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Phylogenetics and comparative morphology of crab spiders (Araneae: Dionycha, Thomisidae)

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Table of contents

Abstract

The higher-level phylogenetic relationships of crab spiders (Thomisidae) are studied from morphological data. 33 taxa are coded for 74 characters (53 binary and 21 multistate). Several analyses using equal, successive and implied weights were carried out. The most parsimonious tree obtained by analysis with successive and implied weights is put forward as the preferred hypothesis of thomisid relationships (length 222 steps, CI 0.74, RI 0.83). Thomisidae emerge monophyletic in all analyses, supported by four unambiguous synapomorphies. It is now apparent that thomisid taxa have been mostly defined on the basis of plesiomorphic character states. A number of taxonomic changes, including the description of new taxa are proposed and the evolution of diverse behaviors of thomisids is studied in light of the new phylogenetic result. Color change behavior evolved once within the family, but eye arrangement patterns of the median ocular quadrangle, thought to be diagnostic for many genera, evolved as much as 10 times independently. The following new species are described: *Borboropactus nyerere* **sp. nov.**, *Cebrenninus srivijaya* **sp. nov.**, *Geraesta lehtineni* **sp. nov.** and *Geraesta mkwawa* **sp. nov.** The following new generic synonymies are proposed: *Bucranium* O. P.-Cambridge, 1881 = *Aphantochilus* O. P.-Cambridge, 1870; *Sanmenia* Song and Kim, 1992 = *Pharta* Thorell, 1891 and *Cupa* Strand, 1906 = *Epidius* Thorell, 1877. The following species are synonymized: *Regillus divergens* Hogg, 1914 and *Borboropactus hainanus* Song, 1993 = *Borboropactus bituberculatus* Simon, 1884 **syn. nov.**, *Epidius ganxiensis* (Yin, Peng & Kim, 1999) = *Epidius rubropictus* Simon, 1909 **syn. nov.**, *Geraesta bilobata* Simon, 1897 = *Geraesta hirta* Simon, 1889 **syn. nov.**, *Sanmenia kohi* Ono, 1995 = *Pharta bimaculata* Thorell, 1891 **syn. nov.** and *Sanmenia zhengi* (Ono & Song, 1986) = *Pharta brevipalpus* (Simon, 1903) **syn. nov.** The following new combinations are proposed: *Aphantochilus taurifrons* (O. P.-Cambridge, 1881) **comb. nov.**, *Epidius typicus* (Bösenberg & Strand, 1906) **comb. nov.**, *Pharta brevipalpus* (Simon, 1903) **comb. nov.**, *Pharta gongshan* (Yang, Zhu and Song, 2006) **comb. nov.**, *Pharta nigra* (Tang, Griswold & Peng, 2009) **comb. nov.** and *Pharta tengchong* (Tang, Griswold & Yin, 2009) **comb. nov.**

Key words: Arachnida, Biodiversity, Character weighting, Cladistics, Color change behavior, implied weights, sampling bias

Introduction

Crab spiders, family Thomisidae, are cryptically colored sit-and-wait predators that generally do not build capture webs. Thomisidae is a speciose family which includes 2146 described species in 177 genera (Platnick 2011).

Recent fieldwork, conducted around the globe (Sri Lanka, Madagascar and South America) by various institutions suggests that this is only a fraction of its true diversity. Crab spiders are mainly active during the day and ambush insects with their well-adapted first and second pairs of legs (Comstock 1948; Homann 1934). Thomisids are a key element in terrestrial ecosystems, acting as predators of agricultural pest (Benjamin *et al.* 2008 and references therein).

Thomisids are behaviorally versatile, exhibiting complex behaviors, like their remarkable ability to change color during migration to flowers of different colors from spring to summer. Thomisids are also ant mimics with several species of crab spiders mimicking a taxonomical diverse range of ants. Sociality and maternal care are also known in thomisids (see Benjamin *et al.* 2008 for a review of these and other behaviors in thomisids). The diversity of their behavior makes them an ideal model system for the study of behavioral evolution. Thus, the reconstruction of the evolutionary history of Thomisidae will enable the study of these behaviors in a comparative context.

Understanding the phylogenetic structure of this large family has always been problematic; see Ono (1988), for a summary of the phylogenetic history of thomisids. Thomisidae are spiders with legs generally extended sideways (laterigrade), instead of being oriented towards the front or back as in most other spiders. Originally, all spiders with laterigrade legs such as Sparassidae and Philodromidae were included. Simon (1895) was the first to propose generic groups for all thomisid genera recognized during his time. His Stephanopsinae contained spiders with cheliceral teeth; Aphantochilinae and Strophiinae contained species with modifications like elongated maxillae related to their ant mimicking habits; Stiphropodinae included species with an enlarged tarsus; spiders that did not fit into the above categories were included in Misumeninae and Philodrominae. Within these subfamilies, species groups were proposed based on eye pattern and shape of prosoma. To date this classification remains mostly unchanged.

Monophyly of thomisids was only recently tested, and was based on molecular synapomorphies (Benjamin *et al.* 2008). Earlier papers on higher-level thomisid relationships present poorly substantiated relationships (Benjamin 2000; Benjamin 2002; Lehtinen 2005; Lehtinen & Marusik 2008; Ono 1988; Wunderlich 2004a, b). The conclusions of these authors are educated guesses, which at the very best are primary hypotheses.

Although thomisid sister group relationships continue to be a puzzle, some issues have become clear: philodromids should be excluded from Thomisidae (Homann 1975) and Aphantochiloids should be placed within Thomisidae (Benjamin *et al.* 2008; Ono 1988). Major questions, such as 'what are the major lineages of Thomisidae?' or 'should *Borboropactus* Simon, 1884 be included within Thomisidae?' remain to be resolved. Wunderlich (2004a, b) elevated *Borboropactus* to family rank, presumably due to the simple reason of being present in amber.

Thomisidae have a rather varied somatic morphology. However, their genitalia, a key character system in spider systematics, are rather uniform. Recent taxonomic studies based on morphology divide Thomisidae into seven subfamilies: Stephanopinae, Thomisinae, Bominae, Stiphropodinae, Dietinae, Strophiinae and Aphantochilinae (Ono 1988). Due to the presence of cheliceral teeth, Stephanopinae O. Pickard-Cambridge, 1871 is considered sister to all other Thomisidae (Ono 1988). Stephanopinae presently includes around 275 described species in 36 genera (13 are monotypic; Platnick 2011). They are distributed widely in the tropics, with most species occurring in South America and in the Old World.

The principal focus of the present paper is to investigate the phylogenetic structure of the stephanopines and to evaluate their placement within a subfamily-level phylogeny for Thomisidae, thus testing its monophyly. This is the first time that a morphological dataset for thomisids and outgroups has been gathered and analyzed in a phylogenetic framework. Thus, another objective of this study was to test the monophyly of Thomisidae. A detailed discussion of the monophyly of all conventional subfamilies is given and several taxa new to science are proposed. Further, the evolution of color change behavior and the eye arrangement patterns of the median ocular quadrangle are explored in light of the preferred phylogenetic hypothesis.

Material and methods

Taxon sampling

Taxon sampling was based on Ono (1988) and Benjamin *et al.* (2008). Up to two species of each genus were selected as exemplars; the type species was included whenever possible. Exemplars were chosen to reflect maximal morphological diversity within genera. Further, exemplars were also chosen from disjunct geographic locations to further maximize the sampling of morphological diversity. *Borboropactus cinerascens* (Doleschall, 1859) and *B.*

nyerere **sp. nov.** represent the *Borboropactus* clade. A number of new taxa were added to the *Epidius* clade and the *Stephanopis* clade. The former is represented in this study by *Epidius parvati* Benjamin, 2000, *E. binotatus* Simon, 1897, *Cebrenninus rugosus* Simon, 1887, *C. srivijaya* **sp. nov.**, *Pharta gongshan* (Yang, Zhu & Song, 2006) **comb. nov.**, *Geraesta hirta* Simon, 1889 and *G. lehtineni* **sp. nov.** The later is represented by *Stephanopis cambridgei* Thorell, 1870, *Sidymella angulata* (Urquhart, 1885), *Onocolus* sp. from Ecuador, *Stephanopis* sp. from Chile and *Sidymella lucida* (Keyserling, 1880). Representatives of two subfamilies not included in Benjamin *et al.* (2008), Stiphropodinae represented by *Stiphropus lugubris* Gerstäcker, 1873, and Strophiinae represented by *Strigoplus* sp. from Sri Lanka and *Strophius* sp. from Panama are included in this study. The genera *Phrynarachne* and *Stephanopoides*, currently included in the subfamily Stephanopinae, are also analyzed in this study. The Thomisus clade is represented by the following genera: *Apyretina* sp. from Madagascar, *Monaeses* sp. from Sri Lanka, *Xysticus fraternus* Banks, 1895 and *X. cristatus* (Clerck, 1757), *Diaea subdola* O. P.-Cambridge, 1885, *Oxytate subvirens* (Strand, 1907), *Thomisus granulifrons* Simon, 1906 and *Mecaphesa asperata* (Hentz, 1847). *Apyretina* and *Oxytate* are currently placed in the subfamily Dietinae, the rest are part of the subfamily Thomisinae. *Aphantochilus rogersi* O. P.-Cambridge, 1870 and *A. taurifrons* O. P.-Cambridge, 1881 **comb. nov.** are also included. The genus *Aphantochilus* was traditionally either placed in its own family or in a separate subfamily within Thomisidae (Levi 1982; Ono 1988). Thus, all traditionally recognized subfamilies are included, except for Bominae, which is excluded due to lack of material. Label data for all examined specimens are given below.

Thomisidae fall within the large clade Dionycha (Coddington & Levi, 1991), characterized by loss of the unpaired tarsal claw. The Dionycha, together with Lycosoidea form part of the RTA clade (Coddington & Levi, 1991; Miller *et al.* 2010). The phylogenetic structure within Dionycha, which is crucial to the placement of Thomisidae, however, has not been fully explored. I have chosen four outgroup taxa representing four families based on the results of Coddington and Levi (1991) and Benjamin *et al.* (2008): *Uduba* (Lycosoidea: Zorocratidae), *Psechrus* (Lycosoidea: Psechridae), *Philodromus* (Dionycha: Philodromidae) and *Onomastus* (Dionycha: Salticidae). Data for *Uduba* sp. was taken from Griswold (1993). Data for *Psechrus* sp was taken from Griswold (1993) and Griswold *et al.* (2005). Data for *Philodromus rufus* Walckenaer, 1826 was taken from Roberts (1995) and (Muster 2009), data for *Onomastus nigricauda* Simon, 1900 was taken from Benjamin (2010).

Character sampling

I have compiled the observed morphological diversity into 74 morphological characters scored across 33 taxa (29 ingroup and 4 outgroup taxa). Of these characters, 53 were binary, 21 were multistate (Appendix A, B). Characters were coded by direct observation of preserved specimens. In some cases, if material was not available or if it was impossible to unambiguously identify the specimens to generic or species level, published studies were used (Bonaldo & Lise 2001; Bryant 1933; Lise 1973, 1979a, b, 1981). Several specimens of a given species and several species of a genus of interest were observed. This resulted in a huge amount of new taxonomical/nomenclatural information. As only a handful of Thomisidae genera are currently diagnosable, the new information is given below in a separate taxonomic section.

Morphology

Digital images were taken with a Nikon DXM1200F camera. Images were edited using an AutoMontage software package. Left structures are depicted unless otherwise stated. Setae are usually not depicted in the final palp drawings. All measurements are given in millimeters and were made with a stereo microscope equipped with a 10x ocular and an ocular micrometer scale. An Amray 1810 housed at the Smithsonian Institution's National Museum of Natural History Scanning Electron Microscope (SEM) facility was used to study and photograph morphological features. Targeted parts were cleaned ultrasonically for 1–3 min and dehydrated with 100% ethanol (transferred from 70% ethanol to absolute ethanol and left overnight), then critical point dried. After critical point drying, the specimens were glued to rounded aluminum rivets using an acetone solution of polyvinyl resin (Paraloid B72) and then Au/Pd coated for examination in the SEM.

Female genitalia were excised using sharpened needles. Abdominal tissue was digested with SIGMA Pancreatin LP 1750 enzyme complex (Alvarez-Padilla & Hormiga 2008), in a solution of sodium borate prepared following methods described in Dingerkus and Uhler (1977). The specimen was then transferred to methyl salicylate (Holm 1979) and temporarily mounted as described in Grandjean (1949) and Coddington (1983) for examination and illustration under microscope.

Abbreviations
AH anterior hood of the epigynum
ALE anterior lateral eyes
ALS anterior lateral spinnerets
AME anterior median eyes
C conductor
CD copulatory duct
CO copulatory opening(s)
DTA dorsal tibial apophysis
E embolus
EF epigynal folds
EL epigynal lip; tongue-shaped appendage of the epigynum
ET epigynal teeth
ETP extra tegular process
FA femoral apophysis
MA median apophysis
MAP major ampullate spigot(s)
mAP minor ampullate spigot(s)
MOA median ocular area
MOA-WA anterior width of MOA
MOA-WP posterior width of MOA
MR median ridge
MTr macro-trichobothrium on palpal tibia
PER posterior row of eyes
PLE posterior lateral eyes
PLS posterior lateral spinnerets
PME posterior median eyes
PMS posterior median spinnerets
PME posterior median eyes
PP posterior pockets
PS peg-like setae
RTA retrolateral/apical tibial apophysis
S spermatheca
STD sperm duct; connects to embolus
TO tarsal organ
TR tegular ridge
VTA ventral tibial apophysis

Institutions
AMNH American Museum of Natural History
ASB Institute of Zoology, Academia Sinica, Beijing
BMNH Natural History Museum, London
CAS California Academy of Sciences, San Francisco
GWU Dr. Gustavo Hormiga’s collection at the George Washington University
MNHU Museum für Naturkunde der Humboldt-Universität, Berlin
MHNG Muséum d`Histoire Naturelle, Genève
MNHN Muséum National d`Histoire Naturelle, Paris
MRAC Koninljik Museum voor Midden-Afrika, Tervuren
NSMT National Science Museum (Natural History), Tokyo
SMF Research Institute Senckenberg, Frankfurt am Main
SMNH Swedish Museum of Natural History, Stockholm
USNM National Museum of Natural History, Smithsonian Institution, Washington, DC

Phylogenetic analysis

Parsimony analysis of the morphological data matrix was performed using PAUP* ver. 4.0 (Swofford 2002) and TNT 1.1 (Goloboff *et al.* 2008b). Mesquite version 1.12 (Maddison & Maddison 2009) was used to build and edit the character matrix. WinClada version 1.00.08 (Nixon 2002) and MacClade 4.0 (Maddison & Maddison 2001) was used to study character evolution. Ambiguous character optimizations were resolved to favor early gains of features with subsequent reversals (Farris optimization or ACCTRAN). All multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971) as no transformation series could be inferred.

In PAUP*, heuristic searches were implemented with 500 random addition sequence replicates, each saving a single tree and using tree bisection reconnection (TBR) branch swapping. MAXTREES was set to 100,000. In TNT, the traditional search (heuristic search) mode was used with 500 random addition sequence replicates, and the TBR swapping algorithm saving 10 trees per replication (see Edwards & Benjamin 2009 for details). As detailed below, bootstrapping and jackknifing was performed to assess branch stability (Farris *et al*. 1996; Felsenstein 1985). Non-parametric bootstrap analysis (Felsenstein 1985) was conducted in PAUP*, with 300 replicates using heuristic searches (10 random addition sequence replicates, each saving at most 100 trees) and TBR branch swapping. Jackknifing was performed for 100 replicates with a removal probability of 40%.

PAUP* was also used to reweight characters (successive weighting) using the rescaled CI. Successive weighting (Farris 1969) is here used to assess the sensitivity of results to weighting against homoplasious characters (Agnarsson 2004; Prendini 2001; Wheeler 1995). Further, *Aphantochilus* and *Borboropactus* were removed, one genus at a time, and the matrix rerun, to analyze its effect on tree structure. Parsimony searches under implied weights (K 1–6) were performed using TNT 1.1 (Goloboff 1993; Goloboff *et al.* 2008b).

Results

Heuristic searches in PAUP generated seven most parsimonious trees, with a length of 222 steps. Traditional searches in TNT resulted in five trees, which were identical to trees found in the PAUP search. Four of these trees and six from the PAUP searches differed from each other by the arrangement of taxa within the Stephanopis clade. In the remaining tree, the two *Borboropactus* exemplars are placed within the Stephanopis clade. However, successive weighting using the maximum value of the rescaled consistency index found a single tree (length 222 steps, CI 0.74, RI 0.83) identical in topology to one of the trees produced in the unweighted analysis. Implied weights (K 1–6) produced the same single tree recovered with successive weighting. I consider this the preferred phylogenetic hypothesis of thomisid relationships (Fig 1).

The removal of *Aphantochilus* did not make a difference, simply rendering *Strigoplus* sp. plus *Strophius* sp. as sister to *Stiphropus lugubris* plus *Apyretina* sp. Similarly, the deletion of *Borboropactus* did not alter the tree topology.

Thomisidae emerge as monophyletic supported by the following synapomorphies, longer and stouter leg pairs I and II (characters 41 and 44), presence of LE tubercles (character 56) and the presence of claw tufts with a pointed end (character 69). Thomisidae splits into 3 major clades, labeled Epidius, Stephanopis and Thomisus (Fig 1). Epidius clade consists of the genera *Epidius*, *Cebrenninus*, *Pharta*, *Geraesta* and *Borboropactus*. Two characters support this grouping: presence of a macro trichobothrium (lost in *Borboropactus*; character 3), embolus closely associated with conductor (character 20), short copulatory ducts (character 33), and the extended claw tufts (character 70). Stephanopis clade includes the genera *Onocolus*, *Stephanopis*, *Sidymella angulata*, *Stephanopis cambridgei* and *Sidymella lucida*. This clade is supported by the projected anterior eye region (character 55). Thomisus clade consists of the genera *Stephanopoides*, *Phrynarachne*, *Stiphropus*, *Apyretina*, *Strigoplus*, *Strophius*, *Aphantochilus*, *Monaeses*, *Oxytate*, *Xysticus*, *Diaea*, *Thomisus* and *Mecaphesa*. It is supported by the presence of a disk shaped tegulum and tegular ridges (characters 11 and 12) and the recurved PER (character 53). Synapomorphies for all nodes are mapped in Fig (1).

Discussion

“Aphantochilidae”, “Borboropactidae” and Philodromidae

Aphantochilus is placed within the Thomisus clade as sister to *Strigoplus* and *Strophius*, in this study. This placing is also supported by molecular data (Benjamin *et al.* 2008). The family Aphantochilidae was erected by Thorell (1873) for a peculiar ant-like spider, *Aphantochilus rogersi*. However, Simon (1895) disagreed, relegating it to subfamilial status within Thomisidae (Aphantochilidae was accepted by others, for example, Petrunkevitch 1928). Given the proposed synonymy of *Bucranium with Aphantochilus* (see taxonomic part), Aphantochilinae now contains just two genera: *Aphantochilus* and *Majellula* (Strand, 1932). *Majellula* is most probably a synonym of *Aphantochilus* (Benjamin unpublished data), leaving Aphantochilinae monogeneric.

In this study, *Borboropactus* is nested within Thomisdae. Further, it is sister to *Geraesta*, supported by the concave MA and presence of ET. The placement of *Borboropactus* within Thomisdae is also supported by molecular data (Benjamin *et al.* 2008). “Borboropactidae” was proposed by Wunderlich (2004b) for the genus *Borboropactus*, citing the presence of a specialized sensory region on the dorsal surface of tarsi (Figs 24C, 24D). Wunderlich (2004b) however, briefly mentions that “Borboropactidae” shares characters, such as the presence of cheliceral teeth, a median apophysis and a conductor with some Stephanopinae, which essentially then is Simon’s (1895) definition of Stephanopinae. Elevating Simon’s Stephanopinae or the Stephanopis clade, in my opinion to family rank would only make sense if all other thomisid subfamilies and clades (named here), are elevated to the same rank. However, I considered this an unnecessary act of splitting. Further, this elevation is uninformative; any classification system should be informative to the end-user.

Philodromids were previously considered derived thomisids (Petrunkevitch 1928; Roberts 1995; Roewer 1954; Suman 1970; Tikader 1980). However, Homann’s (1975) arguments demonstrating that Philodromids and thomisids are not closely related, have now been widely accepted. This study as well as Benjamin *et al.* (2008) places Philodromidae outside of Thomisidae. As suggested by Benjamin *et al.* (2008), Philodromidae might group close to the root of Dionycha.

Thomisidae Sundevall, 1833

The monophyly of Thomisidae is well corroborated. Unambiguous synapomorphies include the long and stout leg pairs I and II (characters 41 and 44), presence of LE tubercles (character 56) and the presence of claw tufts with a pointed end (character 69).

One difference in the topologies obtained from the various analyses is the position of the two *Borboropactus* exemplars. One tree obtained in the analysis with equally weighted characters, differs from the preferred phylogenetic hypothesis (Fig 1), in placing *Borboropactus* as sister to (*Onocolus* sp. (*Stephanopis* sp. + *Sidymella lucida*)) in the *Stephanopis* clade (Fig 2). This grouping is supported by character 43 (the presence of a sclerotized mound with spines on the femora of leg 1; Figs 5B, 6D). This grouping is not supported by molecular evidence (Benjamin *et al.* 2008) and is considered implausible. Moreover, none of the species in the *Stephanopis* clade posses a male palp with a C or MA, which is very characteristic for species of the Epidius clade. Further, both *Geraesta* and *Borboropactus* posses a hyaline C and ET, which are absent in species of the *Stephanopis* clade. Thus, I feel that the placement of *Borboropactus* exemplars in the Epidius clade reflects our current understating of thomisid evolution. It is considered that down weighting characters according to their homoplasy improves reliability of morphological phylogenies (Goloboff *et al.* 2008a). Thus, the use of implied weights is thought to be superior to successive weighting (Goloboff 1993; Goloboff 1995; Goloboff *et al.* 2008a; Ramírez 2003).

Thomisidae relationships

This is the first phylogenetic hypothesis of thomisid relationships based on morphological data. The present hypothesis broadly agrees with the recent molecular phylogeny of Benjamin *et al.* (2008). This study corroborates the basal position of the genera *Epidius*, *Pharta*, *Geraesta* and *Cebrenninus*. However, the presence of cheliceral teeth, a character which was thought to be synapomorphic/diagnostic for basal thomisids (Ono 1988; Wunderlich 2004b), is plesiomorphic. I discuss the monophyly of all “conventional” subfamilies in light of this study and Benjamin *et al.* (2008). However, as only a small percentage of genera are included in both studies, I refrain, at least for now, from presenting a formal classification for the family.

Thomisid clades

Thomisidae clades Epidius, Stephanopis and Thomisus, correspond roughly to clades defined in Benjamin *et al.* (2008). Epidius clade, corresponds to the Epidius clade defined in Benjamin *et al.* (2008). It includes the genera *Borboropactus*, *Epidius*, *Pharta*, *Geraesta* and *Cebrenninus*. Their monophyly is supported by the presence of a macro-trichobothrium on the palpal tibia (lost in *Borboropactus*; character 3) and the presence of claw tufts that extends from the tip towards the tarsus/metatarsus joint (character 70). *Borboropactus* was placed in its own clade by Benjamin *et al.* (2008). The genus *Cupa* is synonymized below with *Epidius*. *Ascurisoma* Strand, 1928, would also group here close to the root of *Cebrenninus* (Benjamin unpublished data). The monophyly of this generic grouping was predicted by Benjamin (2000). However, no morphological synapomorphies were proposed.

The Thomisus clade corresponds to the Thomisus-clade defined in Benjamin *et al.* (2008). This is the largest clade of the family in terms of genera and species. The presence of a disk-shaped tegulum (character 11) and a tegular ridge (character 12) support its monophyly. Most genera within the Thomisus clade (except for *Phrynarachne* and *Stephanopoides*) form a grouping supported by the loss of cheliceral teeth (character 38). However, the composition of the Thomisus clade differs dramatically from the composition of the subfamily Thomisinae Sundevall, 1833 as delineated by Ono (1988). In addition to species from the conventional Thomisinae, this clade includes genera from several other conventional thomisid subfamilies, namely Stephanopinae (*Phrynarachne*, *Stephanopoides*), Stiphropodinae (*Stiphoropus*), Dietinae (*Apyretina*, *Oxytate*), Strophiinae (*Strophius*, *Strigoplus*), and Aphantochilinae (*Aphantochilus*). Although not sampled for this study, most probably Bominae would also fall within this clade, due to the presence of a disk-shaped tegulum (character 11) and a tegular ridge (character 12).

The Stephanopis clade corresponds to the Stephanopis-clade in Benjamin *et al.* (2008). The supporting morphological synapomorphy is the forward projecting eye region (characters 55). As noted in Benjamin *et al.* (2008), none of the Stephanopinae genera of Australia, New Zealand and the Americas are monophyletic. They are badly in need of revision. Further, a considerable number of new species from the specified region as well as South Africa remain undescribed. The instability and lack of support for this clade might be due to these reasons.

Stephanopinae O. Pickard-Cambridge, 1871

Stephanopinae is paraphyletic. Stephanopinae was first proposed as a subfamily in Simon's (1895) revision of the family. The only character taken into consideration at that time was the presence of cheliceral teeth. Recently, Ono (1988) presented a better diagnosis for Stephanopinae. However, none of the proposed diagnostic characters (stout prosomal and leg setae, large PME, PME larger than PLE, cheliceral teeth, truncate labium and maxillae) are synapomorphic for this or any other major clade recovered in this study.

Strophiinae Simon, 1895

Strophiinae as currently circumscribed is polyphyletic. However, only three of the nine genera of the subfamily have been examined. If Strophiinae or a similar grouping is to be retained it should include *Aphantochilus* as well (in this case Aphantochilinae would have priority over Strophiinae). A group that includes *Strigoplus*, *Strophius* and *Aphantochilus* that is supported by the presence of peg-like setae on labium and the elongated endites (character 34 and 39 respectively; Figs 13D, 74B), appears monophyletic. These two characters were proposed by Ono (1988) as diagnostic characters for Strophiinae. Several other diagnostic characters for Strophiinae proposed by Ono, like loss of cheliceral teeth, larger lateral eyes and lack of claw tufts are not synapomorphic. *Smodicinus* Simon, 1895 and related genera also posses elongated endites (Benjamin 2002) and might group with *Strigoplus*,*Strophius* and *Aphantochilus*.

Dietinae Simon, 1895

Dietinae is polyphyletic. I included *Apyretina* and *Oxytate* as exemplars of the subfamily Dietinae. They are not even remotely related (Fig 1). Dietinae appears to be very loosely defined, beginning with Simon's (1895) lumping of a large group of heterogeneous genera. The single character, presence of claw tufts, cited by Petrunkevitch (1928), is homoplasious; so are all diagnostic characters given by Ono (1988).

Bominae Simon, 1886 and Stiphropodinae Simon, 1895

In the preferred phylogenetic hypothesis (Fig 1) *Stiphropus lugubris* groups with *Apyretina* sp., this grouping is supported by three characters: peg-like setae on chelicerae (Character 36), AME 2x PME (character 50) and the smooth dorsal surface of the prosoma (character 63). However, both *S. lugubris* and *Apyretina* sp. are currently placed in two different subfamilies: *S. lugubris* in Stiphropodinae and *Apyretina* sp. in Dietinae (Ono 1988). Apart from *Stiphropus*, Stiphropodinae includes two more genera *Stiphropella* Lawrence, 1952 and *Heterogriffus* Platnick, 1976. Both genera possess peg-like setae on the chelicerae (Platnick, 1976).

Exemplars of Bominae were not included in the present study. Interestingly, most genera currently placed in Bominae possess peg-like setae on the front cheliceral margin as found in *Stiphropus* and *Apyretina* (Figs 54B, 73H; character 36). Bominae that are known to possess peg-like setae are *Holopelus* Simon, 1886, *Parabomis* Kulczynski, 1901 and *Thomisops* Karsch, 1879 (Dippenaar-Schoeman 1986, 1989). *Bomis lavata* L. Koch, 1874, the type species of the genus also posses peg-like setae (Benjamin unpublished data). Another genus, *Pagida* Simon, 1895, currently placed in the subfamily Thomisinae, also posses cheliceral peg-like setae (Benjamin unpublished data). Thus, it appears that the presence of peg-like setae might be synapomorpic for a small group of Old World thomisids, composed mainly of members of Bominae and Stiphropodinae.

Thomisinae Sundevall, 1833

The subfamily Thomisinae includes some of the most colorful and conspicuous thomisids, distributed worldwide. Some Thomisinae possess the ability to change color. Thomisinae was recently circumscribed and diagnosed by Ono (1988). The proposed diagnostic characters of the subfamily, like the presence of lateral eye tubercles (character 56), lack of chelicera teeth (character 38) are plesiomorphic, or very ambiguously defined, like in the case of carapace shape, leg length and “head with developed setae”.

A major conclusion of the molecular study of Benjamin *et al.* (2008) was that none of the conventional subfamilies of Thomisidae were monophyletic. This study provides further evidence.

Character evolution

Thomisids are behaviorally diverse (Benjamin *et al.* 2008). The evolution of these behaviors can now be studied in light of the phylogenetic results detailed here. One of the most remarkable of thomisid behaviors is their ability to change color. It has been known for some time that some thomisids, possibly closely related (e.g., *Misumena*, *Diaea*, *Runcinia* and *Thomisus*), possess the ability to change color and blend into their habitat; in most cases flowers (Comstock 1948; Gabritschevsky 1927; Packard 1905). *Misumena vatia* (Clerck, 1757) changes color during migration to flowers of different color, from spring to the early part of summer (Comstock 1948). Crab spiders are attracted by fragrance components of flowers (Aldrich & Barros 1995; Krell & Kraemer 1998) and use visual and tactile cues for selecting flowers (Greco & Kevan 1994; Morse 1988). They reach their ambush sites in a step-by-step process using several draglines and ballooning events (Homann 1934). Here, I code the color change behavior as follows: (0) color change behavior absent; (1) color change behavior present. This study suggests that color change behavior has evolved just once in the family (Fig 3). However, it should be noted that, even if they are not able to change color, all thomisids are cryptic in their natural surroundings. Cryptic morphology might have been a precursor to the evolution of color change behavior.

Since Simon (1864), eye arrangement in thomisids has been considered of high phylogenetic/taxonomic value. Although eye arrangements, like relative size and relative position, have proven unreliable in other spider families (Levi & Levi 1962), they have been some of the main character systems used in delimiting genera and even subfamilies in thomisids (Lehtinen 2005; Lehtinen & Marusik 2008; Ono 1988; Schick 1965; Suman 1970; Tikader 1971, 1980). Here I coded the arrangement of the median eyes (median ocular quadrangle) as follows: (0) MOA-WA=MOA-WP; (1) MOA-WA<MOA-WP; (2) MOA-WA>MOA-WP. This study suggests that this character requires a minimum of 10 steps on the preferred cladogram (Fig 4).

Taxonomic changes

(*denotes taxa included in the matrix)

Family Thomisidae

Genus *Aphantochilus* O. P.-Cambridge, 1870

Figs 7B, 7H, 10A–E, 11A–F, 12A–D, 13A–F, 14A–F, 15A–D, 16A–F, 17A–F

Type species: *Aphantochilus rogersi* O. P.-Cambridge, 1870
Figs 7B, 10A–E, 11A–F, 12A–D, 13A–F, 14A–F

Bucranium O. P.-Cambridge, 1881: 772: 66, fig 5. Description of juvenile. Type species *Bucranium taurifrons* O. P.-Cambridge, 1881, not examined. **New synonymy**.

Synonymy. The type species of *Bucranium* is here considered a typical member of the genus *Aphantochilus* as it fulfills criteria given in the diagnosis below. *Bucranium* is currently monotypic and thus, taxonomically uninformative. *Aphantochilus* has priority over *Bucranium*.

Diagnosis. Separated from other thomisid genera by the hooked-shaped ventral RTA (Figs 10A, B, 11B, 15A, 16B, C), lack of VTA and DTA, presence of cymbial peg teeth (Figs 10A, 11A–F, 15A, 16A–D), presence of dual spermathecal chambers with a relatively long CD (Figs 10D, E), reduced labium, legs I and II not elongated (leg III is the shortest) and spine-like prosomal projections (Figs 13A, B, 17A-C). Other characters that distinguish *Aphantochilus* are the presence of a femoral apophysis (FA, Figs 11E, 16A), ant mimicking behavior of its members (Oliveira & Sazima 1984) and cymbial modifications of the male palp (which is closely associated with the RTA).

Composition. Four species, *A. cambridgei* Canals, 1933, *A. inermipes* Simon, 1929, *A. rogersi* O. P.-Cambridge, 1870, and *A. taurifrons* O. P.-Cambridge, 1881 **comb. nov.**

Genus *Borboropactus* Simon, 1884

Type species: *Borboropactus squalidus* Simon, 1884
Fig 20C

Diagnosis. *Borboropactus* can be diagnosed by the presence of an epigynal plate or folds (Figs 18D, 19C, 20C, D, 21A, B, 23A, B), the unique sensory patch on tarsi (Figs 24C–E), canoe-shaped tapetum and straight PER. Further, *Borboropactus* can be separated from all other thomisids, except for *Geraesta* and *Angaeus* Thorell, 1881, by presence of a rudimentary RTA in males and ET in females. Both *Geraesta* and *Angaeus* posses a well developed RTA and sometimes DTA/VTA (Figs 39B, 39C, 40E; Tang & Li 2009).

Composition. 15 species, plus the two new species described below; see Platnick (2011) for a listing of all described species.

