1989, A.D. Brescovit *et. al.* (MCNZ-18505); 1 m#, same locality, 29 December 1991, A.B. Bonaldo (MCNZ-21912); 2 m#, same locality, 02 July 1995, Arno A. Lise (MCTP-6714); 1 f#, 03 June 1994, same locality and collector (MCTP-4829); 2 m#, 02 June 1995, same locality and collector (MCTP-8780); 1 m#, 28 April 1995, same locality and collector (MCTP-7543); 1 m#, 09 January 1996, same locality and collector (MCTP-8245); 1 f#, São Sepé,  $30^{\circ}10'41.1"S$   $53^{\circ}33'05.9"W$ , 20 February 1994, E.C. Costa (MCTP-10252); 1 f#, 06 March 1994, same locality and collector (MCTP-10240); 1 m#, 03 June 1994, same locality and collector (MCTP-10244); 1 f#, 01 October 1994, same locality and collector (MCTP-10473); 1 m#, December 1994, same locality and collector (MCTP-10474); 1 m#, same locality, 03 June 1994, Isabel Junqueira (MCTP-8781); **ARGENTINA: Misiones:** 1 m#, Parque Nacional Iguazú,  $25^{\circ}40'42.2"S$   $54^{\circ}26'56.9"W$ , 22-30 August 1986, M.J. Ramírez (MACN-10781); 1 m#, Cerca de Puerto Rico, Gruta India, Ruta 12,  $26^{\circ}49'14.6"S$   $54^{\circ}59'48.7"W$ , Outubro 1977, M.E. Galiano (MACN-1970).

**Diagnosis.** Molina-Gomez and Teixeira, und. sub. [chapter 1]).

**Description. Female (from Santa Maria; MCTP 4011):** Prosoma dorsally dark reddish-brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace. Ten dorsal tubercles in the dorsal posterior slope (Figs 8A-B). Legs I-IV light yellow covered with setae from femur to metatarsus and with macrosetae from tibia to metatarsus. Opisthosoma light-brown, globose with two yellowish-white lateral stains (Fig 8A). Epigynum with a posterior circular concavity wider than long in the deep atrium, and a horizontal fold at the anterior margin of atrium (Figs 8C, E). Copulatory ducts larger than spermathecae (Figs 8D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.070, ALE 0.120, PME 0.070, PLE 0.151, AME-AME 0.215, AME-ALE 0.177, PME-PME 0.281, PME-PLE 0.312, MOQ length 0.288, MOQ width 0.428; leg formula: 1-2-4-3: leg I – femur 0.791/ patella 0.392/ tibiae 0.692/ metatarsus 0.589/ tarsus 0.452/ total 2.916; II – 0.790/ 0.416/ 0.598/ 0.572/ 0.476/ 2.852; III – 0.627/ 0.268/ 0.417/ 0.310/ 0.390/ 2.012; IV – 0.624/ 0.288/ 0.419/ 0.331/ 0.395/ 2.057. Total body length 3.111; prosoma 1.342 length, 1.186 wide; opisthosoma length 1.769; clypeus 0.219 height; sternum 0.638 length, 0.535 width; endites 0.356 length, 0.161 width; labium 0.223 length, 0.114 width.

**Male (from Cachoeira do Sul; MCTP 3534):** Prosoma dorsally dark reddish-brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace. Nine small dorsal tubercles in the dorsal posterior slope (Figs 9A-B). Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma oval with a vertical median whitish stripe and two parallel brown lines in the lateral ends (Fig 9A). Palp with discoid tegulum, short filiform embolus and ventral branch of VTA curved and thicker than narrow, elongated and acuminate lateral branch (Figs 9C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.048, ALE 0.089, PME 0.048, PLE 0.104, AME-AME 0.117, AME-ALE 0.085, PME-PME 0.141, PME-PLE 0.204, MOQ length 0.163, MOQ width 0.279; leg formula: 1-2-4-3: leg I – femur 0.474/ patella 0.238/ tibiae 0.543/ metatarsus 0.388/ tarsus 0.321/ total 1.964; II – 0.477/ 0.263/ 0.546/ 0.302/ 0.263/ 1.851; III – 0.295/ 0.189/ 0.220/ 0.185/ 0.187/ 1.076; IV – 0.305/ 0.189/ 0.224/ 0.189/ 0.182/ 1.836. Total body length 1.836; prosoma 0.847; length, 0.709 wide; opisthosoma length 0.989; clypeus 0.151 height; sternum 0.387 length, 0.328 width; endites 0.223 length, 0.083 width; labium 0.165 length, 0.088 width.

**Distribution.** BRAZIL: Rio Grande do Sul; ARGENTINA: Misiones.

**Distribution.** BRAZIL: Rio Grande do Sul and Santa Catarina.

*Acentroscelus versicolor* Soares, 1942

Figs 10–11.

**Type material: Holotype:** female, Brazil, São Paulo, Osasco, Soares leg. (MZSP-45), examined.

**Other material examined. BRAZIL: São Paulo:** 1 m#, Jundiaí, Serra do Japi, [23°13'S 46°56'W], 15-19 July 2002, Equipe Curso USP (IBSP-120719); 1 f#, Jundiaí, same locality, data and collector (IBSP-120909); 1 m#, same locality, data and collector (IBSP-120913); 1 m#, same locality, data and collector (IBSP-120918); 1 f#, same locality, data and collector (IBSP-120919); 1 m#, same locality, data and collector (IBSP-120921); 1 m#, same locality, data and collector (IBSP-120924); 1 f#, same locality, data and collector (IBSP-120929); 1 f#, same locality, data and collector (IBSP-120933); 1 m#, same locality, data and collector (IBSP-120941); 1 m#, same locality, data and collector (IBSP-120942); 1 m#, same locality, data and collector

(IBSP-120943); 1 f#, same locality, data and collector (IBSP-120949); 1 f#, Guarulhos, Parque Estadual da Cantareira, Núcleo Cabuçu, [23°24'15.1"S 46°31'59.7"W], 16-22 July 2001, Equipe Biota (IBSP-120709); 1 f#, same locality, data and collector (IBSP-120711); 1 m#, same locality, data and collector (IBSP-120712); 1 f#, same locality, data and collector (IBSP-120714); 1 f#, same locality, data and collector (IBSP-120715); 1 f#, same locality, data and collector (IBSP-120716); 1 f#, same locality, data and collector (IBSP-120717); 1 m#, same locality, data and collector (IBSP-120718); 1 m#, same locality, data and collector (IBSP-120719); 1 f#, Guarulhos, 23°24'50.9"S 46°36'00.3"W, 28 October 2000, R. Pinto Da Rocha *et. al.* (MZSP-27984); 2 m#, 22 December 2000, same locality and collectors (MZSP-27985); 1 m#, São Paulo, 23°24'50.9"S 46°36'00.3"W, 2 March 2000, R. Pinto Da Rocha *et. al.* (MZSP-27995); 1 m#, 10 November 2000, same locality and collectors (MZSP-27976); 1 m#, 09 August 2000, same locality and collectors (MZSP-27982); 1 m#, 2 March 2001, same locality and collectors (MZSP-27994); 1 f#, São Paulo, Parque Estadual do Jaraguá, [23°27'32.3"S 46°45'19.1"W], 14-23 October 2002, Equipe Biota (IBSP-120690); 1 m#, same locality, data and collectors (IBSP-120691); 1 m#, same locality, data and collectors (IBSP-120692); 1 f#, same locality, data and collectors (IBSP-120693); 2 m#, São Roque, 23°32'59.0"S 47°09'14.8"W, 07 May 1944, F. Lane (MZSP-9777); 2 m#, 1 f#, 14 May 1944, same locality and collector (MZSP-12835); 1 f#, Osasco, 23°33'07.0"S 46°51'59.6"W, 26 October 1941, Lane (MZSP-45); 1 m#, São Paulo, Reserva Florestal CUASO, Campus USP, 23°33'39.3"S 46°44'13.2"W, July 1985, S.A. Vanin (IBSP-27259); 1 f#, same locality, 29 October 1999, D.F. Candiani (IBSP-32802); 1 f#, São Paulo, Cidade Universitária IBUSP, 23°33'48.4"S 46°43'53.9"W, 13 March 1992, T.P. Amarante (MZSP-13765); 1 m#, Itapevi, 23°34'15.8"S 46°56'54.5"W, I-December 1999, C. Bertim (IBSP-121983); 1 m#, São

Paulo, Vila Água Funda, 23°38'14.9"S 46°37'16.9"W, 07 June 1962, Biasi (MZSP–9776); 1 m#, same locality, 28 March 1952, F. Lane (MZSP–12832); 1 f#, Itapecerica, Embú, 23°39'22.3"S 46°52'04.6"W, 2 October 1949, F. Lane (MZSP–12829); 1 m#, República Nova, Cocaia, 23°42'25.9"S 46°38'50.5"W, 25 January 1948, H. Urbam (MZSP–12833); 1 m#, Guarulhos, Carvalho Araujo, 23°45'42.5"S 46°41'30.5"W, 01 May 1942, A. Zoppei (MZSP–143); 1 f#, same locality, data and collector (MZSP–3542); 1 m#, 03 May 1942, same locality and collector (MZSP–3543); 1 f#, Iporanga, Parque Estadual Turístico do Alto do Ribeira, [24°32'S 48°41'W], 12–18 October 2001, Equipe Biota (IBSP–120907); 1 f#, same locality, data and collector (IBSP–120908); **Paraná:** 1 m#, Ponta Grossa, 25°14'45.9"S 50°01'14.9"W, 02 February 1987, Profaupar (MCTP–42255); 1 f#, Curitiba, Bariguí, 25°31'17.4"S 49°20'57.5"W, 10 February 1959, R. Lanpe (MNHN); 1 f#, 20 Setember 1960, same locality and collector (MNHN–4561); 1 m#, 28 April 1961, same locality and collector (MNHN–4554); **ARGENTINA: Buenos Aires:** 1 m#, San Antonio, Arrollo El Central, 26°03'23.9"S 53°44'08.5"W, Novembro, M.E. Galiano (MACN); **Misiones:** 1 m#, Parque Nacional Iguazú, Sendero Macuco, 25°40'42.2"S 54°26'56.9"W, 08–15 February 1995, M.J. Ramírez (MACN); 1 m#, Parque Nacional Iguazú, 25°40'42.2"S 54°26'56.9"W, October 1978, Galiano (MACN–10780).

**Diagnosis.** Molina-Gomez and Teixeira, und. sub. [chapter 1]).

**Description. Female (from Guarulhos; IBSP 120714).** Prosoma dorsally dark reddish-brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace (Figs 10A-B). Twelve dorsal tubercles in the dorsal posterior slope. Legs I-IV light yellow covered with setae from femur to metatarsus and with macrosetae from tibia to metatarsus. Opisthosoma light-brown, globose with small light brown stains on the entire surface (Fig 10A). Epigynum with an ellipse-shape posterior

concavity longer than wide, in the atrium deep and copulatory ducts shorter than spermathecae (Figs 10C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.072, ALE 0.146, PME 0.098, PLE 0.152, AME-AME 0.210, AME-ALE 0.153, PME-PME 0.220, PME-PLE 0.300, MOQ length 0.287, MOQ width 0.446; leg formula: 1-2-4-3: leg I – femur 0.950/ patella 0.437/ tibiae 0.818/ metatarsus 0.674/ tarsus 0.437/ total 3.316; II – 0.824/ 0.467/ 0.738/ 0.669/ 0.523/ 3.221; III – 0.568/ 0.242/ 0.635/ 0.362/ 0.441/ 2.248; IV – 0.631/ 0.356/ 0.690/ 0.455/ 0.463/ 2.585. Total body length 3.173; prosoma 1.333 length, 1.060 wide; opisthosoma length 1.840; clypeus 0.269 height; sternum 0.653 length, 0.539 width; endites 0.355 length, 0.139 width; labium 0.272 length, 0.146 width.

**Male (from São Paulo; IBSP 120691):** Prosoma dorsally dark reddish-brown with a light-yellow dorsal spot, from the middle posterior eyes to the slope of the carapace. Nine small dorsal tubercles in the posterior slope (Figs 11A-B). Legs I-IV light yellow covered with setae from femur to metatarsus. Opisthosoma eliptic brown with a vertical slight median whitish stripe (Fig 11A). Palp with discoid tegulum, short filiform embolus and a curved ventral projection of VTA shorter than curved and gross lateral branch (Figs 11C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.052, ALE 0.093, PME 0.052, PLE 0.098, AME-AME 0.121, AME-ALE 0.097, PME-PME 0.150, PME-PLE 0.208, MOQ length 0.180, MOQ width 0.262; leg formula: 1-2-4-3: leg I – femur 0.595/ patella 0.211/ tibiae 0.418/ metatarsus 0.315/ tarsus 0.275/ total 1.814; II – 0.612/ 0.211/ 0.450/ 0.283/ 0.322/ 1.778; III – 0.381/ 0.192/ 0.312/ 0.197/ 0.196/ 1.278; IV – 0.477/ 0.192/ 0.227/ 0.197/ 0.192/ 1.285. Total body length 1.779; prosoma 0.834 length, 0.657 wide; opisthosoma length 0.945; clypeus 0.153 height; sternum 0.392

length, 0.307 width; endites 0.229 length, 0.079 width; labium 0.154 length, 0.075 width.

**Distribution.** ARGENTINA: Misiones and BRAZIL: Paraná, Santa Catarina and São Paulo.

***Maeanderion*** Molina-Gomez and Teixeira, und. sub. [chapter 3]).

*Acentroscelus* Simon, 1886: 185

**Type species:** *Maeanderion peruvianus* (Keyserling, 1880)

**Diagnosis.** See Molina-Gomez and Teixeira, und. sub. [chapter 3]).

**Description.** Small spiders (total length 3.10–3.33 in males, 3.67–4.89 in females) with slight sexual size dimorphism. The coloration-pattern is very similar in male and female, brown prosoma with a medium wide strip that varies from dark yellow to brown, from the middle anterior eyes to the more distal region of the carapace (Figs 13A-B and 14A-B). Prosoma longer than wide, long and slope in the posterior region with the margin delineated by small setiferous tubercles with short setae. Middle part of the carapace wider than the rest of the prosoma (Fig 12A). Carapace bristles coming out of conical sockets, distributed from the most anterior part to the posterior margin (Fig 12B). Anterior and posterior eyes disposed in two recurved rows, LE larger than the ME. Vertical clypeus similar or larger than MQO (Fig 12C). Fusiform labium that reaches half the length of the endites, longer than wide (Fig 12D). Sternum longer than wide, with concave anterior edge.

Opisthosoma dark yellow, longer than wide with setae in the whole area, globose in females and more elongated in males. Leg formula: 1–2–4–3; with all bristles covered segments. Femur with two lateral thorns, and tibia and metatarsal provided with three pairs of ventral spines (Fig 13A and 14A).

Females present a large elliptical epiginal plate, wider than long (Figs 13C, E). Epigynum with copulatory opening located in the anterior part. Deep atrium, as long as the epiginal plate (Figs 14D, F). Copulatory ducts with descending entry and longer than the spermatheca (Figs 14D, F).

Male palp with paracimbium (Figs 14C, E). Tegular ridge present (Fig 14E). Males have ventral and retrolateral apophysis on the tibia. RTA about equal to the tibia and VTA not divided (Fig 14E). The tegulum is oval shaped with a tegular ridge with apical-retrolateral direction (Figs 14C, E).

**Composition.** One species: *Acanthonotus peruvianus* (Keyserling, 1880)

**Distribution.** COLOMBIA: Guaviare, Putumayo, Vaupes and Amazonas; ECUADOR: Sucumbios; PERÚ: Loreto and Madre de Dios; BRAZIL: Amazonas and Pernambuco.

**Note.** The original description of *Acanthonotus* applies to any of the three groups worked on in this paper, due to their lack of specificity. To avoid more disorder and confusion in the taxonomy of the group, we decided to use the name *Acanthonotus* (Taczanowski, 1872) although this genus was proposed with *Wittickius guianensis* as a type species. *W. guianensis* corresponds to the genus *Whittickius* described by Mello (1940) and revalidated in this work. In addition, How Keyserling (1880) awarded *A. peruvianus* to this genus, here we decided described *Acanthonotus* based in this entity and do not generate another new category.

*Maeanderion peruvianus* (Keyserling, 1880)

*Acanthonotus peruvianus* Keyserling, 1880: 134, pl. 3, f. 73.

*Acentroscelus peruvianus* Simon, 1895: 995.

Figs 11–12.

**Type material: Syntype series:** Amable Maria, Peru (Missing, not examined).

**Neotype:** female, Peru, Madre de Dios Puerto Maldonado, [02°33' S 60°03'W] (MUSM).

**Other material examined.** **COLOMBIA:** *Guaviare*: 1 f#, San José del Guaviare, 2° 34' 22"N 72° 38' 45"W, October 2013, E. Flórez and Estudiantes de taxonomía animal (ICN-AR-7608); 3m#, same locality and collector (ICN-AR-7615); 2 f#, San José del Guaviare, Vereda Playa Güío, Sector Iracas, finca Galicua, [2°34'24,6"N 72°43'4"W], 16 April 2013, Estudiantes de taxonomía animal (ICN-AR-10238); 1 m#, San José del Guaviare, Vereda Playa Güío. Sendero Los Puentes, 2°34'37.9"N 72°43'5.4"W, 22 October 2012, D. Luna (ICN-AR-5894); 1 f#, 13 April 2013, same locality and collector (ICN-AR-9017); *Vaupes*: 1 m#, 1 f#, Taraira, Lago Taraira, Estación biológica Mosiro Itájura (Caparú), [1°04'S 69°31'W], 01 April 2004, J. Pinzón; 1 f#, same locality, 01 May 2001, J. Pinzón and A. Sabogal (ICN-AR-9149); (ICN-AR-10237); 1 f#, Taraira, Serranía Taraira, Caño Pintadillo, 1°04'S 69°31'W, 04 January 2002, J. Pinzón (ICN-AR-11558); *Putumayo*: 1 f#, Territorio Kofan, 0°21'40.53"N 76°38'30.64"W, 26 September 1998, Valeria Rodríguez (ICN-AR-9031); 1 m#, same locality and data, S. A. Rodríguez (ICN-AR-9034); *Amazonas*: 1 f#, Leticia, 2°53'7"S 69°46'36"W, 17 June 1965, P.R. Craig (CAS-); 1 f#, PNNS Amacayacu, Vereda La Vanguardia, Pozo Azul, 3°02.86'N, 69°59.70'W, 27 August 2001, M. Sharkey and D. Campos (ICN-AR-6142); 1 f#, Leticia, Monilla-Amena, 4°12'55"S 69°56'26"W, 23 March 2004, G. Toldi (ICN-AR-11561); **ECUADOR:** 1 f#, Santa Rosa de Sucumbios, Kofan Indian Village, 0°21'30.72"N 77°7'58.98"W, 26 August 1971, B. Malkin (FMNH-71615); **PERÚ:** 5 m#, 9 f#, Puerto Maldonado, MD. KM 15, [02°33'S 60°03'W], 200 m, 03 June–24 July 1989, Silva (MUSM-); **BRAZIL:** *Amazonas*: 1 m#, 1 f#, Tefé, Estação Ecológica de Mamirauá, 2°13'26.51"S 65°43'18.79"W, 09–13 October 1992, S.H. Borges (MCN Z-22925); 1 m#, Iranduba,

Ilha de Curarí, Paraná,  $3^{\circ}19'52.00''S$   $60^{\circ}5'7.00''W$ , 3 August 1979, J. Adis *et al.* (IBSP-17306); 1 f#, same locality, data and collector (IBSP-17312); 1 f#, Coari, Porto Urucu, Base de Operações Geólogo Pedro de Moura, [ $04^{\circ}52'11''S$   $65^{\circ}08'05''W$ ], September 2006, S. C. Dias *et al.* (MPEG-3283); 1 f#, October 2006, same locality and collector (MPEG-13288); 1 f#, same locality and data, L.O. Man Hung (MPEG-13237).

**Diagnosis.** Prosoma coloration like *Wittickius caxiuana* sp. nov. Similar with *Wittickius echinithorax* sp. nov lack puncturations in the carapace; its bristles leave conical sockets (Figs 12A-B, 13A and 14A). Copulatory opening of epigynum like *Acentroscelus serranus* sp. nov, located in the anterior region of the plate; insite a deep atrium (Figs 13C, E). Unlike the males of *Acentroscelus* and *Wittickius*, embolus with microstructuring and undivided VTA (Figs 14E-F)

**Description. Female (from Amable Maria; MUSM):** Prosoma dark brown with a medium wide strip that varies from dark yellow to brown; longer then wide. Middle part of the carapace wider than the rest of the prosoma (Figs 13A-B). Opisthosoma dark yellow, globose with some white spots distributed laterally (Figs 13A). Epigynum with copulatory opening located in the anterior part. Deep atrium as long as the epiginal plate (Figs 13C, E). Copulatory ducts with descending entry and longer than the spermatheca. Reniform spermatheca, ocuping mostly epiginal plate area (Figs 13D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.07, ALE 0.15, PME 0.09, PLE 0.12, AME-AME 0.10, AME-ALE 0.14, PME-PME 0.14, PME-PLE 0.27, MOQ length 0.27, MOQ width 0.25; leg formula: 1-2-4-3; leg I – femur 1.43/ patella 0.57/ tibiae 1.11/ metatarsus 0.85/ tarsus 0.67/ total 4.62; II – 1.41/ 0.57/ 1.10/ 0.85/ 0.65/ 4.57; III – 0.92/ 0.40/ 0.67/ 0.40/ 0.36/ 2.74; IV – 1.00/ 0.39/ 0.71/ 0.44/

0.40/ 2.94. Total body length 4.63; prosoma 1.42 length, 1.33 wide; opisthosoma length 3.21; clypeus 0.25 height; sternum 0.74 length, 0.63 width; endites 0.42 length, 0.18 width; labium 0.31 length, 0.16 width.