Distribution. Old World, from Africa to New Guinea.

Borboropactus bituberculatus Simon, 1884

Figs 5A, 20A, B, 20D

Borboropactus bituberculatus Simon, 1884: 301.
Regillus bituberculatus (Simon). Simon 1895: 1049, fig 1093.
Regillus divergens Hogg 1914: 57. Hogg 1915: 461, fig 29; Chrysanthus 1964: 89, fig 12–14. Holotype from Setakwa River, South New Guinea, in the BMNH, not examined. **New synonymy**.
Borboropactus hainanus Song, 1993. Male holotype from China, Hainan, Changjiang Co., Bawangling Mountains, 15 May 1990, M.B.Gu, IZCAS-Ar9362, not examined. **New synonymy.**

Type material: Syntypes of *B. bituberculatus*. Two females from New Guinea in MNHN 5460/1572, no more data given, examined (Figs 5A, 20D).

Synonymy. In both instances above, *B. divergens* and *B. hainanus* are well illustrated facilitating unambiguous identification. Further, the former species is from the same locality as *B. bituberculatus*.

Other material examined. INDONESIA: *Irian Jaya:* Waigeo Island, 1 male, Yembekaki, 0–180 m, 20–23 January 2001, A. Riedel (MHNG). ***Urbinasopen:*** 1 male, Gunung Susu, 0–450 m, 25 January 2001, A. Riedel (MHNG). ***Manokwari Province:*** 1 female, Wandammen Bay, Wondiwoi Mts., Wasior, 300–980 m, 3 January 2001, A. Riedel (MHNG). **PAPUA NEW GUINEA: *Madang Province:*** 1 female, Beiteta Road, 3.5 km W of North Coast Road, 80 m, 1 March 1989, Stop # 89–4, D. H. Kavanaugh, G. E. Ball and N. D. Penny (CAS).

Diagnosis. Resembles and likely to be confused with *B. cinerascens*. However, it could be separated from *B. cinerascens* by the large oval MA, broad based E and C (Figs 20A–20B). Females are separated by the stouter ET (Fig 20D).

Description. Habitus as in Fig 5A. Male palps as in Figs 20A–20B. Described in detail elsewhere (Song *et al.* 1999; Chrysanthus 1964; Song & Zhu 1997; Tang & Li 2010).

Distribution. China, Island of New Guinea.

**Borboropactus cinerascens* (Doleschall, 1859)

Figs 18A–E

Thomisus cinerascens Doleschall, 1859: 58, pl. 12, fig 4.
Borboropactus cinerascens (Doleschall). Simon 1884: 300; Benjamin *et al.* 2008: 722, figs 8A–E.
Regillus cinerascens (Doleschall). Thorell 1890a: 318.
Borboropactus mindoroensis Barrion and Litsinger, 1995: 203, figs 116a–g. Synonymized by Benjamin *et al.* (2008).
Borboropactus umaasaeus Barrion and Litsinger, 1995: 203, figs 117a–i. Synonymized by Benjamin *et al.* (2008).
Borboropactus bangkongeus Barrion and Litsinger, 1995: 206, figs 118a–i. Synonymized by Benjamin *et al.* (2008).

Material examined. MALAYSIA: ***P. Pangkor:*** 1 male, 30v150 m, 15–16 December 1997 (MHNG). ***Johor:*** 1 female, Kota Tinggi Waterfall, at the foot of Mt. Muntahak (1° 49' 46.8" N 103° 49' 59.2" E), 170 m, rain forest along stream, 24–26 June 2001, P. Schwendinger (MHNG). 1 male, Gunung Arong (2° 33' 12.1" N 103° 45' 20.5" E), 20 m, rain forest, 15 km N Mersing; 29–30 May 2004, P. Schwendinger (MHNG). ***Gunung Muntaha:*** 1 male, Kota Tinggi Waterfalls (1° 49' 46.8" N 103° 49' 59.2" E), 170 m, rain forest near stream, 15 km NW Kota Tingggi, 26–27 May 2004, P. Schwendinger (MHNG). ***Gunung Pulai*****:** 1 male (1° 34' 50.6" N 103° 30' 36.5" E), 50 m, secondary forest, SW Kulai, 24 May 2004, P. Schwendinger (MHNG). **INDONESIA:** ***Irian Jaya:*** 1 female, Biak Island, Koriam, Roidifu, ca. 100 m, 2 February 2001, A. Riedel (MHNG). **SUMATRA:** ***North Sumatra Province:*** 1 male, Nias Island, disturbed primary forest near road, Gunungsitoli-Hiliduho (1° 15' 59" N, 97° 32' 37" E), 100 m 24 June 2006, P. Schwendinger (MHNG).

Diagnosis. Most closely related to and likely to be confused with *B. bituberculatus*. Males are separated from *B. bituberculatus* by the rounded MA, broad based E and tapering C (Fig 18A). Females are separated by the shape of the AH, which is broader in *B. cinerascens* and the tapering ET; in *B. bituberculatus* the ET is stouter (Figs 18D, 20D).

Description. Male palps as in Figs 18A–C. Epigynum as in Figs 18D, E. Described in detail in Barrion and Litsinger (1995).

Distribution. China, Indonesia, Malaysia, New Guinea, Philippines.

**Borboropactus nyerere* sp. nov.

Figs 6A, B, 19A–E, 22A–F, 23A–F, 24A–F, 25A–F, 26A–D

Type material: Holotype: male, **TANZANIA:** ***Iringa District:*** Uzungwa Scarp Forest reserve, 11 km SE Masisiwe, Kihanga Strm. 8°22'5.7"S 35°58'41.6" E, 1800 m 17–27 May 1997, Understory, ZMJC-SI Exp. 1997 (USNM).

Paratypes: six females, same data as holotype.

Etymology. Named in honor of Julius K. Nyerere (1922–1999) the first President of Tanzania. Used as a noun in apposition.

Diagnosis. Separated by the square-shaped MA, obovate C and stout ET (Figs 22A –E).

Description. Male (holotype): Total length: 5.6; prosoma length: 1.6, width: 2.4. Leg I: femur 2.8, patella 1.1, tibia 2.2, metatarsus 1.5, tarsus 0.8. Prosoma, yellow-brown, laterals darker (Fig 6B). Opisthosoma lighter with white patches and dark markings as in Fig 6B. AER recurved, PER almost straight, ALE = PLE > AME = PME. Opisthosoma triangular, broadening towards the back. Palps as in Figs 19A–B, 22A–F.

Female paratype: Total length: 5.2; prosoma length: 2.5, width: 2.3. Leg I: femur 2.8, patella 1.2, tibia 2.4, metatarsus 1.2, tarsus 0.8. Similar to male, but lighter colored (Fig 6A). Opisthosoma with white patches and dark markings as in Fig 6A. Epigynum and vulva as in Figs 19C–E, 23A–F.

Distribution: Known only from its type locality.

Genus *Cebrenninus* Simon, 1887

Type species: *Cebrenninus rugosus* Simon, 1887
Figs 5C, 5F, 8B, 8E–F, 27A–E, 28A–F, 29A–F

Cebrenninus Simon, 1887: 486. Type species by original designation, *Cebrenninus rugosus* Simon, 1887. Examined.
Libania Thorell, 1890b: 149. Type species by original designation *Libania armillata* Thorell, 1890, type depository unknown. Not examined.

Diagnosis. Separated from other thomisid genera by a combination of the following characters: Presence of a large stout RTA, presence of a free embolus that originates at the center of the bulb and the presence of a SDT inward turn in the male palp. Males also possess a second tegular sclerite, the ETP (Figs 27B, 31A). Females could be separated from all other Thomisidae except for *Ascurisoma* Strand, 1928 by the presence of large globular spermathecae and the presence of a CD that is not longer than the thickness of the wall of S. *Ascurisoma* might be a synonym of *Cebrenninus*.

Composition. 6 species, not well known except for the type species and *Cebrenninus srivijaya* **sp. nov.**,

****Cebrenninus rugosus*** **Simon, 1887**

Figs 5C,5F, 8B, 8E, 8F, 27A–E, 28A–F, 29A–F

Cebrenninus rugosus Simon, 1887: 468. Simon 1897a: 9, figs 1–2.
Libania armillata Thorell, 1890b: 149, types unavailable for study. Synonymized by Simon, 1897a: 9.
Cupa kalawitana Barrion and Litsinger, 1995: 208, figs 119a–f. Holotype not examined. Synonymized by Tang *et al.* (2009).

Type material: Lectotype of *Cebrenninus rugosus*: male, no more data given, MNHN 8652/1572, examined.

Other material examined. THAILAND: ***Southern Isaan:*** 2 females, Khao-Yai National Park, 750 m, 26 July 1962, E. S. Ross and D. Q. Cavagnar (CAS). ***Chiang Mai Province:*** 1 male, near Chiang mai, Doi Suthep, 1150 m, 30 November 1996, P. Schwendinger (MHNG). ***Chumphon Province:*** 1 male 1female, near border Lang Suan-Phato Distr. Khao Kai Jae Waterfall , 80 m, semi evergreen rainforest, 21–22 August 2004, P. Schwendinger (MHNG). **INDONESIA:** ***Sumatra Barat:*** 1 female, Mangani, Mine near Kota Tinggi, 700 m, 21 July 1983, Edward S. Ross (CAS).

Diagnosis. This is the most common and widely distributed species of the genus. Males are separated by the long tapering E and MA. Females are separated by the round anteriorly boarded CO (Figs 27A–E), and the lack of a narrow MR, which is present in *C. srivijaya* **sp. nov.**. Further, this species can also be easily separated by the presence of PME, which is lacking in *C. srivijaya* **sp. nov.**, the only other illustrated species of the genus.

Variation. The specimens examined show some variation in the shape RTA, E and MA (Figs 27B, 27C; Tang & Li 2010; Tang *et al*. 2009).

Distribution. China, Indonesia, Philippines, Singapore, Thailand. Its presence is predicted in Burma, Vietnam and possibly in North India.

Remarks. *Libania* is regarded by Lehtinen (2002) as a synonym of *Cebrenninus*. The variation in the male genitalia of the specimens examined (but not the corresponding female genitalia) might suggest that more than one species is involved.

****Cebrenninus srivijaya*** **sp. nov.**

Figs 6D, 30A–E, 31A–F, 32A–F

Type material: Holotype: Male, **INDONESIA:** ***Bengkulu Province (Sumatra):*** Taba Penanjung – Kepahiang, 630–770 m, evergreen rain forest, shifting, 27 February 2000, P. Schwendinger (MHNG).

Paratypes: 1 male 2 females, same data as holotype.

Etymology. Sri Vijaya is an ancient Hindu kingdom on the island of Sumatra. Used as a noun in apposition.

Diagnosis. Separated from *C. rugosus* by the lack of PME. Further, males can be separated by the short, stout, broad based E and MA (Figs 30A–B, 31A–E). Females can be separated by the presence of a narrow MR, which is lacking in *C. rugosus* (Figs 30C–E).

Description. Male (holotype): Total length: 2.5; prosoma length: 1.3, width: 1.5. Leg I: femur 1.2, patella 0.4, tibia 1.2, metatarsus 0.8, tarsus 0.5. Prosoma dark brown, laterals darker. Opisthosoma light brown with darker patches and black markings as in Fig 6D. AER and PER recurved. ALE > PLE. Leg formula II, I, IV, III. Palp as in Figs 30A, B, 31A–F.

Female paratype: Total length: 6.5; prosoma length: 3.2, width: 1.5. Leg I: femur 1.2, patella 0.4, tibia 1.1, metatarsus 0.6, tarsus 0.5. Color and markings as in male. AER and PER recurved. ALE > PLE. Leg formula II, I, IV, III. Epigynum and vulva as in Figs 30C–E.

Distribution. Known only from its type locality.

Genus *Epidius* Thorell, 1877

Type species: *Epidius longipalpis* Thorell, 1877

Epidius Thorell, 1877: 492 (type species by monotypy *Epidius longipalpis* Thorell, 1877).
Cupa Strand, 1906: in Bösenberg and Strand 1906: 265 (type species by monotypy *Cupa typica* Bösenberg and Strand, 1906). **New synonymy**.

Synonymy. The type species of *Cupa* is here considered a typical member of the genus *Epidius* as it fulfills criteria given in the diagnosis below (Figs 35A, B). I have examined the holotype of *Cupa typica* (SMF 4246); see below for details. This specimen has the, for *Epidius* characteristic oval, dual-chambered spermatheca connected by a C-shaped, thick-walled CD (Figs 35A, B).

Diagnosis. Species of the genus *Epidiu*s can be separated from all other thomisid genera by the following characters. Male palp with a elongated tibia (tibia is longer than the cymbium; Figs 33A–C, 35C; Benjamin 2000). The distal tip of the male palpal tibia furnished with 4 to 6 thick long spines (Figs 33B, 35C, 36A–C; Benjamin, 2000; Tang, *et al.*, 2009); MA fixed (Figs 33B, 35C, 36A–C). Females could be separated from all other thomisid genera by the presence of oval, dual-chambered spermatheca connected by a C-shaped, thick-walled CD (Figs 34A–D, 35A, B, 38F). Living specimens of *Epidiu*s are green in color with a green yellow dorsal folium and live in green live parts of plants (Benjamin 2000; Tang *et al.* 2009). All species of related genera such as *Angaeus, Ascurisoma, Borboropactus*, *Cebrenninus*, *Geraesta* and *Pharta* are dark colored.

Description. See Benjamin (2000) and Tang *et al.* (2009).

Composition. *Epidius bazarus* (Tikader, 1970); *Epidius binotatus* Simon, 1897; *Epidius denisi* Lessert, 1943, *Epidius gongi* (Song & Kim, 1992); *Epidius guineensis* Millot, 1942; *Epidius longipalpis* Thorell, 1877; *Epidius lyriger* Simon, 1897; *Epidius pallidus* (Thorell, 1890), *Epidius parvati* Benjamin, 2000; *Epidius rubropictus* Simon, 1909; *Epidius typicus* (Bösenberg & Strand, 1906) **comb. nov**.

****Epidius binotatus* Simon, 1897**

Figs 33A–C, 34A–D, 38E, F

Epidius binotatus Simon, 1897b: 491. Lessert 1930: 666, fig 36; Lessert 1943: 335, fig 38.

Type material: Syntypes of *Epidius binotatus*: 1 male 1 female 1 juvenile from **SIERRA LEONE**: ‘Freetown’ (MNHN 13670/1574), no more data given, examined (Figs 33A, 34A, B).

Other material examined. **CÔTE D’IVOIRE:** 1 female, Appouesso, FC Bossematié, rain forest, station 1, 13 September 1995, R. Jocqué (MRAC 202642). **DR CONGO:** 3 females, Sankuru, Komi, no more data given (MHNG).1 male 1 female, Poko, no more data given (MHNG). **GABON.**1 male, Route Noayon, Sofor, 11 March 1986, A.Pauly (MRAC 172.760).

Diagnosis. Males can be separated by the hook-shaped E and MA. Both the E and MA are short necked with a rather blunt end (Figs 33A–C). Further, the E is much shorter than that of Asian species. Females can be separated by the CO, which face each other, and also by the C-shaped epigyne (Figs 34A–D, 38E, F).

Epidius rubropictus Simon, 1909

Figs 5I, 35C–E

Epidius rubropictus Simon, 1909: 144.

Philodromus ganxiensis Yin, Peng and Kim, 1999: 356, figs 2a–g. Transferred by Tang *et al.* (2009) from *Philodromus* to *Epidius*. **New Synonymy**.

Epidius ganxiensis (Yin, Peng and Kim, 1999). Tang *et al.*, 2009: 44, figs 3a–j.

Type material: Syntype of *Epidius rubropictus*: **VIETNAM:** 1 male, 'Tonkin' (MNHN 22347), no more data given, examined.

Other material examined. INDONESIA: ***Sumatra:*** 1 female, Utara Deli Serdang Reserve, Naturelle de Sipispis, Region de Dolokmerawan, 380 m, 17 November, 1985, leg. C. Lienhard (MHNG).

Remarks. Tang *et al.*(2009) recognized that *Philodromus ganxiensis* was misplaced in *Philodromus* and transferred it to *Epidius*. The illustrations provided by these authors for *Epidius ganxiensis* and my examination of the type of *E. rubropictus* (MNHN 22347) leave no doubt that both names stand for a single species.

Diagnosis. Males can be separated by the shape of the MA. The MA has a long stalk, ending with a stout rounded tip (Figs 35C). The E is thin and long, originating from the proximal end and extending over the distal end of the tegulum. Females can be separated by the thin, long copulatory ducts and the oval S (Figs 35D, E). Females may also be separated by the disproportionately large spermathecal chambers (Figs 35D, E).

Description. *Female.* from Indonesia: Sumatra. Total length: 3.3; prosoma length: 0.7, width: 1.5. Leg I: femur 2.0, patella 0.5, tibia 2.0, metatarsus 1.6, tarsus 0.9. Male palp as in Fig 35C. Female vulva and epigyne as in Figs 35D, E. For a good description of this species see also Yin *et al.* (1999) and Tang *et al.* (2009).

Distribution. China, Indonesia (Sumatra), Vietnam.

Epidius typicus (Bösenberg & Strand, 1906) comb. nov.

Figs 35A, B

Cupa typica Bösenberg and Strand, 1906: 266: 16, fig 454. Yaginuma 1986: 214, fig 119; Ono 1988: 21, figs 6–10.

Type material: Holotype of *Cupa typica*: **JAPAN:** 'Yunohama Berg bei Saga', Dönitz leg. (SMF 4246), no more data given, examined.

Diagnosis. Separated by the shape of the vulva and copulatory openings (Figs 35A, B). Males remain unknown.

Description. See Ono (1988) for a very detailed description and diagnosis.

Genus *Geraesta* Simon, 1889

Type species: *Geraesta hirta* Simon, 1889

Figs 7F, 39A–E, 40A–F, 41A–F

Geraesta Simon, 1889: 225 (type species by original designation *Geraesta hirta* Simon, 1889). Examined.

Diagnosis. Sister to *Borboropactus*, thus easily confused with it. Separated from *Borboropactus* and all other thomisids by the presence of two to three trichobothria on the dorsal surface of the cymbium of the male palp (Figs 40D, 42B, 43C, 45E). Females can be separated by the presence of an epigynal lip (Figs 41E, 42C, 44D, 46D). Other diagnostic characters are the presence of a colulus (Figs 41F, 46E; also present in *Pharta*, separated from it by the cup-shaped MA) and the presence of a DTA (Fig 39C). Separated from *Epidius* by the absence of an elongated male palp tibia (tibia is longer than the cymbium in *Epidius*; Fig 35C) and the absence of 4 to 6 thick long spines on the distal margin of the tibia of the male palp (Figs 33B, 35C, 36B). Separated from *Cebrenninus* by the presence of a free embolus that originates at the center of the bulb; and the presence of a SDT inward turn in the male palp in *Cebrenninus* (Figs 27A, 30A). Females can be separated from those of *Cebrenninus* by the presence of large globular spermathecae that lack CD in the latter genus (Figs 30D).

Distribution. Madagascar, Tanzania, and possibly all over the rest of Africa.

Remarks. Judging from illustrations in Ledoux (2004) *Prepotelus* Simon, 1898 might be a synonym of *Geraesta*.

*_Geraesta hirta_ Simon, 1889

Figs 7F, 39A–E, 40A–F, 41A–F

Geraesta hirta Simon, 1889: 225. Simon, 1897a: 7, figs 3–4.
Geraesta bilobata Simon, 1897a: 7, fig 5. **New synonymy.**

Type material: Syntype of *Geraesta hirta:* 1 subadult male from Madagascar (MNHN 9317/1573), examined. Syntype of *Geraesta bilobata:* 1 male from Madagascar, should be in MNHN, not found; probably lost.

Other material examined. MADAGASCAR: ***Antsiranana Province:*** 2 male 2 females, P. N. Mt. D'Ambre, 12° 32' S 38°49.10' E, 1100 m, 23–28 November 1993, J. Coddington, N. Scharf, S. Larcher, C. Griswold, R. Andriamanana (USNM). 1 male 1 female, P. N. Mt. D'Ambre, 1.2 km 184° S Joffreville, 12° 31.53.5' S 49°36.8' E, 1000–1200 m, 14–20 December 2005, H. Wood *et. al.*, Montaine rain forest general collecting (CAS CASENT 9024728). ***Mahajanga Province:*** 1 male, Parc National Tsingy de Bemaraha, 10.6 km ESE 123 Antsalova, 19° 42.34' S 44°43.4' E, 150 m, 16–20 September 2001. Tropical dry forest on Tsingy, general collecting night spiders Coll. BL Fisher *et al.* (CAS CASENT 9009314).

Synonymy. This species is recognized by the two dorsal lobs of the prosoma. The examined syntype of *Geraesta hirta* (MNHN 9317/1573) is the male specimen illustrated by Simon (1897a: figs 3–4). It is a sub adult male (penultimate). The outline of the embolus and MA is visible through the exoskeleton of the palp and is figured in Simon's drawing of the male palp (Simon 1897a: figs 3–4). As a subadult male palp it lacks a RTA, as described by Simon (1889). The cheliceral teeth are visible and led him to place the genus in the subfamily Stephanopinae. The type of *G. hirta* is in a very fragile state; I do not consider it prudent to manipulate it further and thus it is not illustrated here. The syntype of *Geraesta bilobata* could not be found at MNHN, although it is listed in the records of the museum. My identification is based on Simon's original description.

Diagnosis. Separated from *G. lehtineni* **sp. nov.** by the thin, tapering RTA (Fig 39B, 40B). Separated from *G. mkwawa* **sp. nov.** by the presence of C and longer RTA (Figs 39B, 40B). Females can be separated by the short EL (Figs 39D, 41E).

Description. Male (MNHN 9317/1573, subadult): Prosoma light yellow, laterals darker. Opisthosoma yellow with white and black patches. AER and PER recurved. All eyes more or less of equal size. Palp as in Figs 39B, C, 40A–F.

Female: Color and markings as in male. Epigynum and vulva as in Figs 39D–E, 41E.

Distribution. Known only from Madagascar. This species has been frequently collected, suggesting that it is widespread compared to other species of the genus.

*_Geraesta lehtineni_ sp. nov.

Figs 42A–D, 43A–F

Type material: Holotype: Male from **MADAGASCAR: *Antananarivo*:** R. S. d'Ambohitantely, Foret d'Ambohitantely, Forest fragment, ca. 20 km NE d' Ankazobe, 18°12'29.6" S 47°17'8.3" E, 1638 m, montane rainforest, 20 March 2003, general coll. night. D. Andriamalala, D. Silva *et al.* (CAS CASENT 9015689).

Paratype: 1 female, same data as holotype.

Other material examined. MADAGASCAR: ***Antananarivo:*** 1 male, R. S. d'Ambohitantely, Foret d'Ambohitantely, Jardin Botanique, 24.1km, 59° NE Ankazobe, 18°10'17" S 47°16'55" E, 1620 m, montane rainforest, 16–21 March 2003, general coll. night. D. Andriamalala, D. Silva *et al.* (CAS CASENT 9013883).

Etymology. Named in honor of Dr. Pekka T. Lehtinen.

Diagnosis. Separated from *G. hirta* by the stouter RTA and the much broader C (Figs 42A, B). Separated from *G. mkwawa* **sp. nov.** by the absence of C and longer, stouter RTA (Figs 42A, B). Note that this species has been found at a much higher elevation than *G. hirta*.

Description. Male: Prosoma light yellow, laterals darker. Opisthosoma, yellow with white and black patches. AER and PER recurved. All eyes are of more or less of equal size. Palp as in Figs 42A, B, 43A–F.

Female: Color and markings as in male. Epigynum and vulva as in Figs 42C, D.

Distribution. Known only from the type locality. Endemic to Madagascar.

Geraesta mkwawa sp. nov.

Figs 6E, 6F, 44A–D, 45A–F, 46A–F

Type material: Holotype: male from **TANZANIA:** ***Iringa District:*** Uzungwa Scarp Forest reserve, 11 km SE Masisiwe, Kihanga Strm. 8°22'5.7" S 35°58'41.6" E, 1800 m, 17–27 May 1997, understory, ZMJC-SI Exp. 1997 (USNM, more specimens are available in USNM and CAS).

Paratypes: 3 male 3 females, same data as holotype.

Etymology. Named after Tanzanian tribal Chief Mkwavinyika Munyigumba Mwamuyinga (1855 –1898) commonly known as Chief Mkwawa. He was a tribal leader in German East Africa (Tanzania) who opposed the German colonization. Mkwawa, meaning "conqueror of many lands" was a very early user of guerrilla warfare. Used as a noun in apposition.

Description. Male (holotype): Total length: 4.0; prosoma length: 2.0, width: 1.7. Leg I: femur 4.0, patella 0.8, tibia 3.8, metatarsus 3.2, tarsus 1.8. Prosoma light yellow, laterals darker. Opisthosoma brown-yellow with white and black patches as in Fig 6E. AER and PER recurved. AME smaller than the rest. Palp as in Figs 44A, 45A–F.
Female: Total length: 5.4; prosoma length: 2.4, width: 2.2. Leg I: femur 3.6, patella 1.2, tibia 3.2, metatarsus 2.4, tarsus 1.2. Color and markings as in male. Epigynum and vulva as in Figs 44C, 44D, 46D.

Genus *Pharta* Thorell, 1891

Type species: *Pharta bimaculata* Thorell, 1891
Figs 5E, 48A–D

Pharta Thorell, 1891: 85. Type species by monotypy *Pharta bimaculata* Thorell, 1891, examined.
Sanmenia Song and Kim, 1992: 142. Type species by original designation *Cupa zhengi* Ono and Song, 1986. **New synonymy**.

Synonymy. The type species of *Sanmenia*, *Cupa zhengi* is here considered a junior synonym of *P. brevipalpus* (Simon, 1903) **comb. nov.**. Illustrations of the type specimens of *Cupa zhengi* by Ono and Song (1986) unambiguously match the type of *P. brevipalpus* examined by me; see below for details. .

Diagnosis. Diagnosed by the presence of posterior epigynal pockets and oval spermatheca. Further, *Pharta* could be separated from all thomisids except for *Ascurisoma*, *Epidius*, *Cebrenninus* and *Geraesta* by the presence of a macro-trichobothrium on the palpal tibia and serrated tarsal setae. Separated from *Epidius* by the absence of an elongated male palp tibia (tibia is longer than the cymbium in *Epidius*; Fig 35C) and the absence of 4 to 6 thick long spines on the distal margin of the tibia of the male palp (Fig 35C, 36A–C). Separated from *Ascurisoma* and *Cebrenninus* by the presence of a free embolus that originates at the center of the bulb, presence of a SDT inward turn in the male palp as well as the proportionately much larger cephalic area in *Ascurisoma* and *Cebrenninus*. Females of *Ascurisoma* and *Cebrenninus* can be separated from *Pharta* by the presence of large globular spermathecae that lack CD in the latter two genera. Separated from *Geraesta* by the absence of a pair of trichobothria on the dorsal surface of the cymbium of the male palp that is present in *Geraesta* (Fig 45E). Females could be separated from those of *Geraesta* by the absence of a scapus (cf. Figs 42C, 46D, showing the scapus in *Geraesta*). Separated from *Borboropactus* by the absence of the following characters found in males and females of *Borboropactus*: C-shaped spermatheca (Fig 18E), the unique sensory patch on tarsi (Figs 24C–E), canoe-shaped tapetum and straight PER (Fig 26C).

Description. This genus is well described under its older name *Sanmenia* (Ono 1995; Ono & Song 1986; Tang *et al.* 2009; Yang *et al.* 2006).

Composition. *Pharta bimaculata* Thorell, 1891; *Pharta brevipalpus* (Simon, 1903) **comb. nov.**; *Pharta gongshan* (Yang, Zhu &Song, 2006) **comb. nov.**; *Pharta nigra* (Tang, Griswold and Peng, 2009) **comb. nov.**; *Pharta tengchong* (Tang, Griswold & Yin, 2009) **comb. nov.**.

Distribution. Burma, China, Japan, Singapore, Vietnam (Ono 1995; Ono & Song 1986; Tang *et al.* 2009; Yang *et al.* 2006).

Pharta bimaculata Thorell, 1891

Figs 5E, 48A–D

Sanmenia kohi Ono, 1995: 162, figs 7-15. **New synonymy.**

Type material: Holotype of *Pharta bimaculata*: 1 subadult female from Singapore (SMNH 1167), examined (Fig 5E).

Other material examined. SINGAPORE: 1 male, Lim Chu Kang Road, abandoned farm, foliage of creeping plant, 29 April 1990, JKH. Koh (USNM). 1 female, Woodlands Road, grasses, 7 April– 15 June 2002, JKH. Koh (USNM).

Synonymy. Several adult specimens from Singapore described in the now invalid genus *Sanmenia* (see above) by Ono (1995), can be unambiguously assigned to *P. bimaculata*, due to their general shape and markings of the prosoma, as well as the two black spots of the opisthosoma (Fig 5E). Further, this is the only known species of the genus from Singapore. As the holotype of *P. bimaculata* is a subadult, genitalic characters cannot be compared. Examination of the types of *Sanmenia kohi* was unnecessary as they are well illustrated.

Diagnosis. Separated from all other species of the genus by the presence of two apical apophyses which originate more or less from the same position of the tibia (Figs 48A, 48B). *Pharta brevipalpus* has two tibial apophyses, of which one is furnished with short, strong hairs (Fig 47C; Ono 1995). *Pharta gongshan* has a single apophysis that diverges into three parts (Fig 47A, B). See also Ono and Song (1986) and Ono (1988).

Description. This species is well described under its older name, *Sanmenia kohi* (Ono 1995).

Distribution. Know only from Singapore (Ono 1995).

Pharta brevipalpus (Simon, 1903) comb. nov.

Fig 47C

Epidius brevipalpus Simon, 1903: 730.
Cupa zhengi Ono and Song, 1986: 26, figs 1–7. Holotype and paratypes in NSMT and ASB; not examined. **New synonymy.**
Sanmenia zhengi (Ono & Song, 1986). Song and Kim 1992: 142 (transferred from *Cupa* to *Sanmenia*).

Type material: Syntype: Male from Phuc-Son, northeastern Vietnam (MNHN 22113/1574), examined.

Synonymy. Both sexes of *Sanmenia zhengi* have been well-illustrated facilitating unambiguous identification. Characteristic is the presence of two apophyses of the tibia of which one is a wide apophysis furnished with short strong hairs (Fig 47C; Ono 1995).

Diagnosis. Separated from all other species of the genus by the presence of two apophyses of the tibia, of which one is furnished with short strong hairs (Fig 47C; Ono 1995).

Description. See Ono and Song (1986) and Ono (1988).

Distribution. China, Japan, Vietnam.

Other material examined (taxa denoted with * were included in the matrix)

Aphantochilus rogersi* O. P.-Cambridge, 1870. **ECUADOR: ***Orellana:*** 1 female, Reserva Etnica Waorani, Transect Ent. 1km S. Onkone Gara Camp 25 June1994, TL. Erwin *et al.* (USNM). **Panama:** ***Canal Zone:*** 1 male, Colon, Humid forest, Canopy fogging, tree, 2–14 July 1979, E. Broadhead *et al.* (USNM).

Aphantochilus taurifrons* (O. P.-Cambridge, 1881) **comb. nov. ECUADOR: ***Orellana:*** 2 males 1 female, Reserva Etnica Waorani, Transect Ent. 1 km S. Onkone Gara Camp, 25 June 1994, TL. Erwin *et al.* (USNM).

Apyretina* sp. **MADAGASCAR: ***Antsiranana Province:*** 2 males 2 females, PN Mt. D'Ambre, 12° 32' S 38°49.10' E. 1100 m, 23–28 November 1993, J. Coddington *et al.* (USNM), Figs 52A–D, 53A–E, 54A–F, 55A–F, 56A–F.

Borboropactus sp. **VIETNAM:** ***Lam Dong Province:*** 7 females; Datanla Waterfall, ca. 5 km S of Da Lat, 11° 54' 02.2"N 108° 26' 54.0"E, 1300 m, evergreen hill forest, 5, 11–12 September 2003, P. Schwendinger (MHNG), Figs 6C, 21A–F.

Borboropactus squalidus Simon, 1884. Female lectotype from Africa: no further details given (MNHN 5045/1572), Fig 20C.

Diaea subdola* O. P.-Cambridge, 1885. **SRI LANKA: ***Central Province:*** 2 males 2 females, Agrapathana, Agra Arboretum, 2003, S. P. Benjamin and M. Bahir (MHNG).

Epidius denisi Lessert, 1943. Female lectotype from **DR CONGO:** no more data given (MRAC 114110).

Epidius guineensis Millot, 1942. Lectotype from **DR CONGO:** ***Bamania:*** 1 male, 1962, R. P. Hulstaert, no more data given (MRAC 122567; Figs 33B, 33C).

Epidius lyriger Simon, 1897. Lectotype from **PHILIPPINES:** ***Manila:*** 1 female, no more details given (MNHN 13705/1574).

Epidius parvati* Benjamin, 2000. **SRI LANKA: ***Western province:*** 1 male 1 female. Colombo, Bellanwila-Attidiya, 14 August 1996, SP. Benjamin (AMNH), Fig 7D.

Mecaphesa asperata* (Hentz, 1847). **USA: ***Kansas:*** 1 male 1 female, 'Cherokee co. 5 mi. N. 3.3 mi. E of Crestiline', 7 May 1984, GF Hevel (USNM), Figs 57A–E, 58A–F.

Monaeses* sp. **SRI LANKA: ***Central Province:*** 1 male 1 female, Agrabopath forest reserve, 18–21 February 2007, 1660–800 m, SP. Benjamin and Z. Jaleel (MHNG), Figs 9A, 9B.

Onocolus* sp. ECUADOR:** ***Orellana:*** 1 male 1 female, Reserva Etnica Waorani, Transect Ent., 1 km S Onkone Gara Camp, 25 June 1994, TL. Erwin *et al.* (USNM), Figs 8A, 59A–G, 60A–F.

Onomastus nigricauda* Simon, 1900. **SRI LANKA: ***Western province:*** 1 male 2 females, Kalutara district, Horane, Bodinagala, 19 July 1996, SP. Benjamin. Same locality, 5 males 6 females, 10 February.2007, leg. SP. Benjamin and Z. Jaleel. ***Sabaragamuwa province:*** 1 male, Ratnapura District, Morningside section, primary forest, 23 February2007, SP. Benjamin and Z. Jaleel (MHNG).

Oxytate subvirens* (Strand, 1907). **SRI LANKA: ***North Western Province:*** 4 males 2 females, Kurunegala District, Kurunegala, Ethagala Mountains, ca. 300 m, 1–28 February 2007, hand collecting, leg. Z. Jaleel (USNM), Figs 61A–E.

Philodromus rufus* Walckenaer, 1826. **USA: ***West Virginia:*** 3 females 5 males, Monongalia Co. WV University forest, Chestnut Ridge, Mixed Oak-Hardwood. Pitfall trap, 22–30 May 1989, DT. Jennings (USNM), Figs 62A–G.

Phrynarachne sp. A. **TANZANIA:** ***Tanga:*** 2 males 1 female, E Usambara Mtns., 12 km SE Amani, kihuhwi-Zigi Forest Reserve, 5° 6.3' S 38°40.6' E, 400–450 m, . 2–4 November 1995, CE. Griswold, N. Scharff, D. Ubick **(**CAS).

Phrynarachne* sp. B. **MADAGASCAR: ***Mahajanga:*** 3 males. Parc National Tsingy de Bemaraha. 3.4 km, 93°E of Bekopaka, Tombeau Vazimba, 6–10 November 2001, 19° 8' 31" S 44°49'41" E, 50 m, EF28 beating low vegetation tropical dry forest, B. L. Fisher *et al.* (CAS), Figs 63A–E, 64A–F.

Pharta gongshan* (Yang, Zhu and Song, 2006). **PR CHINA: ***Fugong**:* 2 males, 2 females, LuMaDeng County, N27.02529° E98.86256°, 1200 m, 23 April 2004, Peng Guang-Xu (USNM), Figs 7C, 8C, 47A, 47B, 47D–F, 49A–F, 50A–F, 51A–D.

Sidymella angulata* (Urquhart, 1885). **NEW ZEALAND: ***South Island:*** 1 male, Marlborough Prov., Pelorus Bridg scenic Reserve, 26 February 2005, D. Silva and H. Wood (CAS CASENT 9023857), Figs 65A, B.

Stephanopis cambridgei Thorell, 1870. **Holotype:** 1 adult female, **AUSTRALIA**, Thorell's collection (SMNH 1163), Figs 5D, 5G.

Stephanopis cambridgei* Thorell, 1870. **AUSTRALIA: ***Australian Capital Territory:*** 1 male 1 females, Black Mt. Canberra, 35° 18'S: 149° 08'E, 650 m, open *Eucalyptus* woodland, 7 August 1990, CE. Griswold and TC. Meikle (USNM). ***Western Australia:*** 1 male 1 female, Tinglewood near cabins, 6.98 km 5^0 N Walpole, disturbed *Eucalyptus* forest, S 34° 54' 51.0" E 116° 43' 50.9", 24 February 2006. G. Hormiga and L. Lopardo (GWU), Figs 66A–G, 67A–E.

Stephanopis* sp. **CHILE: ***Region X:*** 2 females, Parque National Puyehue, Forest behind Cabanas de la Fundaction de las Raices, Between Rte 215 and Rio Gol Gol, ca. 3 km E Entre Lagos, S 40° 39' 59.0" W 72° 10' 19", 22–24 January 2003, beating vegetation, SE. Lew (CAS CASENT 9016500), Figs 68A, 68B, 69A–F.

Stiphropus lugubris* Gerstäcker, 1873. **KENYA: 3 males, Kakamega Forest, 0° 22' N 34°50' E ,2001–2003, canopy fogging, W. Freund (ZEmk Ar. 092), Figs 70A, 70B, 73A–H. Remarks: the original material (a dried out sub-adult male) was collected by Baron Karl Klaus (Carl Claus) von der Decken on one of his expeditions to Mount Kilimanjaro (Gerstäcker 1873) and is lost (type depository unknown). *Stiphropus lugubris* is identified here based on the original description. The material is from the type locality.

Strophius* sp. **PANAMA: ***Canal Zone:*** 5 male 2 females, Colon, humid forest, canopy fogging, tree, 2–14 July 1979, E. Broadhead *et al.* (USNM), Figs 70C, 70D–F, 71A–F, 72A–F.

Strigoplus* sp. **SRI LANKA: ***North Western Province:*** 2 males, Kurunegala District, Kurunegala, Ethagala Mountains, ca. 300 m, 1–28 February 2007, hand collecting, Z. Jaleel (USNM), Figs 74A–F, 75A–F.

Thomisops sp. **SRI LANKA:** ***Central Province:*** 1 male 1female, Matale District, Riverstone, Knuckles range, ca. 1100 m, 07°31'42"N, 80° 44'17"E, 10 March 1998, hand collecting, SP. Benjamin (MHNG), Fig 7E.

Thomisus granulifrons* Simon, 1906. **SRI LANKA: ***Western Province:*** 1 male 1 female, Bellanwila-Attidiya, 1 February–30 March 1998, SP. Benjamin (USNM), Figs 7A, 8D.

Xysticus cristatus* (Clerck, 1757). **SPAIN: no further data, 1 male 1 female, (USNM), Figs 9C, 9D.

Xysticus fraternus* Banks, 1895. **USA: ***West Virginia:*** 4 males 2 females, Monongalia Co., WV University forest, Chestnut Ridge. Mixed Oak-Hardwood, pitfall trap, 22–30 May 1989, DT Jennings, (USNM), Figs 9E, 9F.

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References

Agnarsson, I. (2004) Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society*, 141, 447–626.

Aldrich, J.R. & Barros, T.M. (1995) Chemical attraction of male crab spiders (Araneae, Thomisidae) and kleptoparasitic flies (Diptera, Milichiidae and Chloropidae). *Journal of Arachnology*, 23, 212–214.

Alvarez-Padilla, F. & Hormiga, G. (2008) A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. *Journal of Arachnology*, 35, 538–542.

Badcock, H.D. (1918) Ant-like Spiders from Malaya, collected by the Annandale-Robinson Expedition 1901-1902. *Proceedings of the Zoological Society of London*, 1917, 277-321.

Barrion, A.T. & Litsinger, J.A. (1995) *Riceland Spiders of South and Southeast Asia.* CAB International, Wallingford, Oxon, v–xix, 1–700 pp.

Benjamin, S.P. (2000) *Epidius parvati* sp. n., a new species of the genus *Epidius* from Sri Lanka (Araneae: Thomisidae). *Bulletin of the British Arachnological Society*, 11, 284–288.

Benjamin, S.P. (2001) The genus *Oxytate* L. Koch 1878 from Sri Lanka, with description of *Oxytate taprobana* sp. n. (Araneae:

Thomisidae). *Journal of South Asian Natural History*, 5, 153–158.

Benjamin, S.P. (2002) *Smodicinodes schwendingeri* sp. n. from Thailand and the first male of *Smodicinodes* Ono, 1993, with notes on the phylogenetic relationships in the tribe Smodicini (Araneae: Thomisidae). *Revue Suisse de Zoologie*, 109, 3–8.

Benjamin, S.P. (2010) Revision and cladistic analysis of the jumping spider genus *Onomastus* (Araneae: Salticidae). *Zoological Journal of the Linnean Society*, 159, 711–745.

Benjamin, S.P., Dimitrov, D., Hormiga, G. & Gillespie, R.G. (2008) Family ties: molecular phylogeny of crab spiders (Araneae: Thomisidae). *Cladistics*, 24, 708–722.

Bonaldo, A.B. & Lise, A.A. (2001) A review of the neotropical spider genus *Stephanopoides* (Araneae: Thomisidae, Stephanopinae). *Biociencias*, 9, 63–80.

Bösenberg, W. & Strand, E. (1906) Japanische Spinnen. *Abhandlungen derSenckenbergischen naturforschenden Gesellschaft*, 30, 93–422.

Bristowe, W.S. (1941) *The Comity of Spiders.* Ray Society London, 560 pp.

Bryant, E.B. (1933) Notes on Types of Urquhart's Spiders. *Records of the Canterbury Museum*, 4, 1–27.

Chrysanthus, F. (1964) Spiders from South New Guinea, VI. *Nova Guinea, Zoology*, 28, 87-104.

Coddington, J.A. (1983) A temporary slide-mount allowing precise manipulation of small structures. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* (NF) 26, 291–292.

Coddington, J.A. & Levi, H.W. (1991) Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics*, 22, 565–592.

Comstock, J.H. (1948) *The Spider Book*. Comstock Publishing Company, Inc., Ithaca, New York, 729 pp.

Dingerkus, G. & Uhler, L.D. (1977) Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology*, 52, 229–232.

Dippenaar-Schoeman, A.S. (1986) The crab spiders of southern Africa (Araneae: Thomisidae). 7. The genus *Holopelus* Simon, 1886. *Phytophylactica*, 18, 187–190.

Dippenaar-Schoeman, A.S. (1989) The crab-spiders of Africa (Araneae: Thomisidae). 8. The genus *Thomisops* Karsch, 1879. *Phytophylactica*, 21, 319–330.

Doleschall, C.L. (1859) Tweede Bijdrage tot de Kenntis der Arachniden van den Indischen Archipel. *Acta Societatis scientiarum Indo-Neerlandicae*, 5, 1–60.

Dondale, C.D. (2005) Thomisidae. *In:* Ubick, D., Paquin, P., Cushing, P.E. & Roth, V. (Eds.) *The Spiders of North America. An Identification Manual,*Americal Arachnological Society, 246–247.

Edwards, G.B. & Benjamin, S.P. (2009) A first look at the phylogeny of the Myrmarachninae, with rediscovery and redescription of the type species of *Myrmarachne* (Araneae: Salticidae). *Zootaxa*, 2309, 1–29.

Farris, J.S. (1969) A successive approximations approach to character weighting. *Systematic Zoology*, 18, 374–385.

Farris, J.S., Albert, V.A., Kallersjo, M., Lipscomb, D. & Kluge, A. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12, 99–124.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791.

Fitch, W.M. (1971) Towards defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology*, 20, 406–416.

Foelix, R.F. (1996a) *Biology of Spiders*. Oxford University Press, Oxford, 330 pp.

Foelix, R.F. (1996b) How do crab spiders (Thomisidae) bite their prey? *Revue Suisse de Zoologie*, H.S. 1, 203–210.

Gabritschevsky, E. (1927) Experiments on color changes and regeneration in the crab-Spider, *Misumena vatia*. *Journal of Experimental Zoology*, 47, 251–266.

Gerstäcker, A. (1873) Gliedertiere. *In*, Barron C. C. von der Decken's Reisen in Ost Afrika in 1859-61, Leipzig, pp. 1–542.

Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–91.

Goloboff, P.A. (1995) Parsimony and weighting: a reply to Turner and Zandee. *Cladistics*, 11, 91–104.

Goloboff, P.A., Carpenter, J.M., Arias, S.J. & Esquivel, D.R.M. (2008a) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, 24, 1–16.

Goloboff, P.A., Farris, J.S. & Nixon, K. (2008b) TNT: a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.

Grandjean, F. (1949) Observation et conservation des très petits arthropodes. *Bulletin du Muséum National d'Histoire naturelle*, 21, 363–370.

Greco, C.F. & Kevan, P.G. (1994) Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decisions by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). *Canadian Journal of Zoology*, 72, 1583–1588.

Griswold, C.E. (1993) Investigations into the phylogeny of the Lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). *Smithsonian Contributions to Zoology*, 539, 1–39.

Griswold, C.E., Coddington, J.A., Hormiga, G. & Scharff, N. (1998) Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society*, 123, 1–99.

Griswold, C.E., Ramírez, M.J., Coddington, J.A. & Platnick, N.I. (2005) Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments of their phylogeny. *Proceedings of the California Academy of Sciences*, 56, 1–324.

Hogg, H.R. (1914) Spiders collected by the wollaston and British ornithological union expeditions in Dutch New Guinea. *Proceedings of the Zoological Society of London (Series C Abstracts)*, 137, 56–58.

Hogg, H.R. (1915) Report on the spiders collected by the British ornithologists union expedition and the wollaston expedition in Dutch New Guinea. *Transactions of the Zoological Society of London*, 20, 425–484.

Holm, A. (1979) A taxonomic study of European and East African species of the genera *Pelecopsis* and *Trichopterna* (Araneae, Linyphiidae), with descriptions of a new genus and two new species of *Pelecopsis* from Kenya. *Zoologica Scripta*, 8, 255–278.

Homann, H. (1934) Beiträge zur Physiologie der Spinnenaugen. IV. Das Sehvermögen der Thomisiden. *Zeitschrift für vergleichende Physiologie*, 20, 420–429.

Homann, H. (1975) Die Stellung der Thomisidae und der Philodromidae im System der Araneae (Chelicerata, Arachnida). *Zeitschrift für Morphologie und Ökologie der Tiere*, 80, 181–202.

Huber, B.A. (1995) The retrolateral tibial apophysis in spiders- shaped by sexual selection. *Zoological Journal of the Linnean Society*, 113, 151-163.

Jackson, R.R. & Pollard, S.D. (1996) Predatory behavior of jumping spiders. *Annual Review of Entomology*, 41, 287–309.

Jackson, R.R., Taylor, P.W., McGill, A.S. & Pollard, S.D. (1995) The web and prey-capture behaviour of *Diaea* sp., a crab spider (Thomisidae) from New Zealand. . *Records of the Western Australian Museum*, *Supplement*, 52, 33–37.

Jocque, R. & Dippenaar-Schoeman, A.S. (2007) *Spider Families of the World*. Royal Museum of Central Africa, Tervuren, 336 pp.

Krell, F. & Kraemer, F. (1998) Chemical attraction of crab spider (Araneae, Thomisidae) to a flower fragrance component. *Journal of Arachnology*, 26, 117–119.

Ledoux, J.-C. (2004) Araignées de l'île de La Réunion: I. Hahniidae, Ctenidae, Thomisidae et Clubionidae (Araneae). *Revue Arachnologique*, 14, 159-191.

Lehtinen, P.T. (2002) Generic revision of some thomisids related to *Xysticus* C.L.Koch, 1835 and *Ozyptila* Simon, 1864. *In:* Toft, S. & Scharff, N. (Eds.) *European Arachnology 2000: Proceedings of the 19th European Colloquium of Arachnology.* Aarhus Univ. Press, Aarhus, pp. 315–327.

Lehtinen, P.T. (2005) Taxonomic notes on the Misumenini (Araneae: Thomisidae: Thomisinae), primarily from the Palaearctic and Oriental regions. *In:* Logunov, D.V. & Penney, D. (Eds.) *European Arachnology 2003 (Proceedings of the 21st European Colloquium of Arachnology, St. -Petersburg, 4–9 August 2003,* pp. 147–184.

Lehtinen, P.T. & Marusik, Y.M. (2008) A redefinition of *Misumenops* F. O. Pickard-Cambridge, 1900 (Araneae, Thomisidae) and review of the New World species. *Bulletin of the British Arachnological Society*, 14, 173–198.

Lessert, R., de. (1930) Araignées du Congo recueillies au cours de l'expédition organisée par l'American Museum (1909-1915). Quatrième partie. *Revue Suisse de Zoologie*, 37, 613-672.

Lessert, R. de. (1943) Araignées du Congo belge (Troisième partie). *Revue Suisse de Zoologie*, 50, 305–338.

Levi, H.W. (1982) Araneae. *In:* Parker, S.P. (Ed.) *Synopsis and Classification of Living Organisms*. McGrew Hill, New York, pp. 77–95.

Levi, H.W. & Levi, L.R. (1962) The genera of the spider family Theridiidae. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 127, 1–71.

Lise, A.A. (1973) Contribuiçao ao conhecimento do género *Sidyma* no Brasil, com descriçao de uma nova espécie (Araneae: Thomisidae). *Iheringia (Zoologia)*, 43, 3–47.

Lise, A.A. (1979a) Tomisideos neotropicais I: *Onoculus garruchus* sp.n. (Araneae: Thomisidae: Stephanopsinae). *Iheringia (Zoologia)*, 54, 67–76.

Lise, A.A. (1979b) Tomisideos neotropicais IV: *Onocolus mitralis* sp.n. (Araneae: Thomisidae, Stephanopsinae). *Revista Brasileira de Biologia*, 39, 487–492.

Lise, A.A. (1981) Tomisideos neotropicais VI: *Sidyma kolpogaster* Lise, 1973 descriçao do macho e nova ocorrencia (Araneae, Thomisidae, Stephanopsinae). *Iheringia (Zoologia)*, 57, 129–135.

Loerbroks, A. (1984) Mechanik der Kopulationsorgane von *Misumena vatia* (Clerck, 1757) (Arachida: Araneae: Thomisidae). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, (NF) 27, 383-403.

Maddison, W.P. & Maddison, D.R. (2001) MacClade: Analysis of Phylogeny and Character Evolution. Sinauer Associates, Sunderland, Massachusetts

Maddison, W.P. & Maddison, D.R. (2010) Mesquite: a modular system for evolutionary analysis. Version 2.72. Available from: http://mesquiteproject.org (accessed 30 August 2007).

Miller, J.A., Carmichael, A., Ramírez, M.J., Spagna, J.C., Haddad, C.R., Rezac, M., Johannesen, J., Kral, J., Wang, X. & Griswold, C.E. (2010) Phylogeny of entelegyne spiders: Affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). *Molecular Phylogenetics and Evolution*, 55, 786–804.

Millot, J. (1941) Les Araignées de l'Afrique Occidentale française, Thomisidae. *Mémoires de l'Academide des Sciences de Paris*, 65, 1–82.

Morse, D.H. (1988) Cues associated with patch-choice decisions by foraging crab spiders *Misumena vatia*. *Behaviour*, 107, 297–313.

Muster, C. (2009) Phylogenetic relationships within Philodromidae, with a taxonomic revision of *Philodromus* subgenus *Artanes* in the western Palearctic (Arachnida: Araneae). *Invertebrate Systematics*, 23, 135–169.

Nixon, K.C. (2002) WinClada. Published by the Author, Ithaca, New York. Available from: http://www.cladistics.com/about_winc.htm (accessed 5 June 2010).

Oliveira, P.S. & Sazima, I. (1984) The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biological Journal of the Linnean Society*, 22, 145–155.

Ono, H. (1980) Thomisidae aus dem Nepal-Himalaya. III. Das Genus *Stiphropus* Gerstaecker 1873, mit Revision der asiatischen Arten (Arachnida : Araneae). *Senkenbergiana biologica*, 61, 57–76.

Ono, H. (1988) *A revisional study of the spider family Thomisidae (Arachnida, Araneae) of Japan.* National Science Museum, Tokyo, 252 pp.

Ono, H. (1995) Four East Asian spiders of the families Eresidae, Araneidae, Thomisidae and Salticidae (Arachnida, Araneae). *Bulletin of the national science museum, Series A (Zoology)*, 21, 157-156.

Ono, H. & Song, D.X. (1986) A new Sino-Japanese species of the genus *Cupa* (Araneae: Thomisidae) from the coastal areas of the East China Sea. *Bulletin of the National Science Museum, Series A (Zoology)*, 12, 25–29.

Packard, A.S. (1905) Change of color and protective coloration in a flower-spider (*Misumena vatia* Thorell). *Journal of the New York Entomological Society*, 13, 85–96.

Petrunkevitch, A. (1928) Systema Araneorum. *Transactions of the Connecticut Academy of Arts and Sciences*, 29, 1–270.

Pickard-Cambridge, O. (1881) On some New Genera and Species of Araneida. *Proceedings of the Zoological Society of London*, 1881, 765–775.

Platnick, N.I. (1976) Notes on the spider genus *Doliomalus* (Araneae: Gnaphosidae). *Revue de Zoologie Africaine*, 90, 975-983.

Platnick, N.I. (2011) The World Spiders Catalog, Version 11.5, American Museum of Natural History, New York. Available from: http://research.amnh.org/entomology/spiders/catalog81-87/index.html (accessed 16.III.2011).

Prendini, L. (2001) Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology*, 50, 290–300.

Ramírez, M.J. (2003) The spider subfamily Amaurobioidinae (Araneae, Anyphaenidae): A phylogenetic revision at the generic level. *Bulletin of the American Museum of Natural History*, 277, 1–262.

Roberts, M.J. (1995) *Spiders of Britain & Northern Europe*. Harper Collins, London, 383 pp.

Roewer, C.F. (1954) *Katalog der Araneae von 1758 bis 1940, bzw 1954*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 1–923 pp.

Schick, R.X. (1965) The crab spiders of California (Araneida : Thomisidae). *Bulletin of the American Museum of Natural History*, 129, 1–180.

Simon, E. (1864) Histoire naturelle des Araignées (Aranéides). 1–540.

Simon, E. (1884) Description d'une nouvelle famille de l'ordre des Araneae (Bradystichidae). *Annales de la Société entomologique de Belgique. Comptes Rendus [Les comptes Rendus sont réunis en un bulletin, placé après les Annales]*, 28, 297–301.

Simon, E. (1887) Espèces et genres nouveaux de la famille des Sparassidae. *Bulletin de la Société Zoologique de France*, 12, 466–474.

Simon, E. (1889) Etudes arachnologiques. 21e Mémoire. XXXI. Descriptions d'espèces et de genres nouveaux de Madagascar et de Mayotte. *Annales de la Société entomologique de France*, 6, 223–236.

Simon, E. (1894) *Histoire naturelle des Araignées.* Roret, Paris, 1 (1), 1–256 pp.

Simon, E. (1895) *Histoire naturelle des Araignées.* Roret, Paris, 1 (4), 761–1084 pp.

Simon, E. (1897a) *Histoire naturelle des Araignées.* Roret, Paris, 2 (1), 1–192 pp.

Simon, E. (1897b) Etudes arachnologiques. 27e Mémoire. XLII. Descriptions d'espèces nouvelles de l'ordre des Araneae. *Annales de la Société entomologique de France*, 65, 465–510.

Simon, E. (1903) Etudes arachnologiques. 33e Mémoire. LIII. Arachnides recueillis à Phuc-Son (Annam) par M. H. Fruhstorfer (nov.-déc. 1899). *Annales de la Société entomologique de France*, 71, 725–736.

Simon, E. (1909) Etude sur les Arachnides du Tonkin (1ère partie). *Bulletin scientifique de la France et de la Belgique*, 42, 69–147.

Song, D. & Kim, J.P. (1992) A new species of crab spider from China, with description of a new genus (Araneae: Thomisidae). *Korean Arachnology*, 7, 141–144.

Song, D.X., Zhu, M.S. & Chen, J. (1999) *The Spiders of China*. Hebei Sci. Technol. Publ. House, Shijiazhuang, 640 pp.

Song, D.X. & Zhu., M.S. (1997) *Fauna Sinica: Arachnida: Araneae: Thomisidae, Philodromidae*. Science Press, Beijing, viii + 259 pp.

Suman, T.W. (1970) Spiders of the family Thomisidae in Hawaï. *Pacific Insects*, 12, 773–864.

Swofford, D.L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, Massachusetts

Tang, G. & Li, S. (2009) *Paraborboropactus* gen. nov., with description of three new species of crab spiders from Xishuangbanna, Yunnan, China (Araneae, Thomisidae). *Acta Zootaxonomica Sinica*, 34, 712–721.

Tang, G. & Li, S. (2010) Crab spiders from Hainan Island, China (Araneae, Thomisidae). *Zootaxa*, 2369, 1–68.

Tang, G., Yin, C.M., Peng, X.J. & Griswold, C.E. (2009) Six crab spiders of the subfamily Stephanopinae from southeast Asia (Araneae: Thomisidae). *Raffles Bulletin of Zoology*, 57, 39–50.

Thorell, T. (1873) *Remarks on synonyms of European spiders. Part IV.* Uppsala, 375–645. pp.

Thorell, T. (1877) Studi sui Ragni Malesi e Papuani. I. Ragni di Selebes raccolti nel 1874 dal Dott. O. Beccari. *Annali del Museo civico di storia naturale di Genova*, 10, 341–634.

Thorell, T. (1890a) Aracnidi di Pinang raccolti nel 1889 dai Signori L. Loria e L. Fea. *Annali del Museo civico di storia naturale di Genova*, 2, 269–383.

Thorell, T. (1890b) Diagnoses Aranearum aliquot novarum in Indo-Malesia inventarum. *Annali del Museo civico di storia naturale di Genova*, 2, 132–172.

Thorell, T. (1891) Spindlar från Nikobarerna och andra delar af södra Asien, etc. *Konglige Svenska Vetenskaps-Akademiens Handlingar*, 2, 1–149.

Tikader, B.K. (1971) Revision of Indian crab spiders (Araneae, Thomisidae). *Memoirs of the Zoological Survey of India*, 15, 1–90.

Tikader, B.K. (1980) *Thomisidae (Crab-spiders)*. Zoological Survey of India, Calcutta, 1–247 pp.

Wheeler, W.C. (1995) Sequence alignment and parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology*, 44, 321–331.

Wunderlich, J. (2004a) Fossil crab spiders (Araneae: Thomisidae) in Baltic and Dominican amber. *Beiträge zur Araneologie*, 3, 1747–1760.

Wunderlich, J. (2004b) The new spider (Araneae) family Borboropactidae from the tropics and fossil in baltic amber.*Beiträge zur Araneologie*, 3, 1737–1746.

Yaginuma, T. (1986) *Spiders of Japan in Color (new edition)*. Hoikusha, Osaka, 305 pp.

Yang, Z.Z., Zhu, M.S. & Song, D.X. (2006) A new species of the genus *Sanmenia* Song & Kim, 1992 (Araneae, Thomisidae) from Yunnan Province, China. *Zootaxa*, 1151, 41–46.

Yin, C.M., Peng, X.J. & Kim, J.P. (1999) Three new species of the genus *Philodromus* from China (Araneae: Philodromidae). *Korean Journal of Biological Sciences*, 3, 355–358.

Appendix A. Characters and character state descriptions.

Male genitalia

1. Tibia of male palp: (0) shorter than cymbium; (1) longer than cymbium.
Femur and tibia of male palps of *Epidius* are characteristically elongated (Figs 33A, 35C; Benjamin 2000). The elongation of the femur and tibia is diagnostic for *Epidius*. This character and to a lesser extent characters 2 and 3, were previously recognized (Badcock 1918; Lessert 1930; Millot 1941; Simon 1897a).

2. Tibial macrosetae: (0) absent; (1) present.
The distal tip of the male palpal tibia of all known species of *Epidius* possesses 4 to 6 thick long macrosetae (Figs 35C, 36B, 36C; Tang *et al.* 2009). This character is diagnostic for *Epidius* (Benjamin 2000).

3. Macro-trichobothrium on palpal tibia (0) absent; (1) present.
A macro trichobothrium (which is thicker and longer than the other trichobothria) is present in the genera *Epidius*, *Cebrenninus*, *Pharta* and *Geraesta* (Figs 28A, 28D, 31C, 35C, 36C, 40C, 45F, 49E).

4. Retrolateral tibia apophysis (RTA): (0) absent; (1) present.
Apophyses of the male palpal tibia may occur on different surfaces of the tibia (Griswold *et al.* 2005). I recognize three different structures, RTA, VTA and DTA. They are three different homology hypotheses for this study. If a single apophysis is present, I have scored it as a RTA and further subdivided it in terms of position. RTA is the first male structure to contact the female genital system and is inserted in to hood/pockets of the epigyne (Huber 1995). Most thomisids have a single apophysis either on the retrolateral or retroventral surface of the tibia (see character 5). Other thomisids have two or three additional apophyses (Ono 1988; Schick 1965).

5. Position of RTA: (0) retrolateral; (1) retroventral.
The RTA of *Epidius*, *Pharta* and *Aphantochilus* originate from the retroventral surface of the tibia, rather than the retrolateral surface (Figs 10B, 11B, 33B, 47A). This distinction only applies when a single tibial process is present. See also definition of character 6 and 7.

6. Ventral tibial apophysis (VTA): (0) absent; (1) present.
If two tibial processes are present, the process originating from the ventral surface of the tibia is termed VTA. This distinction applies when a second apophysis is present (see character 4).

7. Dorsal tibial apophysis (DTA): (0) absent; (1) present.
DTA is a retrolateral/dorsal process of the male palpal tibia. It is present in *Geraesta* (Fig 40E) and other thomisids, e.g. *Smodicinodes* Ono, 1993 (Benjamin 2002).

8. Cymbium peg-like setae: (0) absent; (1) present.
The presence of cymbium peg-like setae are unique to *Aphantochilus* (Figs 10A, 11A–F, 16D).

9. Cymbial trichobothria: (0) absent; (1) present.
The presence of cymbial trichobothria is unique to *Geraesta* (Figs 40D, 42B, 43C).

10. Paracymbium: (0) cymbium smooth; (1) simple; (2) complex.
Various types of paracymbia are present in thomisids. When present they are coded as simple or complex. A simple paracymbium is present in *Aphantochilus*, *Stephanopis cambridgei*, *Strigoplus* sp., *Strophius* sp., *Stiphropus lugubris* and *Apyretina* sp. (Figs 10B, 15A, 16C, 70B, 73A, B. 75B). The complex paracymbia are found in *Thomisus granulifrons, Xysticus, Diaea subdola* and *Mecaphesia asperata* (Figs 57C, D; Roberts 1995; Schick 1965). The paracymbium is defined as any outgrowth or modification arising from the margin of the cymbium. This definition is similar to the definition of the paracymbium in Araneoidea (Griswold *et al.* 1998; Griswold *et al.* 2005). A simple paracymbium may not be directly associated with the embolus. A complex paracymbium that accommodates the embolus and functionally supplants the conductor is present in thomisids, and has been termed a tutaculum (Schick 1965). The paracymbium might have independently originated several times within Araneae.

11. Tegulum shape: (0) oval; (1) disk-shaped; (2) irregular; (3) cylindrical.
Most spiders have a tegulum that is more or less oval, with the subtegulum partly visible. However, in thomisids there are two types: the oval-shaped tegulum (Figs 27A, 33A, 40B) and the disk-shaped tegulum (Figs 15A, 52A, 53B, 63A, 66A). In neither type is the subtegulum visible ventrally. *Onomastus* have an irregular shaped tegulum (Benjamin, 2010).

Psechrus, which has a cylindrical tegulum, is scored based on the description and illustrations in Griswold *et al.* (2005).

12. Tegular ridge: (0) absent; (1) present.
This is any raised section or ridge on the ventral surface of the tegulum of the male palp (tegulum-rinne in Loerbroks 1984, tegular rim in Lehtinen & Marusik 2008). It is usually a low and morphologically longitudinal structure (16C, 16F, 70C, 71A, 75A; Schick 1965). Tegular ridges are pockets that accommodate the VTA, facilitating rotation of the tegulum during copulation (Huber 1995).

13. Conductor: (0) absent; (1) present.
The tegulum of most spiders bears apophyses, absent in most thomisids. The conductor is a tegular process that is closely associated (relative position) with the embolus that serves to guide the embolus. Some thomisids have an immoveable tegular outgrowth of the same appearance as the tegulum, situated close to the embolus (Figs 18A, 19A, 20A, 39B, 42B, 73B; Tegulum-Fortsatz in Loerbroks 1984), which might also serve to guide the embolus (see character 16).

14. Conductor type: (0) sclerotized; (1) hyaline.
Most conductors do not differ much in color and texture from the tegulum. In contrast, a hyaline conductor is transparent and thin (Figs 18A, 18B, 20A, 39B, 42A). In slow optimization this character is synapomorphic for *Borboropactus* and *Geraesta*.

15. Conductor shape: (0) longer than wide; (1) rounded; (2) digitiform; (3) *Onomastus*; (4) filiform.
A longer-than-wide conductor is present in *Geraesta* (Figs 39B, 42A). A rounded conductor is present in *Borboropactus* (Figs 18A, 19A, 22E). A digitiform conductor is as in *Philodromus rufus* and *Stiphropus lugubris* (Figs 62A, 62B, 73B). A filiform conductor is as in *Epidius parvati* (Fig 36B). The unique conductor of *Onomastus* is described in detail in Benjamin (2010).

16. Median apophysis: (0) absent; (1) present.
The embolus is easily located as the sperm duct opens at the tip of it. When a palp has a second tegular structure in addition to the embolus, it is scored here as the median apophysis, rather than a conductor as in Griswold *et al.* (2005). If there is a third structure and it is associated with the embolus, it is a conductor, if not it is an extra tegular process. A MA is present in all Thomisidae from the Epidius clade (Figs 18A, 19A, 20A, 27A, 30A, B, 39B, 42B, 47A).

17. Median apophysis types: (0) concave; (1) hook; (2) filiform.
The MA is variable in shape, it is concave in *Borboropactus* and *Geraesta* (Figs 18A, 19A, 19B, 22E, 33B, 35C); it is hook-shaped in *Epidius*, *Pharta* and *Cebrenninus* (Figs 27B, 47A, 47C. 48A). *Onomastus* has a bifurcate MA (Benjamin, 2010).