**Male (from Amable Maria; MUSM):** Prosoma like females, varying the intensity of coloration (Figs 14A-B). Opisthosoma dark yellow, elliptical and thin (Figs 14A). Male palp with paracimbium. Embolus short, thicker at the base and apex with microstructuring screw-shaped denticles. RTA about equal to the tibia and VTA not divided, in retrolateral direction (Figs 14C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.06, ALE 0.14, PME 0.09, PLE 0.11, AME-AME 0.11, AME-ALE 0.12, PME-PME 0.13, PME-PLE 0.29, MOQ length 0.30, MOQ width 0.23; leg formula: 1-2-4-3: leg I – femur 1.37/ patella 0.553/ tibiae 1.15/ metatarsus 0.95/ tarsus 0.62/ total 4.65; II – 1.33/ 0.53/ 1.06/ 0.46/ 0.59/ 3.52; III – 0.81/ 0.37/ 0.66/ 0.37/ 0.37/ 2.58; IV – 0.94/ 0.37/ 0.70/ 0.46/ 0.36/ 2.82. Total body length 3.14; prosoma 1.36 length, 1.21 wide; opisthosoma length 1.75; clypeus 0.21 height; sternum 0.69 length, 0.63 width; endites 0.37 length, 0.15 width; labium 0.26 length, 0.12 width.

**Distribution.** COLOMBIA: Putumayo, Vaupes, Guaviare and Amazonas; ECUADOR: Sucumbios; PERU: Madre de Dios; BRAZIL: Amazonas and Pernambuco.

**Note.** The type material of this species was not found during the performance of this work. The identification of the material was made using the descriptions provided by Keyserling (1880), based on the illustrations of his work. For the numerous records and the presence of material in the type locality, we award a neotype for this entity, previously described.

***Whittickius* (Mello–Leitão, 1940)**

**Type species:** *Whittickius singularis* Mello–Leitão, 1940

**Diagnosis.** See Molina-Gomez and Teixeira, und. sub. [chapter 3]).

**Description.** Tiny spiders (total length 2.62–4.13 in males, 3.10–4.26 in females) with slight sexual size dimorphism. The coloration–pattern is very similar in all species of the genus, prosoma dark brown to light brown sometimes with a light–yellow dorsal spot, from the middle anterior eyes to the slope of the carapace (Figs 16-24 A). Prosoma longer than wide, with a slope in the posterior region with the margin delineated by large setiferous tubercles with long setae (Figs 15A-B, D-F). In most species, carapace with lateral short setae coming out of punctures and in general, bright and glabrous appearance (Fig 15A, E). Both anterior and posterior eyes disposed in two recurved rows: LE larger than the ME. Vertical clypeus similar or larger than MQO (Figs 15A-B). Fusiform labium reaching half the length of the endites, longer than wide. Sternum cup–shaped with concave anterior edge (Fig 15C).

Opisthosoma longer than wide, from light to dark yellow, globose in females and more elongated in males. Leg formula: 1–2–4–3; all legs light yellow without thorns but exhibit abundant setae in all segments (Figs 16-24 A).

Male palpus filiform to ribbon–shape embolus. RTA reduced, thin and similar to a conical tooth, shorter than VTA. Ectal branch of VTA excavated and longer than mesial branch (Figs 17C-F).

Epyginal plate septum present, with deep or shallow atrium. Spermathecae equal or shorter than copulatory ducts (Figs 16C-F).

**Composition.** Five species: *Whittickius singularis* Mello–Leitão, 1940; *W. guianensis* (Taczanowski, 1872); *W. granulosus* Mello–Leitão, 1929; *W. echinithorax* sp. nov., *W. caxiuana* sp. nov.

**Updated distribution.** From Trinidad Island (Trinidad and Tobago) to Jujuy (Argentina).

*Whittickius caxiuana* sp. nov.

Figs 16–17.

**Type material: Holotype:** f#, Colombia Putumayo Valle Del Guamuez, [0°21'40.53"N 76°38'30.64"W] (ICN–AR–952). **Paratype:** m#, Brazil, Pará, Belém, Reserva Mocambo, [01°26'28,7"S 48°24'46,2"W] (MPEG-15563).

**Other material examined.** COLOMBIA: *Putumayo*: 2 m#, 1 f#, Valle Del Guamuez, Territorio Kofan, 0°21'40.53"N 76°38'30.64"W, 1000 m, 20 September 1998, Ligia Benavides (ICN–AR–952); 3 m#, 1 f#, same locality and data, A. Rodríguez (ICN–AR–10236); REPUBLIC OF TRINIDAD AND TOBAGO: *Trinidad Island*: 1 m#, Arima, Creat of pass arima valley, 10°39'11.2"N 61°17'23.3"W, February 1964, S.S. Ross (CAS); BRAZIL: *Amazonas*: 2 m#, 1 f#, Japurá, Parí Cachoeira, 0°18'48.9"S 69°49'18.9"W, 4 June 1949, Javarete (MZSP–12826); *Pará*: 1 j#, Belém, Reserva Mocambo, 01°26'28,7"S 48°24'46,2"W, 14 December 2007, B.V.B Rodrigues (MPEG–15561); 1 f#, same locality, data and collector (MPEG–15562); 1 m#, same locality and data, N.C. Bastos (MPEG–15564); 1 m#, same locality, 11 December 2007, S.C. Dias (MPEG–15563); 2 f#, same locality, data and collector (MPEG–15565); 1 f#, Altamira, Castelo dos Sonhos, 08°17'15"S 54°59'55"W, 12 November 2005, J.O. Dias (MPEG–4408); 1 m#, same locality, 10 November 2005, D.R. Santos–Souza (MPEG–4326); 1 f#, Novo Progresso, Cachimbo, Campo de Provas Brigadeiro Velloso, 09°21'89"S

55°02'01"W, 16 March 2004, J.A.P. Barreiros (MPEG–15543); 1 f#, same locality, 24 March 2004, J. Ricetti (MPEG–15544); 1 f#, Belém, 1°25'36.5"S 48°25'47.2"W, August 1953, J.P. Duret (MACN–10786); 1 j#, same locality and data (MACN–10785); 2 f#, same locality, January 1965, E. Dense (MZSP–9768); 1 f#, same locality, August 1970, C.M. Galiano (MACN–10781); 1 m#, August 1971, same locality and collector (MACN–10782); 3 m#, 1 f#, 3–20 August 1971, same locality and collector (MACN–10784); 1 m#, Melgaço, Caxiuanã, 1°50'55.0"S 51°41'42.2"W, 11 August 1996 (MCTP–9507); 1 m#, Rio Gurupi, 2°42'10.3"S 46°45'02.3"W, 7–15 April 1963, B. Maclain (MZSP–3354); 1 f#, 2–30 May 1963, same locality and collector (MZSP–3296); **Mato Grosso:** 1 m#, Canarana/Querência, Fazeenda Tangueo, antiga Fazenda Morro Azul, 12°49'47.6"S 52°27'28.0"W, 09 June 2006, D.F. Candiani (MPEG–15558); 1 f#, same locality and data, N.F. Lo-Man-Hung (MPEG–15559); 1 f#, same locality, 27 May 2006, N.F. Lo-Man-Hung (MPEG–15560); **Bahia:** 1 f#, Una, Reserva Biológica de Una, 15°10'29.0"S 39°06'12.2"W, 15–28 November 2000, A.D. Brescovit *et al.* (IBSP–47142); **BOLIVIA: La Paz:** 1 f#, Coroico, Rio Anorimillo, 16°11'15.5"S 67°43'43.5"W, Hubent (LNK).

**Diagnosis.** General form of the male palpus as *W. singularis*, differentiated by having the ventral branch of the VTA longer than the retrolateral (Figs 17C, E). Epiginal plate without atrium like *W. echinithorax* sp. nov., with copulatory ducts shorter than kidney-shape spermathecae like *W. guianensis* and *W. singularis* (Figs 16C-F).

**Description. Female (from Belém; MCTP–10781):** Dark brown prosoma with a yellow midline from the anterior middle eyes, to the posterior slope (Figs 16A-B). Margin of the posterior decline with five long tubers from which long bristles emerge. Legs and opisthosoma as described to the genus (Fig 16A). Epiginal plate wider than

long without atrium and median ridge present (Figs 16C, E). Spermathecae as long as epiginal plate and larger than copulatory ducts (Figs 16D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.11, ALE 0.22, PME 0.11, PLE 0.16, AME-AME 0.13, AME-ALE 0.14, PME-PME 0.25, PME-PLE 0.37, MOQ length 0.30, MOQ width 0.35; leg formula: 1-2-4-3: leg I – femur 1.29/ patella 0.53/ tibiae 0.95/ metatarsus 0.74/ tarsus 0.49/ total 3.94; II – 1.28/ 0.45/ 0.98/ 0.78/ 0.40/ 3.89; III – 0.91/ 0.40/ 0.60/ 0.46/ 0.37/ 2.74; IV – 1.05/ 0.38/ 0.68/ 0.48/ 0.41/ 3.00. Total body length 3.49; prosoma 1.53 length, 1.14 wide; opisthosoma length 1.96; clypeus 0.30 height; sternum 0.64 length, 0.50 width; endites 0.38 length, 0.17 width; labium 0.24 length, 0.17 width.

**Male (from Putumayo; ICN-AR-10236):** Prosoma coloration similary to females. Margin of posterior slope with seven tubercles shorter than females (Figs 17A-B). Legs and opisthosoma as females (Figs 17A). Palp with disk shape tegulum with tegular ridge present in apical-retrolateral direction (Figs 17C-F). Tibial process as in the other species of the genus.

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.20, PME 0.11, PLE 0.16, AME-AME 0.14, AME-ALE 0.15, PME-PME 0.18, PME-PLE 0.37, MOQ length 0.27, MOQ width 0.34; leg formula: 1-2-4-3: leg I – femur 1.47/ patella 0.55/ tibiae 1.25/ metatarsus 0.95/ tarsus 0.67/ total 4.90; II – 1.49/ 0.53/ 1.24/ 0.97/ 0.60/ 4.84; III – 0.92/ 0.46/ 0.71/ 0.46/ 0.44/ 2.99; IV – 1.06/ 0.40/ 0.79/ 0.53/ 0.47/ 3.25. Total body length 3.25; prosoma 1.53 length, 1.14 wide; opisthosoma length 1.72; clypeus 0.29 height; sternum 0.64 length, 0.56 width; endites 0.39 length, 0.13 width; labium 0.25 length, 0.15 width.

**Distribution.** COLOMBIA: Putumayo; REPUBLIC OF TRINIDAD AND TOBAGO: Trinidad Island; BRAZIL: Amazonas, Pará, Mato Grosso, Bahia and BOLIVIA: La Paz.

*Whittickius echinithorax* sp. nov.

Figs 18–19.

**Type material: Holotype:** f#, Brazil, Roraima Alto Alegre Ilha de maracá, Estação Ecológica de Maracá, [2°02'58.4"N 50°25'40.7"W] (MCTP-769). **Paratype:** m#, Brazil, Pará, Novo Progresso, Cachimbo, Campo de Provas Brigadeiro Velloso, [09°16'49"S 54°56'32"W] (MPEG-5454).

**Other material examined. BRAZIL: Pará:** 2 m#, Novo Progresso, Cachimbo, Campo de Provas Brigadeiro Velloso, 09°16'49"S 54°56'32"W, 09 Setember 2003, D.R. Santos-Souza (MPEG-5454); 1 f#, 15 October 2003, same locality and collector (MPEG-5406); 1 f#, same locality, data and collector (MPEG-5328); 3 m#, same locality, data and collector (MPEG-5405); 1 m#, same locality, 09 Setember 2003, A.B. Bonaldo (MPEG-5458); 1 f#, 15 November 2003, sme locality and collector (MPEG-5337); 1 m#, same locality, 20 March 2004, J.A.P. Barreiros (MPEG-5361); **Minas Gerais:** 1 f#, Marliéria, Parque Estadual do Rio Doce, [19°43'33.6"S 42°34'43.6"W ], 1–10 November 2005, Equipe Biota (IBSP-120705); **Roraima:** 1 m#, 1 f#, Alto Alegre, Ilha de maracá, Estação Ecológica de Maracá, 2°02'58.4"N 50°25'40.7"W, 31 January–14 February 1992, Arno A. Lise (MCTP-1769); 1 m#, 1 f#, same locality, data and collector (MCTP-7550); 1 m#, same locality, data and collector (MCTP-7549); 1 f#, same locality, data and collector (MCTP-22700); **Mato Grosso do Sul:** 1 m#, Bonito, [21°06'04.9"S 56°42'33.7"W], 133 m, 14–23 October 2002, Equipe Biota (IBSP-120677); **São Paulo:** 1 m#, Teodoro Sampaio, Parque Estadual do Morro do Diabo,

[ $22^{\circ}31'S$   $52^{\circ}18'W$ ], 2 m, 24–31 March 2003, Equipe Biota (IBSP–120654); 1 f#, same locality, data and collector (IBSP–120658).

**Diagnosis.** This is the only species of the genus that lacks punctured socks on the carapace (Figs 12F, 18A-B). As in *W. granulosus*, it has multiple tubercles evenly distributed along the dorsal prosoma but differs from that has a conical socket in each of these structures (Figs 12F, 18A-B). In addition, both females and males have the largest tubercles of the posterior decline compared to the other species of *Whittickius* (Figs 18 and 19 A-B). Is the only one with ectal branch of VTA smaller than mesial branch (Figs 19C-F) and similar to *W. granulosus* has a spermathecae longer than copulatory ducts (Figs 18D, F).

**Description. Female (from Alto Alegre; MCTP–1769):** Prosoma dark brown with a light yellow middleline triangular. Dorsal slope with eight great tubercles (Fig 18A). Clypeus with two light spots under the middle anterior eyes (Fig 18B). Opisthosoma globose with an anterior and two median clear and triangular stines, and two horizontal and concave stripes in the middle (Fig 18A). Copulatory opening in anterolateral portion of epiginal plate, without atrium (Fig 18C, E). Copulatory ducts equal than spermathecae and descending entry in the epyginum (Fig 18D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.09, ALE 0.18, PME 0.11, PLE 0.15, AME–AME 0.14, AME–ALE 0.14, PME–PME 0.41, PME–PLE 0.35, MOQ length 0.32, MOQ width 0.31; leg formula: 1–2–4–3: leg I – femur 1.21/ patella 0.47/ tibiae 0.90/ metatarsus 0.68/ tarsus 0.48/ total 3.73; II – 1.17/ 0.49/ 0.88/ 0.68/ 0.49/ 3.71; III – 0.81/ 0.36/ 0.60/ 0.40/ 0.41/ 2.58; IV – 0.93/ 0.32/ 0.65/ 0.48/ 0.39/ 2.78. Total body length 3.47; prosoma 1.44 length, 1.28 wide; opisthosoma length 2.03; clypeus 0.28 height; sternum 0.67 length, 0.53 width; endites 0.35 length, 0.13 width; labium 0.27 length, 0.15 width.

**Male (from Novo Progresso; MPEG-5454):** Prosoma coloration like females. Dorsal slope with twelve tubercles smaller than in females (Fig 19A). Like females, clypeus with two light spots under the middle anterior eyes (Fig 19B). Opisthosoma globose, wider than long (Fig 19A). Embolous length 1/2 of the tegulum circumference (Figs 19C, E). VTA as long as the RTA and perpendicular to this. Ribbed RTA with pointed apex (Figs 19C-F).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.21, PME 0.11, PLE 0.19, AME-AME 0.20, AME-ALE 0.17, PME-PME 0.25, PME-PLE 0.38, MOQ length 0.31, MOQ width 0.38; leg formula: 1-2-4-3; leg I – femur 1.62/ patella 0.66/ tibiae 1.36/ metatarsus 1.06/ tarsus 0.67/ total 5.38; II – 1.58/ 0.70/ 1.35/ 1.08/ 0.66/ 5.37; III – 1.10/ 0.43/ 0.78/ 0.48/ 0.46/ 3.25; IV – 1.10/ 0.35/ 0.77/ 0.59/ 0.49/ 3.29. Total body length 3.30; prosoma 1.76 length, 1.43 wide; opisthosoma length 1.54; clypeus 0.36 height; sternum 0.71 length, 0.61 width; endites 0.48 length, 0.16 width; labium 0.31 length, 0.13 width.

**Distribution.** BRAZIL: Pará, Minas Gerais, Roraima, Mato Grosso and São Paulo.

*Whittickius granulosus* (Mello-Leitão, 1929) **comb. Nov.**

Figs 20.

*Acentroscelus granulosus* Mello-Leitão, 1929: 177, fig. 59.

*Acentroscelus granulosus* Rinaldi, 1984: 113.

*Whittickius granulosus* Molina-Gómez and Teixeira, (IN PROCESS).

**Type material: Holotype:** female, Brazil, Bahia, Santo Antônio da Barra, E. Simon leg. (MNHN-11504, examined)

**Other material examined.** ARGENTINA: *Jujuy*: 1 juvenil, Calilegua, Parque Nacional Calilegua, 23°40'24.3"S, 64°52'30.8"W, 27 September 1995, M. Ramírez and P. Goloboff (MACN). BRAZIL: *Minas Gerais*: 1 f#, Belo Horizonte, Museu de História Natural e Jardim Botânico da UFMG, [19°53'34,4"S, 43°54'47,1"W], September–October 2014, P.H. Martins (UFMG–16082).

**Diagnosis.** This species is the only one that has granules or tubers on the entire surface of the carapace with punctured sockets (Figs 12G-20A-B). Females of *A. granulosus* are different of all species of *Whittickius* by present small tubercles in the slope margin (Fig 20A). Couulatory ducts equal to spermathecae like *W. echinithorax* sp. nov (Figs 20D, F).

**Description. Female (from Belo Horizonte; UFMG–16082):** Prosoma dorsally light reddish–brown with a light–yellow dorsal line, from the middle posterior eyes to the slope of the carapace (Figs 20A-B). The carapace shows small granules with strong punctures apically (Fig 12G). Twelve dorsal tubercles in the dorsal posterior slope (Fig 20A). Legs I and II light yellow from coxa to patella and light brown in the most distal segments; legs III and IV light yellow and all legs covered with setae on the entire surface. Opisthosoma light–yellow, globose with brownish–yellow irregular stains on the entire back of the abdomen (Fig 20A). Anterior region of epiginal plate with deep atrium divided in two regions (Figs 20C, E), short copulatory ducts with descending entry and reniform spermathecas (Figs 20D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.10, ALE 0.18, PME 0.08, PLE 0.14, AME–AME 0.18, AME–ALE 0.16, PME–PME 0.26, PME–PLE 0.37, MOQ length 0.29, MOQ width 0.45; leg formula: 1–2–4–3: leg I – femur 1.07/ patella 0.41/ tibiae 0.68/ metatarsus 0.45/ tarsus 0.56/ total 3.17; II – 1.14/ 0.43/ 0.44/ 0.52/ 0.55/ 3.16; III – 0.76/ 0.31/ 0.52/ 0.35/ 0.37/ 2.31; IV – 0.87/ 0.39/ 0.61/ 0.32/ 0.31/

2.50. Total body length 3.32; prosoma 1.37 length, 1.18 wide; opisthosoma length 1.98; clypeus 0.26 height; sternum 0.65 length, 0.54 width; endites 0.36 length, 0.15 width; labium 0.27 length, 0.15 width.

**Distribution.** ARGENTINA: Calilegua and BRAZIL: Belo Horizonte.

**Note.** The male of *A. granulosus* is unknown. The description realized by Rinaldi (1984), as in the case of the species *A. albipes*, was carried out using samples corresponding to an entity other to *A. granulosus*. We had access to the material analyzed and determined by Rinaldi (1984; MZSP-9768), so we can know that the male identified with the name of *A. granulosus* really corresponds to a male of the *W. caxiuana* sp. nov species, described for the first time in this work. For this reason, the description made for the male of *A. granulosus* is void and currently is not possible due to lack of available material in biologic collections.