18. Median apophysis attachment: (0) fixed; (1) flexibly attached.
When present, MA is flexibly attached in Thomisidae (Figs 18A, 19A, 19B, 22B, 22E, 27A, 27B, 30A, 30B), except for *Epidius* (Figs 33A, B). *Uduba* also has a flexibly attached MA (Griswold 1993).

19. Extra tegular process: (0) absent; (1) present.
Additional structures that do not fit the description of E, C or MA are termed “extra” tegular process. Several thomisids like *Cebrenninus*, *Xysticus* and *Ozyptila* possess various tegular outgrowths (Figs 27A, 28A, 30B, 31A, 31E; Roberts 1995; Schick 1965), I do not consider them homologous to the C or MA. The presence of an ETP supports the monophyly of *Cebrenninus* (Figs 1, 2). See also the definitions of character 13 and 16.

20. Resting position of embolus: (0) on tegulum; (1) on conductor; (2) below conductor; (3) on cymbium; (4) within paracymbium; (5) free.
The resting position of the embolus is scored as follows: resting on the tegulum in *Stephanopis cambridgei*, *Aphantochilus taurifrons*, *Thomisus*, *Monaeses*, *Strigoplus*, *Strophius* sp., *Oxytate*, *Apyretina*, *Sidymella lucida*, *S. angulata* and *Phrynarachne* sp. (Figs 15A, 65A, 70C). Closely associated or resting on conductor (Figs 18A, 19A, 39B, 42A). Below conductor in *Epidius* and *Pharta* (Figs 33A, B, 47A, 47C). The embolus rests on the cymbium in *Aphantochilus rogersi* (Figs 10A, 11B). The embolus is closely associated with the tutaculum in *Xysticus* and *Diaea*. The embolus is free in *Cebrenninus* (Figs 27A, 28B, 30A).

21. Embolus origin: (0) embolus originates from the lateral part of the tegulum; (1) embolus originates from median part of the tegulum; (2) embolus originates from below the tegulum; (3) embolus originates from within the alveola cavity.
In *Onomastus*, the embolus originates from within the alveolar cavity (Benjamin, 2010) and in *Psechrus* and *Uduba* from below the tegulum.

22. Sperm duct trajectory (STD): (0) circular; (1) with loops.
In thomisids, the sperm duct follows a circular peripheral course through the tegulum (Figs 15A, 18A, 33B, 42A, 70A, 70C), with a minimal inward shift in *Cebrenninus* and *Aphantochilus* (Figs 10B, 27A, 30A). The circular path of the sperm duct trajectory is diagnostic for thomisids (Ono 1988). Loops are present in both philodromids and many salticids (Benjamin 2010; Muster 2009).

23. SDT number of loops: (0) one; (1) two or more.
SDT loops are absent in thomisids. A single loop is present in philodromids (Muster 2009) and two in *Onomastus* (Benjamin 2010). The presence of a single U-shaped SDT loop in philodromids is diagnostic (Muster 2009).

24. STD inward turn:(0) absent; (1) present.
The STD inward turn is synapomorphic for *Cebrenninus* (Figs 27A, 30B). I think that this character is independent from character 21 in the case of *Cebrenninus*, as, although not very obvious in *Cebrenninus rugosus*, in *C. srivijaya* **sp. nov.** it first moves inwards and then towards the periphery and then again inwards at the base of E, forming a loop. However, it must have independently originated in *Aphantochilus* to accommodate the centrally positioned embolus (Fig 10B).

Female genitalia

25. Epigynal folds: (0) absent; (1) present.
This character codes for the ventral folds present in *Borboropactus* (Figs 21A, B, 23A, 23B). Epigynal folds are broad wrinkle-like structure on the ventral surface of the epigynum. They do not necessarily separate the two CO.

26. Epigynal teeth: (0) absent; (1) present.
Lateral lobes of *Borboropactus* and *Geraesta* are furnished with teeth as in Figs 18C, D, 19C–E, 20C, D, 23A–C, 39D, E, 41E, 44D, 46D. The presence of epigynal teeth is synapomorphic for *Borboropactus* and *Geraesta* (Figs 1).

27. Epigynal lip: (0) absent; (1) present.
This character codes for the ventral lip-like projection present in the epigynal area of *Geraesta* (Figs 39D, 42C, 44C, 46D).

28. Anterior hood: (0) absent; (1) present.
An anterior hood is present in *Onocolus* sp., *Mecaphesa asperata* and *Stephanopis* sp. (Figs 58E, 68A, B)

29. Posterior pockets:(0) absent; (1) present.
Present in *Pharta* (Figs 47D, 47E, 48C, 51A) and *Oxytate* (Fig 61D; Benjamin 2001).

30. Median ridge: (0) absent; (1) present.
The median ridge is a narrow sclerotized septum that separates the two CO. A median ridge is present in the following species examined: *Cebrenninus srivijaya* **sp. nov.**, *Onocolus* sp., *Xysticus fraternus*, *Strophius* sp. *Apyretina pentagona*, *Mecaphesa asperata*, *Stephanopis* sp. and *Stephanopoides* sp. (Figs 52C, 55F, 68A, 70E).

31. Number of spermathecae chambers: (0) one; (1) two or more.

32. Shape of spermathecae: (0) globular; (1) C-shaped; (2) oval; (3) membranous pouch; (4) sclerotized duct.

33. Copulatory duct type: (0) duct; (1) *Epidius*; (2) wall of spermathecae; (3) membranous pouch; (4) sclerotized cylinder.
The CDs of taxa studied are as follows. Membranous pouches are non-sclerotized membranous structures; ducts are sclerotized tubular structures of equal diameter throughout its length. Sclerotized cylinder is a CD that is sclerotized and cylindrical in shape. *Epidius* has a C-shaped, thick-walled CD (Figs 35A, B).
Somatic morphology

34. Peg-like setae on endites and labium: (0) absent; (1) present.
Stout setae of unknown function (“strong hairs” in Ono 1988) are present in *Strigoplus*, *Strophius* and *Aphantochilus* (Figs 13C, D, 74B). This character is synapomorphic for *Strigoplus, Strophius* and *Aphantochilus* (Fig 1).

35. Labial peg-like setae density: (0) less than 4; (1) more than 4.
Refers to the number of setae discussed in character 34.

36. Peg-like setae on the promargin of the chelicerae: (0) absent; (1) present.
The frontal chelicerae margin of *Stiphropus lugubris* and *Apyretina* sp. are furnished with short, stout, peg-like setae ("Small denticles" in Jocque & Dippenaar-Schoeman 2007; bacilliform cusps in Platnick 1976: fig 1; "spinulose" in Dippenaar-Schoeman 1986; Figs 54B, 73H). The number of peg-like setae varies between genera. Around 5 to 8 setae are found in *Stiphropus* (Figs 54B, 73H; Ono 1980), while in *Thomisops* most of the anterior margin is covered by peg-like setae (Dippenaar-Schoeman 1986, 1989). Other genera that are known to posses peg-like setae on the promargin of the chelicerae are *Bomis, Holopelus*, *Pagida and Parabomis*; see main text for discussion.

37. Peg-like setae on tip of the female palp: (0) absent; (1) present.
Peg-like setae are present on the tip of the female palp of *Aphantochilus* (Fig 13E).. Similar setae are also present on the cymbium of the male palp of *Aphantochilus* (Figs 10A, 11A, B, 16A, 16B, 16D).

38. Cheliceral teeth: (0) absent; (1) present.
This is a major character (and sometimes the only character) used by most authors in the classification of thomisids. However, cheliceral teeth are primitively present in spiders and have been retained in some thomisids (Figs 24A, B, 60B), but have been secondarily lost in most others (Figs 72B, 73H, 75F).

39. Macrosetae on the anterior surface of chelicerae: (0) absent; (1) present.
Cheliceral anterior surface is furnished with prominent stout setae of unknown function in *Strigoplus*, *Strophius* and *Aphantochilus* (Figs 17F, 72A, B, 75E, 75F). This character is synapomorphic for *Strigoplus*, *Strophius* and *Aphantochilus* (Fig 1).

40. Endites: (0) more of less the length of the labium; (1) approximately 2x the length of labium.
Endites are generally elongated (endite longer than 2x labium) in the genus *Aphantochilus*. Due to the elongated endites the labium is mostly constricted (Figs 13C, 17D).

41. Leg pair I longer and stouter than III and IV: (0) not conspicuously longer than III and IV; (1) longer and stronger than III and IV.
Leg pairs I and II are generally much longer and stouter than III and IV in thomisids (see also character 44). These two characters have been known for some time (Dondale 2005; Homann 1975; Jocque & Dippenaar-Schoeman 2007), but are included for the first time in a cladistic analysis within Thomisidae. The stronger legs I and II are attributed to the ambush predatory life style of thomisids (Bristowe 1941; Foelix 1996a, b) and is considered diagnostic for Thomisidae (Ono 1988). These two characters are reversed in *Aphantochilus*. In *Philodromus rufus*, leg II is the longest, followed by leg I (Muster 2009).
42. Leg I tarsus/metatarsus joint: (0) flexible; (1) non-flexible.
This character is unique to *Stiphropus* (Ono 1980), it also occurs in *Pagida* (Benjamin unpublished data).

43. Leg I femora: (0) smooth; (1) furnished with sclerotized mound and spines.
Present in spiders of the Epidius clade, except for *Epidius* (Fig 6D).

44. Leg II longer and stouter than III and IV: (0) not conspicuously longer than III and IV; (1) longer and stronger than III and IV.
See description of character 41. I consider this character to be independent of character 41. In my opinion each appendage pair can evolve independently.

45. Tarsal trichobothrial pattern: (0) in a straight line; (1) in two or more rows; (2) *Borboropactus*.
Trichobothria in thomisids are either distributed in a straight line (Figs 7A–B) or scattered in several rows (Figs 7C–D, F). *Borboropactus* has a sensory pit (24C–E).

46. PME: (0) absent; (1) present.
PME's are absent in *Cebrenninus srivijaya* **sp. nov.**

47. Tapetum: (0) grate-shaped; (1) canoe-shaped; (2) absent.
All thomisids have a grate-shaped tapetum, except for *Borboropactus* which has a canoe-shaped (Homann 1934). Philodromids and salticids do not have a tapetum (Homann 1975).

48. Relative size of ALE and AME: (0) sub equal; (1) ALE 2x AME; (2) AME 2x ALE.

49. Relative size of PLE and PME: (0) sub equal; (1) PLE 2x PME.

50. Relative size of AME and PME: (0) sub equal; (1) PME 2x AME; (2) AME 2x PME.

51. Number of eye rows: (0) 2; (1) 3.

52. AER: (0) straight; (1) ALE behind AME; (2) recurved.

53. PER: (0) straight; (1) PLE behind PME; (2) recurved.

54. Horn between lateral eyes: (0) absent; (1) present.
Present in *Aphantochilus* (Figs 13A, 17B).

55. Anterior eye region: (0) at level of clypeus; (1) projects beyond the clypeus
In several thomisids, especially species of the Stephanopis clade, the eye region projects beyond the anterior margin of the clypeus. Apart from species of the Stephanopis clade the following species included in this study exhibit this character: *Borboropactus cinerascens*, *Borboropactus nyerere* **sp. nov.**, *Pharta gongshan* and *Geraesta hirta*.

56. LE tubercles: (0) absent; (1) present.
Lateral eyes in thomisids are situated on prominent pale tubercles. Lateral eyes are often larger than the median eyes in thomisids. The presence of LE tubercles has been previously considered diagnostic for thomisidae (Dondale 2005; Jocque & Dippenaar-Schoeman 2007; Ono 1988). It is included for the first time in a cladistic analysis.

57. LE turbercle type: (0) tubercles separate; (1) tubercles joined.
LE turbercles are joined (or overlap each other) in *Diaea*, *Thomisus* and *Mecaphesa*. This character is synapomorphic for these three taxa.

58. LE tubercle color: (0) color of prosoma; (1) white.

59. ALS MAP number in female: (0) 1; (1) 2.
In all thomisids females have a pair of ALS MAP and a pair of PMS mAP (Figs 55B, 55E). In contrast males have a single ALS MAP and PMS mAP (Figs 12B, 56B, C).

60. PMS mAP number in female: (0) 1; (1) 2.
See description of character 59.

61. Colulus: (0) absent, smooth or reduced a few special setae; (1) present, as a fleshy knob-like protuberance. Most thomisids lack colulus (or it is reduced to a few setae). But it is present in *Pharta* and *Geraesta* (Figs 41F, 46E, 50F). Homann (1975) states that all thomisids posses modified setae instead of a colulus. This is mistaken, as seen in Figs 41F, 46E, 50F.

62. Body coloration: (0) red/brown; (1) green; (2) gray.
Living specimens of *Epidiu*s, *Oxytate* and some species of *Monaeses* are green in color with red or yellow markings (Benjamin 2000; Benjamin 2001; Tang *et al.* 2009).

63. Prosoma dorsal surface: (0) smooth; (1) rough; (2) blobs; (3) finger print.
The dorsal surface texture of the prosoma of most thomisids is rough, sometimes with fine blobs as in *Xysticus fraternus* and several other taxa (Figs 9E, 9F, 13F, 17A–C, 60D). In *Stephanopis* sp., *Stephanopis cambridgei*, *Onocolus* sp. and *Phrynarachne* sp. the entire surface of the prosoma is covered with large blobs, in some cases furnished with setae (Figs 67A, B, 69D). In *Epidius*, *Stiphropus* and *Apyretina*, the prosoma dorsal surface is smooth without any blobs (Fig 54A). In *Borboropactus*, the surface has a frilled texture, termed here as finger print (Fig 26D).

64. Prosoma dorsal setae: (0) smooth ordinary; (1) scaled ordinary; (2) oval leaf; (3) elongated, bean shaped; (4) ordinary-round based; (5) feathered with a pointed end.
Smooth-ordinary setae are as in *Xysticus fraternus* (Figs 9E, 9F, 54A). Scaled ordinary setae are as in *Cebrenninus rugosus* (Fig 8F). Oval leaves-like setae are as in *Onocolus* sp. (Fig 60D). Elongated bean shaped setae are as in *Geraesta* (Figs 46A, B). Ordinary-round based setae are as in *Aphantochilus rogersi* (Figs 13F, 17A–C). Setae that are feathered and with a pointed end are found in *Philodromus rufus*. *Borboropactus* has two types of setae, oval leaf and bean shaped (Fig 26D).

65. Sternum surface: (0) smooth; (1) fine-blobs.
The surface texture of the sternum of most thomisids is smooth (Figs 9B, 53E, 60F). In a few of the examined taxa, such as *Aphantochilus rogersi*, the surface of the sternum is covered with fine blobs (Fig 17E).

66. Sternum setae: (0) smooth ordinary; (1) feathered point; (2) bean shaped; (3) feathered-club; (4) ordinary round-based; (5) feathered leaf-shaped.
Smooth ordinary setae are unbranched hairs as in *Apyretina* sp. and *Monaeses* sp. (Fig 53E). Feathered-pointed setae are finely branched with a tapering end (Fig 46C). Bean-shaped setae are flattened in cross-section. Feathered-club shaped setae are thickly feathered, given them a club-like appearance as in *Onocolus* sp. and *Borboropactus* (Figs 26B, 60F). Feathered leaf-shaped setae have branches that render them leaf-shaped (Fig 71E).

67. 3rd tarsal claw: (0) absent; (1) present.
Absent in thomisids and salticids, but present in *Psechrus* and *Uduba* sp.
(Griswold, *et al.* 2005).

68. Tarsal claw tufts: (0) absent; (1) present.
Absent in *Uduba* sp. (Griswold, *et al.* 2005). Present in all thomisids included in this study.

69. Type of claw tufts: (0) pointed-end; (1) brush; (2) spoon; (3) *Onomastus*.
Claw tufts with a pointed end are as in *Borboropactus* (Figs 24F, 32F, 46F), brush-like claw tufts are as in *Monaeses* and *Xysticus cristatus* (Figs 9A, C, D), spoon-shaped claw tufts are as in *Philodromus rufus* and *Strigoplus minor* (Figs 62F, 74E; Homann 1975). In *Onomastus* every single setae of the claw tuft has large number of cilia at its tip, forming sort of a “claw tuft” in itself (Figs 61F–H).

70 Position of tarsal claw tufts (0) confined to tarsus tip (1) extends from the tip towards the tarsus/metatarsus joint.
In some thomisids the tarsal claw tufts extend away from the tarsal tip towards the metatarsus, which in this case is sometimes called the scopula (Figs 38C, 46F) as seen in all exemplars of the Epidius clade (except for *Borboropactus*). Some species outside the Epidius clade also posses extended claw tufts (Figs 54E, 62F). It is thought that claw tufts improve the grip of slippery surfaces or prey.

71. Tarsal setae: (0) smooth ordinary; (1) serrated; (2) branched; (3) oval leaf; (4) smooth screw. Ordinary setae are as in *Aphantochilus* and *Thomisus* (Fig 7B, 8D), serrated setae are as in *Borboropactus*, *Cebrenninus*, *Epidius*, *Geraesta* and *Pharta* (Figs 8B, 8C, 24E, 32F, 38A, B, 45F), branched setae are as in *Strigoplus* (Fig 74C, 74D), oval leaf setae are as in *Onocolus* (Fig 8A), smooth screw is found in *Philodromus rufus* (Fig 62F).

72. Calamistrum: (0) absent; (1) present.
Absent in thomisids and salticids, but present in *Psechrus* and *Uduba* sp.
(Griswold, *et al.* 2005).

73. Capture web: (0) absent; (1) present.
Absent in thomisids and salticids, but present in *Psechrus* and *Uduba* sp.
(Griswold, et al. 2005). However, a single species of *Diaea* from New Zealand has been reported to build a rudimentary web used for prey capture (Jackson *et al.* 1995). Some salticids also do build webs (Jackson & Pollard 1996).

74. Fovea: (0) absent; (1) present.
Absent in thomisids, but present in *Psechrus* (Griswold *et al.* 2005).
Appendix B. Phylogenetic data matrix.

The first state is ‘‘0’’, followed by ‘‘1’’, etc., ‘‘?’’ denotes missing data, ‘‘–’’ is inapplicable.

	Characters																													
										1										2										3
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Psechrus sp.	0	0	0	0	-	0	0	0	0	0	3	0	1	0	4	0	-	-	0	1	2	0	-	-	0	0	0	0	0	0
Uduba sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	1	1	1	1	1	2	0	-	-	0	0	0	0	0	1
Philodromus rufus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	-	-	0	1	0	1	0	0	0	0	0	0	?	?
Onomastus nigricuda	0	0	0	0	-	0	0	0	0	0	2	0	1	0	3	1	2	1	1	1	3	1	1	0	0	0	0	0	0	0
Borboropactus cinerascens	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	-	0	1	1	0	0	0	0
Borboropactus nyerere	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	-	0	1	1	0	0	0	0
Epidius parvati	1	1	1	1	0	0	0	0	0	0	0	0	1	0	4	1	1	0	0	2	0	0	-	0	0	0	0	0	0	0
Epidius binotatus	1	1	1	1	0	0	0	0	0	0	0	0	0	-	-	1	1	0	0	2	1	0	-	0	0	0	0	0	0	0
Pharta gongshan	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	1	1	1	0	2	0	0	-	0	0	0	0	0	1	0
Cebrenninus rugosus	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	1	1	1	1	5	1	0	-	1	0	0	0	0	0	0
Cebrenninus srivijaya	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	1	1	1	1	5	1	0	-	1	0	0	?	0	0	1
Stephanopis cambridgei	0	0	0	1	0	1	0	0	0	1	0	0	0	-	-	0	-	-	0	0	2	0	-	1	0	0	?	0	0	0
Onocolus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	-	-	0	5	0	0	-	?	0	0	0	1	0	1
Geraesta hirta	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	1	0	0	-	0	0	1	1	0	0	0
Geraesta lehtineni	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	1	1	0	-	0	0	1	1	0	0	0
Aphantochilus rogersi	0	0	0	1	1	0	0	1	0	1	0	1	0	-	-	0	-	-	0	3	1	0	-	1	0	0	0	0	0	0
Aphantochilus taurifrons	0	0	0	1	1	0	0	1	0	1	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	0
Thomisus granulifrons	0	0	0	1	0	1	0	0	?	2	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	0
Monaeses sp.	0	0	0	1	0	1	0	0	0	0	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	0
Xysticus cristatus	0	0	0	1	0	1	0	0	?	2	1	1	0	-	-	0	-	-	1	4	0	0	-	0	0	0	0	0	0	0
Xysticus fraternus	0	0	0	1	0	1	0	0	0	2	1	1	0	-	-	0	-	-	1	4	0	0	-	0	0	0	0	0	0	1
Diaea subdola	0	0	0	1	0	1	0	0	0	2	1	1	0	-	-	0	-	-	0	4	0	0	-	0	0	0	0	0	0	0
Strigoplus sp.	0	0	0	1	0	1	0	0	?	1	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	?	?	?	?
Strophius sp.	0	0	0	1	0	1	0	0	0	1	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	1
Oxytate subvirens	0	0	0	1	0	1	0	0	0	0	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	1	?
Stiphropus lugubris	0	0	0	1	0	1	0	0	0	1	1	0	1	0	2	0	-	-	0	1	0	0	-	0	0	0	0	0	0	0
Apyretina sp.	0	0	0	0	-	0	0	0	0	1	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	1
Mecaphesa asperata	0	0	0	1	0	1	0	0	0	2	1	1	0	-	-	0	-	-	0	3	0	0	-	0	0	0	0	1	0	1
Stephanopis sp.	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	?	0	0	0	1	0	1
Sidymella lucida	0	0	0	1	0	0	0	0	?	?	0	0	0	-	-	0	-	-	0	0	0	0	-	?	0	0	?	?	?	?
Sidymella angulata	0	0	?	1	0	0	0	0	?	1	0	0	0	-	-	0	-	-	0	0	2	0	-	1	0	0	?	?	?	?
Phrynarachne sp.	0	0	0	1	0	1	0	0	0	0	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	0
Stephanopoides sp.	0	0	?	0	-	0	0	0	0	0	1	1	0	-	-	0	-	-	0	0	0	0	-	0	0	0	0	0	0	1

	Characters																													
										4										5										6
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Psechrus sp.	1	0	0	0	-	0	0	1	0	0	0	0	0	0	?	0	0	0	0	0	2	0	0	0	0	0	-	-	2	2
Uduba sp.	1	4	0	0	-	0	0	1	0	0	0	0	0	0	?	0	1	0	0	0	2	0	0	0	0	0	-	-	2	2
Philodromus rufus	0	2	0	0	-	0	0	1	0	0	0	0	0	1	?	0	2	0	0	0	0	2	2	0	0	0	-	-	1	1
Onomastus nigricuda	0	2	2	0	-	0	0	1	0	0	0	0	0	0	?	0	2	2	1	2	1	1	1	0	0	0	-	-	0	0
Borboropactus cinerascens	1	1	0	0	-	0	0	1	0	0	1	0	1	0	2	0	1	0	0	0	0	2	0	0	1	1	0	0	1	1
Borboropactus nyerere	1	1	0	0	-	0	0	1	0	0	1	0	1	0	2	0	1	1	0	0	0	2	0	0	1	1	0	0	1	1
Epidius parvati	0	0	1	0	-	0	0	1	0	0	1	0	0	1	1	0	?	1	0	1	0	2	0	0	0	1	0	0	1	1
Epidius binotatus	0	0	1	0	-	0	0	1	0	0	1	0	0	1	?	0	?	1	0	1	0	2	0	0	0	1	0	0	1	1
Pharta gongshan	1	2	2	0	-	0	0	1	0	0	1	0	1	1	1	0	0	1	0	1	0	2	2	0	1	1	0	0	1	1
Cebrenninus rugosus	0	0	2	0	-	0	0	1	0	0	1	0	1	1	?	0	0	1	1	0	0	2	2	0	0	?	0	?	1	1
Cebrenninus srivijaya	0	0	2	0	-	0	0	1	0	0	1	0	1	1	1	1	0	1	-	-	0	2	-	0	0	1	0	0	1	1
Stephanopis cambridgei	0	1	0	0	-	0	0	1	0	0	1	0	0	1	0	0	?	1	0	1	0	1	0	0	1	1	0	0	1	1
Onocolus sp.	?	?	?	0	-	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	2	0	0	1	?	0	?	1	1
Geraesta hirta	1	0	0	0	-	0	0	1	0	0	1	0	1	1	1	0	0	1	0	1	0	2	2	0	1	1	0	0	1	1
Geraesta lehtineni	1	0	0	0	-	0	0	1	0	0	1	0	1	1	?	0	?	1	0	1	0	?	?	0	0	1	0	0	1	1
Aphantochilus rogersi	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	2	2	1	0	1	0	0	1	1
Aphantochilus taurifrons	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	2	2	1	0	1	0	0	1	1
Thomisus granulifrons	0	3	4	0	-	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	2	0	0	1	1	?	1	1
Monaeses sp.	?	?	?	0	-	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	1	0	?	1	1
Xysticus cristatus	0	1	0	0	-	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	1	0	?	1	1
Xysticus fraternus	0	1	0	0	-	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	1	0	?	?	?
Diaea subdola	0	4	3	0	-	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	2	2	0	0	1	1	1	1	1
Strigoplus sp.	?	?	?	1	1	0	?	0	1	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	1	0	1	?	1
Strophius sp.	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	?	0	?	1	1
Oxytate subvirens	0	0	0	0	-	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	2	0	0	1	0	1	1	1
Stiphropus lugubris	?	4	?	0	-	1	0	0	0	0	1	1	0	1	0	0	0	1	1	2	0	2	2	0	0	1	0	0	?	?
Apyretina sp.	?	0	0	0	-	1	0	0	0	0	1	0	0	1	?	0	0	1	1	2	0	2	2	0	0	1	0	0	1	1
Mecaphesa asperata	?	?	?	0	-	0	0	0	0	0	1	0	0	1	?	0	0	0	0	0	0	2	2	0	0	1	1	1	1	1
Stephanopis sp.	0	4	0	0	-	0	?	1	0	0	1	0	1	1	?	0	0	1	0	2	2	2	2	0	1	1	0	0	?	?
Sidymella lucida	?	?	0	0	-	0	0	1	0	0	1	?	?	1	?	0	?	1	0	?	2	1	0	0	1	?	?	?	?	?
Sidymella angulata	?	?	?	0	?	0	0	1	0	0	1	0	?	1	?	0	0	1	0	1	2	2	0	0	1	?	?	?	?	?
Phrynarachne sp.	0	0	3	0	-	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	2	2	2	0	0	1	0	1	?	?
Stephanopoides sp.	0	0	0	0	-	0	0	1	0	0	1	0	0	1	?	0	?	1	0	0	2	2	2	0	0	?	0	?	?	?

	Characters												
									7				
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4
Psechrus sp.	0	2	?	?	?	?	0	1	2	0	0	1	1	1
Uduba sp.	0	0	?	?	?	?	0	0	-	-	?	1	1	?
Philodromus rufus	0	0	0	1/5	0	1	1	1	2	1	1/4	0	0	0
Onomastus nigricuda	0	1	3	0	?	?	1	1	3	0	1	0	0	0
Borboropactus cinerascens	?	0	?	?	?	?	1	?	?	?	?	0	0	0
Borboropactus nyerere	0	0	3	2/3	0	2/3	1	1	0	0	1	0	0	0
Epidius parvati	0	1	0	0	?	?	1	1	0	1	1	0	0	0
Epidius binotatus	?	1	?	?	?	?	1	?	?	?	?	0	?	0
Pharta gongshan	1	0	1	?	?	?	1	1	0	1	1	0	0	0
Cebrenninus rugosus	0	0	1	1	0	0	1	1	0	1	1	0	0	0
Cebrenninus srivijaya	0	0	?	?	?	?	1	1	0	1	1	0	0	0
Stephanopis cambridgei	0	0	2	2	?	?	1	?	?	?	1/3	0	0	0
Onocolus sp.	0	0	2	2	0	3	1	1	0	0	3	0	0	0
Geraesta hirta	1	0	1	3	?	1	1	1	0	1	1	0	0	0
Geraesta lehtineni	?	0	1	3	0	0	1	1	0	1	1	0	0	0
Aphantochilus rogersi	0	0	1	4	1	4	1	1	0	0	0	0	0	0
Aphantochilus taurifrons	0	0	1	4	?	4	1	?	?	?	?	0	0	0
Thomisus granulifrons	0	0	?	?	?	?	1	1	1	1	0	0	0	0
Monaeses sp.	0	1	1	0	0	?	1	1	1	0	0	0	0	0
Xysticus cristatus	0	0	?	?	?	?	1	1	1	0	0	0	0	0
Xysticus fraternus	0	0	1	0	0	0	1	1	1	1	0/4	0	0	0
Diaea subdola	0	0	1	0	?	?	1	1	2	0	0/1	0	0	0
Strigoplus sp.	0	0	1	0	0	0	1	1	2	0	2	0	0	0
Strophius sp.	0	0	1	0	0	5	1	1	2	0	2	0	0	0
Oxytate subvirens	0	1	?	?	?	?	1	1	2	0	0	0	0	0
Stiphropus lugubris	?	0	0	0	0	0	1	1	0	0	2	0	0	0
Apyretina sp.	0	0	0	0	0	0	1	1	0	1	2	0	0	0
Mecaphesa asperata	0	0	1	0	0	0	1	0	-	-	?	0	0	0
Stephanopis sp.	?	0	2	2/3	1	3	1	1	0	1	1	0	0	0
Sidymella lucida	?	0	?	?	?	?	1	?	?	?	?	0	0	?
Sidymella angulata	?	0	?	?	?	?	1	?	?	?	?	0	0	?
Phrynarachne sp.	0	0	2	4	1	0	1	1	0	0	1	0	0	0
Stephanopoides sp.	?	0	?	?	?	?	1	1	?	0	0	0	0	?

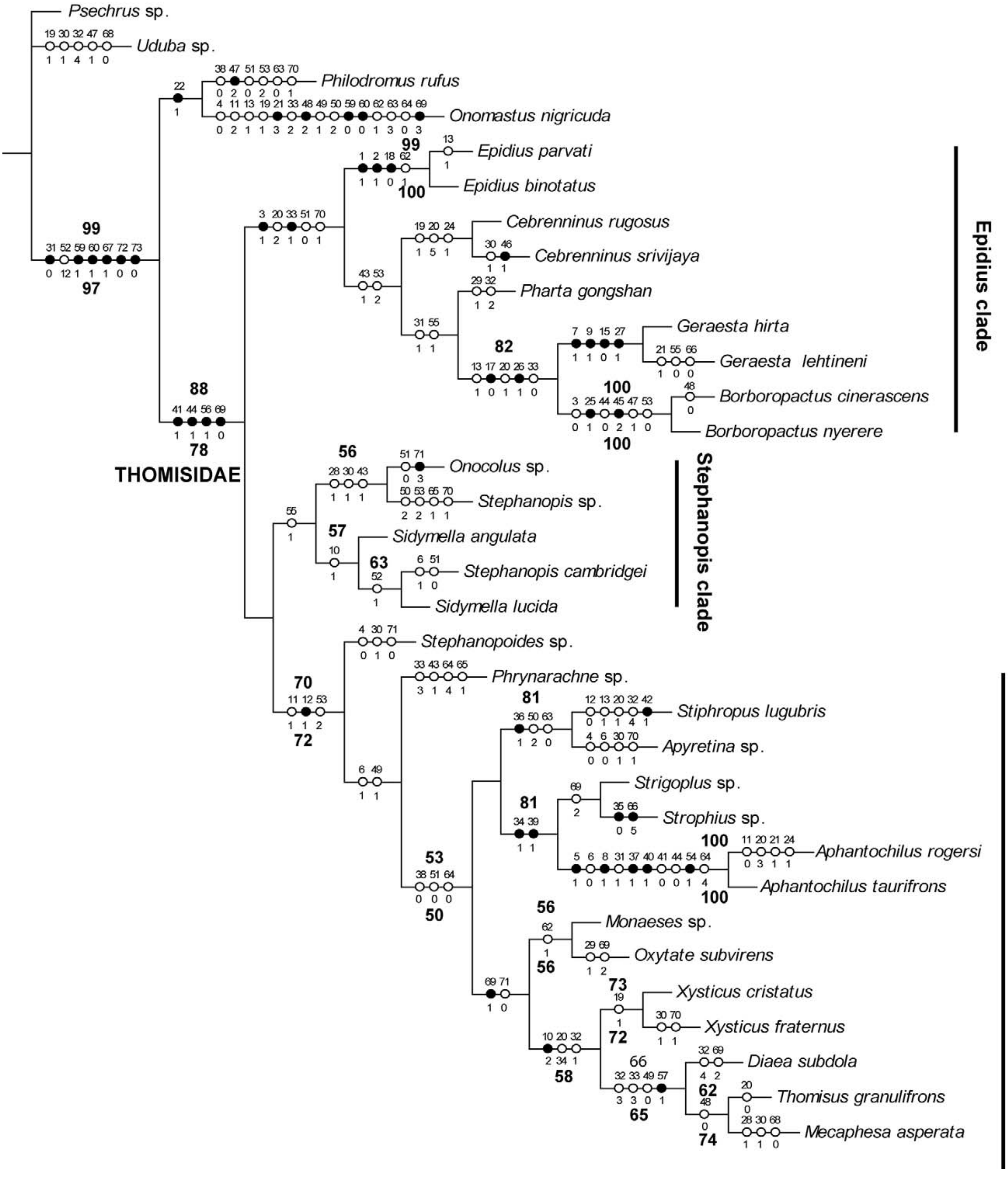

FIGURE 1. The preferred phylogenetic hypothesis of thomisid relationships obtained by analysis with implied weights (L 222, CI 0.74, RI 0.83). Unambiguous character state changes are mapped using Farris optimization. Numbers at nodes represent Bootstrap (above branches) and Jackknife values (below branches) above 50%.

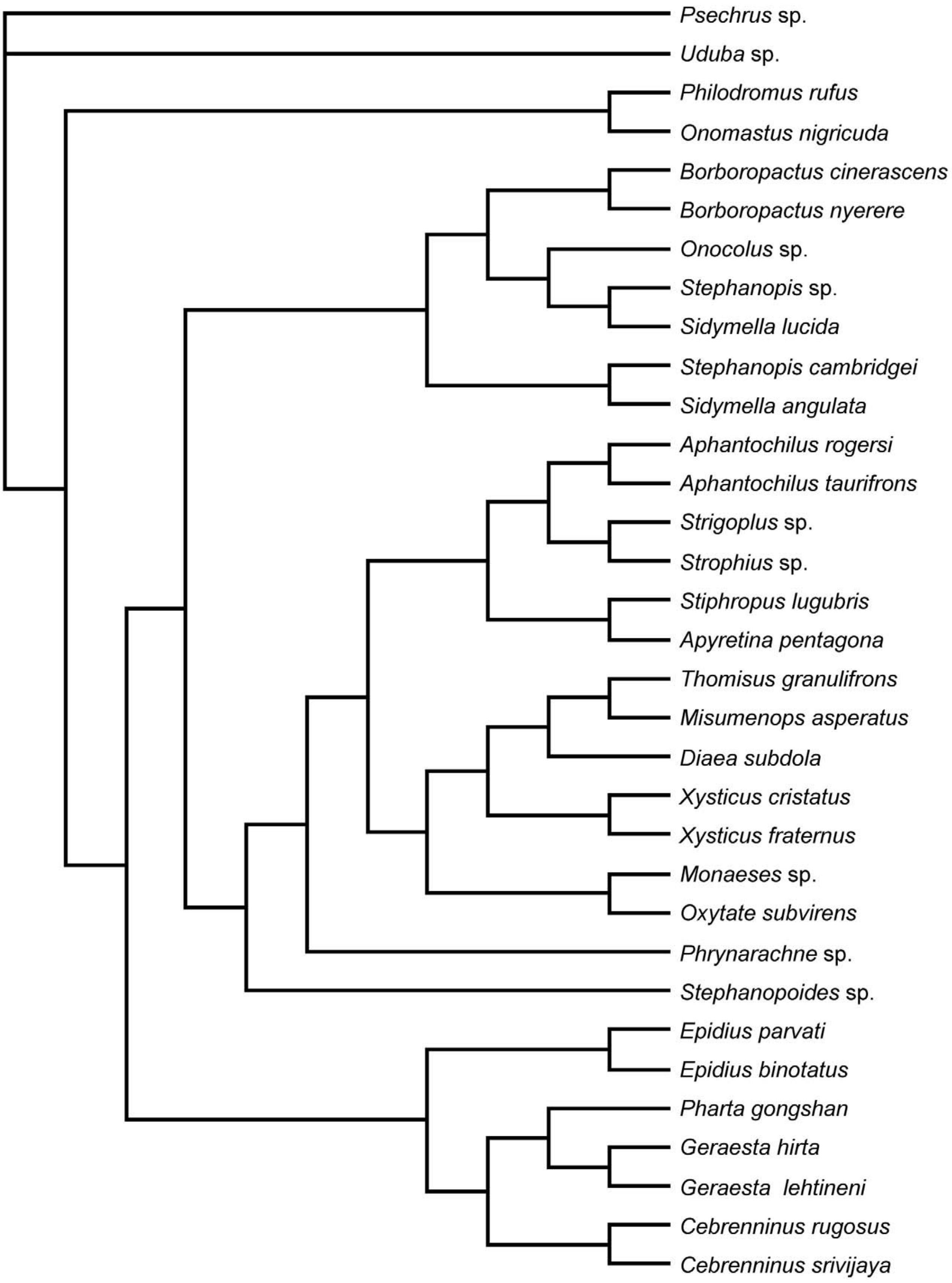

FIGURE 2. One of the trees found in the analysis with equal weights (L 222, CI 0.52, RI 0.68). In this tree, the two *Borboropactus* exemplars are placed within the Stephanopis clade.

FIGURE 3. Parsimony reconstruction of the evolution of color change behavior in Thomisidae. Coded as follows: (0) color change behavior absent; (1) color change behavior present. This study suggests that color change behavior evolved just once in the family. See text for details.

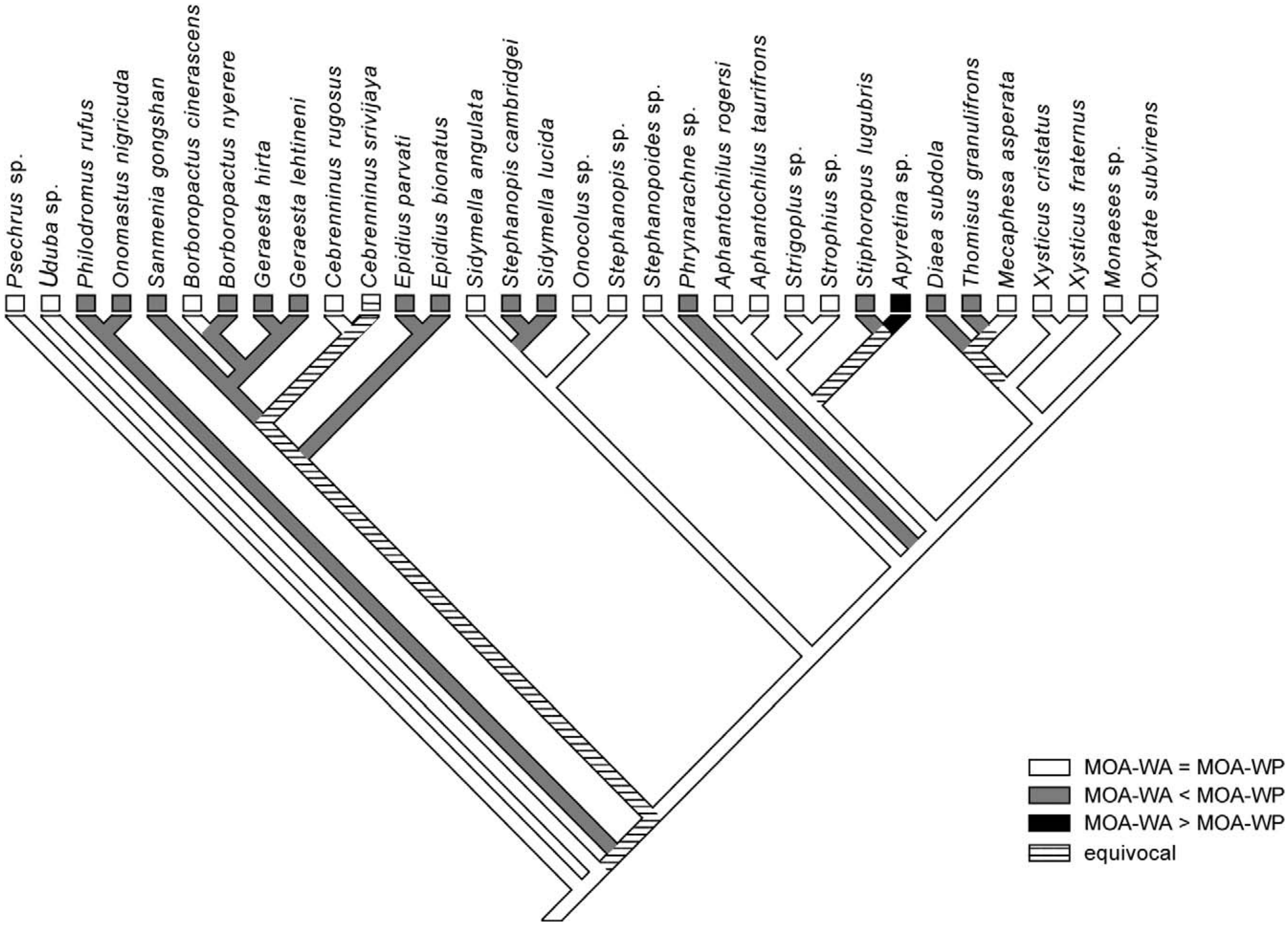

FIGURE 4. Parsimony reconstruction of the ratio of anterior width to posterior width of median ocular area, coded as follows: (0) MOA-WA=MOA-WP; (1) MOA-WA<MOA-WP; (2) MOA-WA>MOA-WP. Thus mapped, this character system requires a minimum of 10 steps on the preferred cladogram. See text for details.

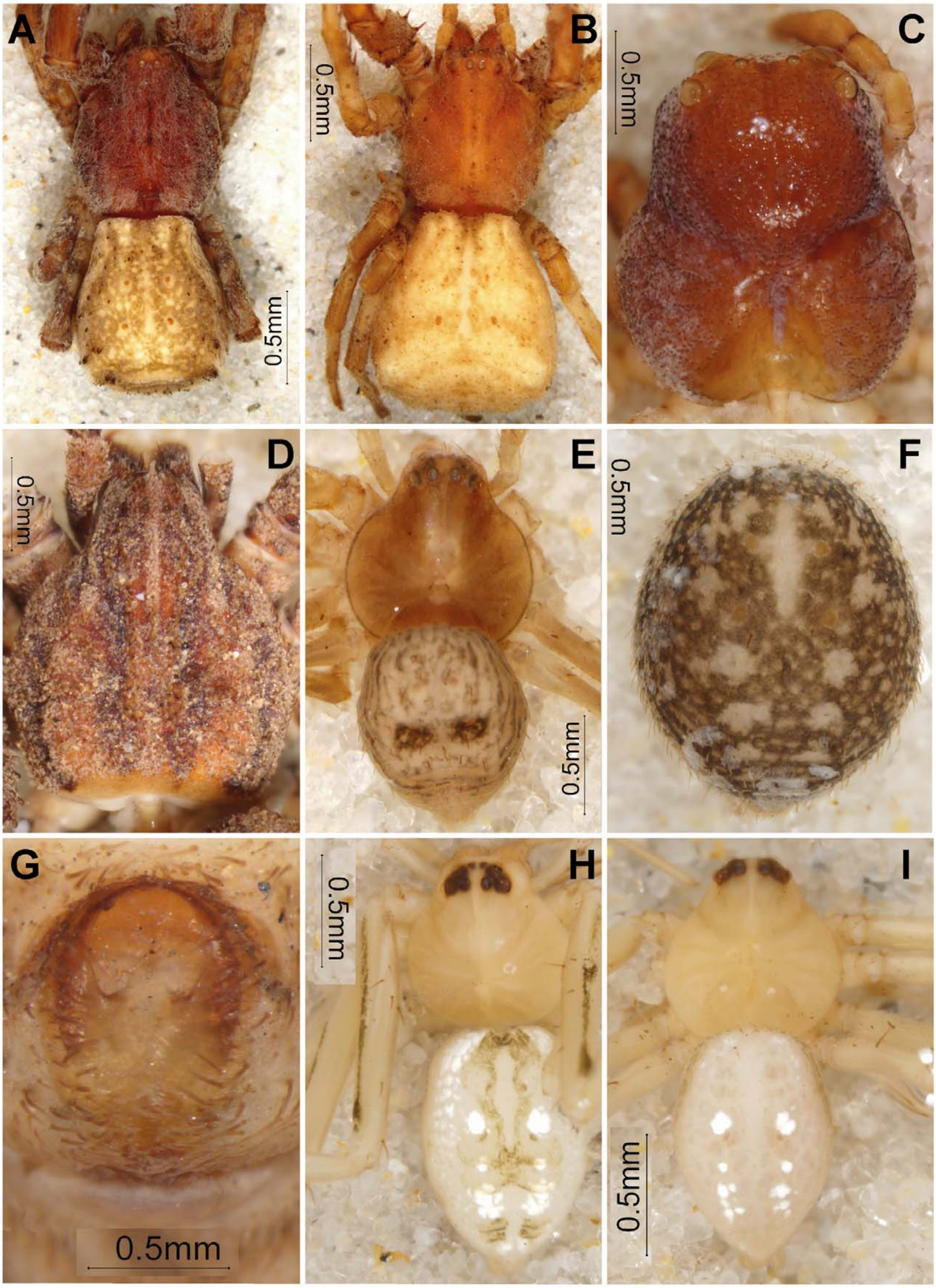

FIGURE 5. Photographs of Thomisidae. A *Borboropactus bituberculatus* (MNHN 5460/1572); B *Borboropactus squalidus* (MNHN 5045/1572); C *Cebrenninus rugosus* **(**MNHN 8652/1572), prosoma; D *Stephanopis cambridgei* (SMNH 1163); E lectotype of *Pharta bimaculata* (SMNH 1167); F *C. rugosus*, opisthosoma; G *S. cambridgei* (SMNH 1163), epigynum; H *Epidius lyriger* (13705); I *Epidius rubropictus* (MNHN 22347).

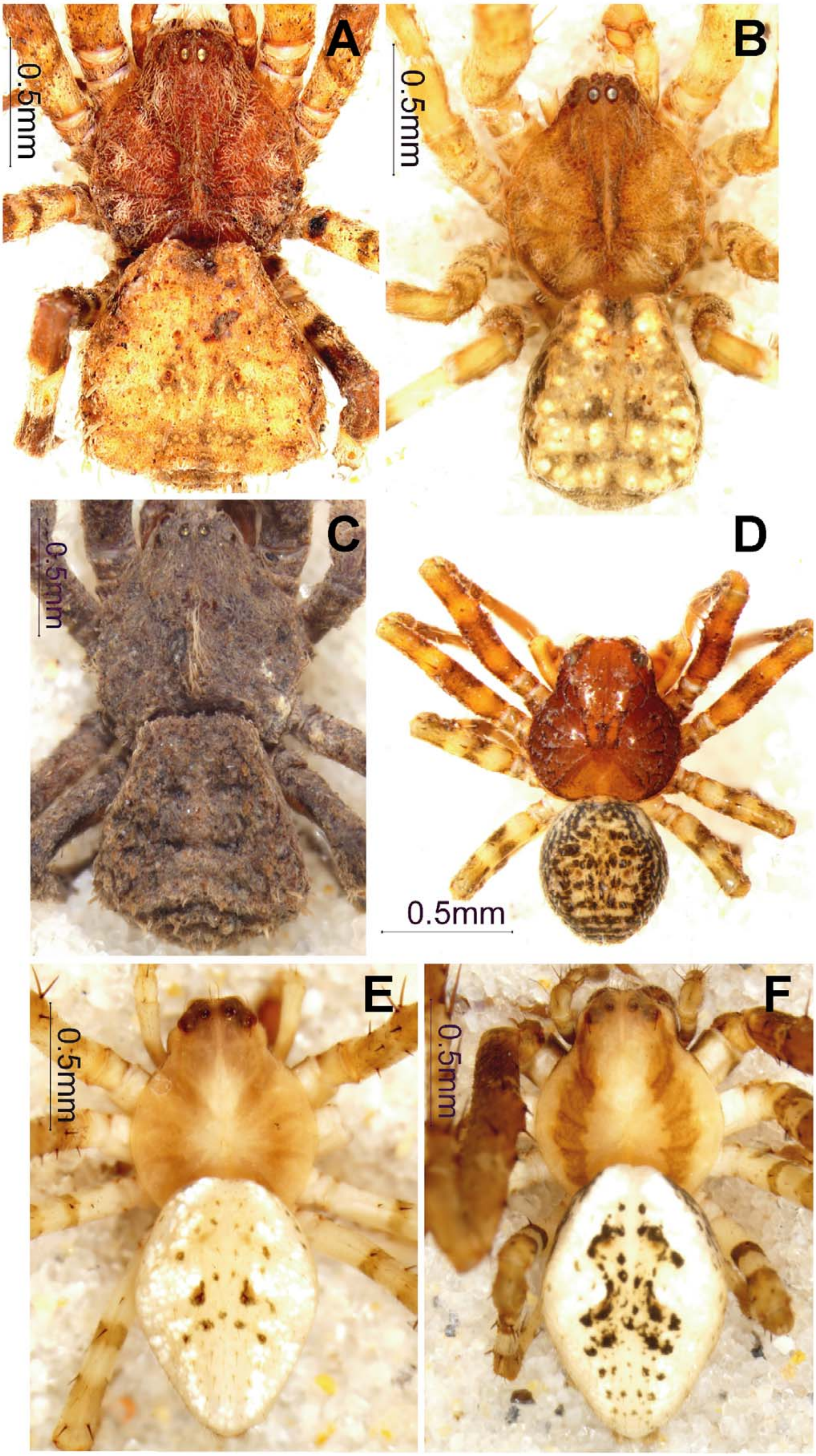

FIGURE 6. Photographs of Thomisidae. A *Borboropactus nyerere* **sp. nov.**, female; B ditto, male; C *Borboropactus* sp., female; D *Cebrenninus srivijaya* **sp. nov.**, male; E *Geraesta mkwawa* **sp. nov.**, male; F ditto, female.

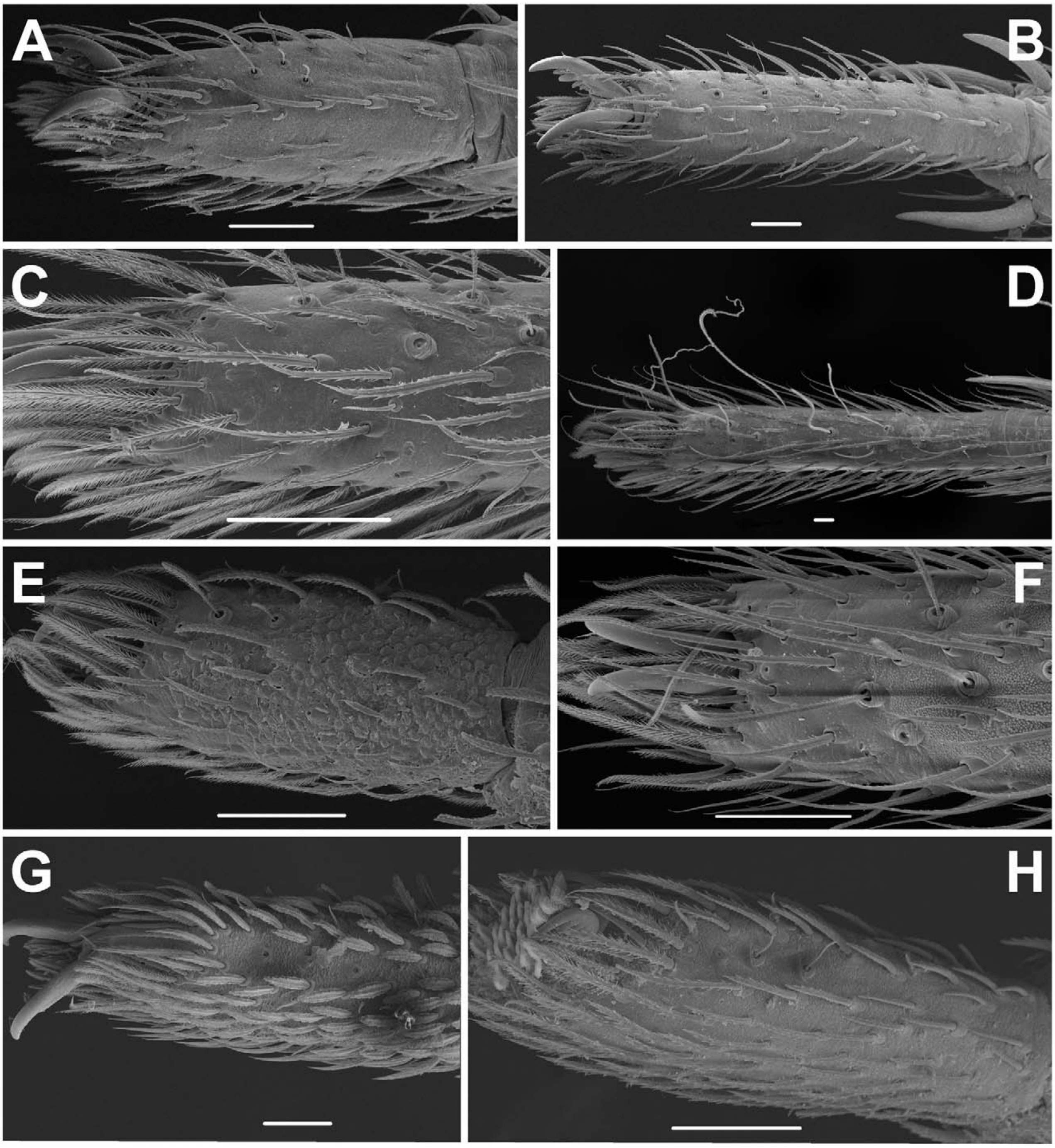

FIGURE 7. Tarsi of Thomisidae, tarsi showing trichobothrial number and pattern, dorsal view. A, B, D–H female; C male. A *Thomisus granulifrons*; B *Aphantochilus rogersi*, left leg 4; C *Pharta gongshan*, left leg 1; D *Epidius parvati*, left leg 4; E *Thomisops pupa*, left leg 1; F *Geraesta hirta*, left leg 1; G *Stephanopis cambridgei*, left leg I; H *Aphantochilus taurifrons*, left leg 4. Scale bars = 20 µm (D), 100 µm (A–C, E–H).

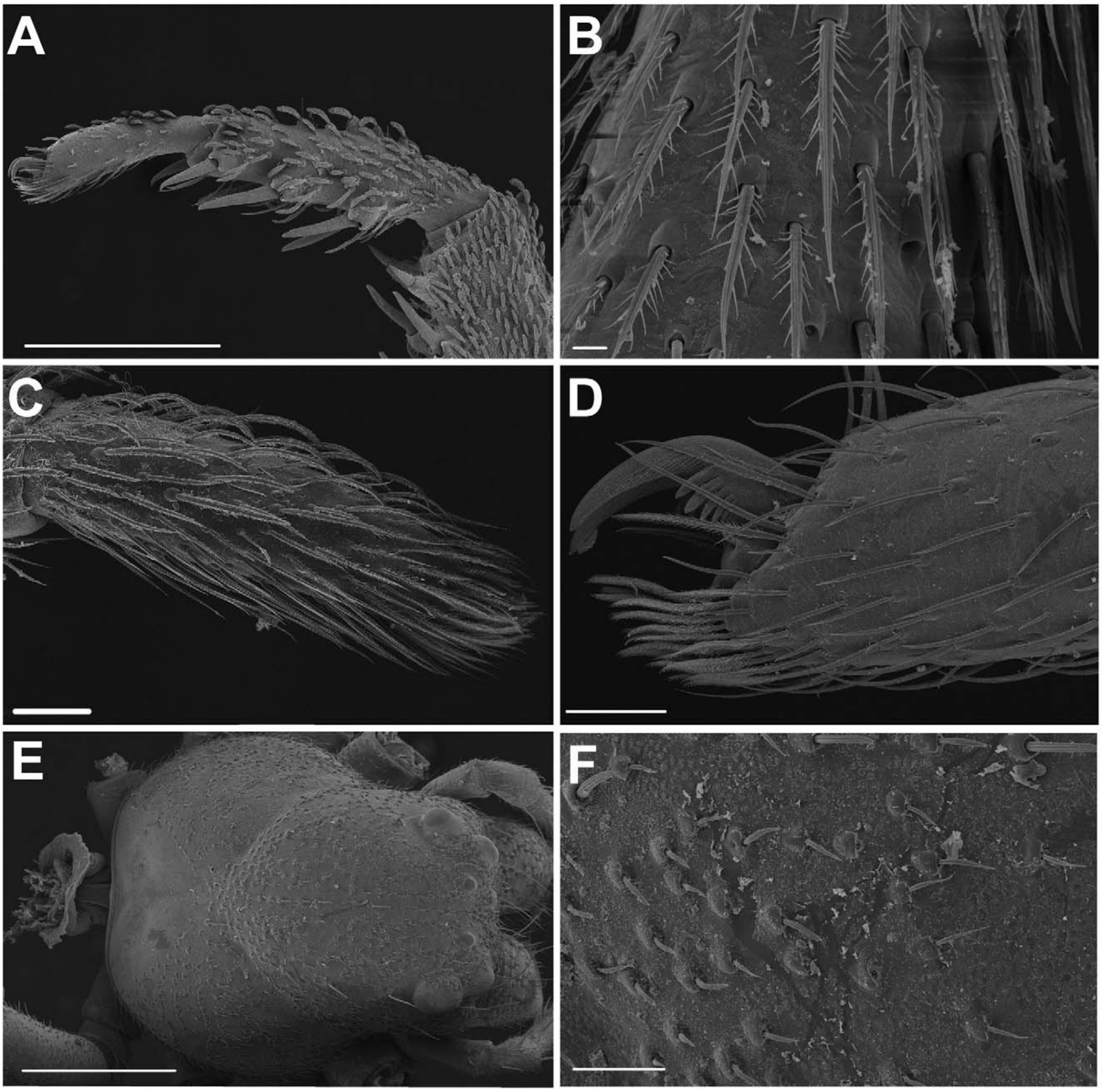

FIGURE 8. Setae of thomisids. A *Onocolus* sp. from Ecuador, female, left leg I, lateral view; B *Cebrenninus rugosus* female from Sumatra, left leg IV, dorsal view; C *Pharta gongshan*, female, left leg I, lateral view; D *Thomisus granulifrons*, female, left leg I, lateral view; E *Cebrenninus rugosus*, female prosoma, dorsal view; F ditto, detail, dorsal view. Scale bars = 10 µm (B), 100 µm (C–F), 1 mm (A).

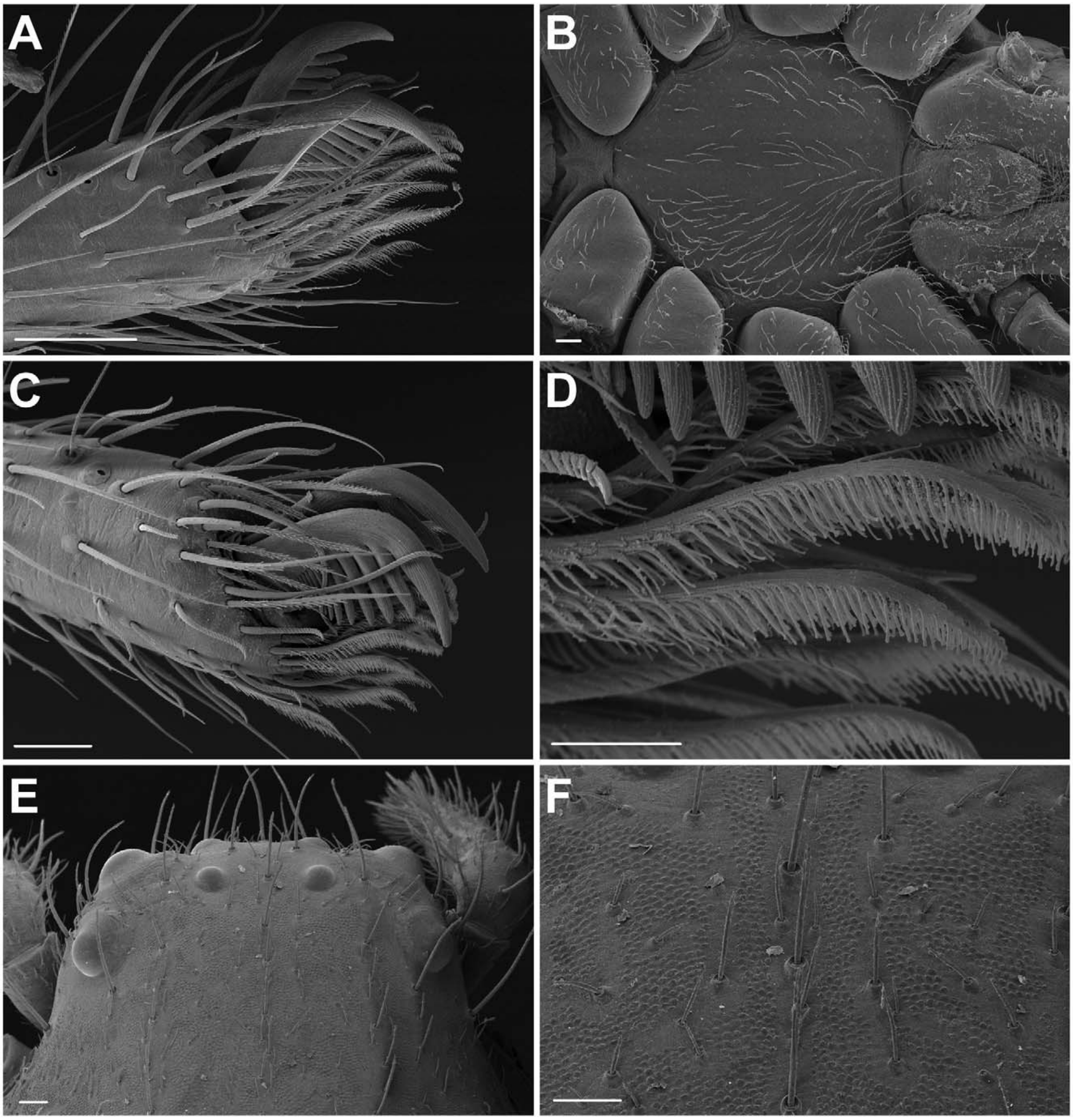

FIGURE 9. Setae of thomisids. A female left leg I *Monaeses* sp. from Sri Lanka, lateral view; B ditto, sternum, ventral view; C female, *Xysticus cristatus*, left leg I; D ditto, detail; E *X. fraternus*, female prosoma, dorsal view; F ditto, detail. Scale bars = 20 µm (D), 50 µm (C) 100 µm (C, D), 1 mm (A, B, E, F).

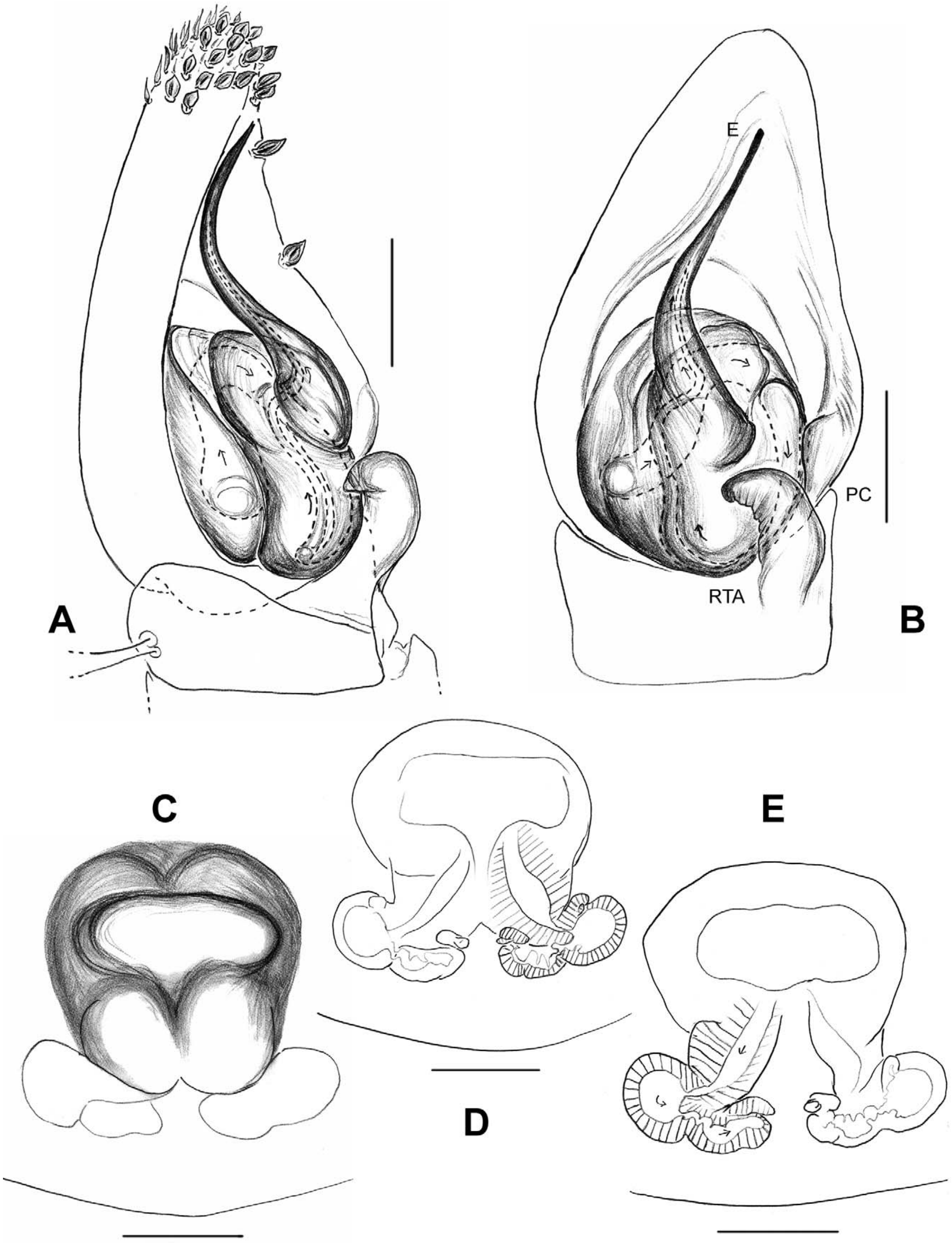

FIGURE 10. *Aphantochilus rogersi*. A–B male palp (A retrolateral, B ventral); C epigynum, ventral; D–E vulva (D ventral, E dorsal). Scale bars = 0.2 mm.