*Whittickius singularis* (Mello-Leitão, 1940)

Figs 21–22

**Type material: Holotype:** f#, Guiana (BENH-3493, examined).

**Other material examined.** BRAZIL: **Pará:** 1 m#, Juruti, Vale do Igarapé Mutum, Platô do Rio Juruti, 02°36'11.2"S 56°12'36.3"W, 04 August 2004, D.R. Santos-Souza (MPEG-8768); **Amapá:** 3 m#, 3 f#, Serra do Navío, Território de Amapá, 1°48'24.4"N 52°13'48.5"W, June 2003, Galiano (MACN-10783); **Amazonas:** 1 m#, 1 f#, Manaus, Reserva Ducke, 2°57'37.2"S 59°55'32.0"W, August 1971, M.E. Galiano (MACN-19120); 7 m#, 5 f#, same locality, data and collector (MACN-10778); 1 m#, same locality, 11 April 1973, P. Alboquerque (INPA-22681); 1 f#, same locality, data and collector (INPA-22682); 2 f#, same locality, data and collector (INPA-22683); 1 m#, same locality, data and collector (INPA-22684); 1 m#, same locality, data and

collector (INPA-22685); 1 m#, same locality, data and collector (INPA-22686); 1 m#, same locality, data and collector (INPA-22687); **FRENCH GUIANA: Saint-Laurent-du-Maroni:** 4 m#, 2 f#, Saül, Belvérè,  $3^{\circ}37'16.1''N$   $53^{\circ}12'35.6''W$ , 31 March 2010, V. Vedel (MCTP-42634); 6 m#, 5 f#, same locality, data and collector (MCTP-42638); 1 m#, Maripasoula,  $3^{\circ}38'58.7''N$   $54^{\circ}02'40.5''W$ , 2014, V. Vedel (MCTP-41730); 1 f#, same locality, data and collector (MCTP-41731); 1 m#, same locality, data and collector (MCTP-41732); 1 m#, same locality, data and collector (MCTP-41739); 1 m#, 1 f#, Saint-Élie, Réserve Naturelle de La Trinité,  $4^{\circ}05'19.1''N$   $52^{\circ}40'47.1''W$ , 10 April 2010, V. Vedel (MCTP-42637); 3 f#, Regina, Station de Recherche des Nouragues, Inselberg, Terra firme,  $4^{\circ}05'19.1''N$   $52^{\circ}40'47.1''W$ , 09 Setember 2010, Hoppier (MCTP-42636); 1 m#, same locality, 15 March 2010, V. Vedel (MCTP-41733); 1 m#, same locality, data and collector (MCTP-41734); 1 f#, same locality, data and collector (MCTP-41735); 1 f#, same locality, data and collector (MCTP-41737); 1 m#, 09 March 2010, same locality and collector (MCTP-42635); 1 f#, same locality, data and collector (MCTP-41738); 1 m#, 1 f#, 2 j#, 23-09 May 2010, same locality and collector (MCTP-42633); 1 m#, 2013, same locality and collector (MCTP-41740).

**Diagnosis.** This is the only one with tubercles clearer and differentiated than the color of carapace (Figs 21A, 22A). It has a pair of medium-sized tubercles larger than the rest of the tubers at the posterior slope (Figs 21B, 22B). Male palp with an embolous length 1/4 of the tegulum circumference like *W. caxiuana* sp. nov. but differs from the apex direction of the embolous and in the ectal branch tha is thinner and longer than mesial branch (Figs 22C, E). Females with deep atrium in the middle of epiginal plate like *W. guianensis* (Figs 22D, F).

**Description. Female (from Manaus; MACN-19120):** Prosoma evenly brown with bright appearance (Figs 21A-B). Opisthosoma and legs according to the genus description. Dorsal slope with nine tubercles of different size (Figs 21A-B). Epiginal plate full of folds in the posterior region and atrium delimited posteriorly (Figs 21C, E). Copulatory ducts with descending entry, short and curved, smaller than spermathecae. Reniform spermathecae with visibly separated internal chambers (Figs 21D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.11, ALE 0.20, PME 0.08, PLE 0.15, AME-AME 0.11, AME-ALE 0.13, PME-PME 0.35, PME-PLE 0.37, MOQ length 0.26, MOQ width 0.32; leg formula: 1-2-4-3: leg I – femur 1.54/ patella 0.61/ tibiae 1.18/ metatarsus 0.89/ tarsus 0.68/ total 4.90; II – 1.50/ 0.65/ 1.21/ 0.93/ 0.56/ 4.85; III – 1.00/ 0.47/ 0.77/ 0.53/ 0.42/ 3.20; IV – 1.13/ 0.42/ 0.83/ 0.56/ 0.43/ 3.38. Total body length 3.63; prosoma 1.55 length, 1.25 wide; opisthosoma length 2.08; clypeus 0.31 height; sternum 0.70 length, 0.58 width; endites 0.46 length, 0.19 width; labium 0.31 length, 0.12 width.

**Description. Male (from Saint Laurent du Maroni; MCTP-42634):** Prosoma, legs and opisthosoma like females. Dorsal slope with eleven tubercles of different size (Figs 22A-B). Palp with cymbium widened at the base with an agglomerate of dense and long bristles on the VTA. Apex embolous in tape format. Tibial apophysis like genus description (Figs 22A-B).

Measurements: eyes diameters and eyes interdistances: AME 0.09, ALE 0.18, PME 0.10, PLE 0.15, AME-AME 0.09, AME-ALE 0.12, PME-PME 0.14, PME-PLE 0.33, MOQ length 0.28, MOQ width 0.28; leg formula: 1-2-4-3: leg I – femur 1.57/ patella 0.57/ tibiae 1.27/ metatarsus 1.00/ tarsus 0.71/ total 5.13; II – 1.57/ 0.55/ 1.31/ 1.00/ 0.70/ 5.12; III – 0.92/ 0.41/ 0.73/ 0.52/ 0.40/ 2.98; IV – 1.11/ 0.39/ 0.77/ 0.55/ 0.42/ 3.24. Total body length 2.97; prosoma 1.37 length, 1.10 wide; opisthosoma length

1.60; clypeus 0.26 height; sternum 0.59 length, 0.57 width; endites 0.40 length, 0.15 width; labium 0.26 length, 0.14 width.

**Distribution.** BRAZIL: Pará, Amapá and Amazonas; FRENCH GUIANA: Saül, Mana, Saint-Élie and Regina.

**Note.** We described for the first time the male of *W. singularis*, belonging to the same type locality. Based on this species we revalidate and redescribed to *Whittickius* because it was the type species proposed by Mello-Leitão, 1940 when described the genus originally.

*Whittickius guianensis* (Taczanowski, 1872)

Figs 23–24

**Type material: Syntype series:** f#, m# Saint Laurent de Maroni, French Guiana (examined).

**Other material examined.** COLOMBIA: *Meta*: 1 m#, 1 f#, Villavicencio, Vereda La Llanerita, Finca Cataguala, 4°8'56.37"N 73°37'59.19"W, 20–21 April 2005, Estudiantes de sistemática animal (ICN-AR-10235); 1 j#, San Martín, Finca El Caduceo, Río Camoa, 3°39'54.27"N 73°39'27.04"W, 400 m, 13 May 2006, G. Aveo (ICN-AR-11559); *Vaupes*: 1 m#, 1 f#, Taraira, Lago Taraira, Estación biológica Mosiro Itájura (Caparú), 1°04'S 69°31'W, October–November 2004, J. Pinzón (ICN-AR-7643); 1 j#, Territorio Kofán, 0°21'40.53"N 76°38'30.64"W, 780 m, 27 September 1998, J. Rodriguez (ICN-AR-11560); BRAZIL: *Pará*: 2 f#, Altamira, Castelo dos Sonhos, 08°17'15"S 54°59'55"W, 12 November 2005, D.F. Candiani (MPEG-4329); 1 m#, Santa Bárbara do Pará, Parque Ecológico do Guma, [01°12'44"S 48°17'28"W], 16 February 2010, G.H.F. Azevedo *et al.* (UFRJ-9558) *Sergipe*: 1 m#, Itabaiana, Estação Ecológica da Serra de Itabaiana, 10°40'S 37°25'W, 68 m, 14–20 Setember 1999, A.D.

Brescovit *et al.* (IBSP–120702); **Bahia:** 1 m#, Camacan, 15°25'11.7"S 39°29'47.1"W, (IBSP–15814); **Mato Grosso:** 1 m#, Chapada do Guimarães, 15°18'33.2"S 55°50'44.6"W, 15–26 July 1992, A.A. Lise (MCTP–2177); 1 m#, Pantanal, 17°38'51.8"S 57°28'30.6"W, 04–10 August 1992, A.A. Lise (MCTP–2353); **Roraima:** 1 m#, Alto Alegre, Ilha de maracá, Estação Ecológica de Maracá, 2°02'58.4"N 50°25'40.7"W, 01 May 1952, Marcelo Nascimento (MCTP–1959); 1 f#, same locality, 07 December 1987, Arno A. Lise (MCN Z–17518); 1 m#, 1 f#, 07 December 1987, same locality and collector (MCN Z–17517); 1 f#, same locality, 14 February 1990 (MCTP–1770); **Espírito Santo:** 1 f#, 20°25'57.0"S 41°01'12.0"W, 14 Setember 1942, Soares (MZSP–685); **Mato Grosso do Sul:** 2 m#, Bonito, [21°06'04.9"S 56°42'33.7"W], 99 m, 14–23 October 2002, Equipe Biota (IBSP–120673); 1 f#, 17 m, same locality, data and collector (IBSP–120674); 1 m#, 2 m, same locality, data and collector (IBSP–120675); 1 f#, 34 m, same locality, data and collector (IBSP–120676); 1 f#, 45 m, same locality, data and collector (IBSP–120678); 1 m#, 54 m, same locality, data and collector (IBSP–120679); **São Paulo:** 1 m#, Ribeirão Preto, 21°10'30.5"S 47°48'38"W, 36 m, January 2005, L. Garcia (IBSP–66450); **ARGENTINA: Misiones:** 1 f#, Parque Nacional Iguazú, Parque Nacional Iguazú, Sendero Macuco y picadas aledañas, 25°40'43"S 54°26'57"W, 18–21 January 2005, C. Grismado (MACN–27641); **PERU: Loreto:** 2 m#, 5 f#, Rio Samiria, 5°07'17.4"S 75°33'37.3"W, May–June 1990, T. Erwin *et al.* (MUSM); 1 m#, same locality, data and collector (MUSM); 1 m#, same locality, data and collector (MUSM); 1 m#, 2 f#, same locality, data and collector (MCTP–17306).

**Diagnosis.** Like *W. singularis* atrium smaller than epiginal plate and copulatory openings arranged in deep atrium, differs from that in *W. guianensis* the median ridge divided the atrium (Figs 23C, E). Is the only one that present copulatory ducts with

ascending entry (Figs 23D, F). Also differs to *W. singularis* in that male palp present a filiform embolous shorter (Figs 24C-F).

**Description. Female (from Alto Alegre; MCTP-1770):** Prosoma mostly dark brown, with middle region cleared up (Fig 23A). Middle tubercle larger than the other eight in the posterior slope (Figs 23B). Legs and opisthosoma like genus description. Deep atrium smaller than epiginal plate with median ridge present (Figs 23C, E). Copulatory ducts ascending shorter than reniform spermathecae. This last presents visible internal chambers (Figs 24D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.11, ALE 0.21, PME 0.10, PLE 0.20, AME-AME 0.21, AME-ALE 0.19, PME-PME 0.33, PME-PLE 0.44, MOQ length 0.30, MOQ width 0.43; leg formula: 1-2-4-3: leg I – femur 1.79/ patella 0.66/ tibiae 1.29/ metatarsus 0.96/ tarsus 0.68/ total 5.39; II – 1.69/ 0.70/ 1.35/ 1.01/ 0.72/ 5.47; III – 1.23/ 0.56/ 0.90/ 0.57/ 0.58/ 3.85; IV – 1.41/ 0.52/ 0.98/ 0.62/ 0.52/ 4.05. Total body length 3.48; prosoma 2.05 length, 1.63 wide; opisthosoma length 2.84; clypeus 0.45 height; sternum 0.81 length, 0.66 width; endites 0.52 length, 0.20 width; labium 0.32 length, 0.16 width.

**Male (from Alto Alegre; MCTP-1959):** Prosoma and legs than females. Opisthosoma thinner than females and with a wide longitudinal whitish line (Figs 24A-B). Palp with discoid cymbium and short and filiform emboulus (Figs 24C, E). Branches of VTA equal longer and wider. Bristle of ectal branch longer than another of the tibia (Figs 24D, F). RTA like genus description.

Measurements: eyes diameters and eyes interdistances: AME 0.08, ALE 0.20, PME 0.10, PLE 0.15, AME-AME 0.16, AME-ALE 0.16, PME-PME 0.21, PME-PLE 0.34, MOQ length 0.31, MOQ width 0.30; leg formula: 1-2-4-3: leg I-femur 1.64/ patella 0.64/ tibiae 1.30/ metatarsus 1.01/ tarsus 0.63/ total 5.11; II – 1.51/ 0.61/ 1.38/

1.01/ 0.63/ 5.10; III – 1.06/ 0.47/ 0.87/ 0.51/ 0.41/ 3.32; IV – 1.15/ 0.44/ 0.83/ 0.53/ 0.53/ 3.40. Total body length 3.48; prosoma 1.67 length, 1.34 wide; opisthosoma length 1.81; clypeus 0.37 height; sternum 0.65 length, 0.52 width; endites 0.45 length, 0.15 width; labium 0.32 length, 0.14 width.

**Distribution.** BRAZIL: Pará, Sergipe, Bahia, Roraima, Mato Grosso Espírito Santo, Mato Grosso do Sul and São Paulo; ARGENTINA: Misiones; PERU: Loreto.

### *Species inquirenda*

The types of the following nominal species are immature; therefore, it is not possible to determine them as undoubted entities. The descriptions and original illustrations of these species also do not provide enough information for their clear identification, for this reason these species are here considered as *nomina dubia*.

*Acentroscelus gallinii* Mello–Leitão, 1943

*Acentroscelus gallini* Mello–Leitão, 1943: 117, fig. 19 (Holotype immature from Argentina, Córdoba, Maquinista Gallini, M. Birabén leg., deposited in (MLPA–15810), examined).

*Acentroscelus nigrianus* Mello–Leitão, 1929

*Acentroscelus nigrianus* Mello–Leitão, 1929: 117 (Holotype immature from São Paulo de Olivença, Amazonas, Brazil, E. Simon leg., deposited in (MNHN–9327), examined).

*Acentroscelus secundus* Mello–Leitão, 1929

*Acentroscelus secundus* Mello–Leitão, 1929: 176, fig. 18 (Holotype immature from Brazil, Rio de Janeiro, Petrópolis [22°32'24.0"S, 43°09'40.3"W] (MNRJ–878), examined).

### **Acknowledgement**

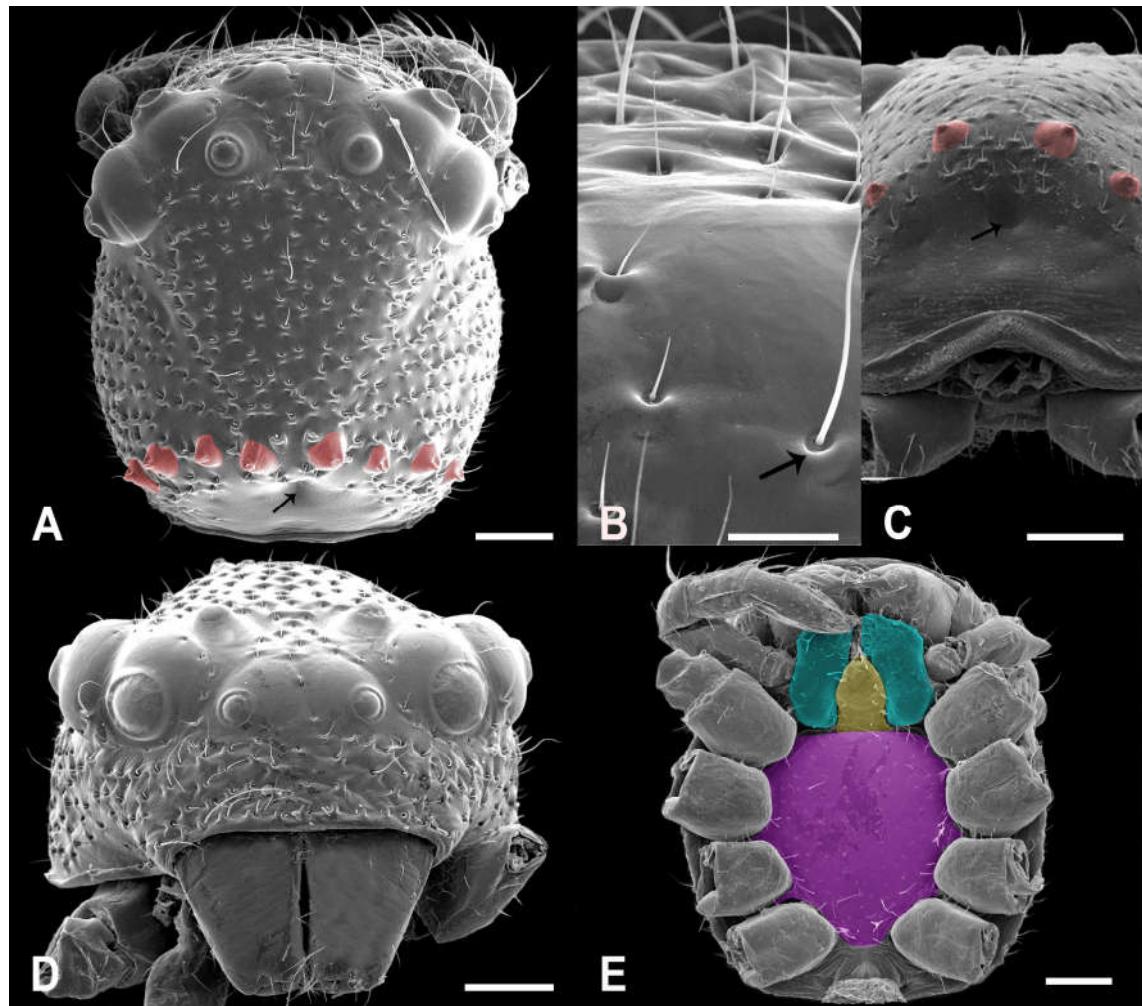
We thank the curators for the borrow of the specimens useful for carrying out this work.

We also thank the technicians of CEMM of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS) for the support. DMG was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) [number 131807/2018–8].

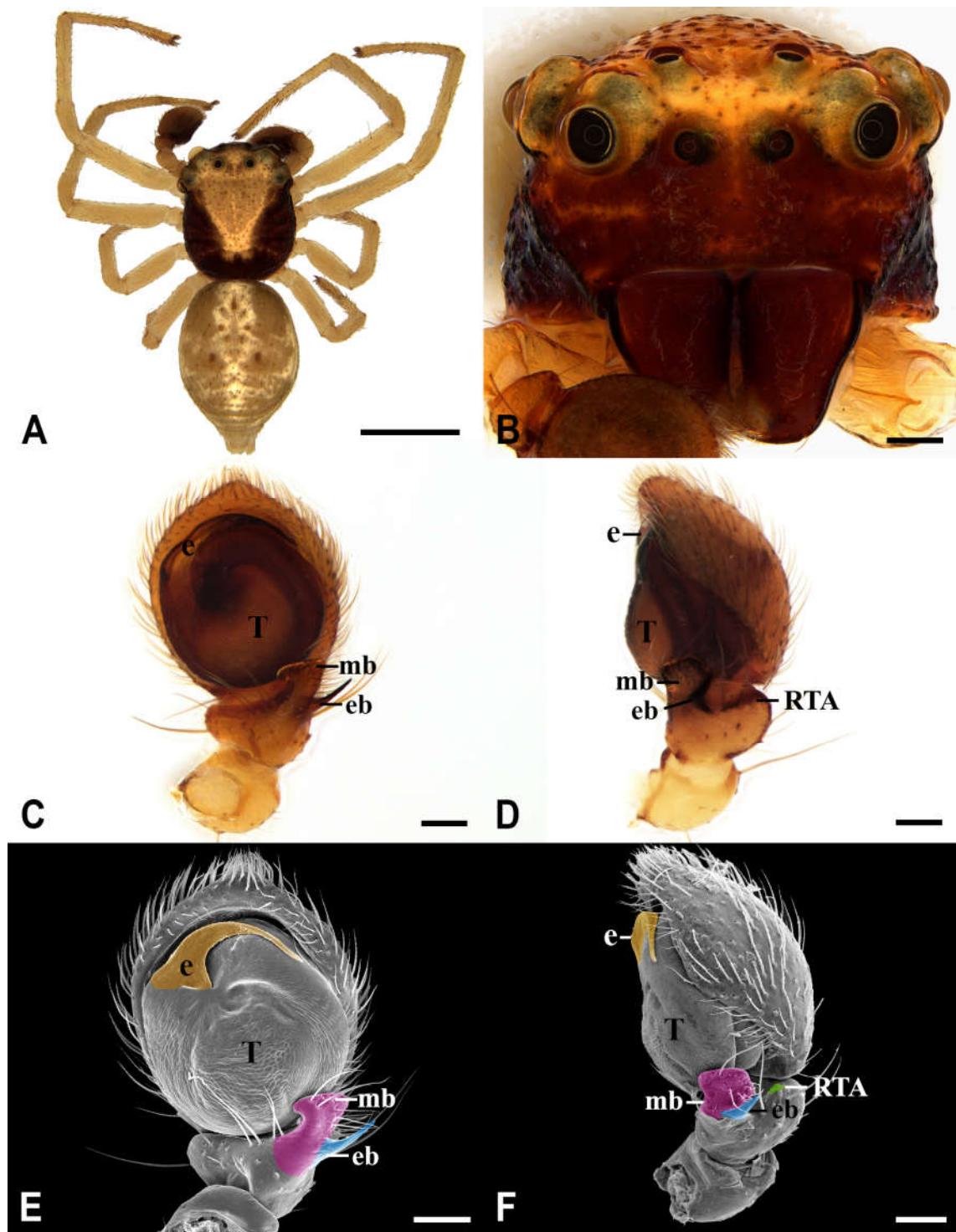
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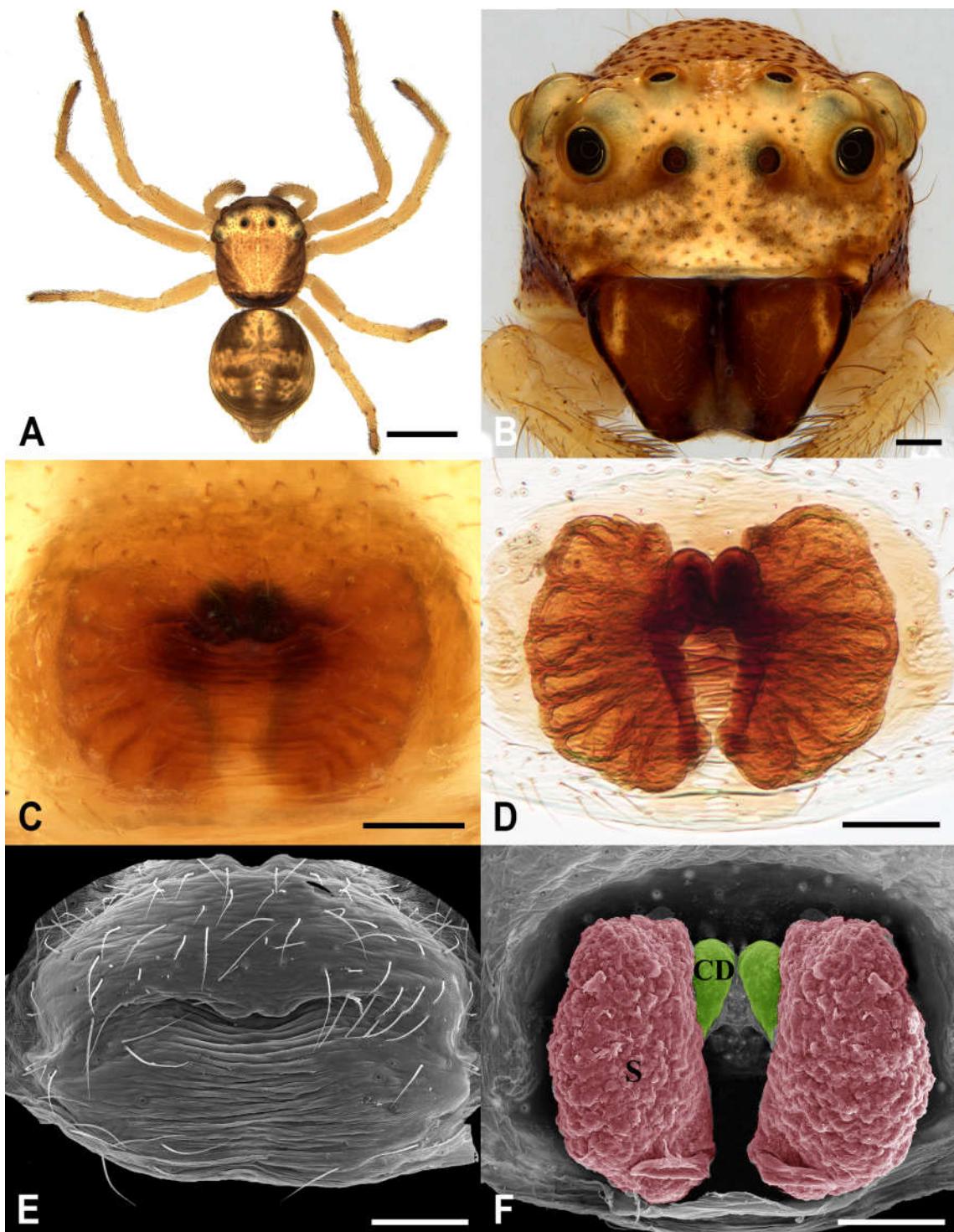
## Figures



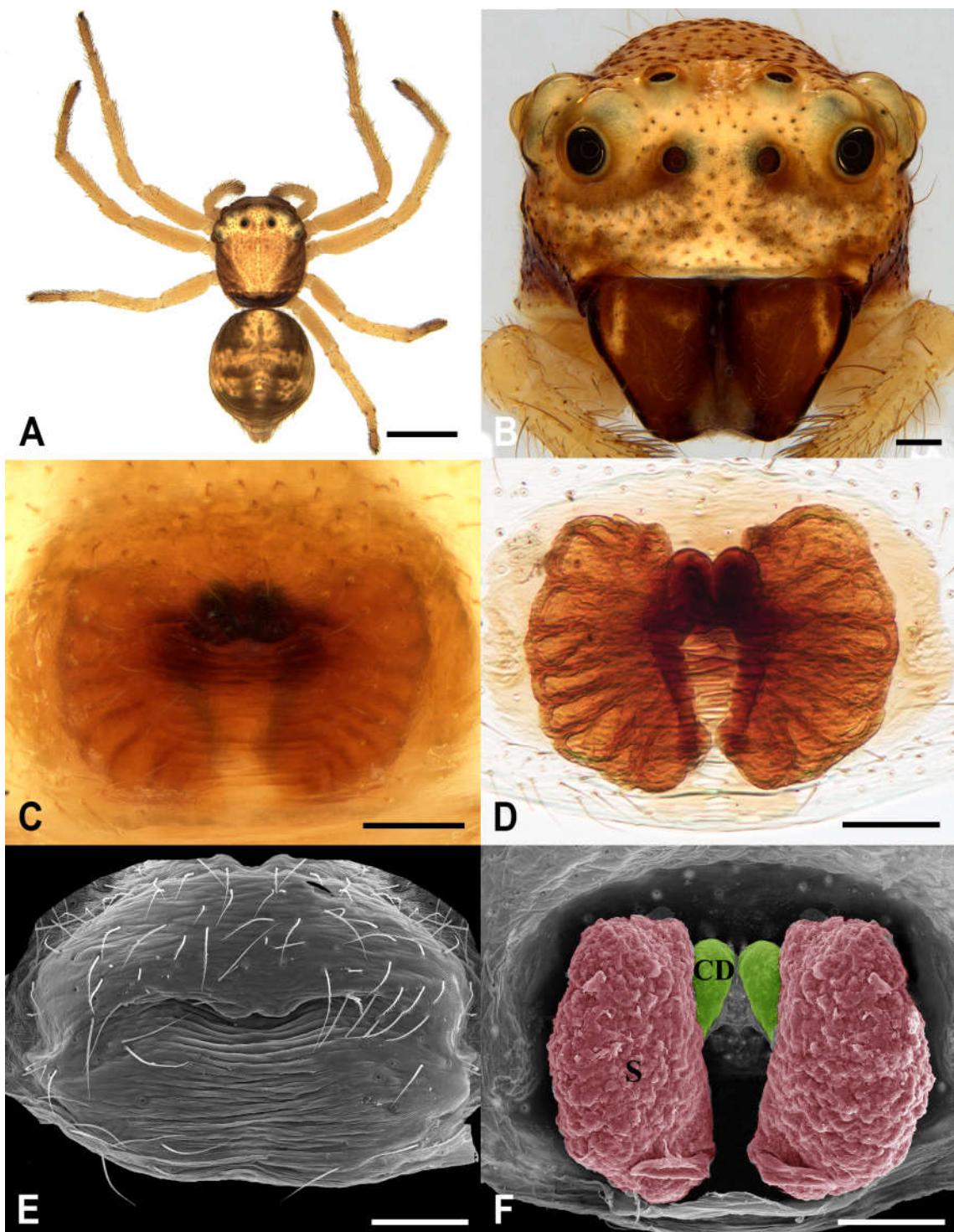
**FIGURE 1.** *Acentroscelus albipes*, female (IBSP-120875). A, dorsal view of carapace. Setiferous tubercles in the margin of posterior slope (red) and median depression (arrow). B, dorsal surface of the carapace. Punctures (arrow). C, *Acentroscelus serranus* sp. nov. (MCNZ-25487) posterior view of the carapace. Setiferous tubercles in the margin of posterior slope (red) and median depression (arrow). *Acentroscelus albipes*. D, Front view. Ocular region. E, Ventral view of carapace. Endites (blue), labium (yellow) and sternum (magenta). Scale bars: 0.2 mm (A, C-E) and 0.05 mm (B).



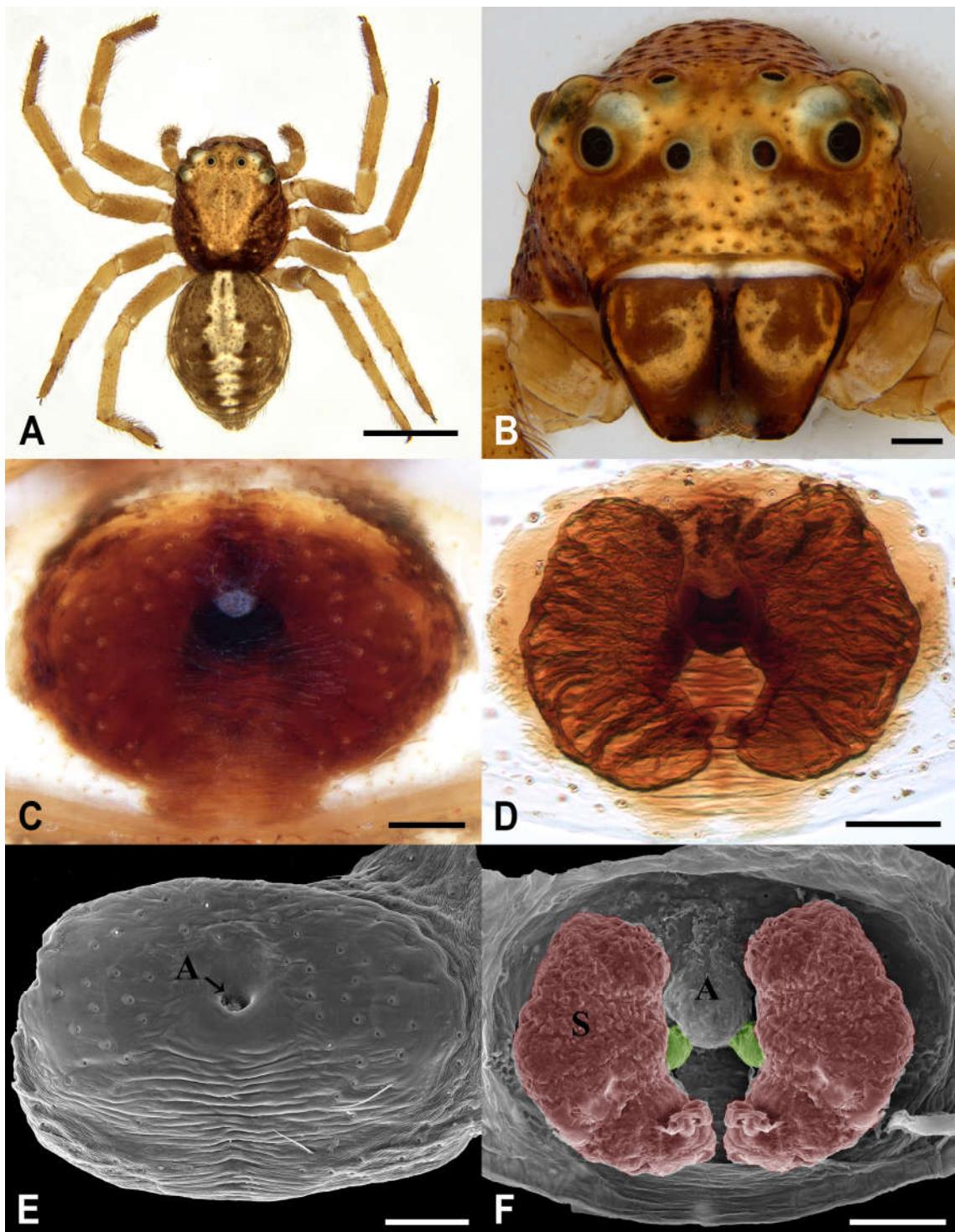
**FIGURE 2.** *Acentroscelus marmoratus* sp. nov., male (MZSP-27978). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



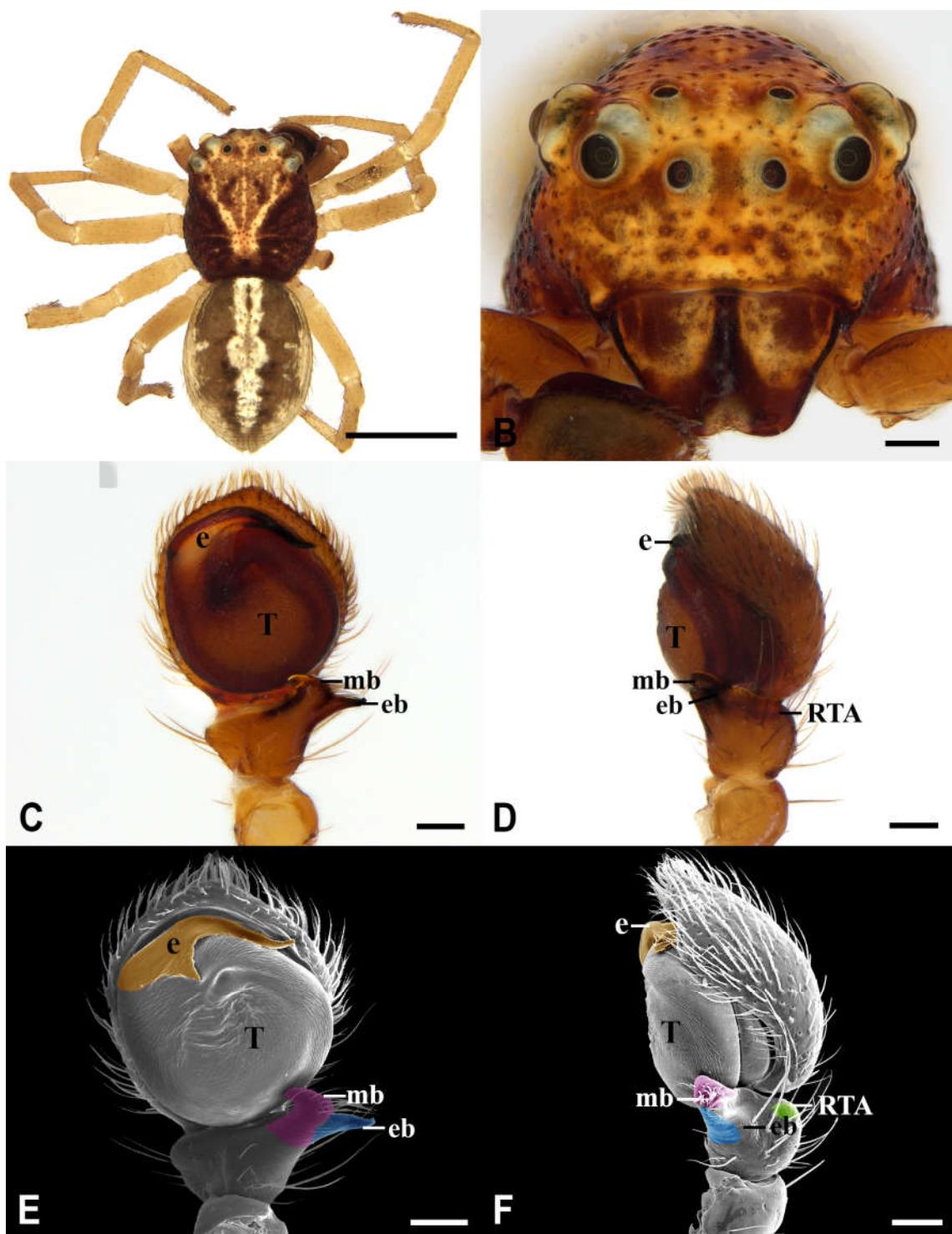
**FIGURE 3.** *Acentroscelus marmoratus* sp. nov., female (MZSP-27992). A, B habitus (A dorsal, B frontal); epigynal plate. C, ventral view. D, dorsal view with spermathecae and copulatory ducts. E, ventral view. F, dorsal view with spermathecae (red) and copulatory ducts (green). Scale bars: 0.1 mm (A–F).



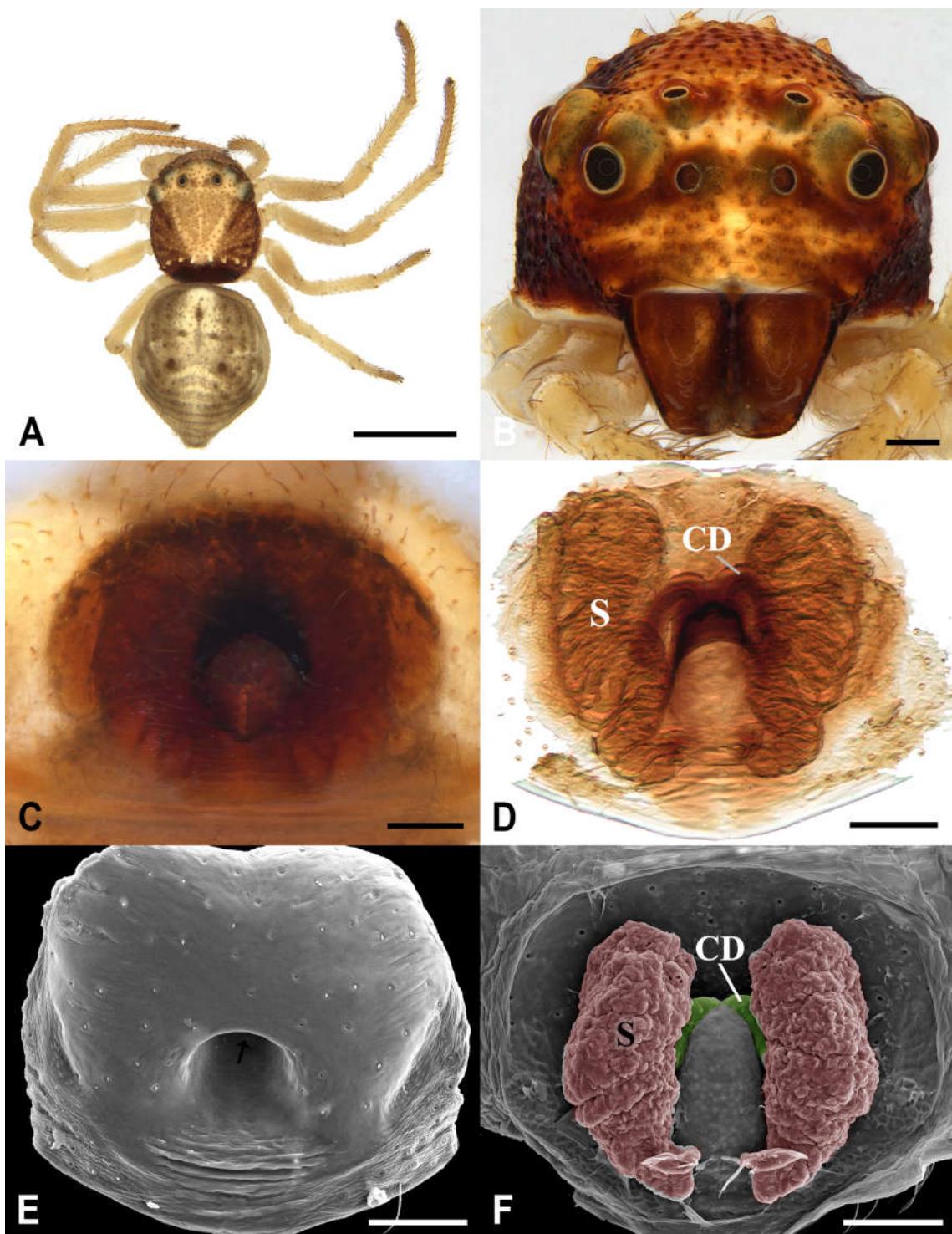
**FIGURE 3.** *Acentroscelus marmoratus* sp. nov., female (MZSP-27992). A, B habitus (A dorsal, B frontal); epigynal plate. C, ventral view. D, dorsal view with spermathecae and copulatory ducts. E, ventral view. F, dorsal view with spermathecae (red) and copulatory ducts (green). Scale bars: 0.1 mm (A–F).