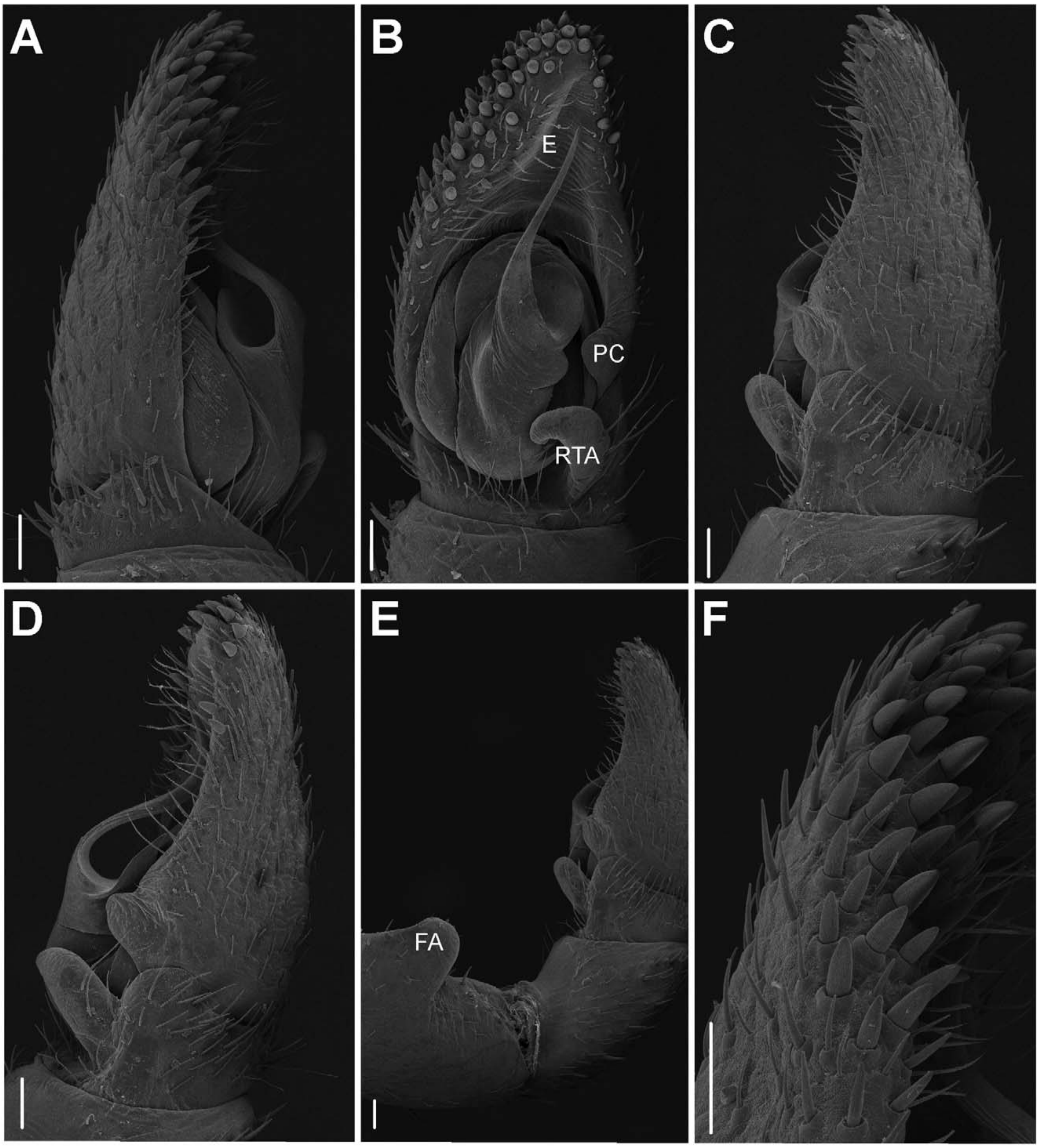

FIGURE 11. Scanning electron micrographs of *Aphantochilus rogersi*. A–E male palp (A prolateral, B ventral, C–E retrolateral); F tip of cymbium. Scale bars = 100 µm.

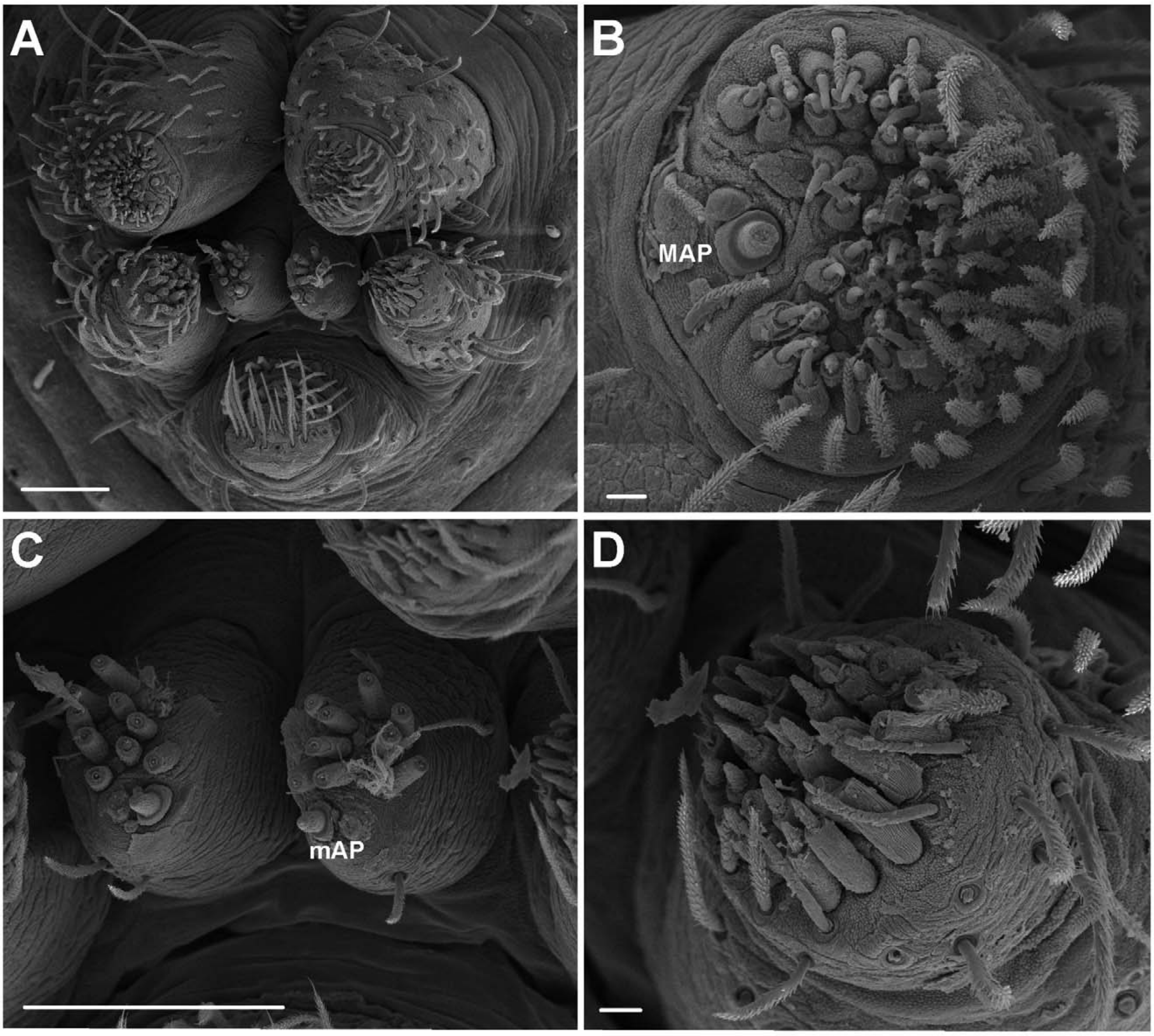

FIGURE 12. Scanning electron micrographs of *Aphantochilus rogersi*, male. A spinnerets; B ALS; C PMS; D PLS. Scale bars = 10 µm (A, C), 100 µm (B, D).

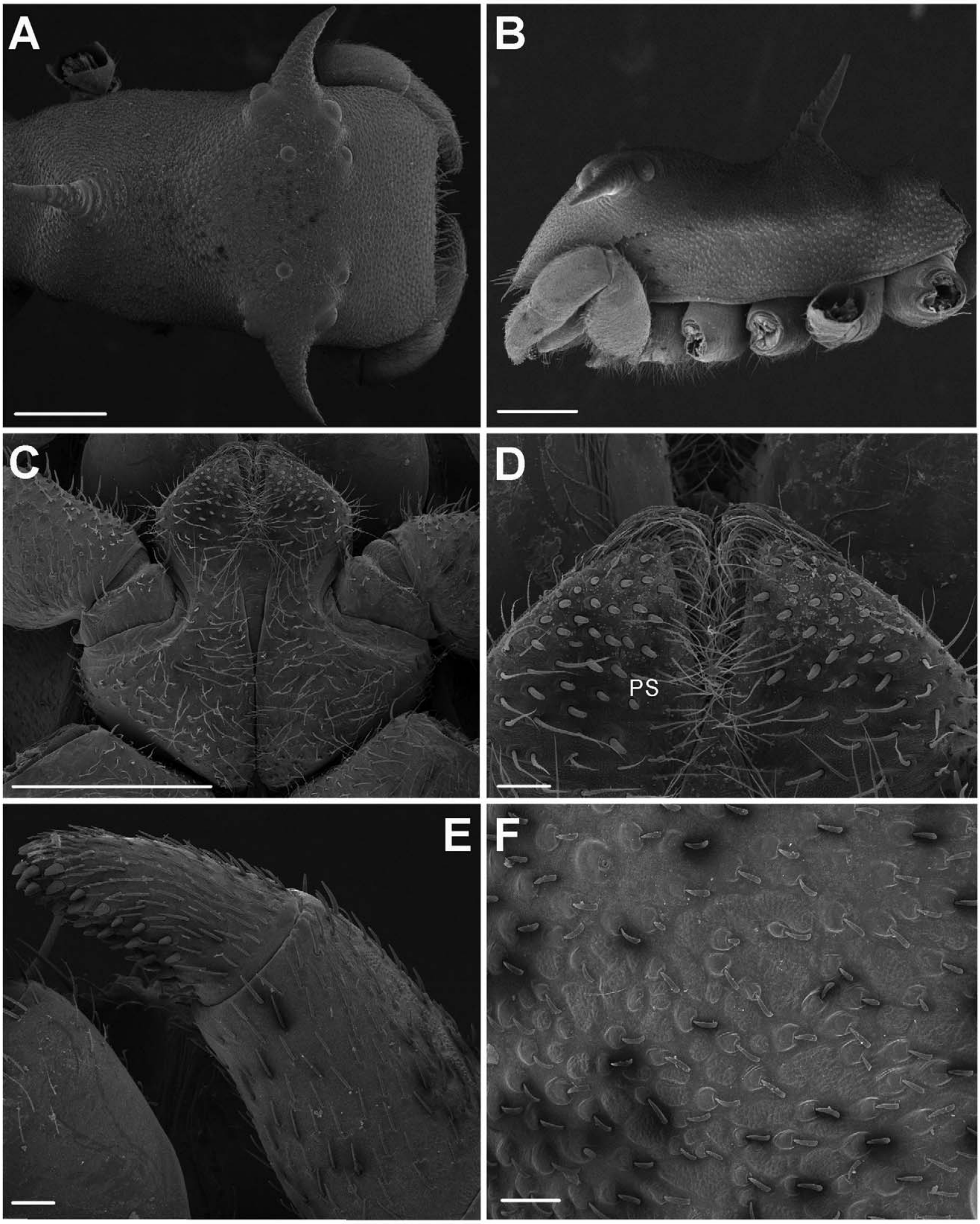

FIGURE 13. Scanning electron micrographs of *Aphantochilus rogersi*, female. A, B, F prosoma (A, F dorsal, B lateral); C endites and labium, ventral view; D detail of endites; E palp, ventral view. Scale bars = 100 µm (D–F), 1 mm (A–C).

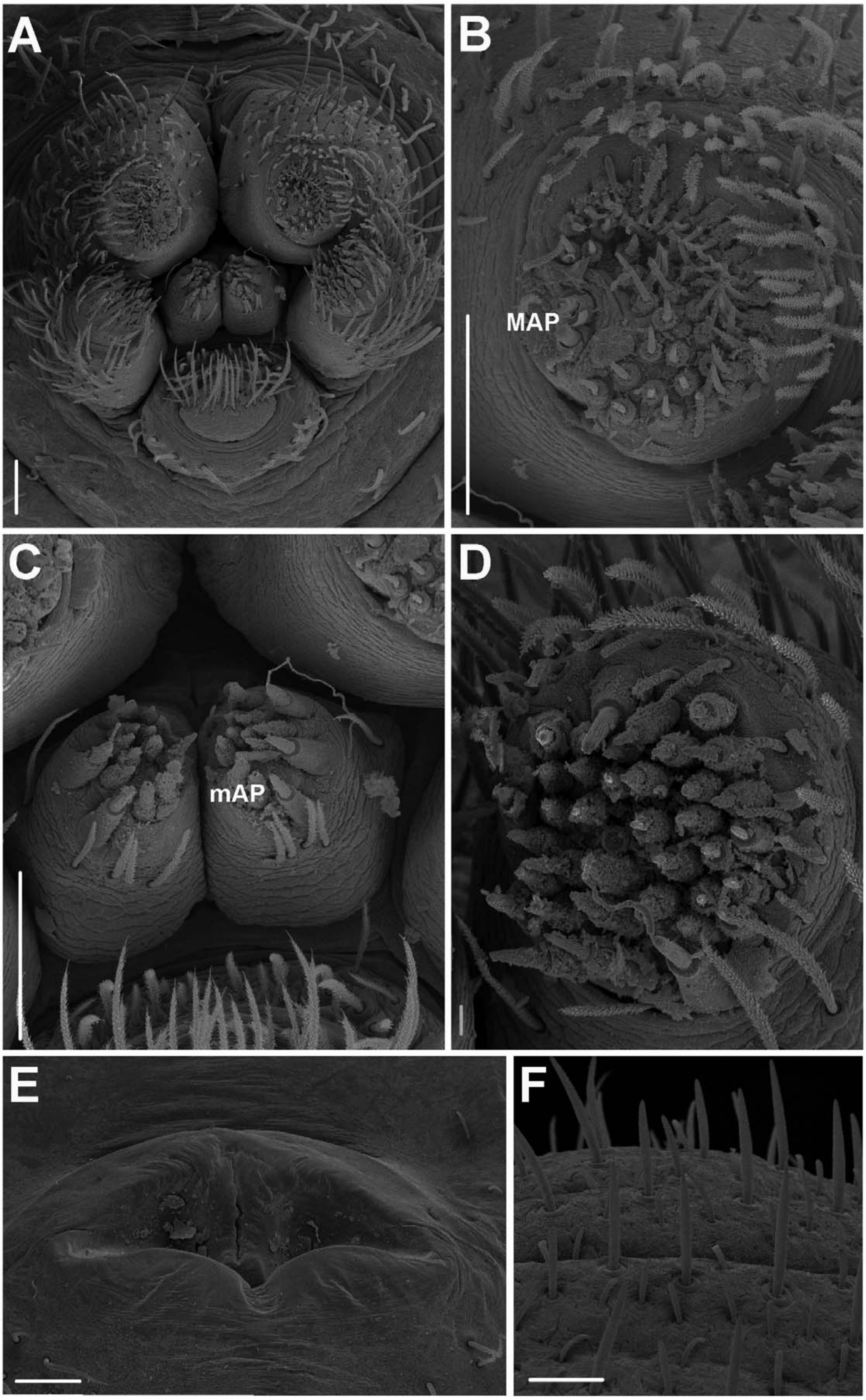

FIGURE 14. Scanning electron micrographs of *Aphantochilus rogersi*, female. A spinnerets; B ALS; C PMS; D PLS; E epigynum, ventral view; F opisthosomal setae, lateral view. Scale bars = 10 µm (D), 100 µm (A–C, E, F).

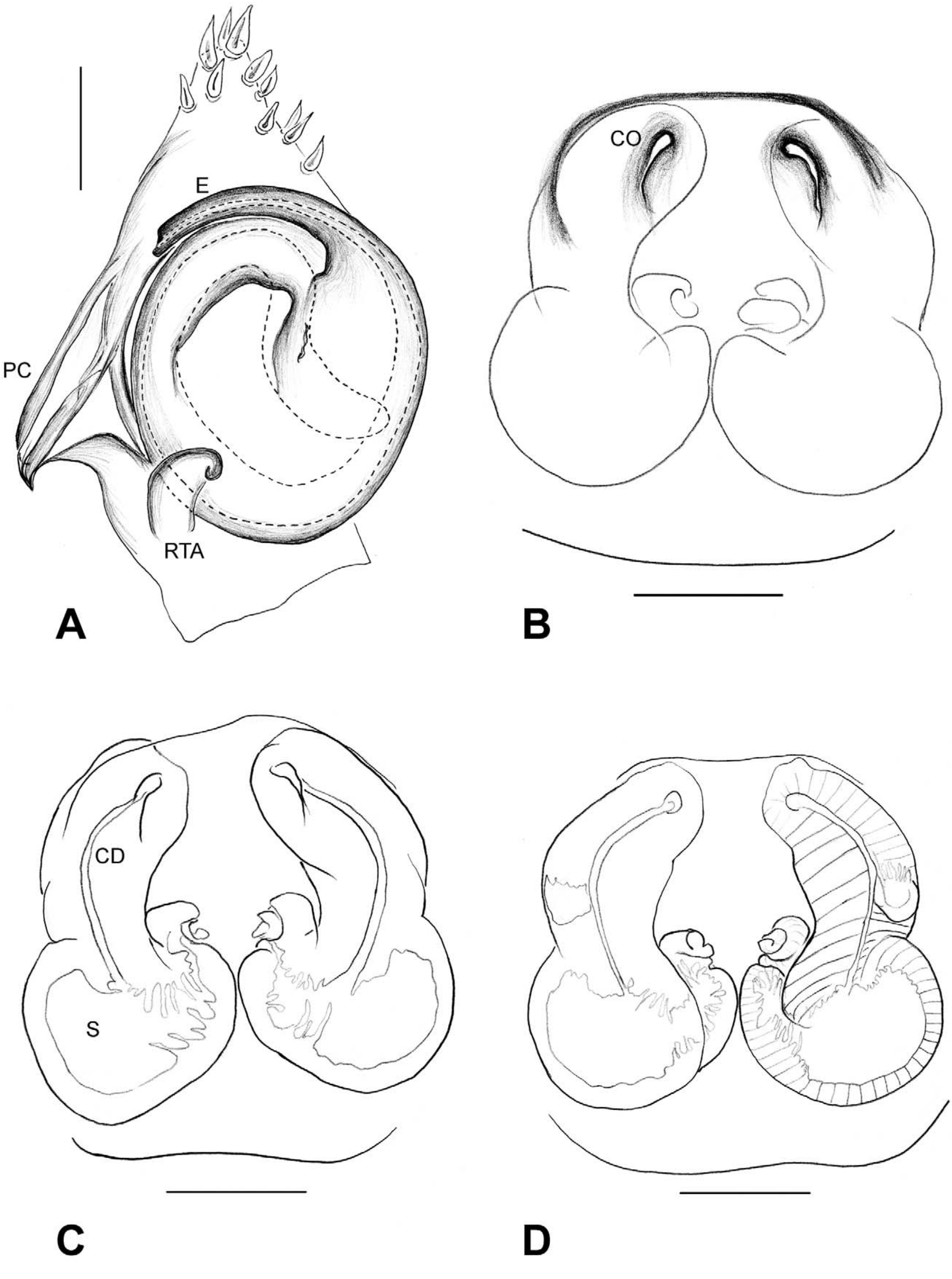

FIGURE 15. *Aphantochilus taurifrons*. A male palp, ventral view; B epigynum, ventral view; C–D vulva (C ventral, D dorsal). Scale bars = 0.1 mm.

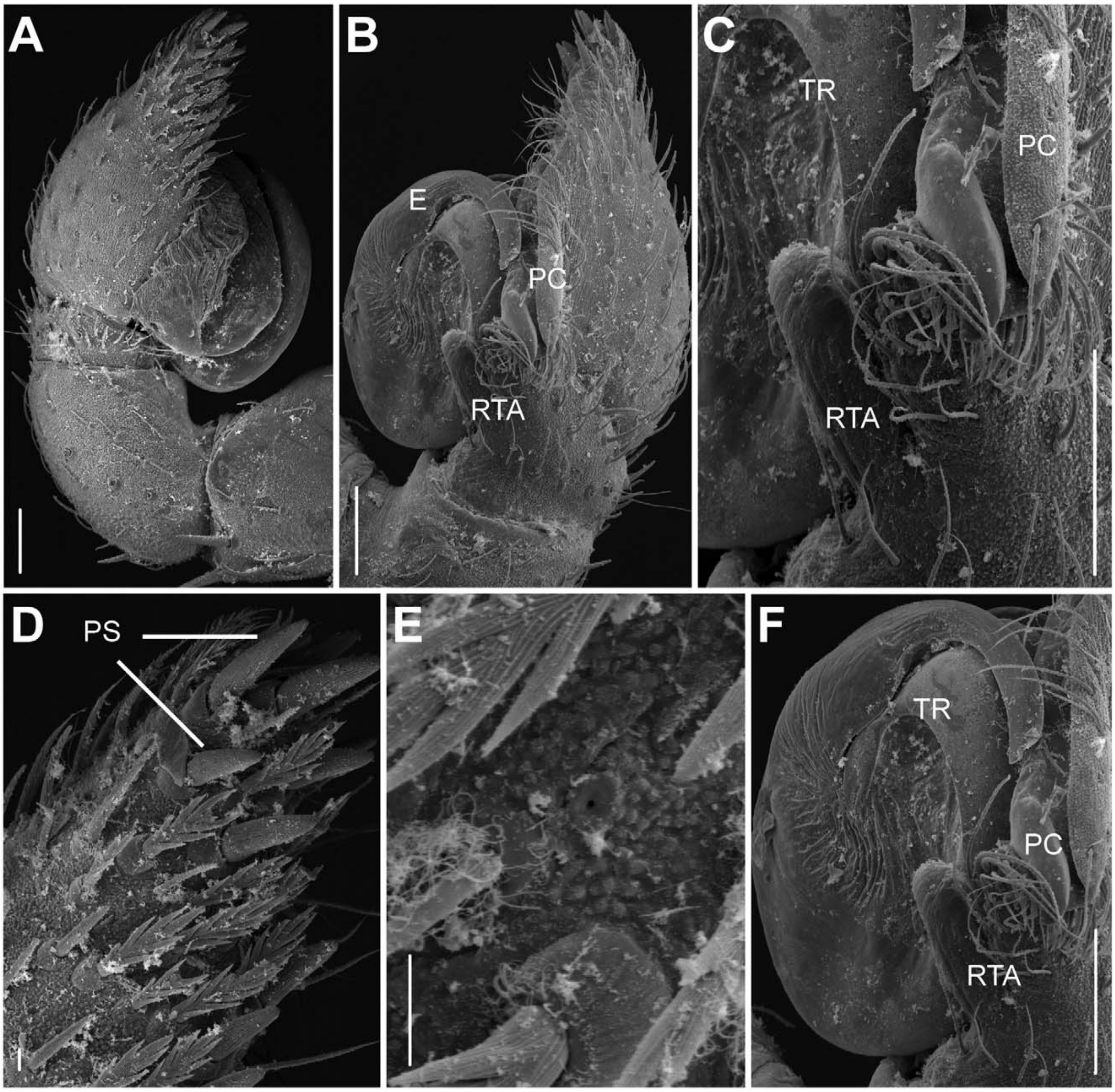

FIGURE 16. Scanning electron micrographs of *Aphantochilus taurifrons*, male. A–C, F, palp (A prolateral, B, C, F retrolateral); D tip of cymbium, prolateral view; E tarsal organ, dorsal view. Scale bars = 10 µm (D, E), 100 µm (A–C, F).

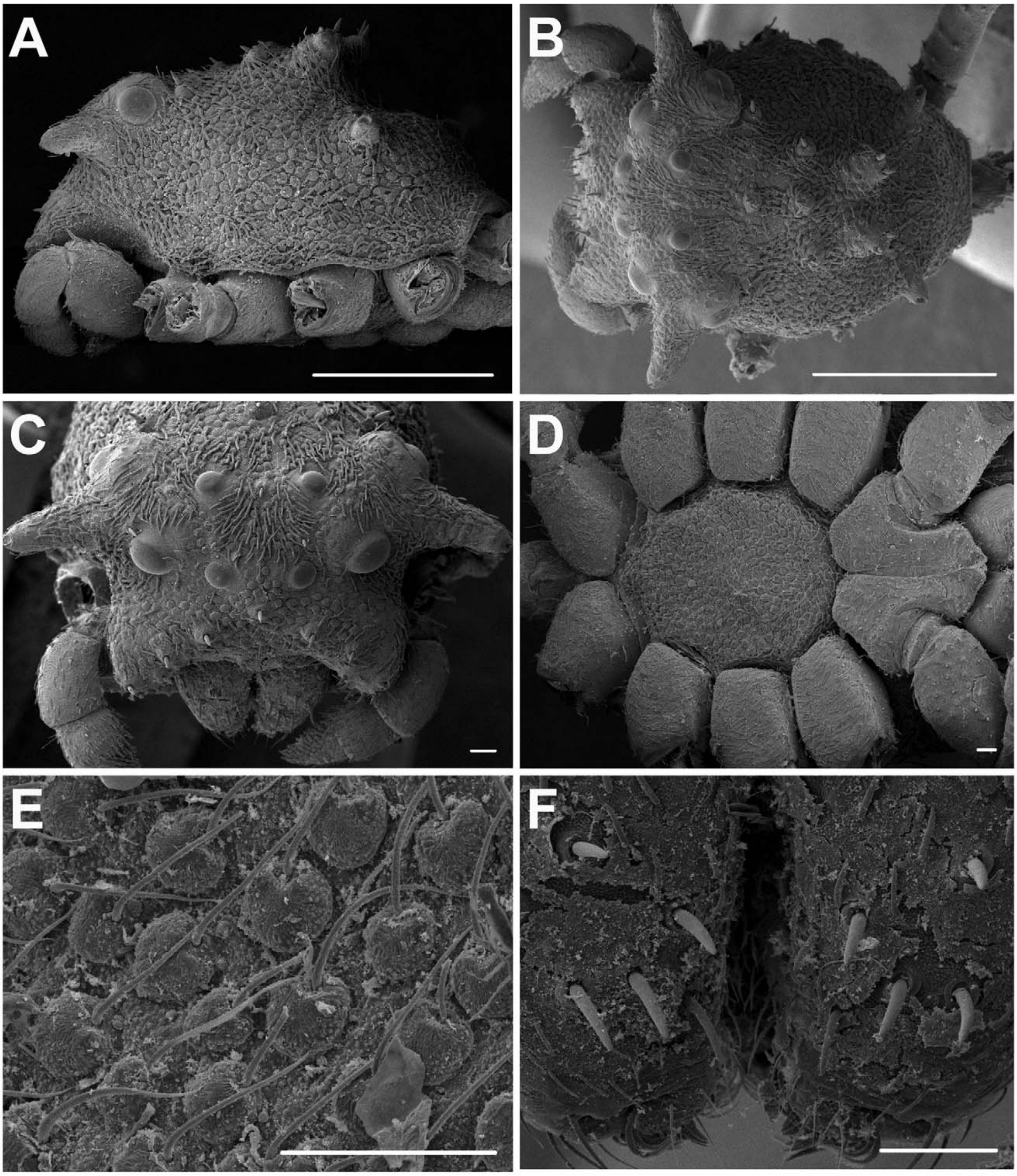

FIGURE 17. Scanning electron micrographs of *Aphantochilus taurifrons*, female. A–D prosoma (A lateral, B dorsal, C frontal, D ventral); E, sternum detail, ventral view; F chelicerae, front view. Scale bars = 100 µm (A, C–F), 1 mm (B).

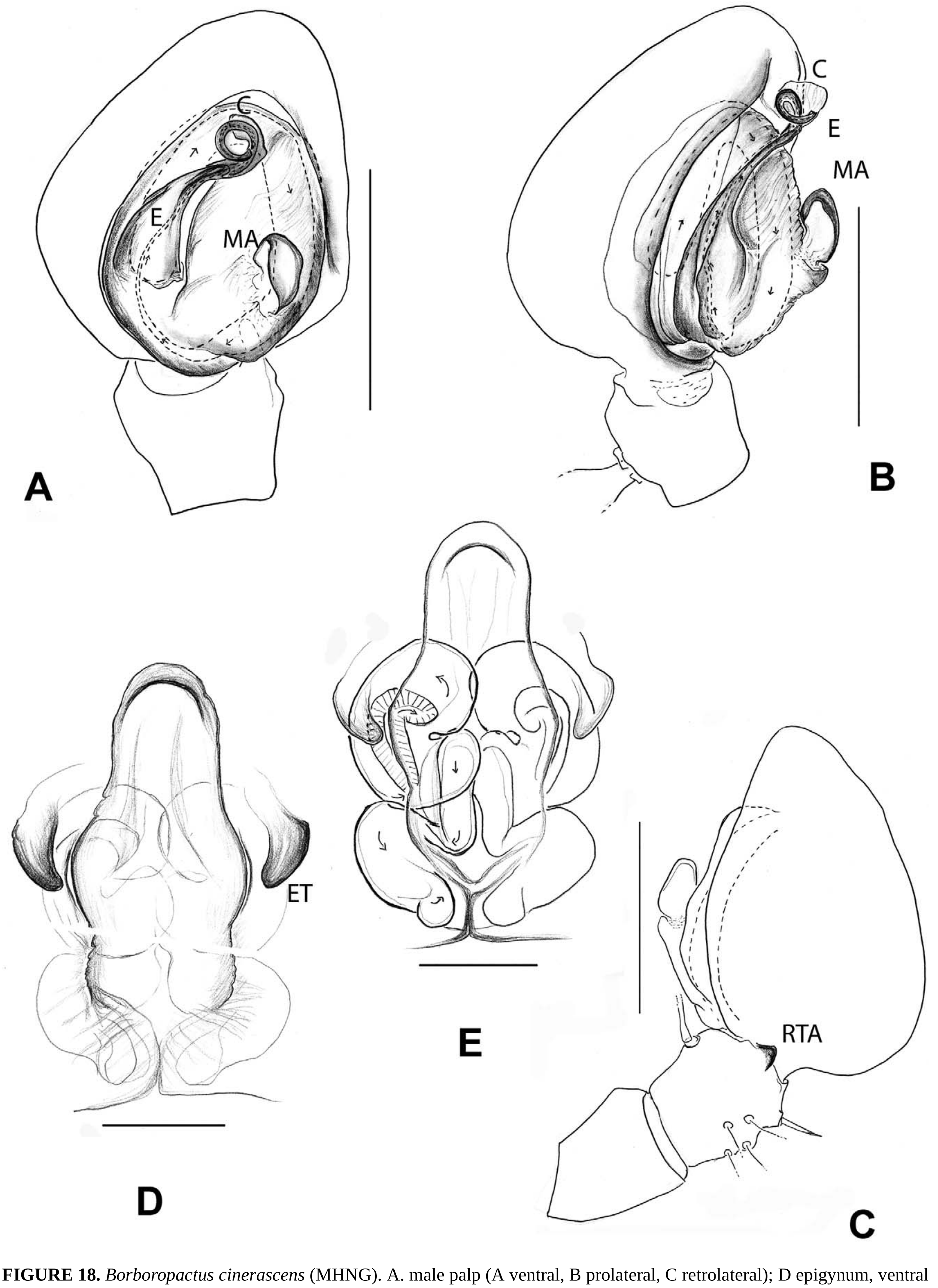

FIGURE 18. *Borboropactus cinerascens* (MHNG). A. male palp (A ventral, B prolateral, C retrolateral); D epigynum, ventral view; E vulva, ventral view. Scale bars = 0.2 mm (D, E), 0.5 mm (A–C).