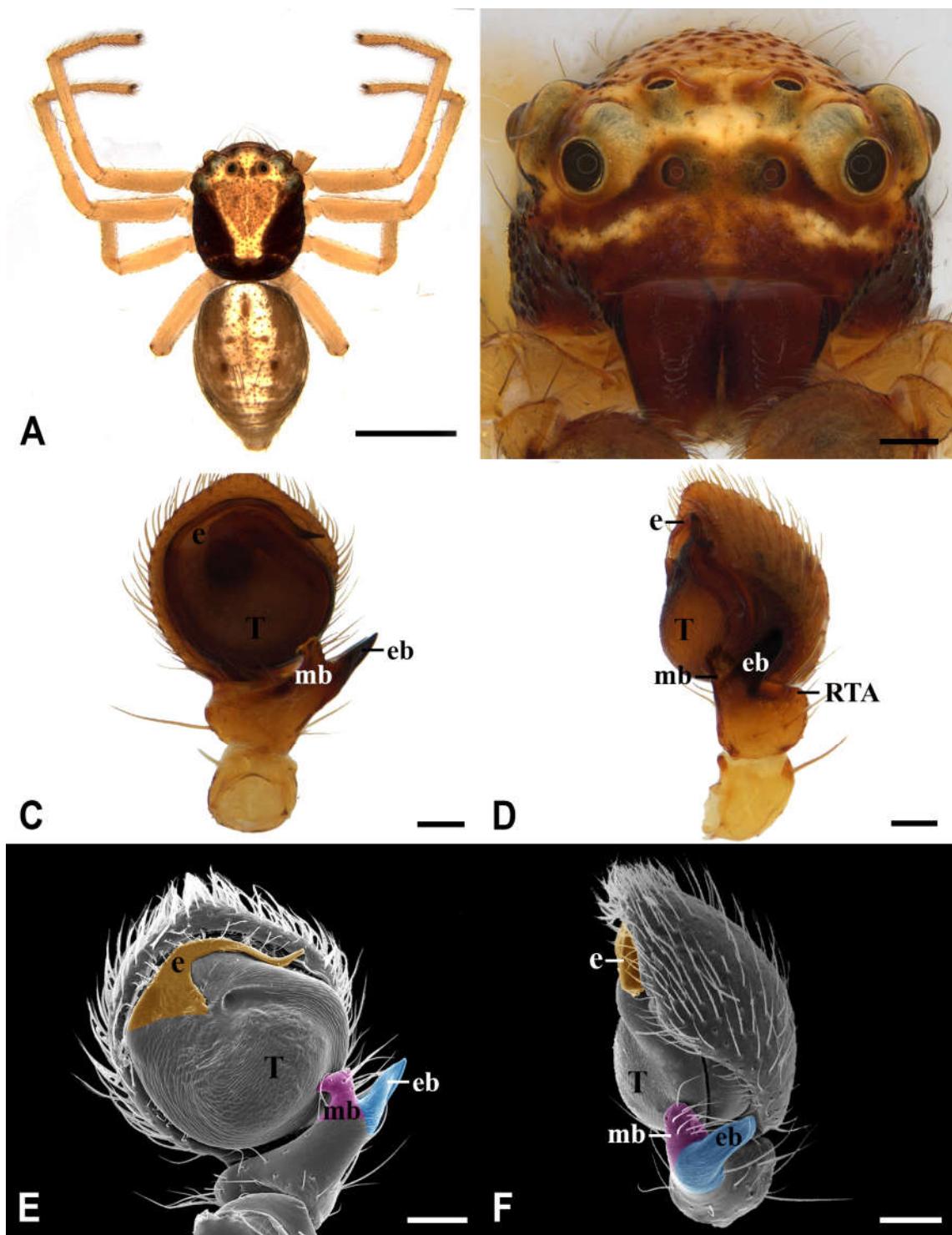
**FIGURE 4.** *Acentroscelus serranus* sp. nov., female (MCNZ-25487). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epigynal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



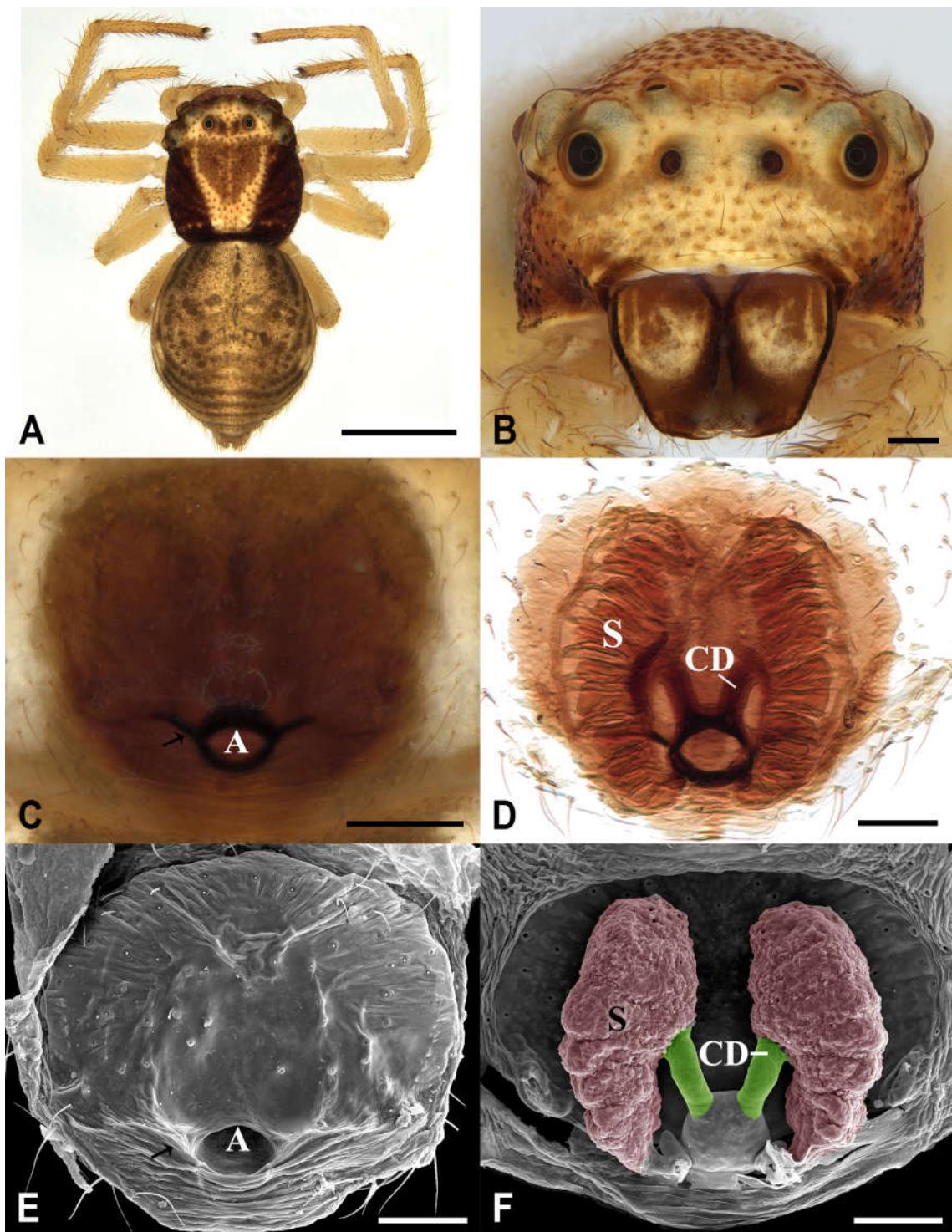
**FIGURE 5.** *Acentroscelus serranus* sp. nov, male (MCNZ–25487). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



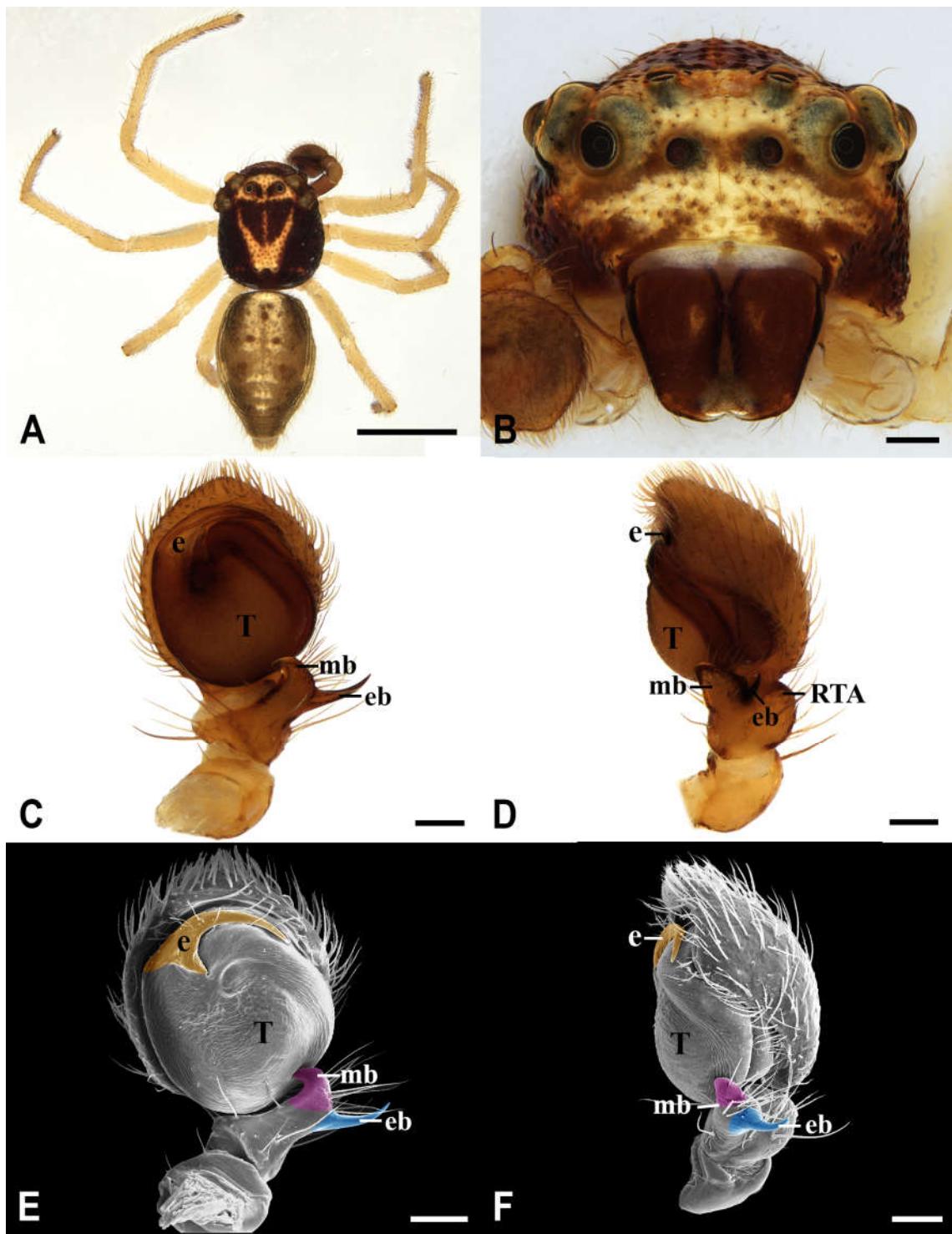
**FIGURE 6.** *Acentroscelus albipes* Simon, 1886, female (IBSP-120875). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



**FIGURE 7.** *Acentroscelus albipes* Simon, 1886, male (MNRJ). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



**FIGURE 8.** *Acentroscelus ramboi* Mello-Leitão, 1943, female (IBSP-121001). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S), copulatory ducts (CD) and horizontal fold at the anterior margin of atrium (arrow). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red), copulatory ducts (CD, green) and horizontal fold at the anterior margin of atrium (arrow). Scale bars: 0.1 mm (A-F).



**FIGURE 9.** *Acentroscelus ramboi* Mello-Leitão, 1943, male (MCTP-8780). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T, magenta), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA,

green).

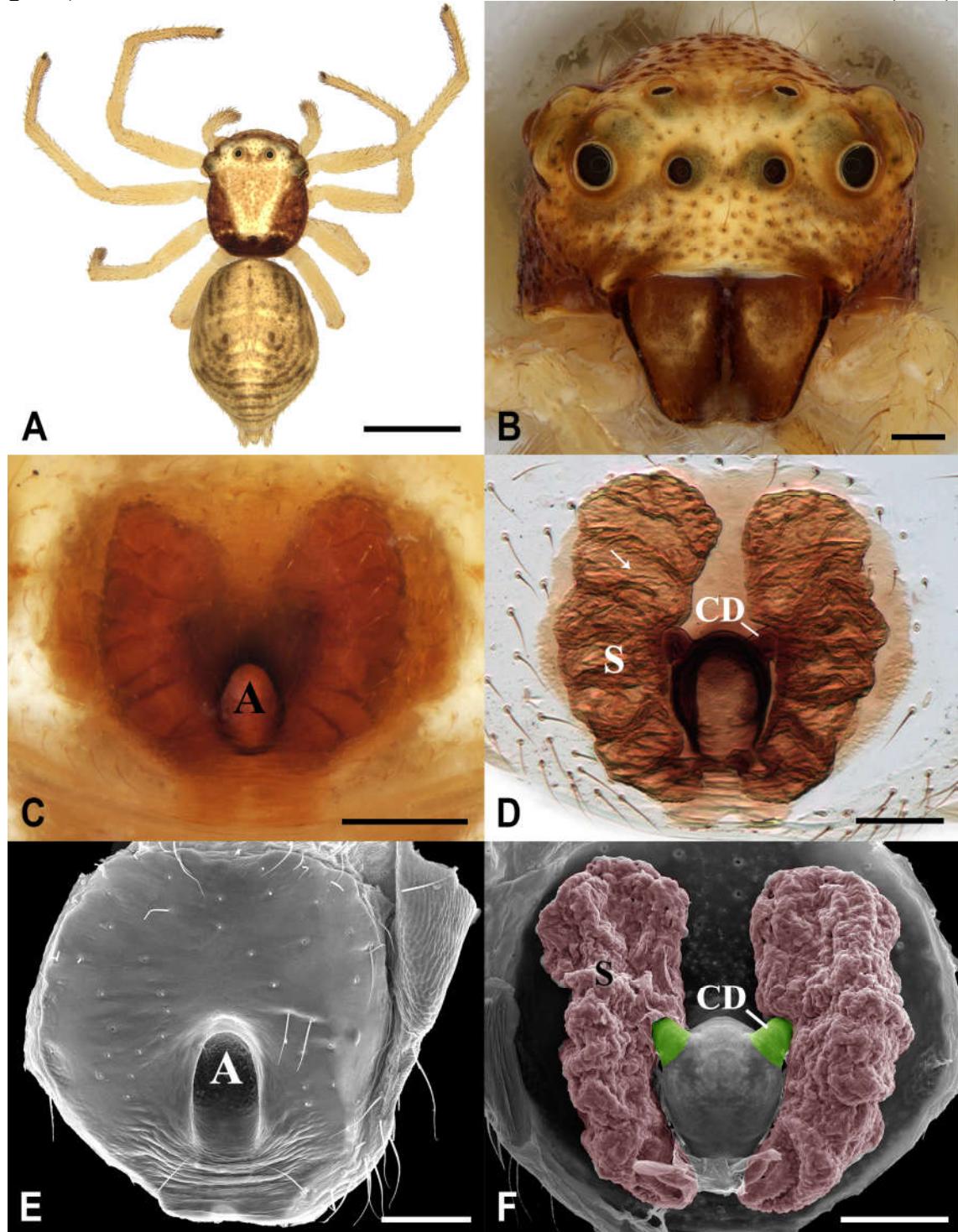
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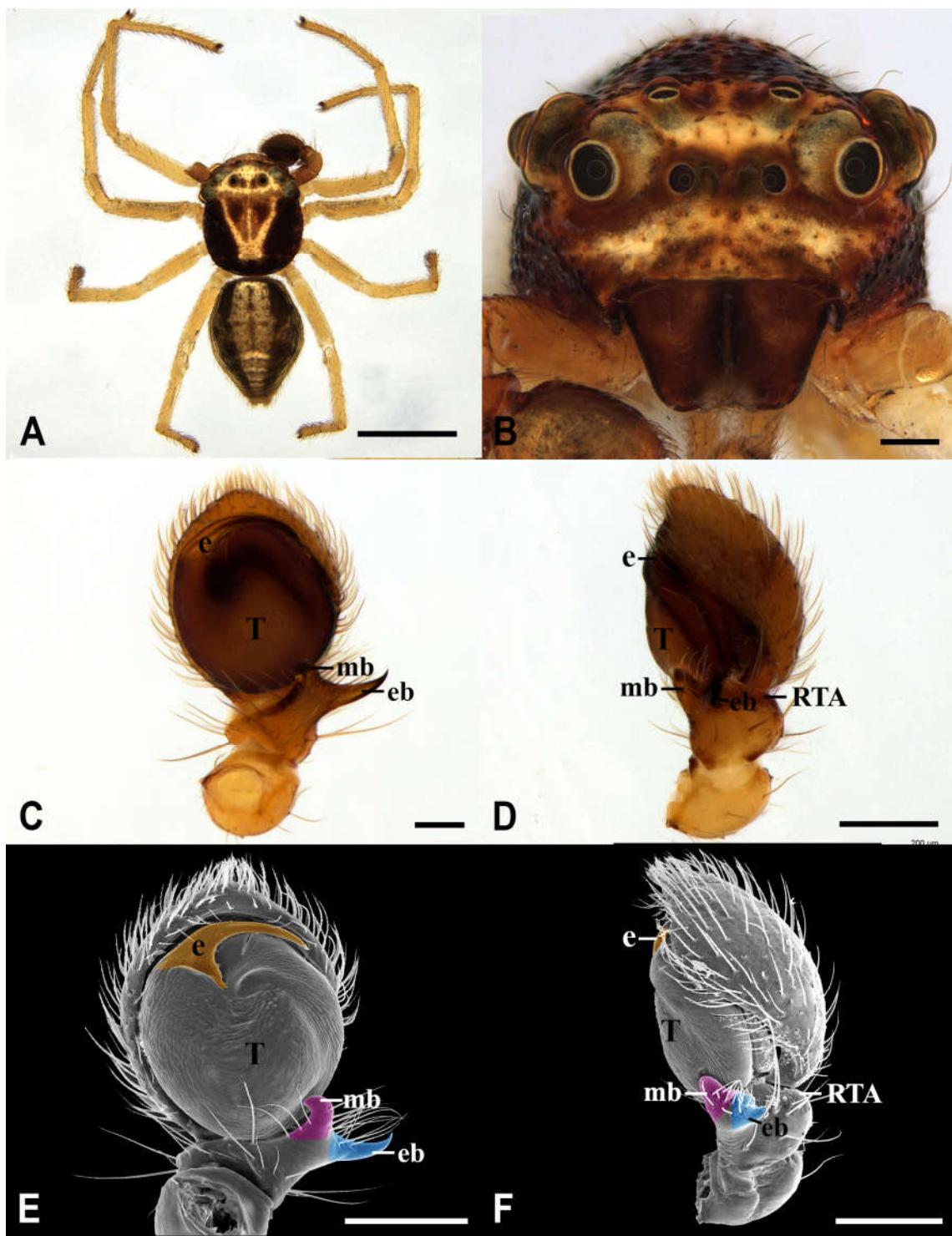
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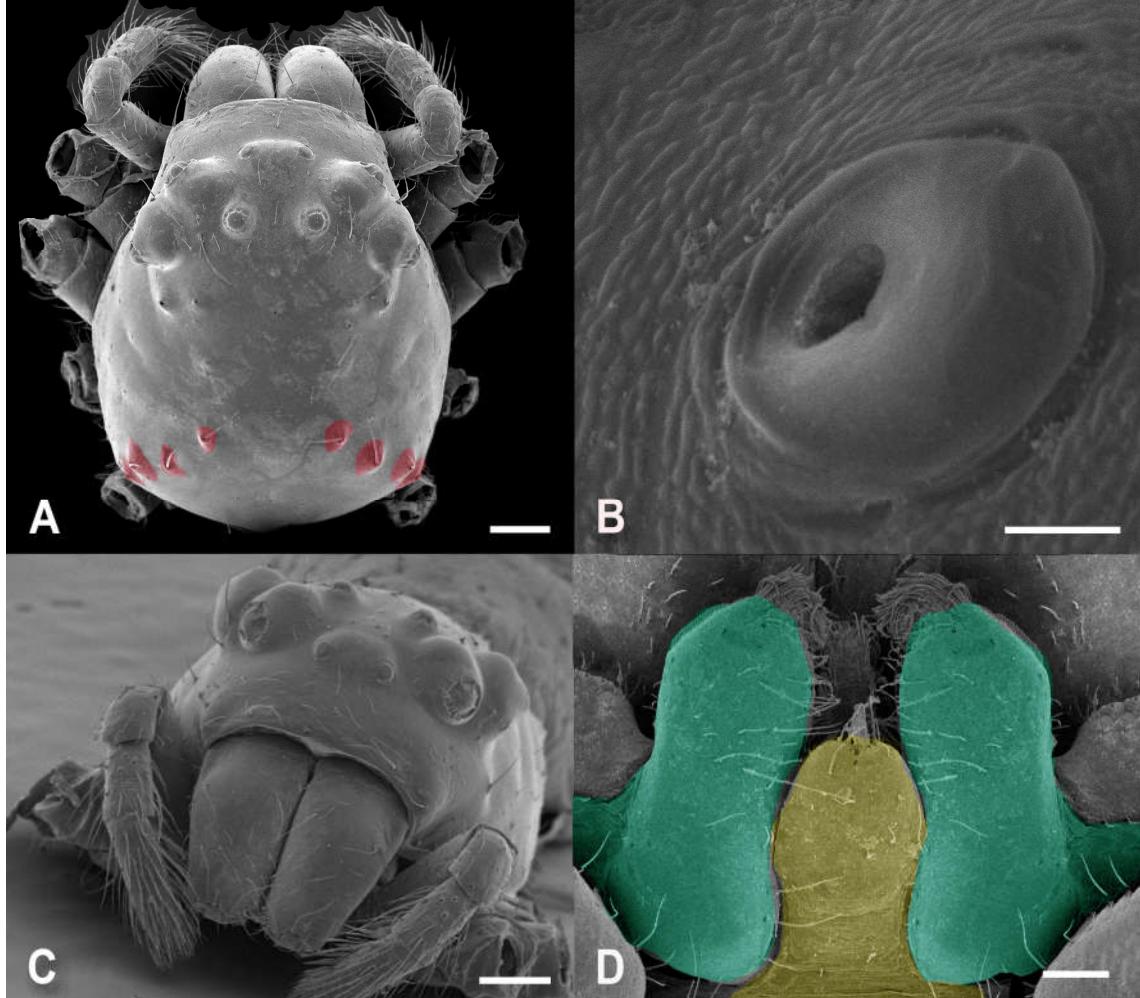


**FIGURE 10.** *Acentroscelus versicolor* Soares, 1942, female (IBSP-120690). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).

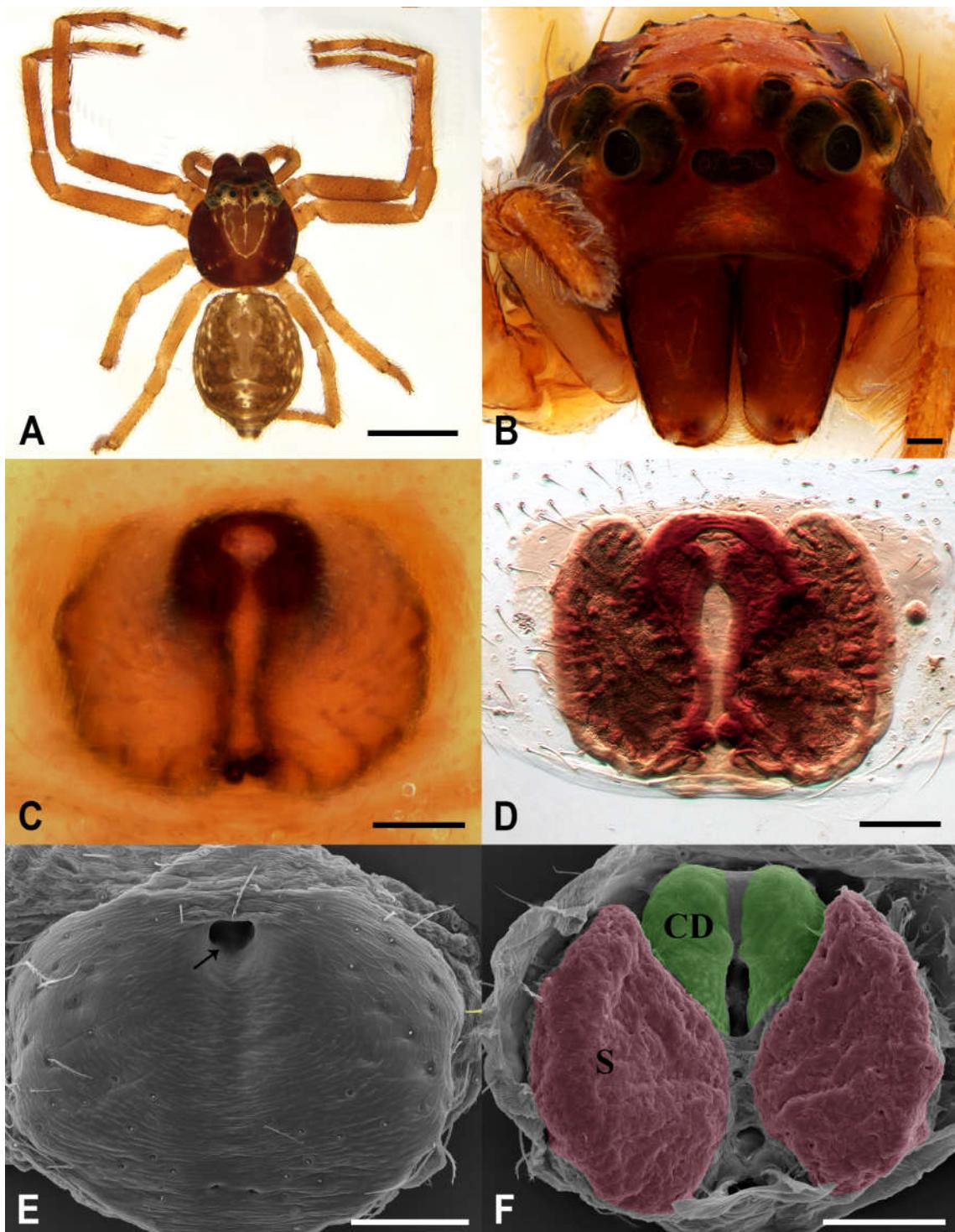


**FIGURE 11.** *Acentroscelus versicolor* Soares, 1942, male (IBSP-120712). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA,

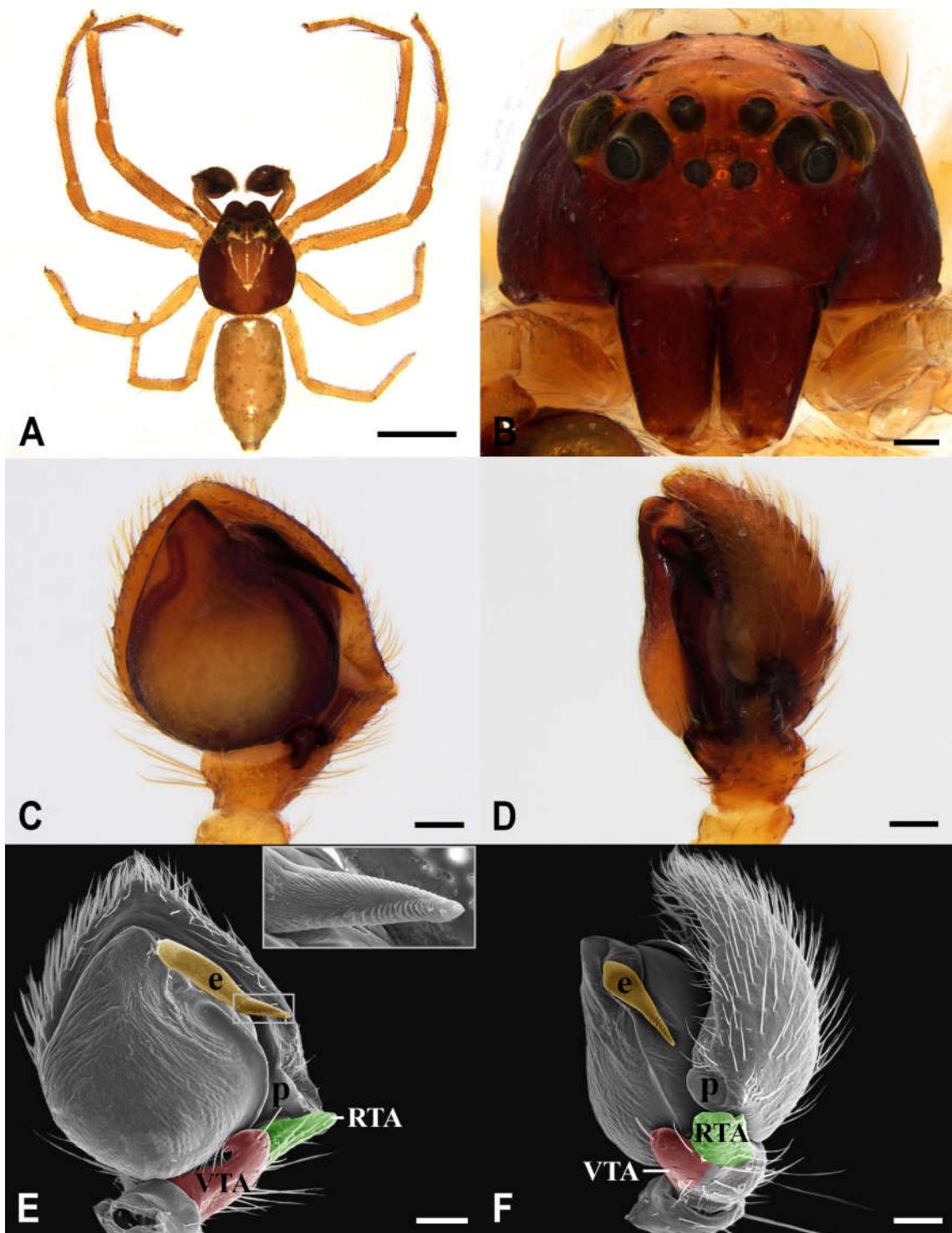
green). Scale bars: 0.1 mm (A–F).



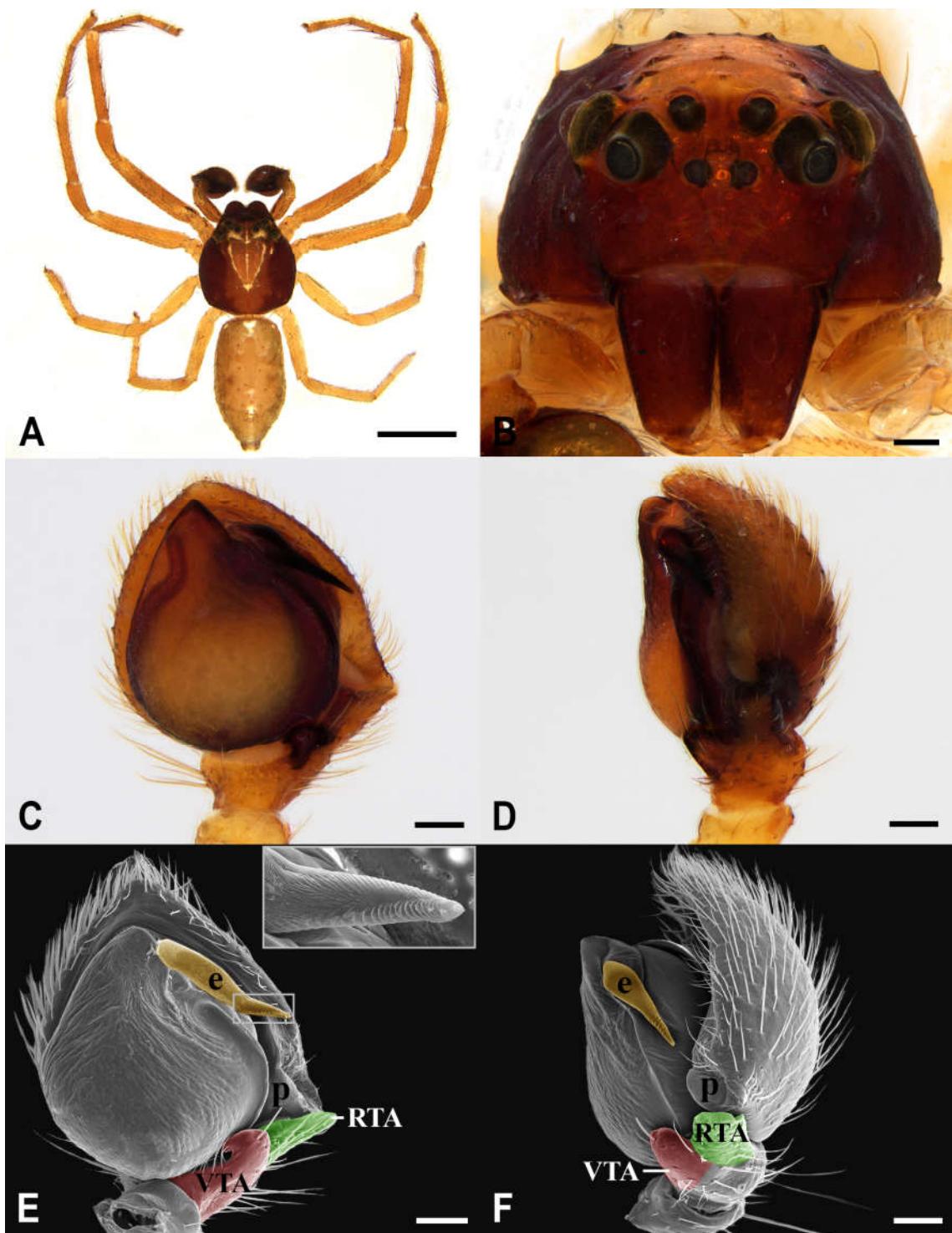
**FIGURE 12.** *Maeanderion peruvianus*, (Keyserling, 1880), female (MUSM). A, dorsal view of carapace. Setiferous tubercles in the margin of posterior slope (red). B, Dorsal surface of carapace, conical sockets. C, Front view. Ocular region. D, Ventral view of carapace. Endites (green) and labium (yellow). Scale bars: 0.2 mm (A, C) and 0.05 mm (B, D).



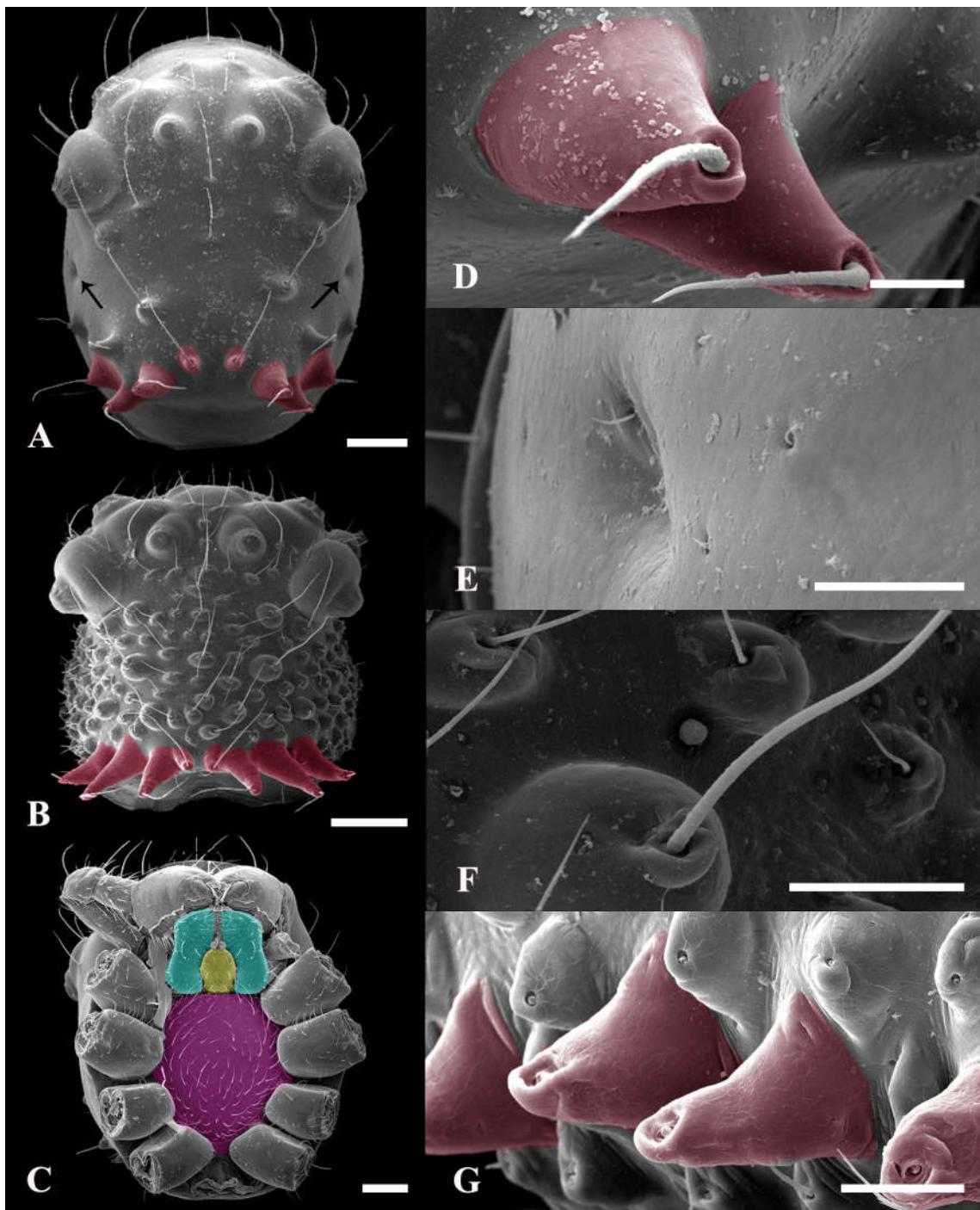
**FIGURE 13.** *Maeanderion peruvianus* (Keyserling, 1880), female (MUSM). A, B habitus (A dorsal, B frontal); epigynal plate. C, ventral view. D, dorsal view with spermathecae and copulatory ducts. E, ventral view. Deep atrium localized in the anterior region of the epigynal plate with two lateral copulatory openings. F, dorsal view with spermathecae (red) and copulatory ducts (green). Scale bars: 0.1 mm (A–F).



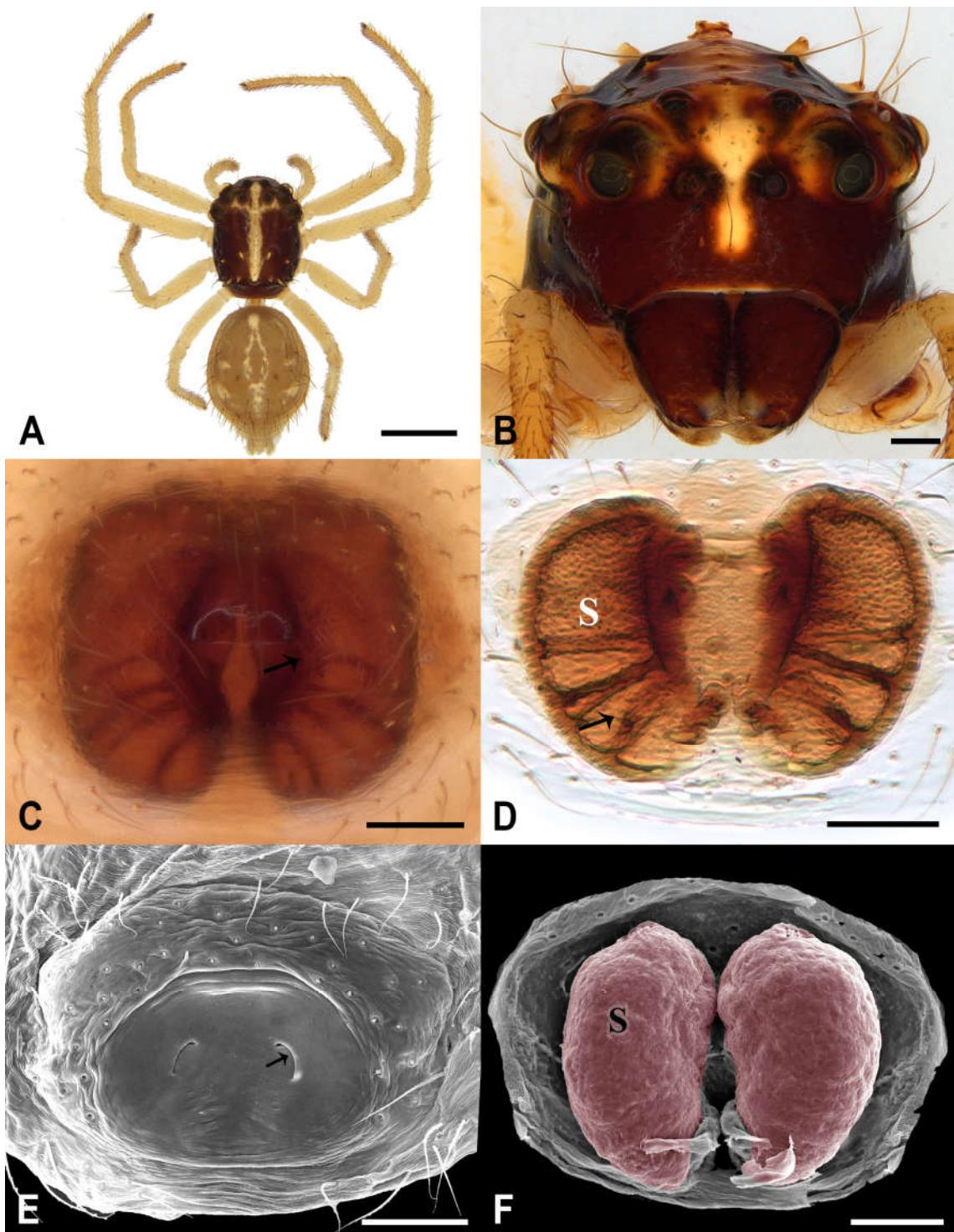
**FIGURE 14.** *Maeanderion peruvianus* (Keyserling, 1880), male (MUSM). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), ventral tibial apophysis (VTA) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), ventral tibial apophysis (VTA, red) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