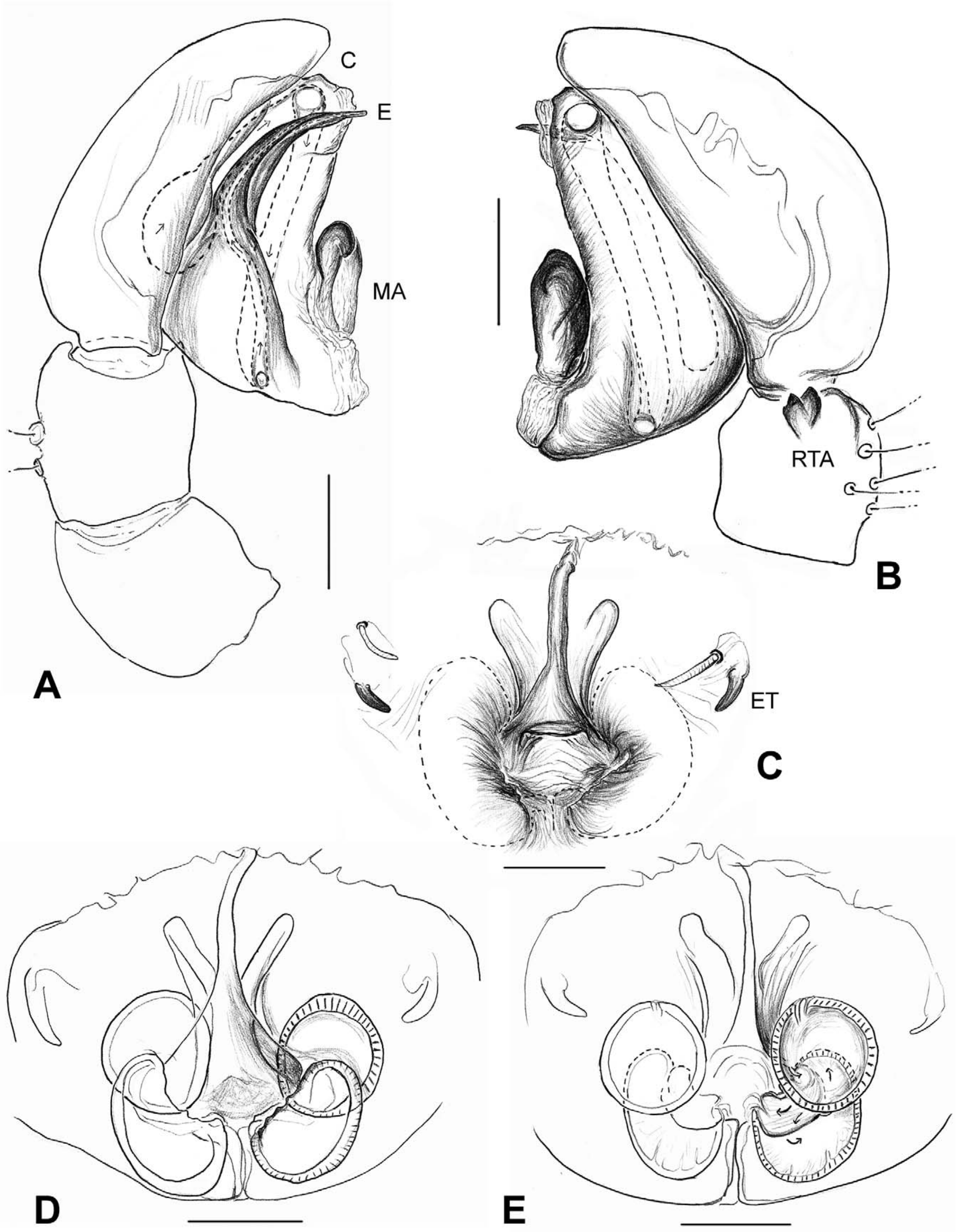

FIGURE 19. *Borboropactus nyerere* **sp. nov.** (USNM). A–B male palp (A prolateral, B retrolateral); C epigynum, ventral view; D–E vulva (D ventral, E dorsal). Scale bars = 0.1 mm.

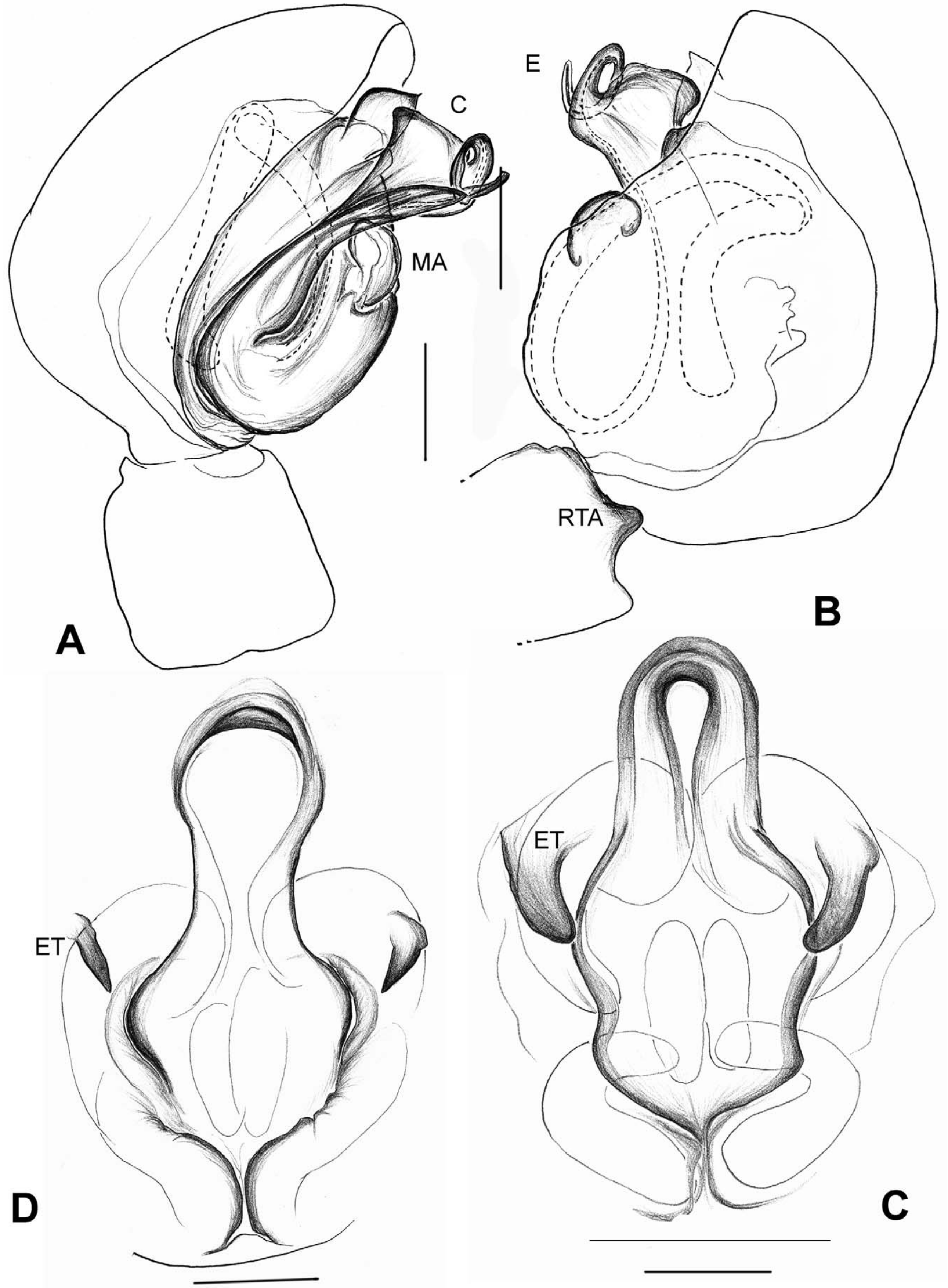

FIGURE 20. A, B, D *Borboropactus bituberculatus*. C *Borboropactus squalidus* (MNHN 5045/1572). A–B male palp from Irian Jaya, Waigeo Island (A prolateral, B retrolateral); C, D epigynum, ventral view (MNHN 5460/1572). Scale bars = 0.2 mm.

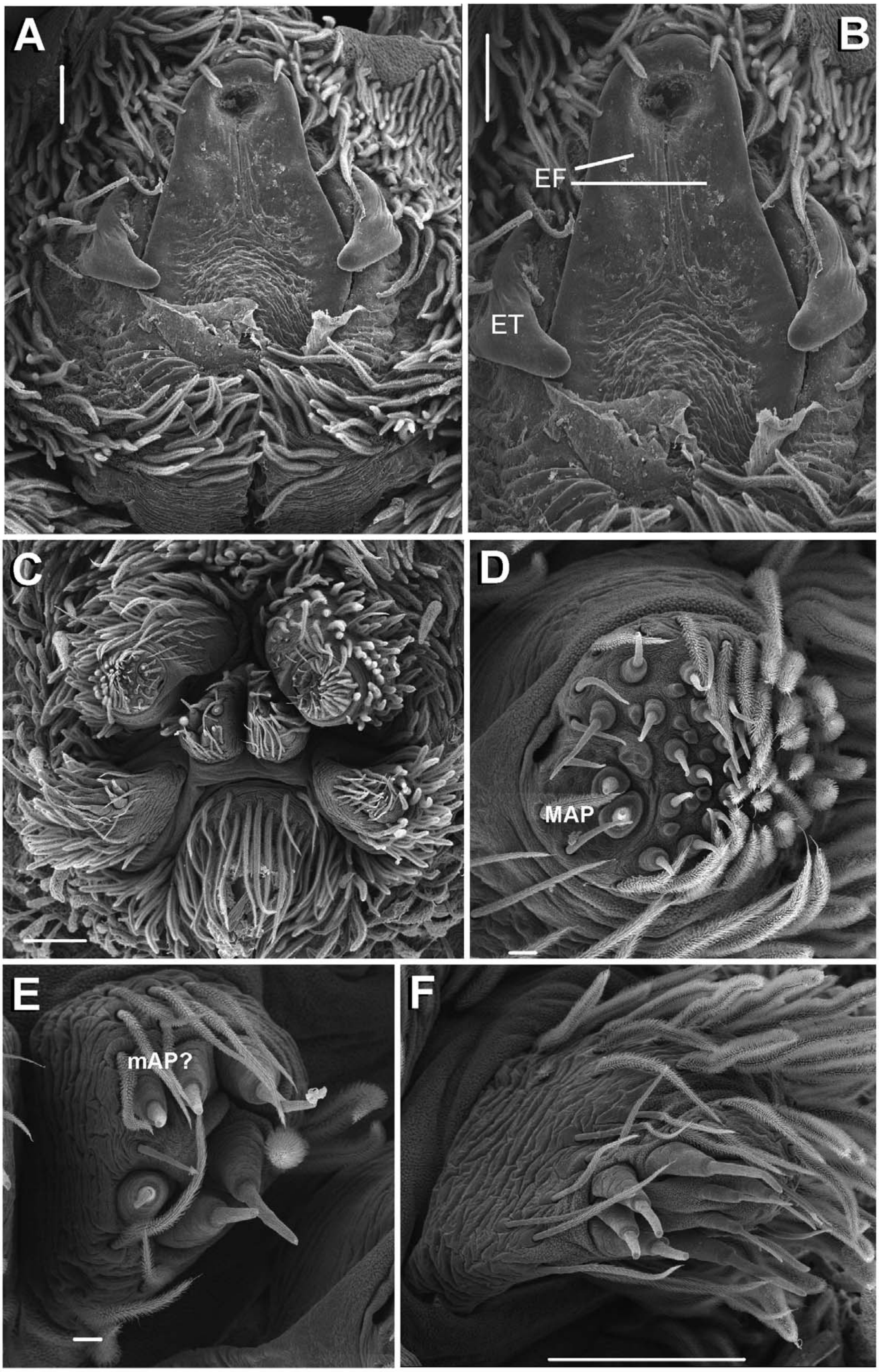

FIGURE 21. Scanning electron micrographs of *Borboropactus* sp. (MHNG). A, B epigynum, ventral view; C spinnerets; D ALS; E PMS; F PLS. Scale bars = 10 µm (D, E), 100 µm (A–C, F).

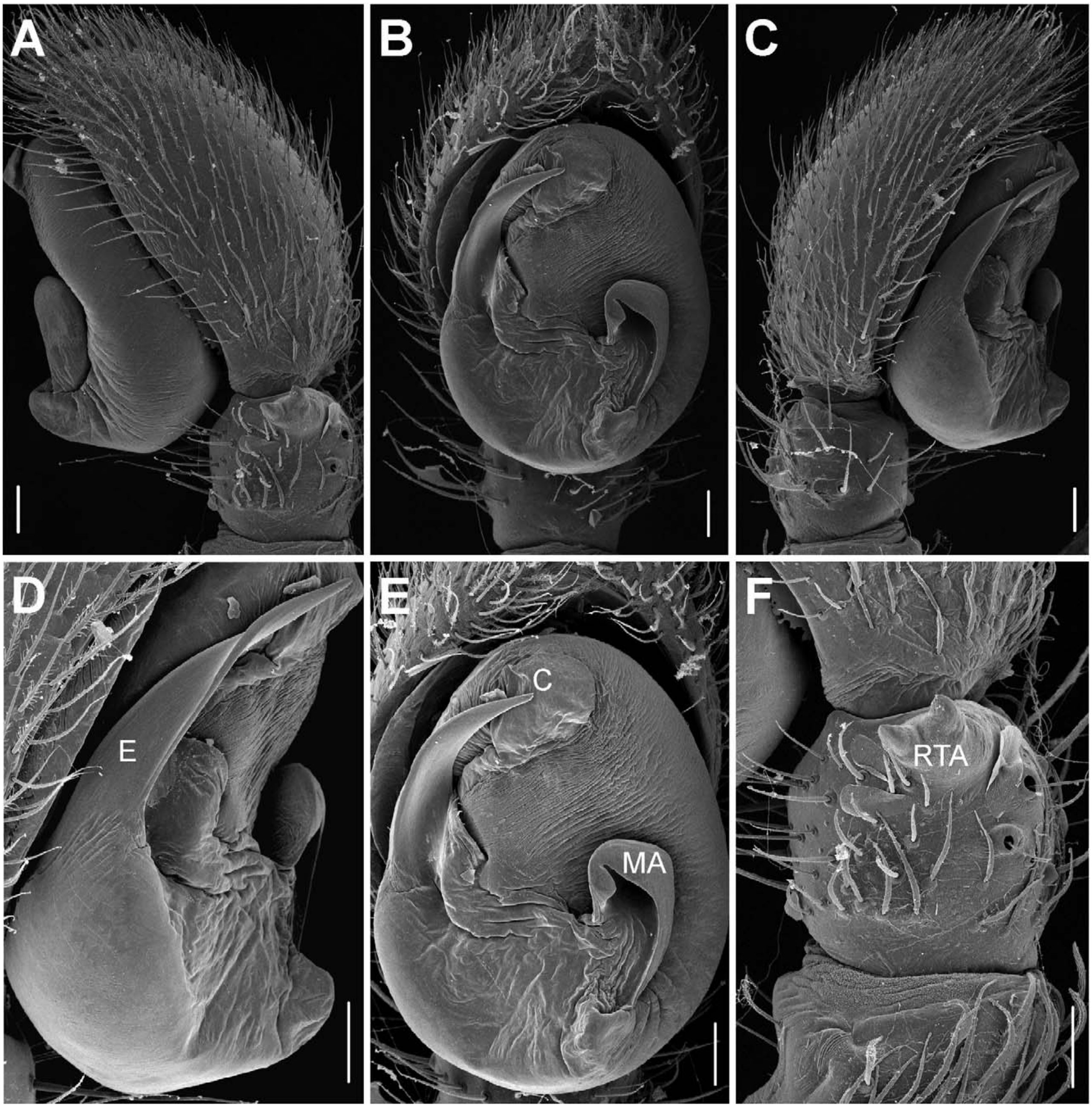

FIGURE 22. Scanning electron micrographs of *Borboropactus nyerere* **sp. nov.** (USNM). A–F male palp (A, F retrolateral, B, E ventral, C, D prolateral). Scale bars = 100 µm.

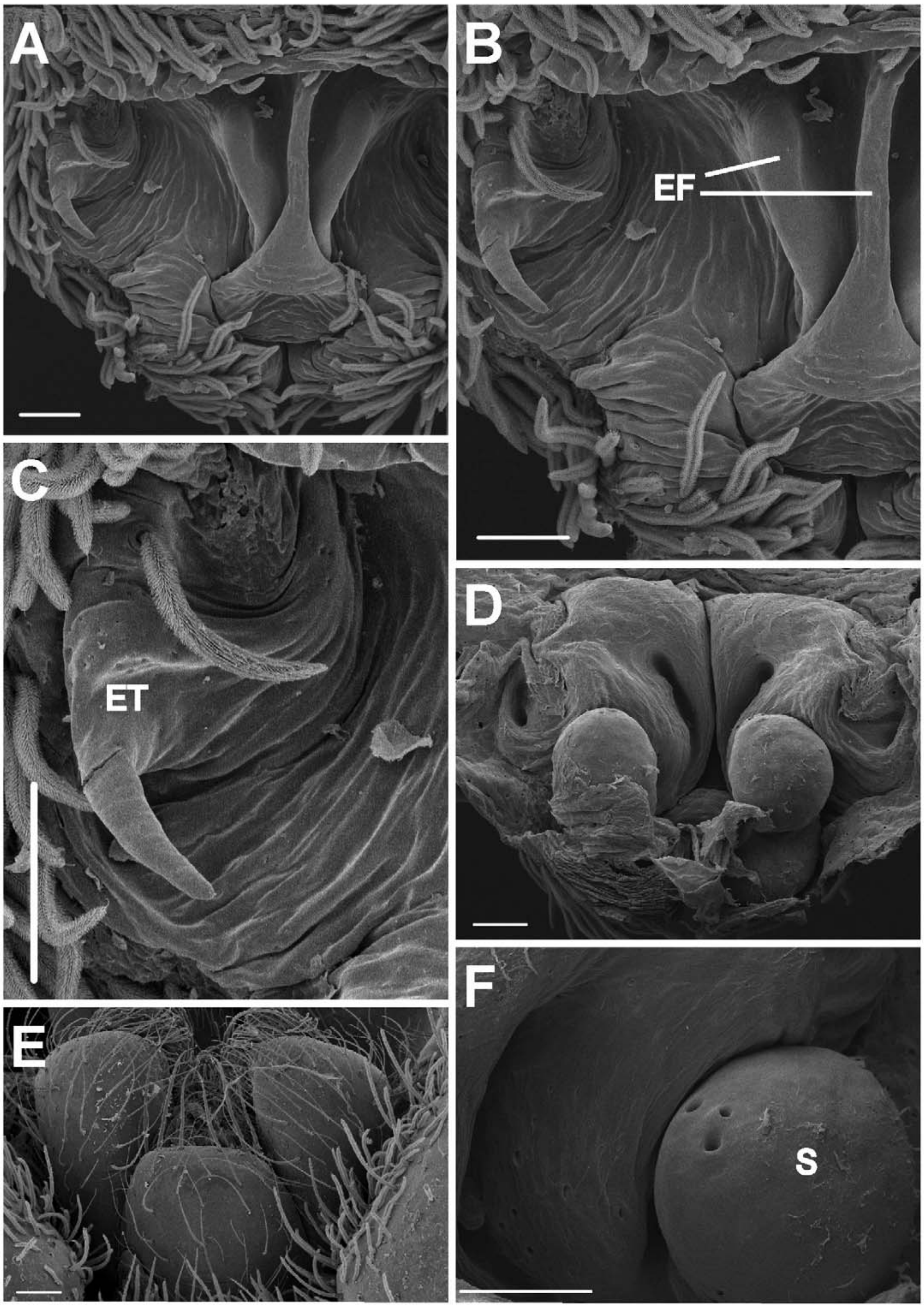

FIGURE 23. Scanning electron micrographs of *Borboropactus nyerere* **sp. nov.** (USNM). A–C epigynum, ventral view; D, F vulva, dorsal view; E Labrum, ventral view. Scale bars = 100 µm.

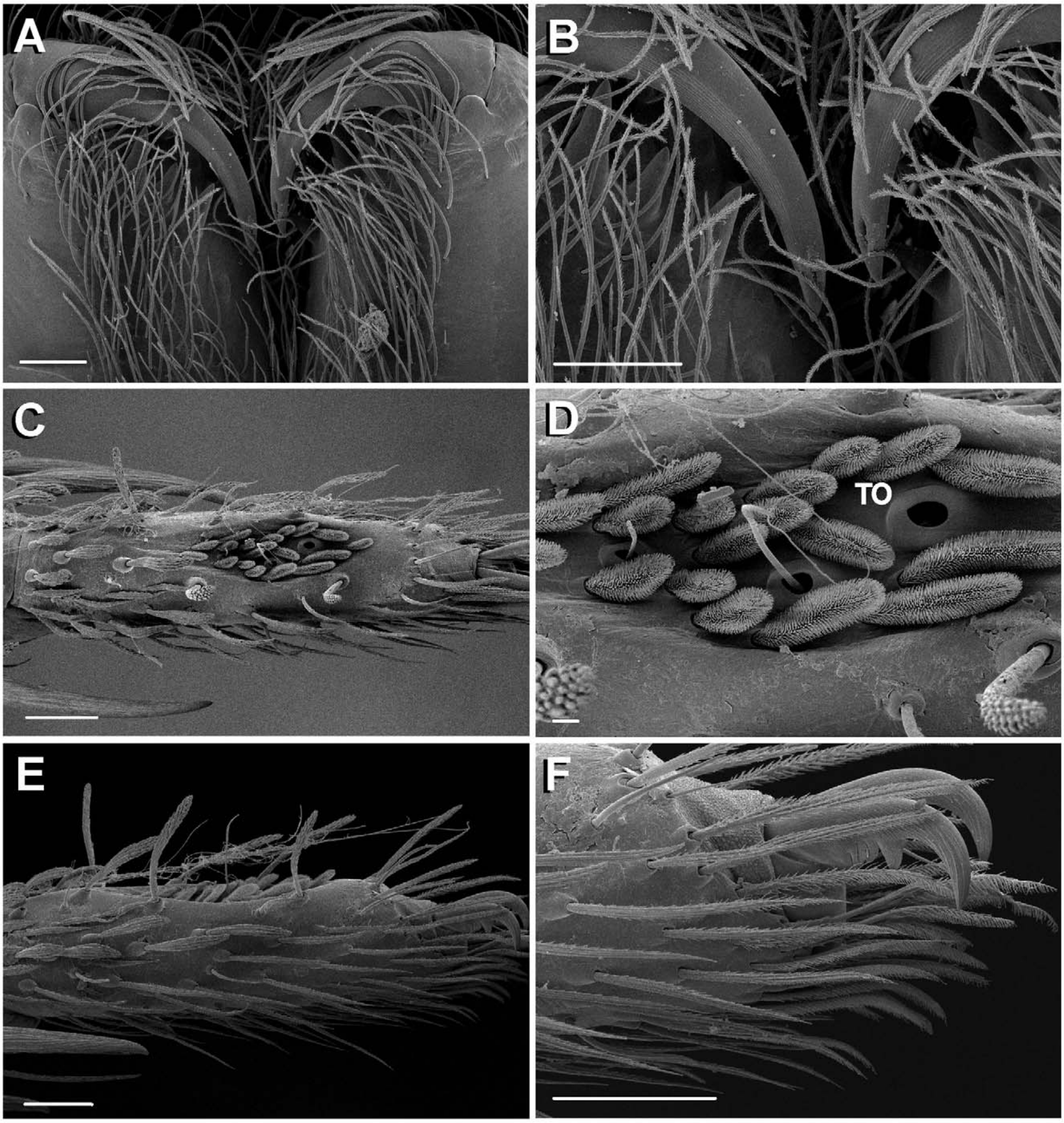

FIGURE 24. Scanning electron micrographs of *Borboropactus nyerere* **sp. nov.** (USNM), female. A, B Chelicera; C–F left leg 1 (C, D dorsal, E, F lateral). Scale bars = 10 µm (D,) 100 µm (A–C, E, F).

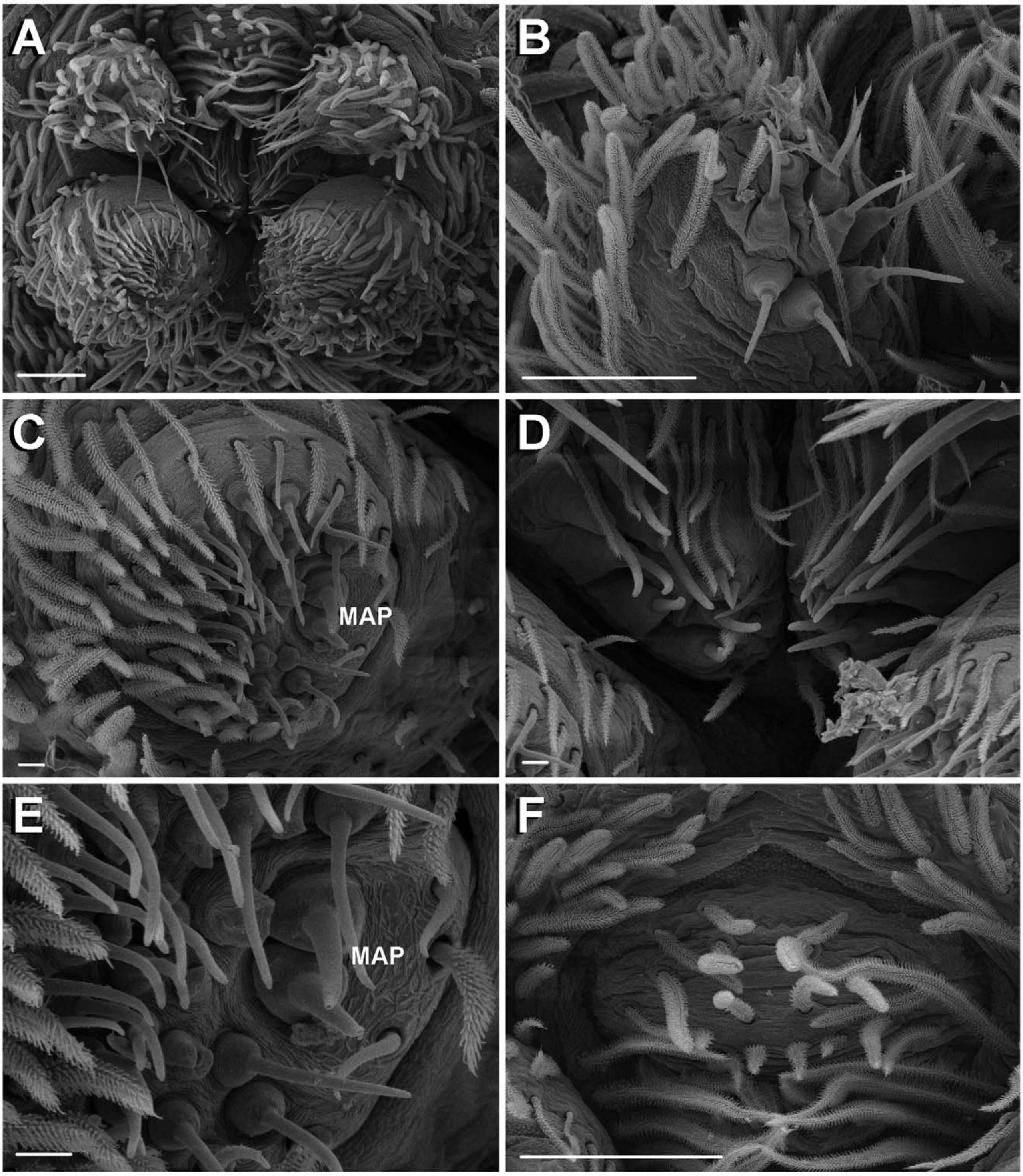

Figure 25. Scanning electron micrographs of *Borboropactus nyerere* **sp. nov.** (USNM), female. A spinnerets; B PLS; C, E ALS; D PMS; F anal tubercle. Scale bars = 10 µm (C, D, E), 100 µm (A, B, E, F).

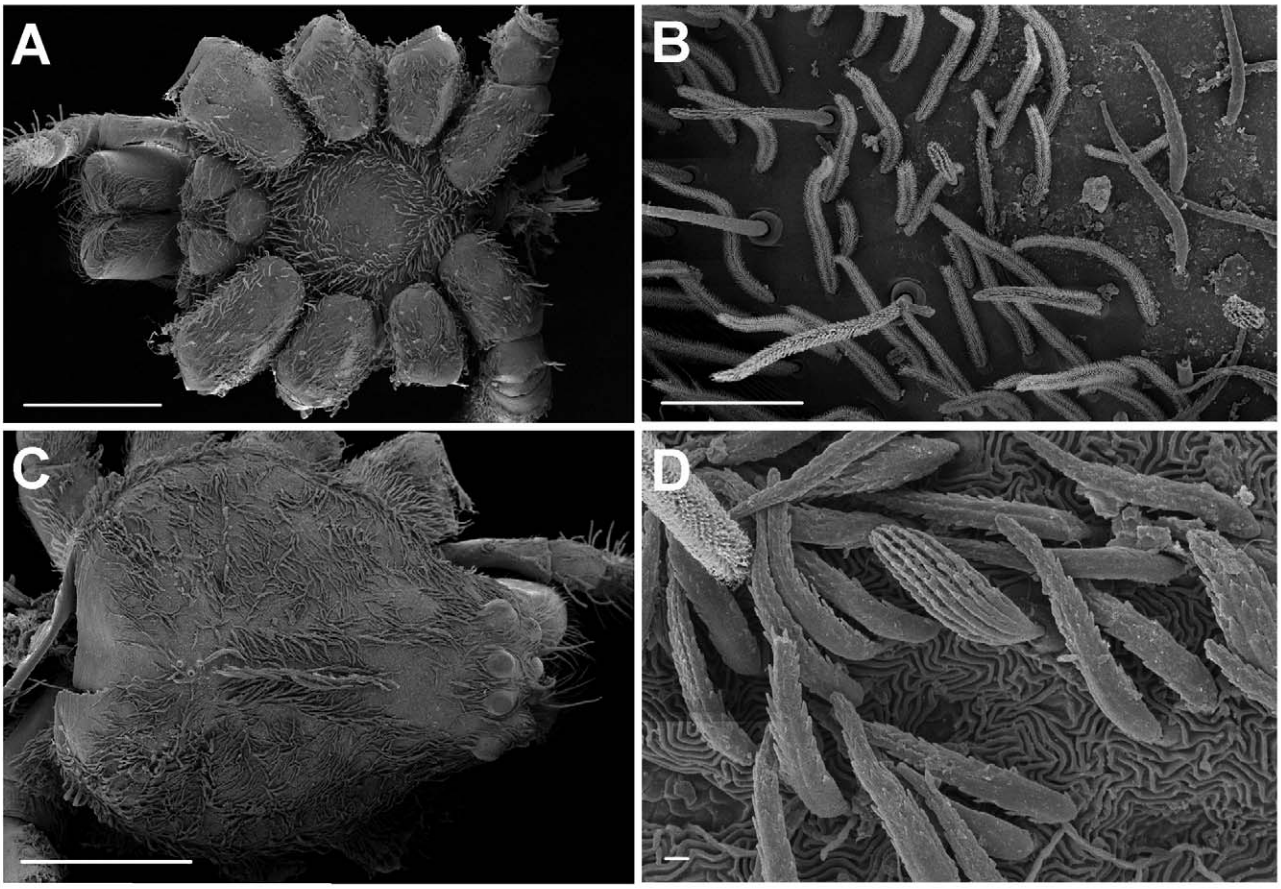

FIGURE 26. Scanning electron micrographs of *Borboropactus nyerere* **sp. nov.** (USNM). A, C, D prosoma (A ventral, C dorsal, D details); B Sternum, detail. Scale bars = 10 µm (D), 100 µm (B), 1 mm (A, C).

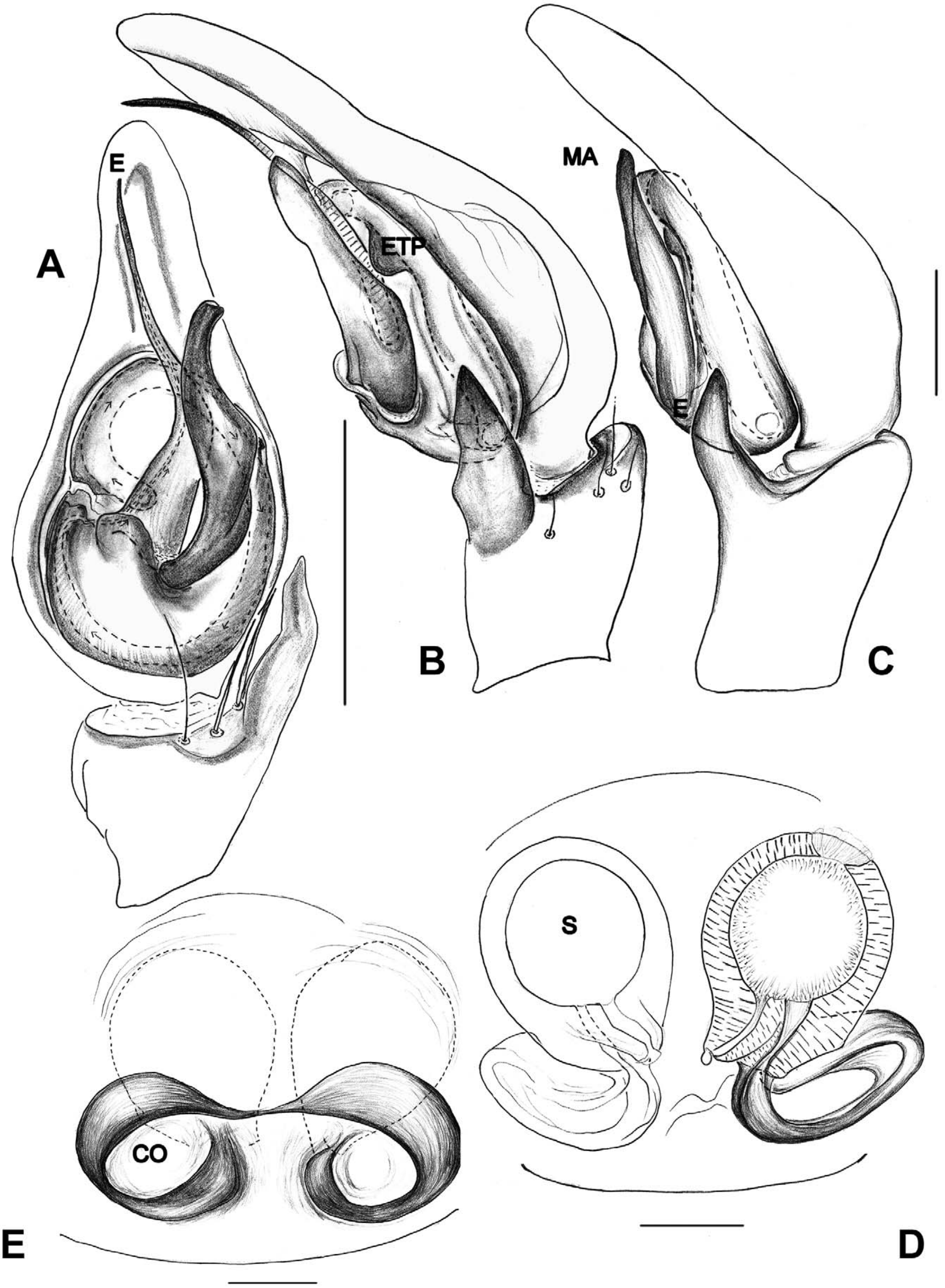

FIGURE 27. *Cebrenninus rugosus*. A, B male from Thailand (MHNG), left palp (A ventral, B retrolateral); C male palp, retrolateral view (lectotype MNHN 8652/1572); D, E female from Thailand (D epigynum, ventral view, E vulva, dorsal view). Scale bars = 0.1 mm (E, D) 0.2 mm (C), 0.5 mm (A, B).