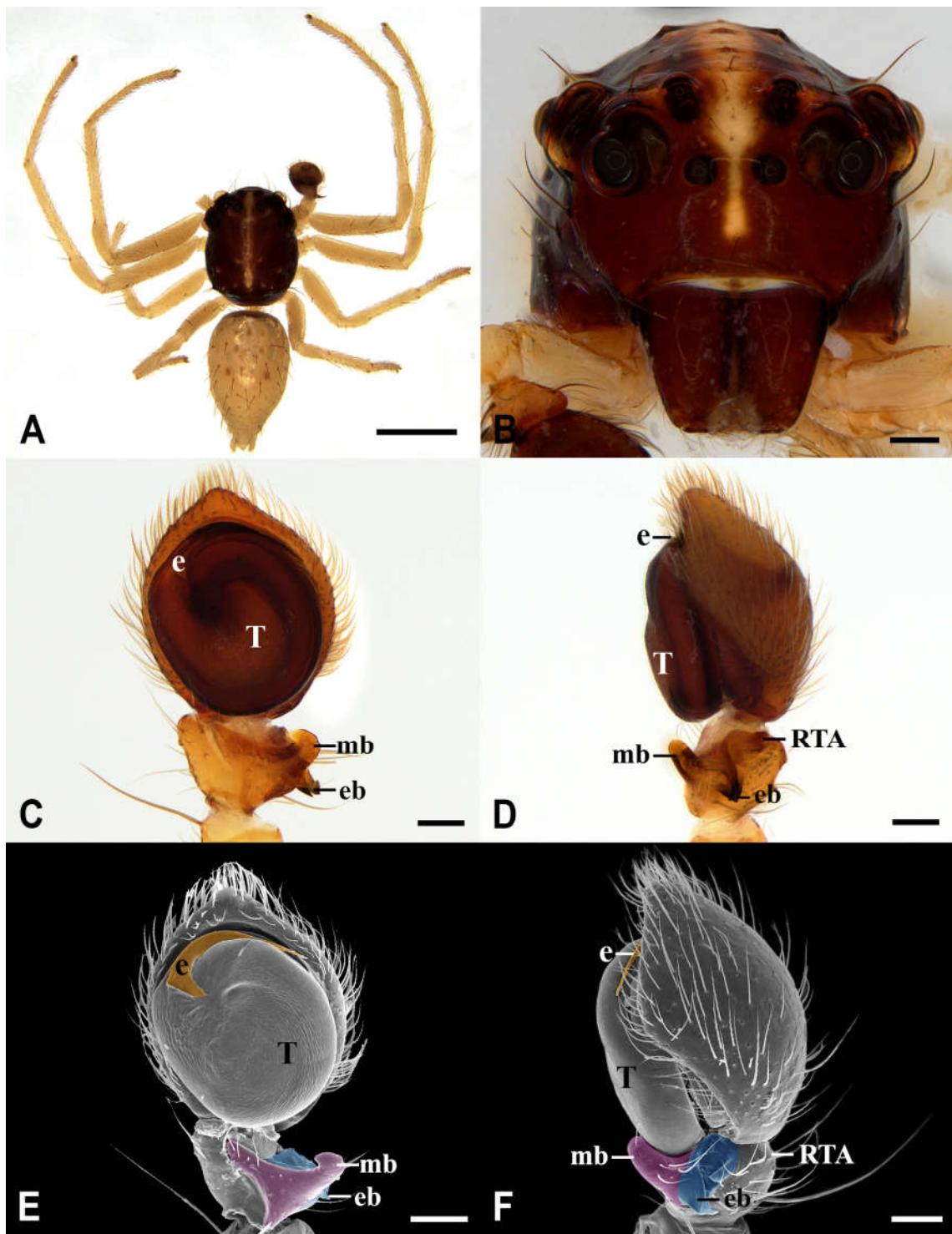
**FIGURE 14.** *Maeanderion peruvianus* (Keyserling, 1880), male (MUSM). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), ventral tibial apophysis (VTA) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), ventral tibial apophysis (VTA, red) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



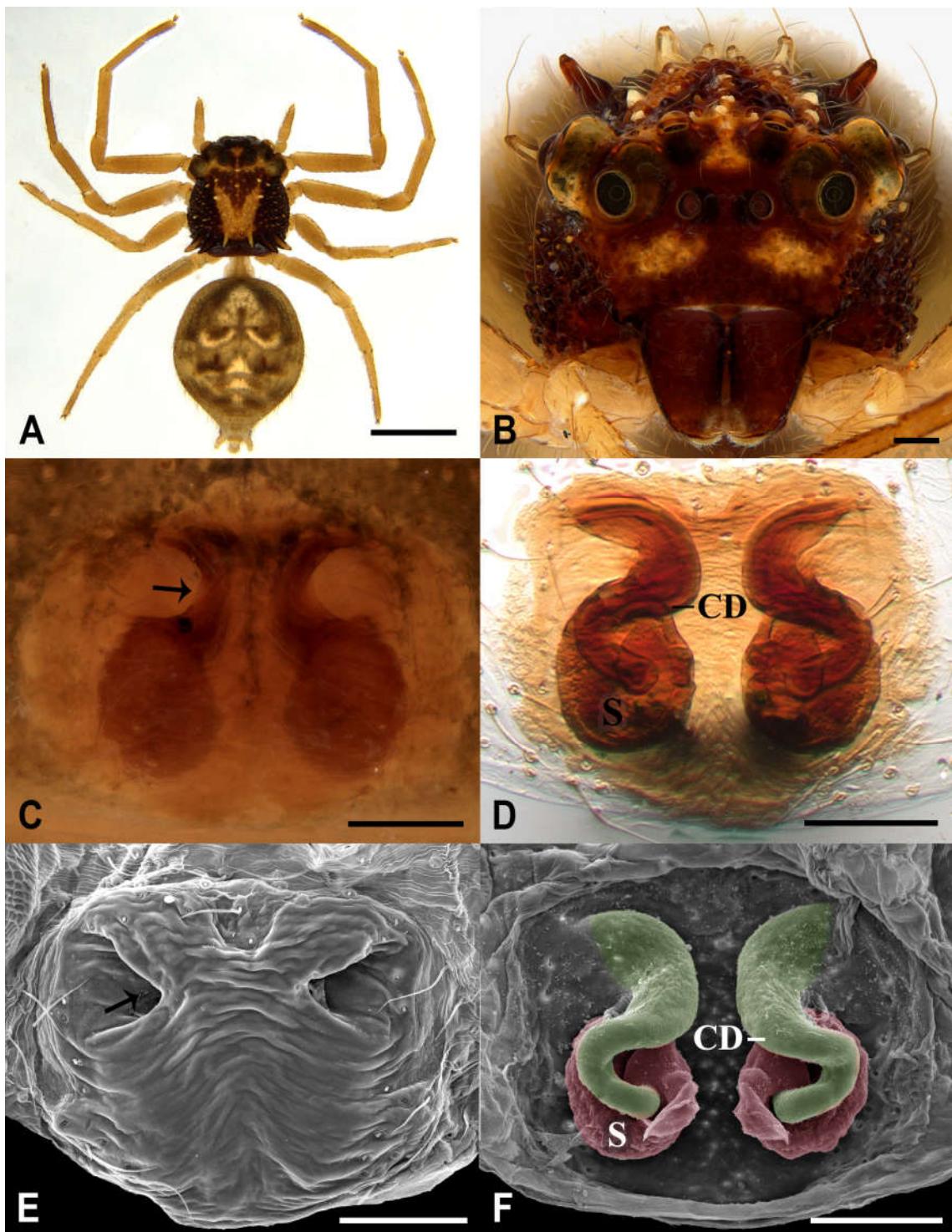
**FIGURE 15.** A, *Whittickius singularis* (Mello-Leitão, 1940), female (MACN-19120). Dorsal view of carapace. Setiferous tubercles in the margin of posterior slope (red) and lateral short setae coming out of punctures (arrow). B, *Whittickius echinithorax* sp. nov., female (MCTP-1769). Dorsal view of carapace. Setiferous tubercles in the margin of posterior slope (red). *Whittickius singularis* (Mello-Leitão, 1940), female (MACN-19120). C, Ventral view of carapace. Endites (blue), labium (yellow) and sternum (magenta). D, Setiferous tubercles in the margin of posterior slope (red) like a conical socket. E, lateral short setae coming out of punctures. *Whittickius granulosus* (Mello-Leitão, 1929), female (UFMG-16082). F. Dorsal surface of carapace with conical sockets. G. Setiferous tubercles in the margin of posterior slope (red) and conical sockets around. Scale bars: 0.2 mm (A-C) and 0.05 mm (D-G).



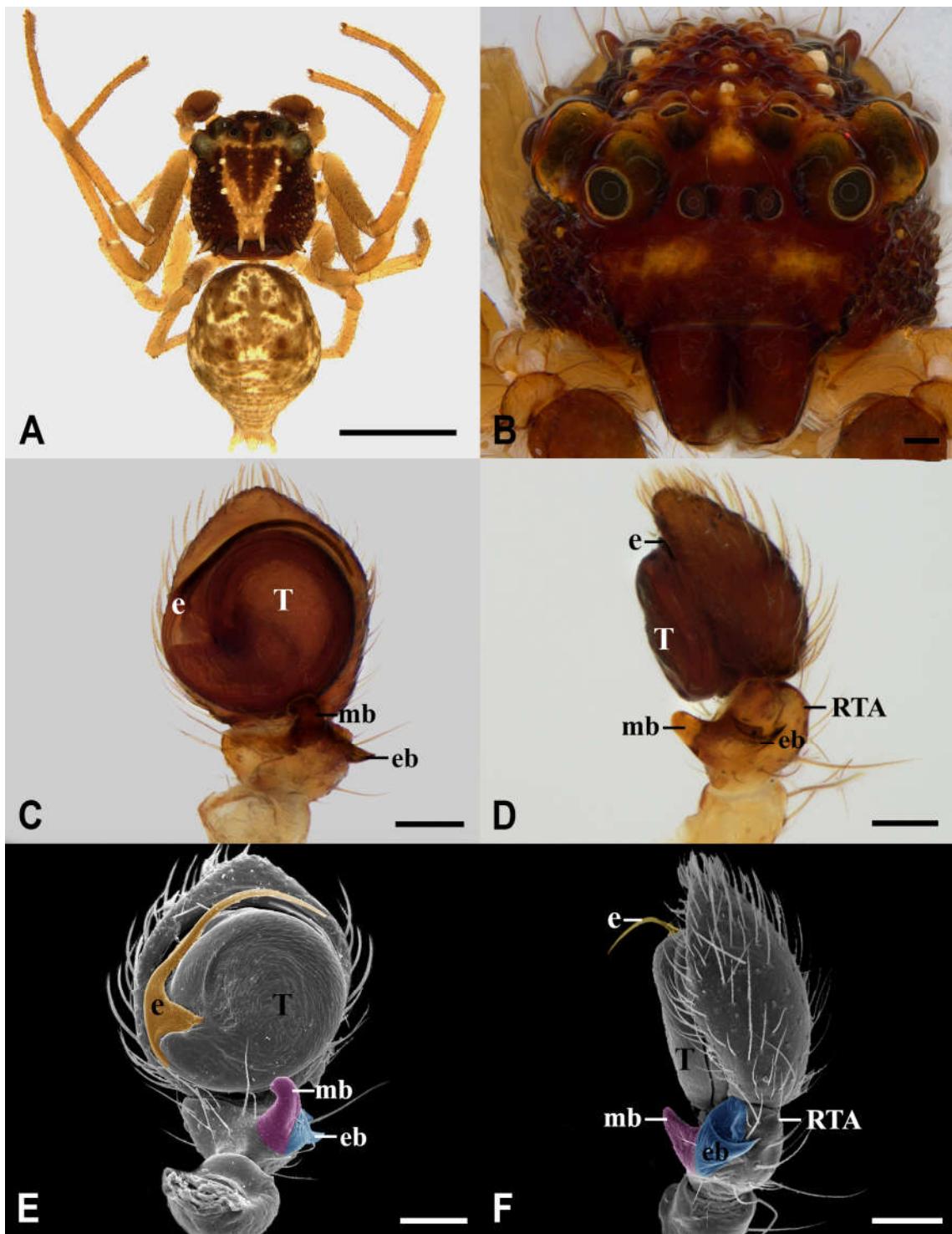
**FIGURE 16.** *Whittickius caxiuana* sp. nov., female (MCTP–10781). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epigynal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



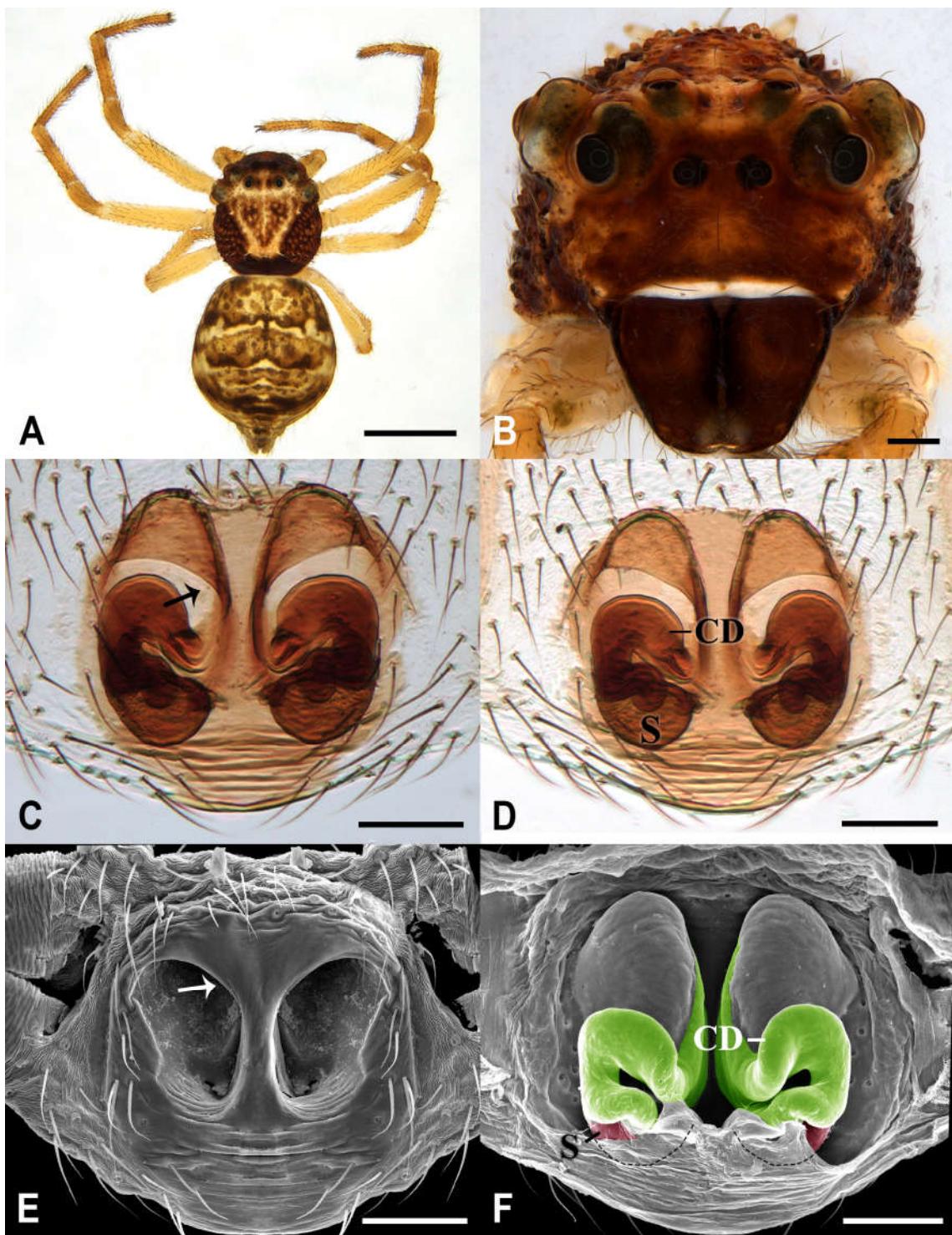
**FIGURE 17.** *Whittickius caxiuana* sp. nov., male (ICN-AR-10236). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



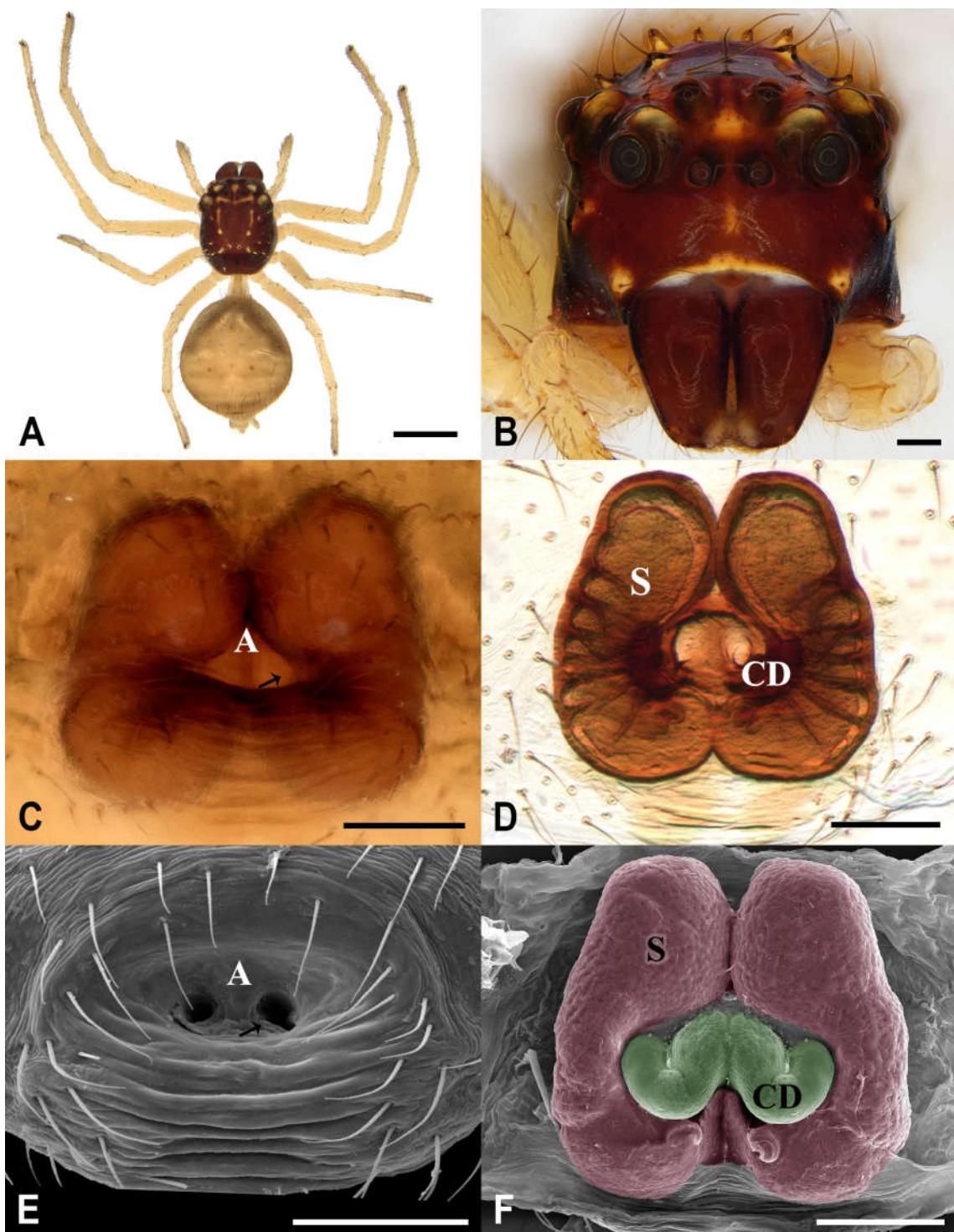
**FIGURE 18.** *Whittickius echinithorax* sp. nov., female (MCTP-1769). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



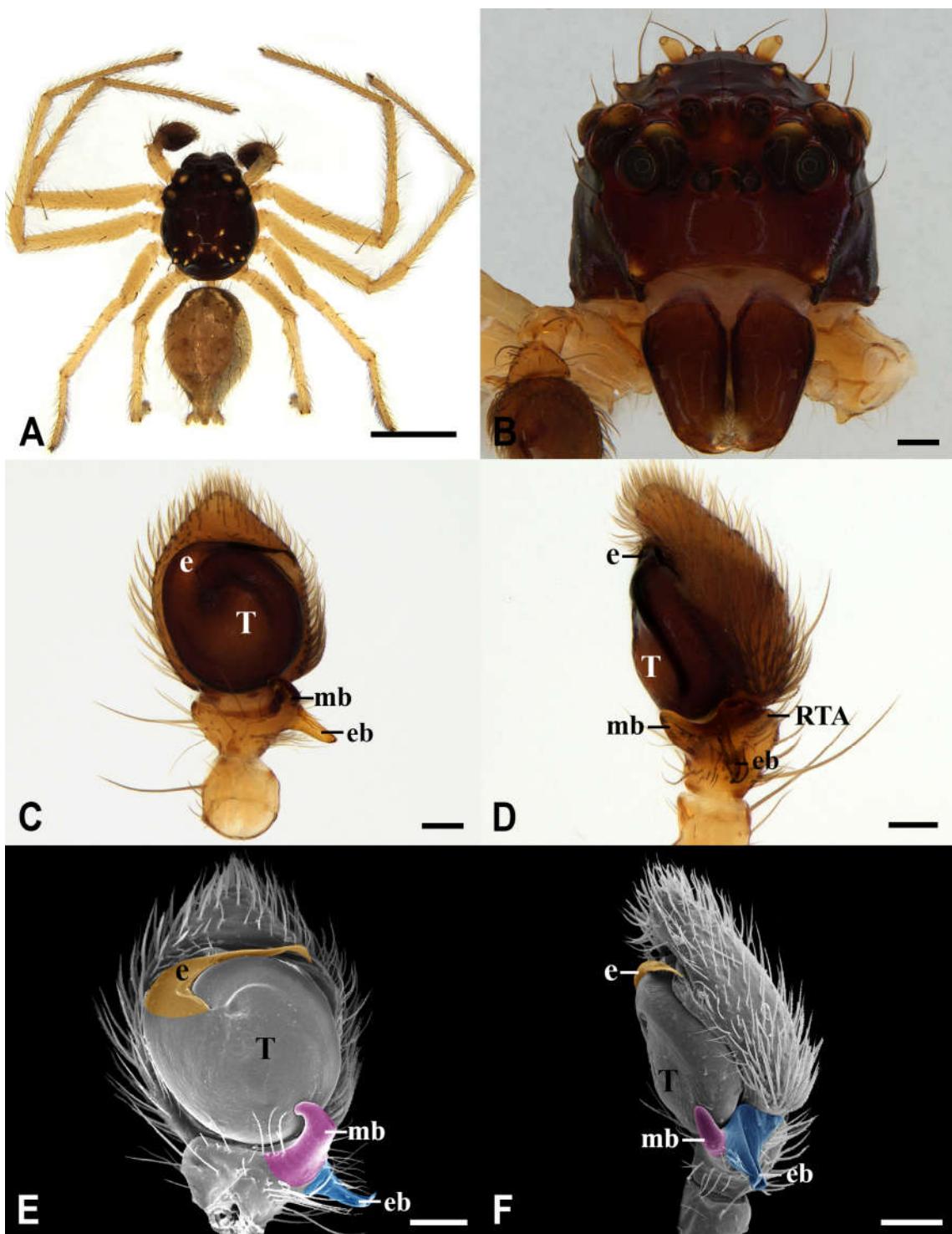
**FIGURE 19.** *Whittickius echinithorax* sp. nov., male (MPEG-5454). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



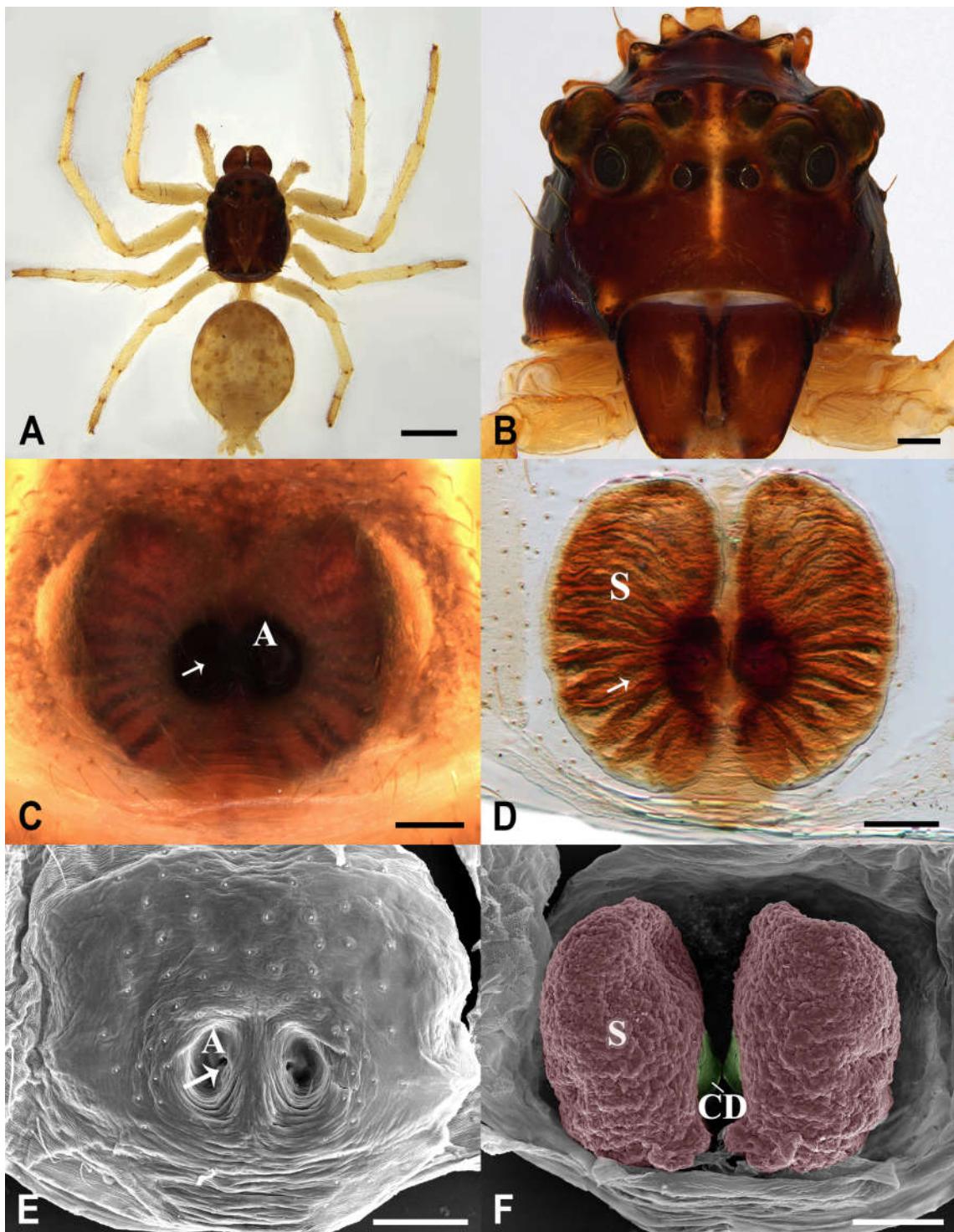
**FIGURE 20.** *Whittickius granulosus* (Mello-Leitão, 1929), female (UFMG-16082). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



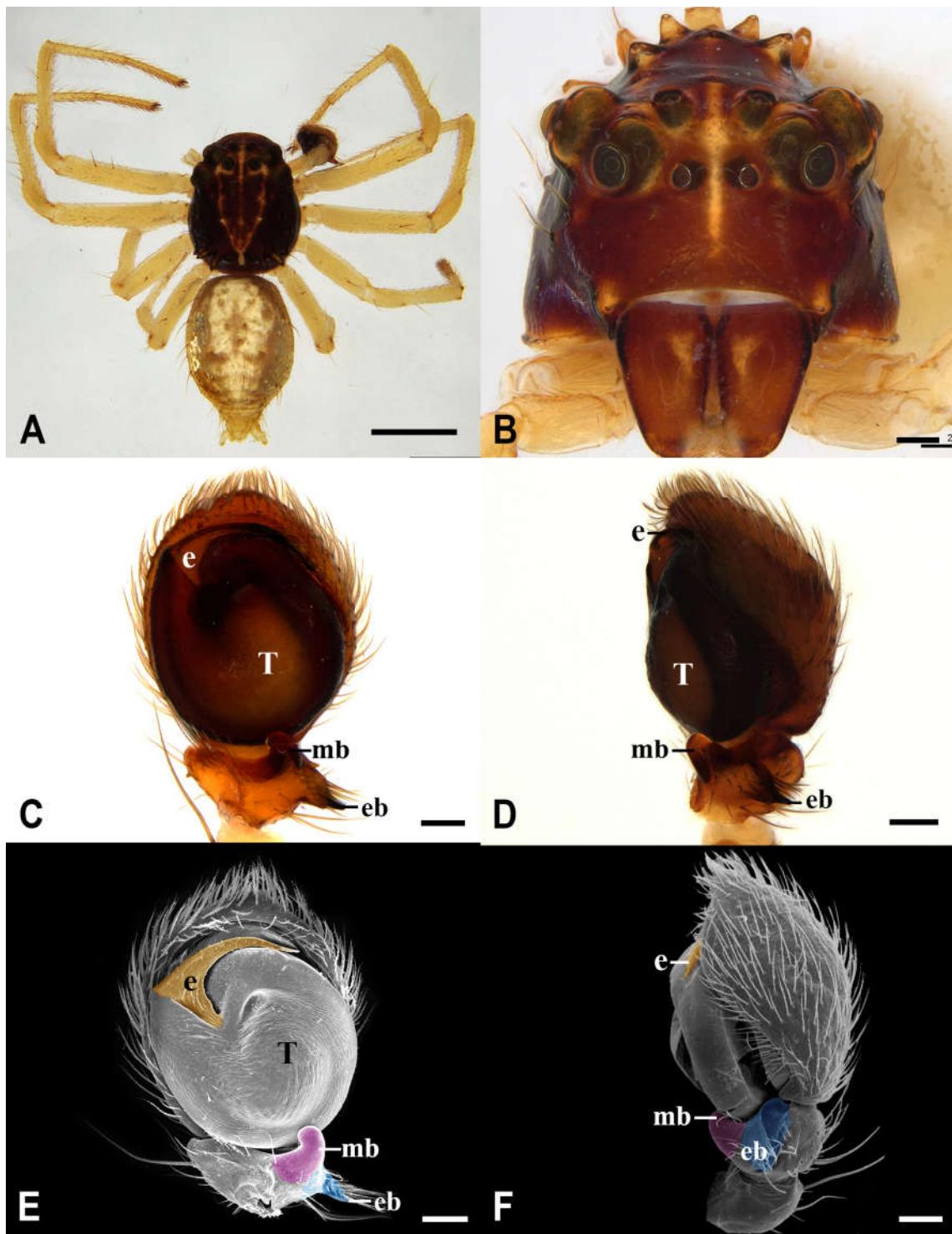
**FIGURE 21** *Whittickius singularis* (Mello-Leitão, 1940), female (MACN-19120). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



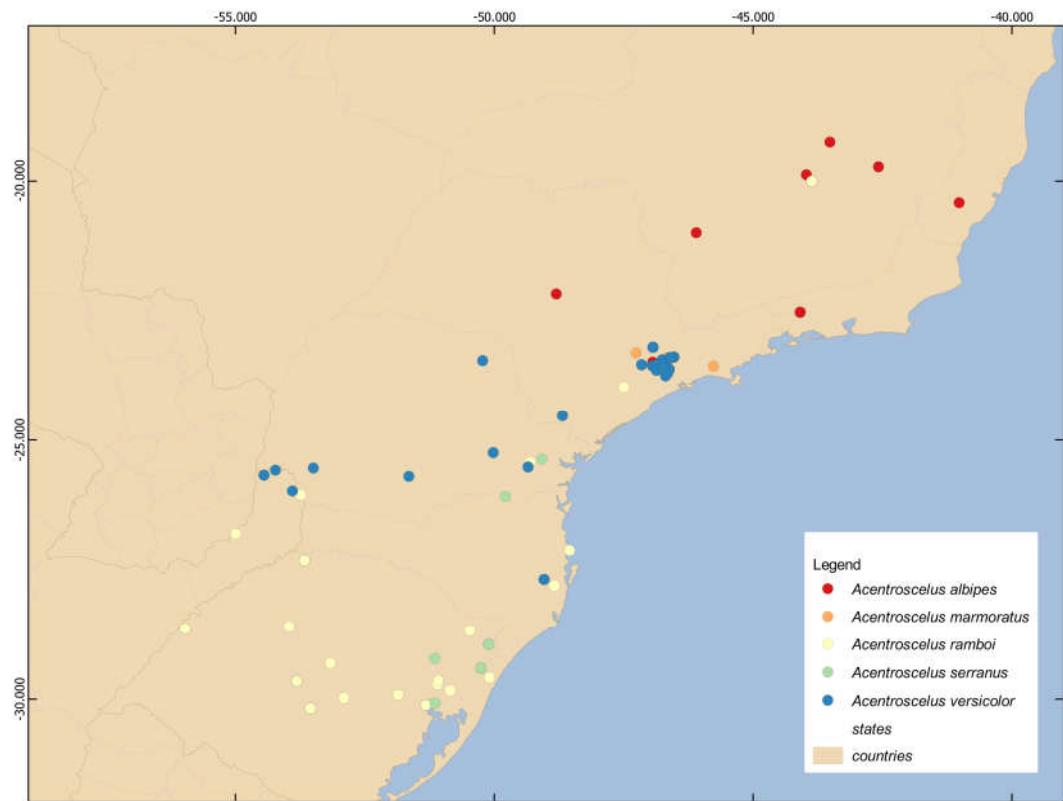
**FIGURE 22.** *Whittickius singularis* (Mello-Leitão, 1940), male (MCTP-42634). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



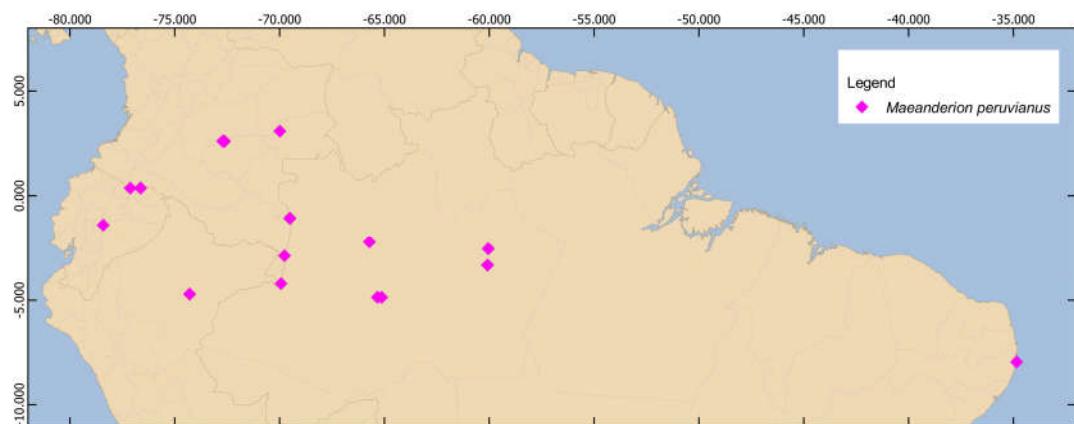
**FIGURE 23.** *Whittickius guianensis* (Taczanowski, 1872), female (MCTP-1770). A, dorsal habitus; B, frontal habitus; epigynal plate C, ventral view and D, dorsal view with spermathecae (S) and copulatory ducts (CD). E, ventral view. Deep atrium localized in the anterior region of the epiginal plate with two lateral copulatory openings. F, dorsal view with spermathecae (S, red) and copulatory ducts (CD, green). Scale bars: 0.1 mm (A–F).



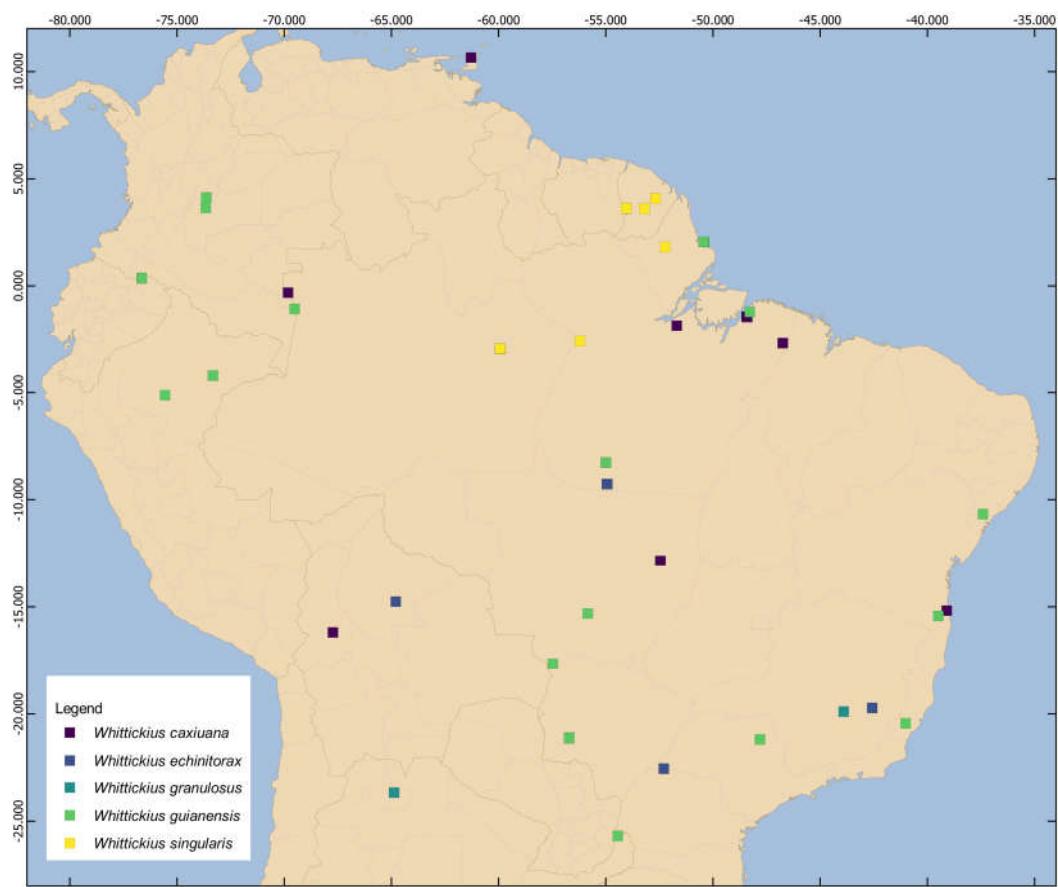
**FIGURE 24.** *Whittickius guianensis* (Taczanowski, 1872), male (MCTP-1959). A, dorsal habitus; B, frontal habitus; photography of the left palp in C, frontal view and D, retrolateral view, embolous (e), tegulum (T), mesial branch (mb), ectal branch (eb) and retrolateral tibial apophysis (RTA); photography with scanning electron microscopy in E, frontal view and F, retrolateral view, embolous (e, orange), tegulum (T), mesial branch (mb, magenta), ectal branch (eb, blue) and retrolateral tibial apophysis (RTA, green). Scale bars: 0.1 mm (A–F).



**FIGURE 25.** Geographic distribution of *Acentroscelus* species.



**FIGURE 26.** Geographic distribution of *Maeanderion* species.



**FIGURE 27.** Geographic distribution of *Whittickius* species.

## CONCLUÕES FINAIS

Análise morfométrica recuperou distinção na morfologia tanto na carapaça quanto no pedipalpo dos machos de *Acentroscelus versicolor* e *Acentroscelus ramboi*, o que corroborou a manutenção das duas entidades taxonômicas. (Capítulo 1)

Análise filogenética resgatou *Acentroscelus* latu sensu como um grupo filogenético, mas com baixo índice de suporte em todos os ramos; porém, com linagens bem suportadas por um conjunto de sinapomorfias que foi considerado significante para que estas fossem descritas em diferentes gêneros. Assim, *Acentroscelus* foi redefinido. *Whittickius* revalidado e um gênero novo foi proposto: *Maeanderion*. (Capítulo 2)

Outros exemplares com as mesmas características de *Maeanderion* tem sido encontrados na coleção, mas ainda estão em fase de análises para que mais evidências sejam encontradas e definidas oportunamente. (Capítulo 2)

Todos os três gêneros foram revisados de modo que: *Acentroscelus* ficou composto por 5 espécies, 2 foram descritas como novas. *Whittickius* ficou composto por 5 espécies, 2 foram descritas como novas. *Maeanderion* ficou composto por 1 espécie. No entanto nenhuma das novas espécies de *Maeanderion* uma vez que estas estão representadas por poucos exemplares e uma amostra mais extensa que ainda está em revisão.



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