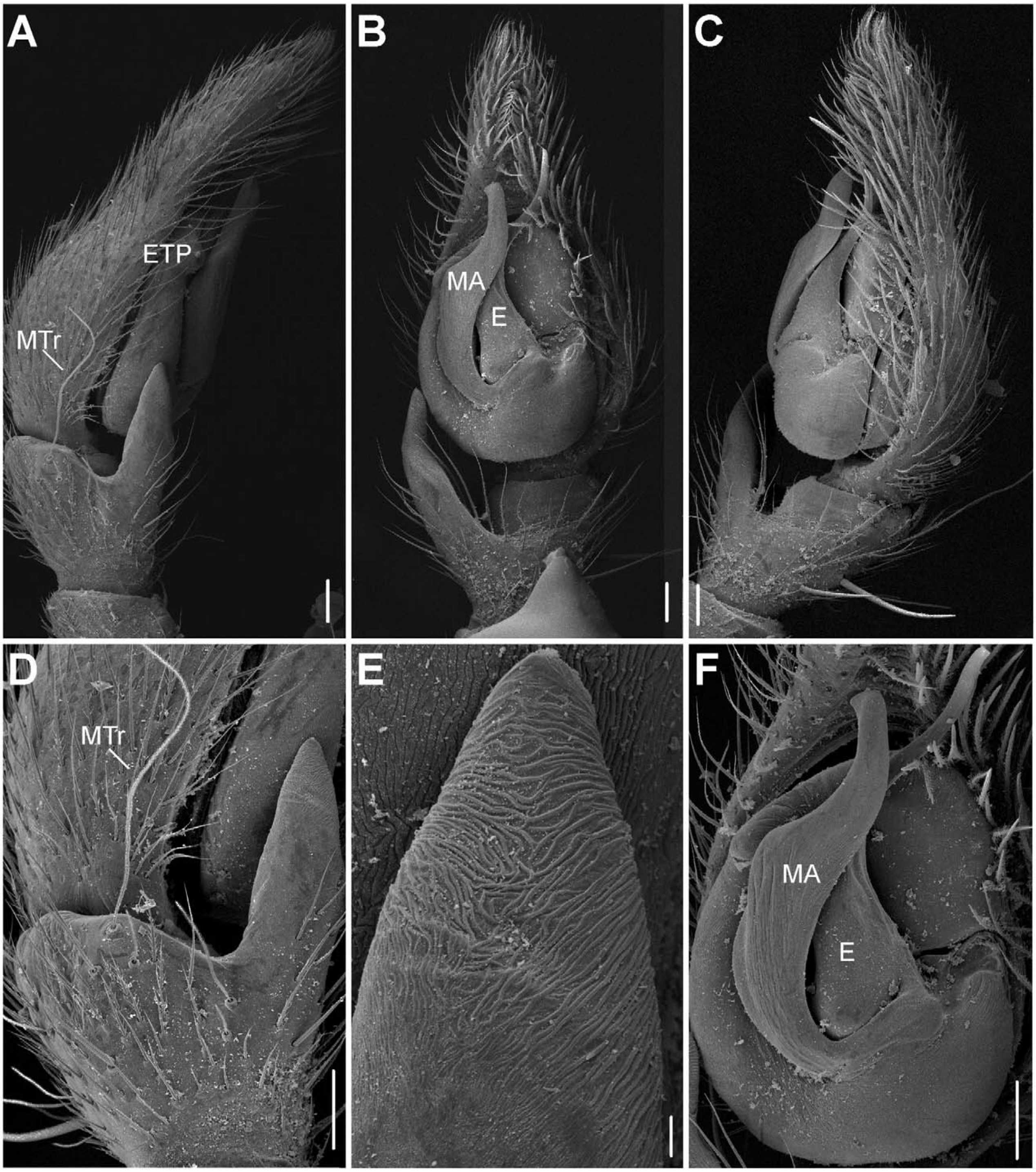

FIGURE 28. Scanning electron micrographs of *Cebrenninus rugosus* male from Sumatra (MHNG). A–F right male palp (A, D, E retrolateral, B, F ventral, C prolateral). Scale bars = 10 µm (E), 100 µm (A–D, F).

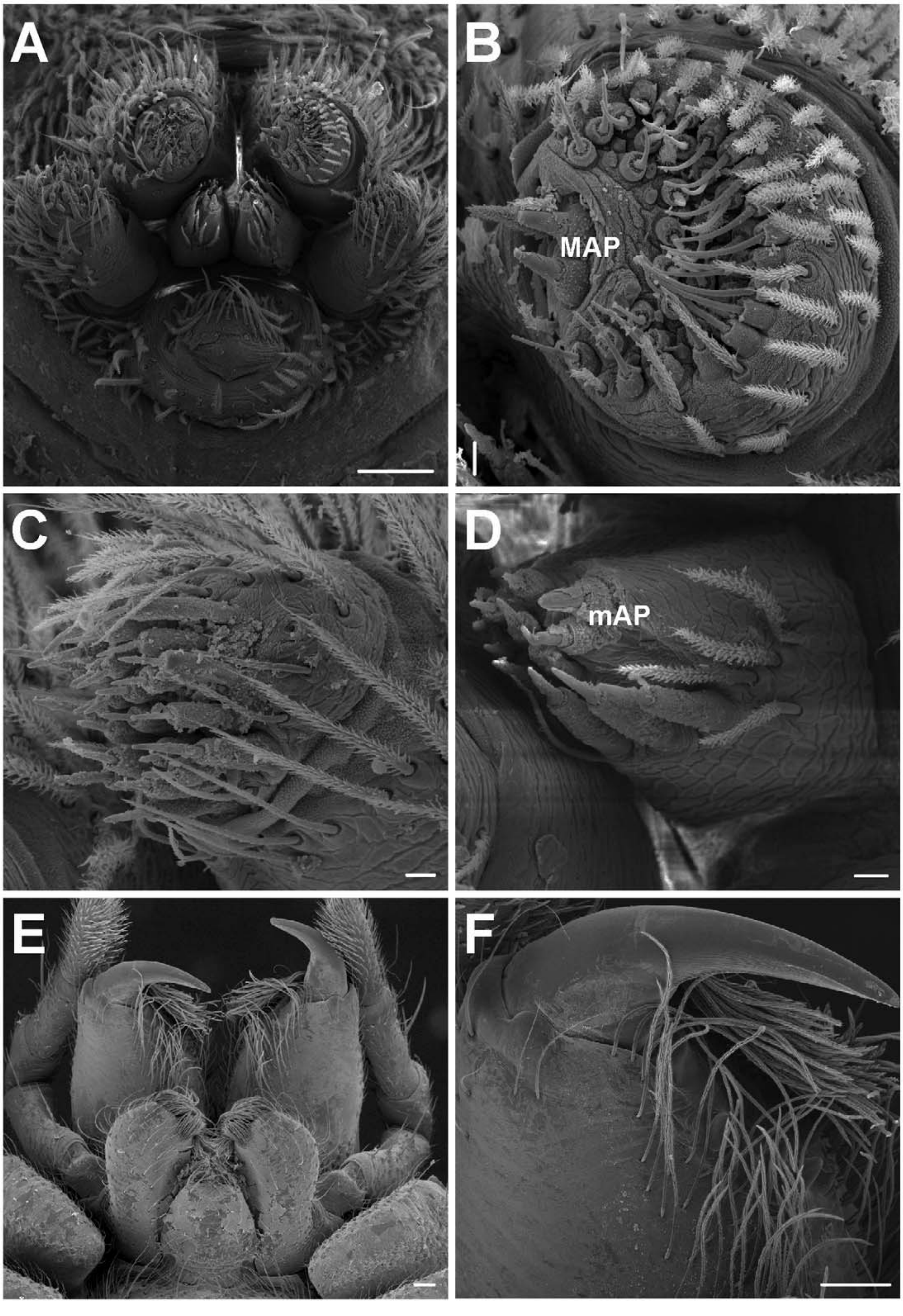

FIGURE 29. Scanning electron micrographs of *Cebrenninus rugosus* female from Sumatra (MHNG). A Spinnerets; B ALS; C PMS; D PLS; E Labium, ventral view; F Chelicera, ventral view. Scale bars = 10 µm (B, D–F), 100 µm (A, C).

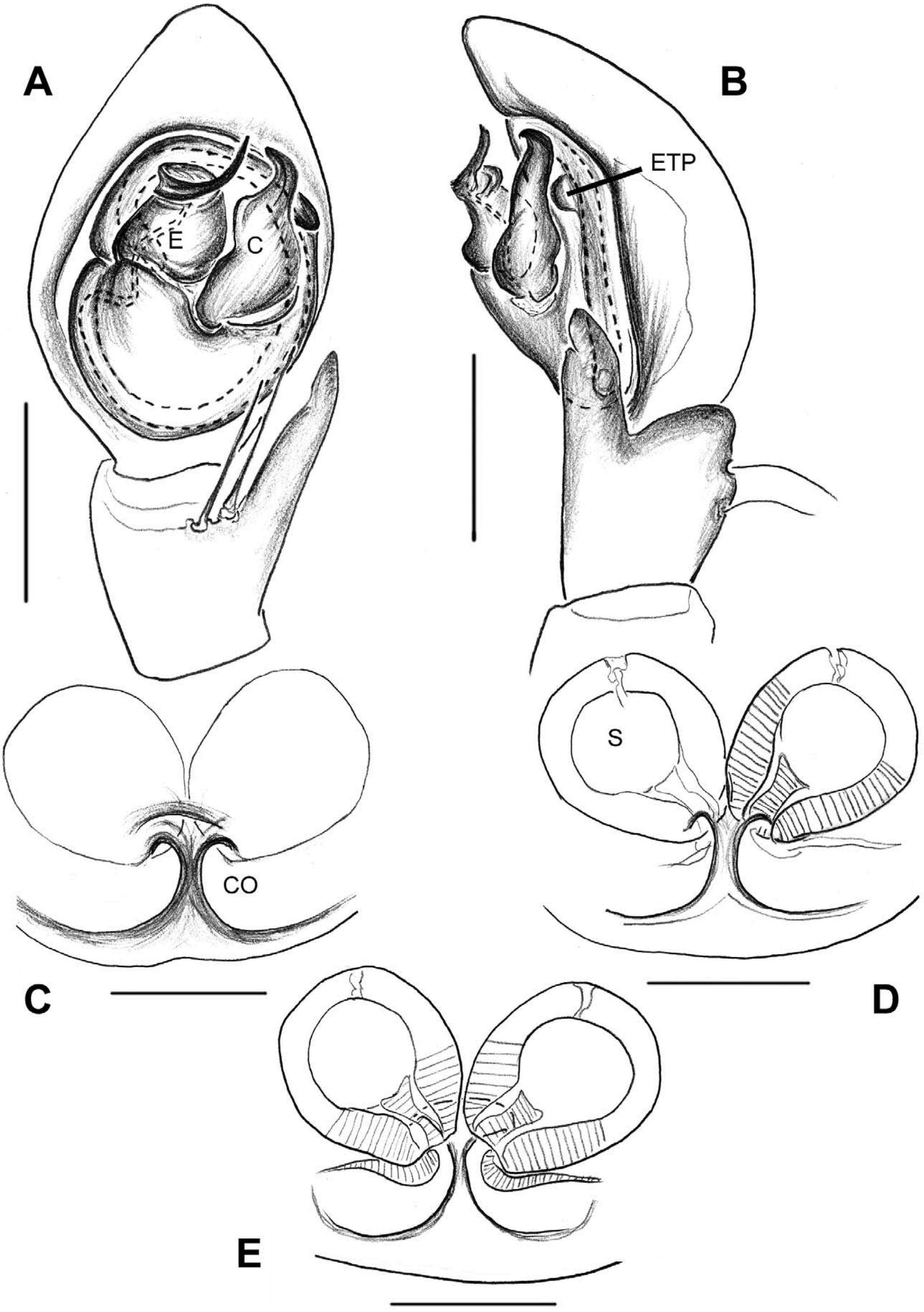

FIGURE 30. *Cebrenninus srivijaya* **sp. nov.**, male holotype and female paratype from Sumatra (MHNG). A, B male palp (A ventral, B retrolateral); C epigynum, ventral view; D–E vulva (D ventral, E dorsal). Scale bars = 0.1 mm (C–E), 0.2 mm (A, B).

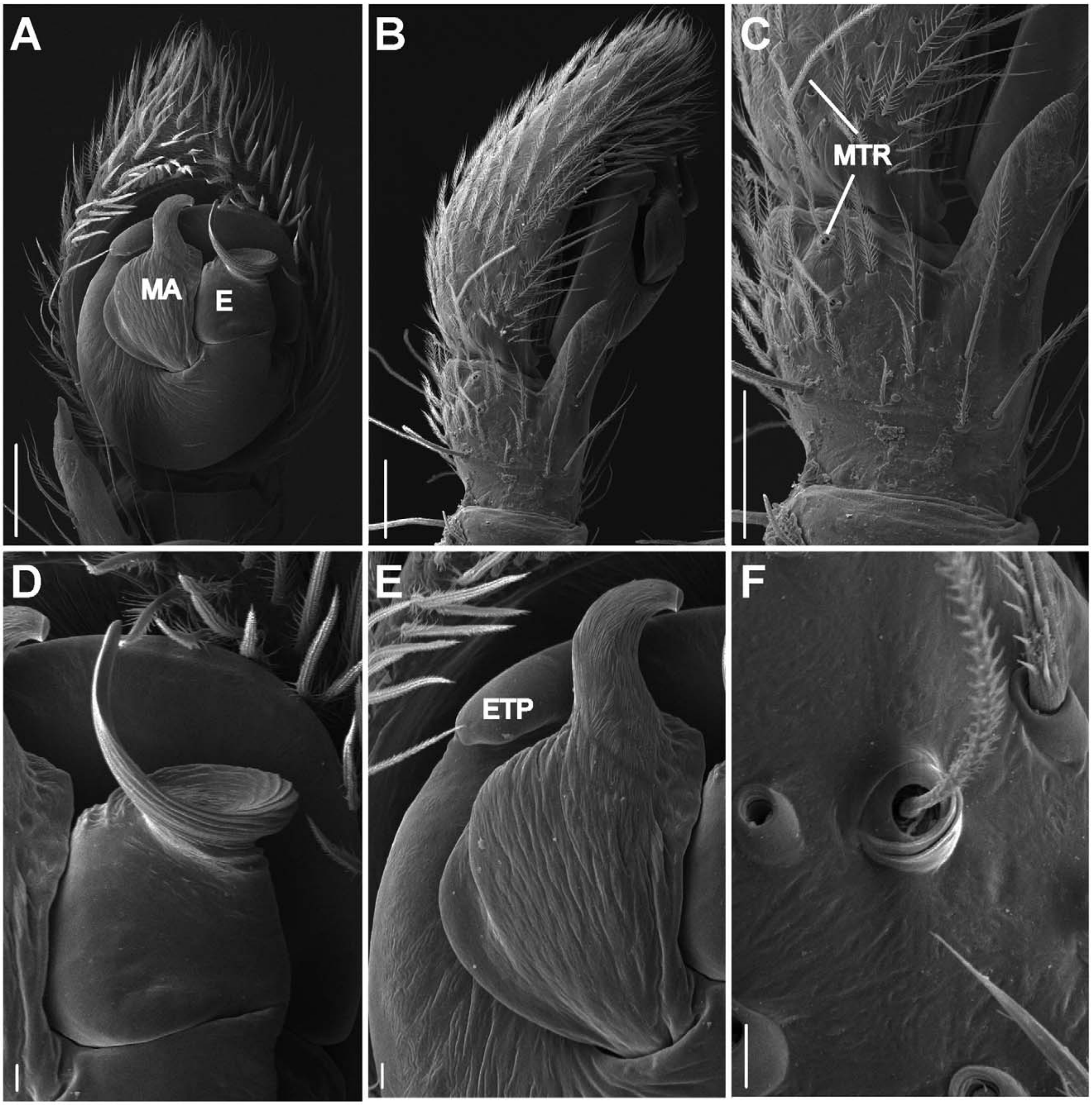

FIGURE 31. Scanning electron micrographs of *Cebrenninus srivijaya* **sp. nov.**, male paratype from Sumatra (MHNG). A–F Right male palp (A, D, E ventral, B, C, F retrolateral). Scale bars = 10 µm (A–C), 100 µm (D–F).

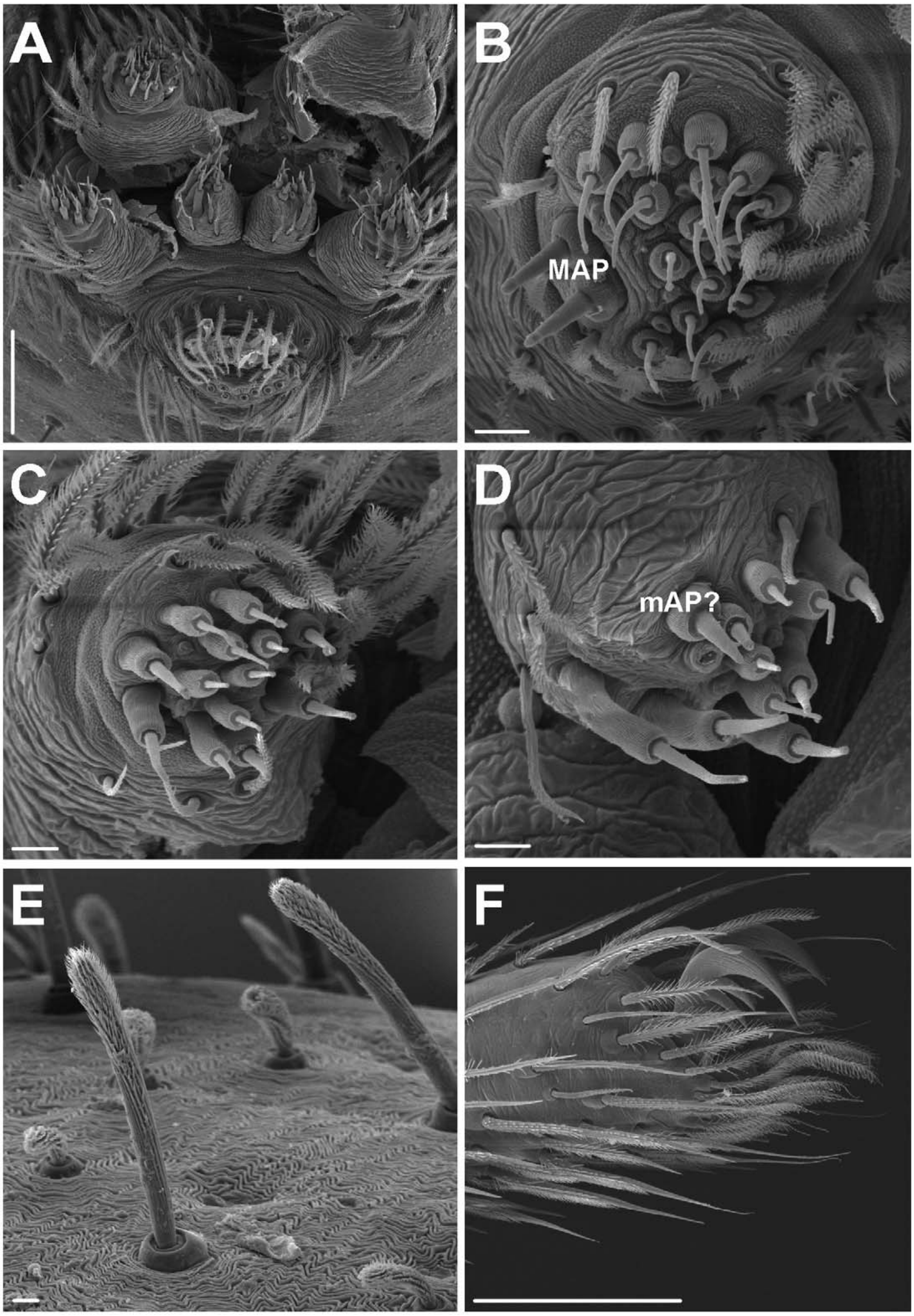

FIGURE 32. Scanning electron micrographs of *Cebrenninus srivijaya* **sp. nov.**, female paratype from Sumatra (MHNG). A Spinnerets; B ALS; C PLS; D PMS; E opisthosoma, dorsal view; F Left leg 1, lateral view. Scale bars = 10 µm (B –E), 100 µm (A, F).

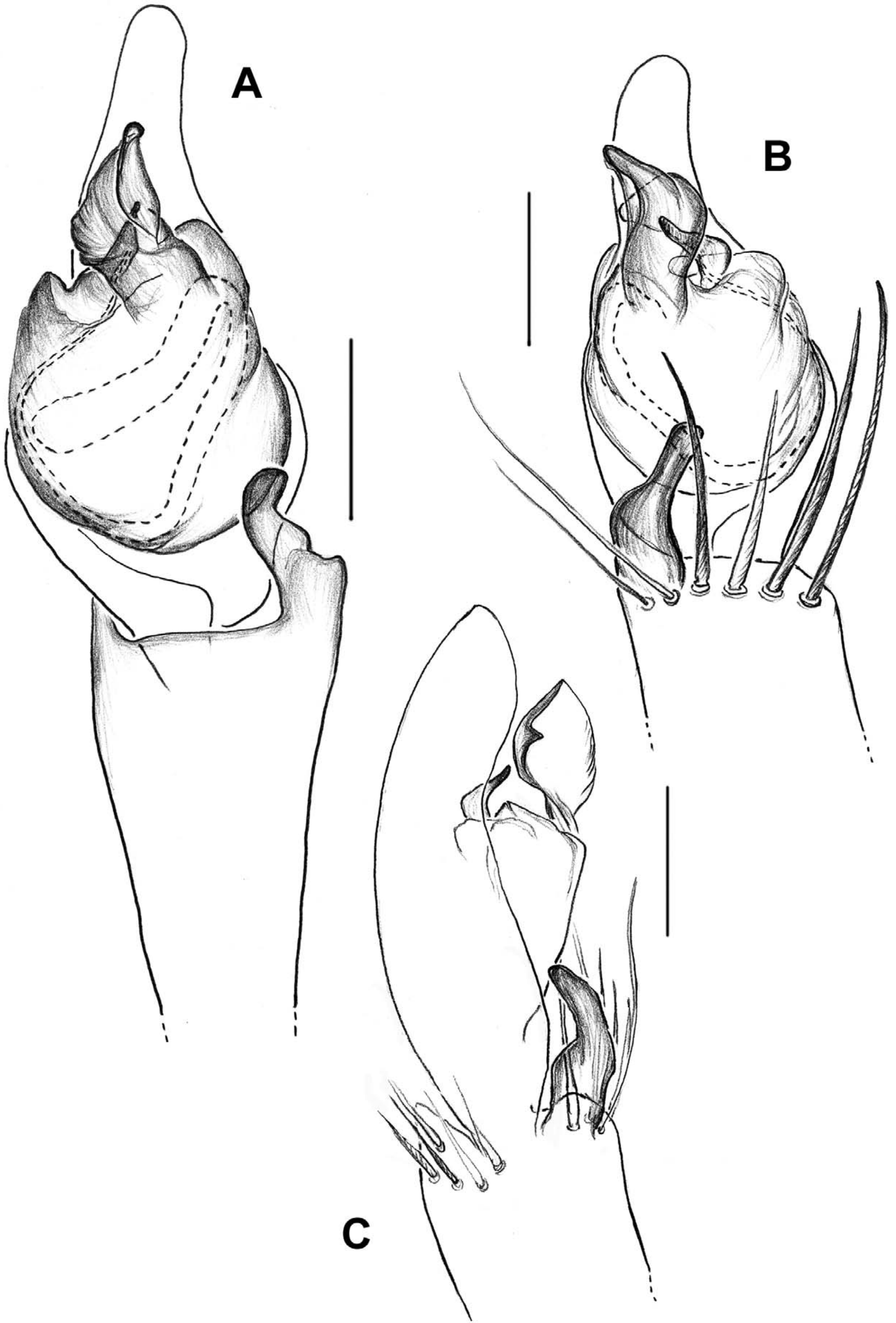

FIGURE 33. *Epidius binotatus* (MNHN 13670/1574). A ventral view of left male palp. B, C *Epidius binotatus guineensis* (MRAC 122567), right male palp (B ventral, C retrolateral). Scale bars = 0.2 mm.

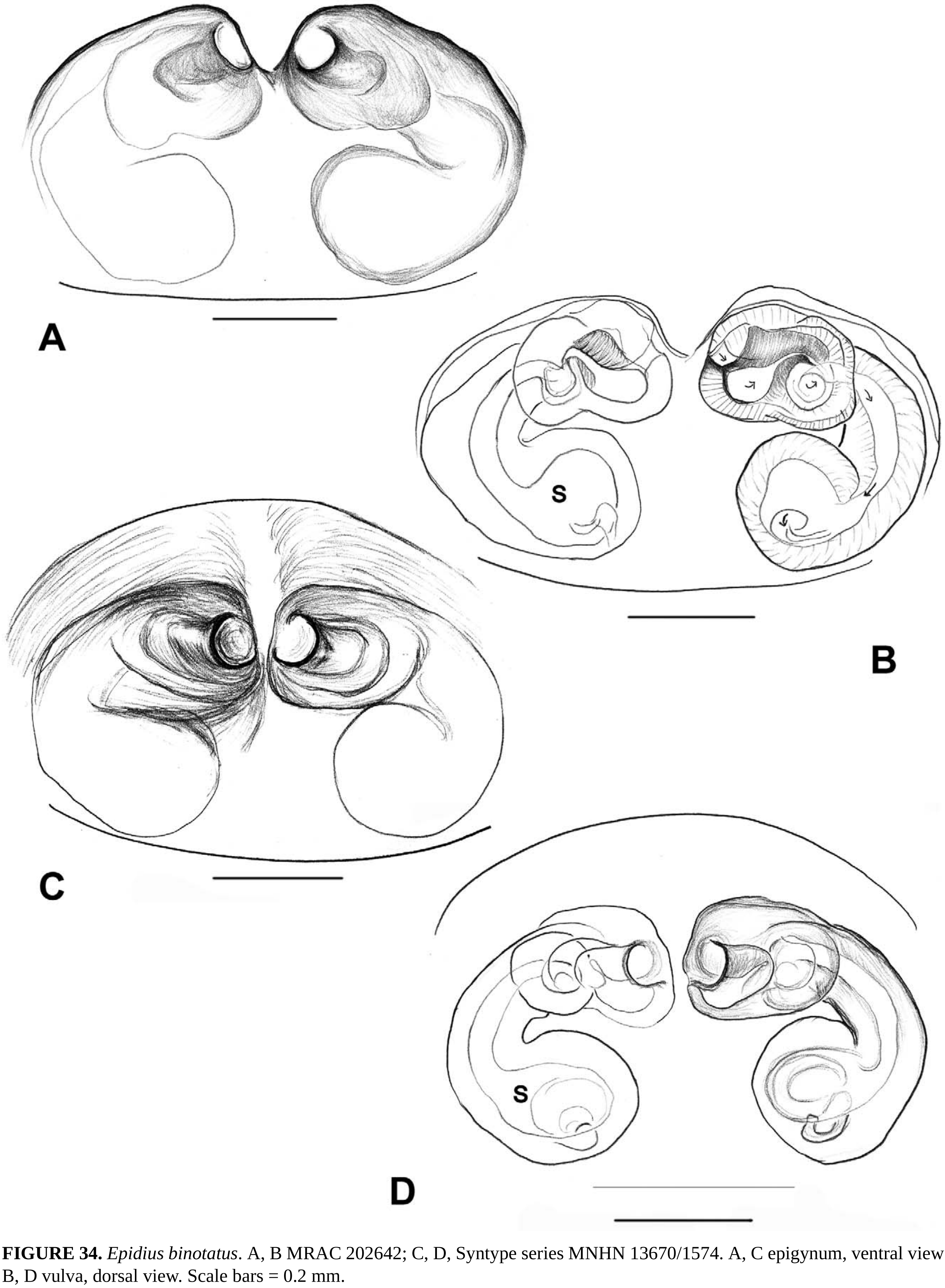

FIGURE 34. *Epidius binotatus*. A, B MRAC 202642; C, D, Syntype series MNHN 13670/1574. A, C epigynum, ventral view; B, D vulva, dorsal view. Scale bars = 0.2 mm.

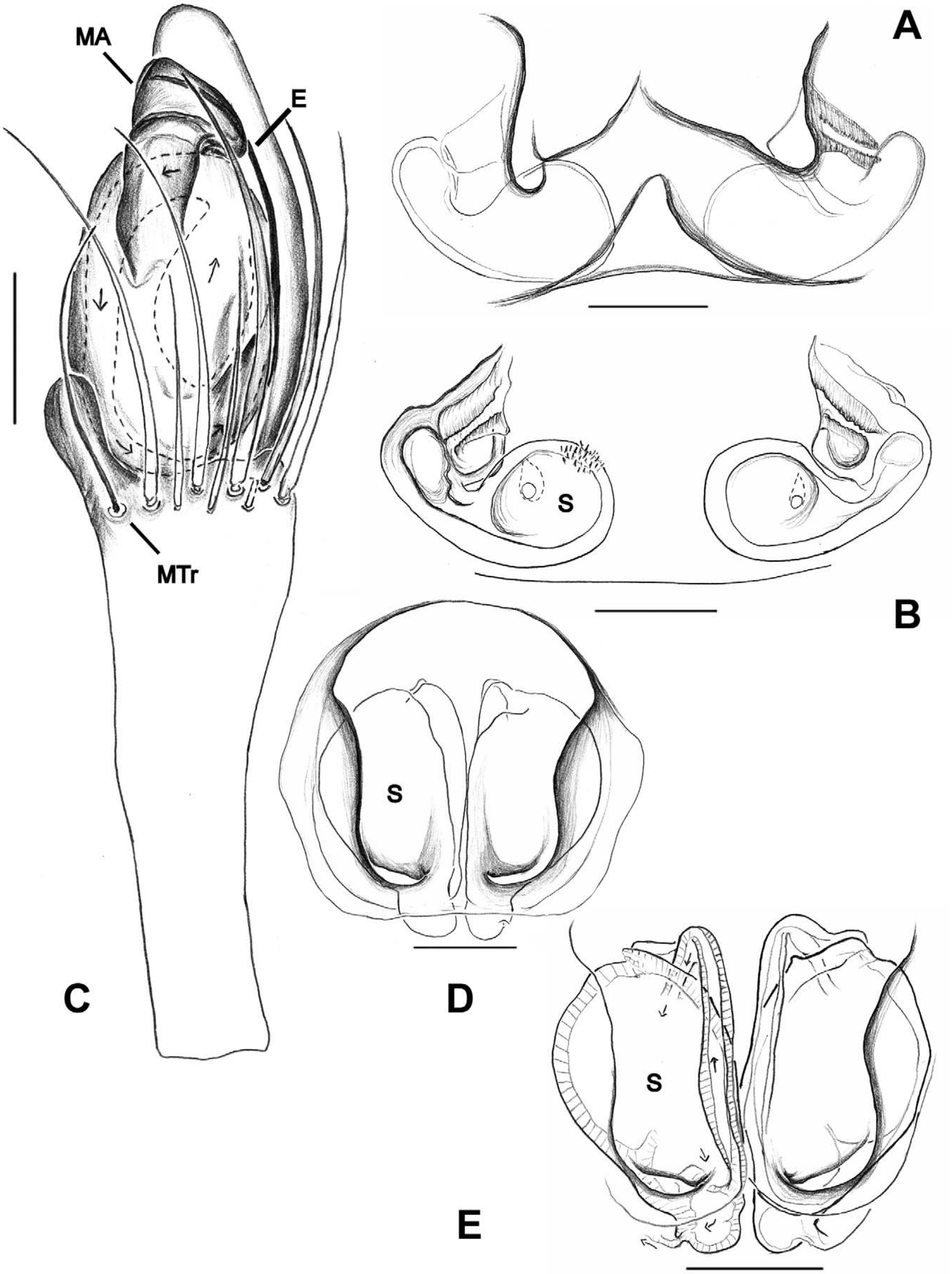

FIGURE 35. A, B *Epidius typicus* (SMF 4246). A epigynum, ventral view; B vulva, ventral view. C, D, E *Epidius rubropictus*. C right male palp, ventral view (MNHN 22347); D–E female from Sumatra (D epigynum, ventral view, E vulva, ventral view). Scale bars = 0.2 mm.

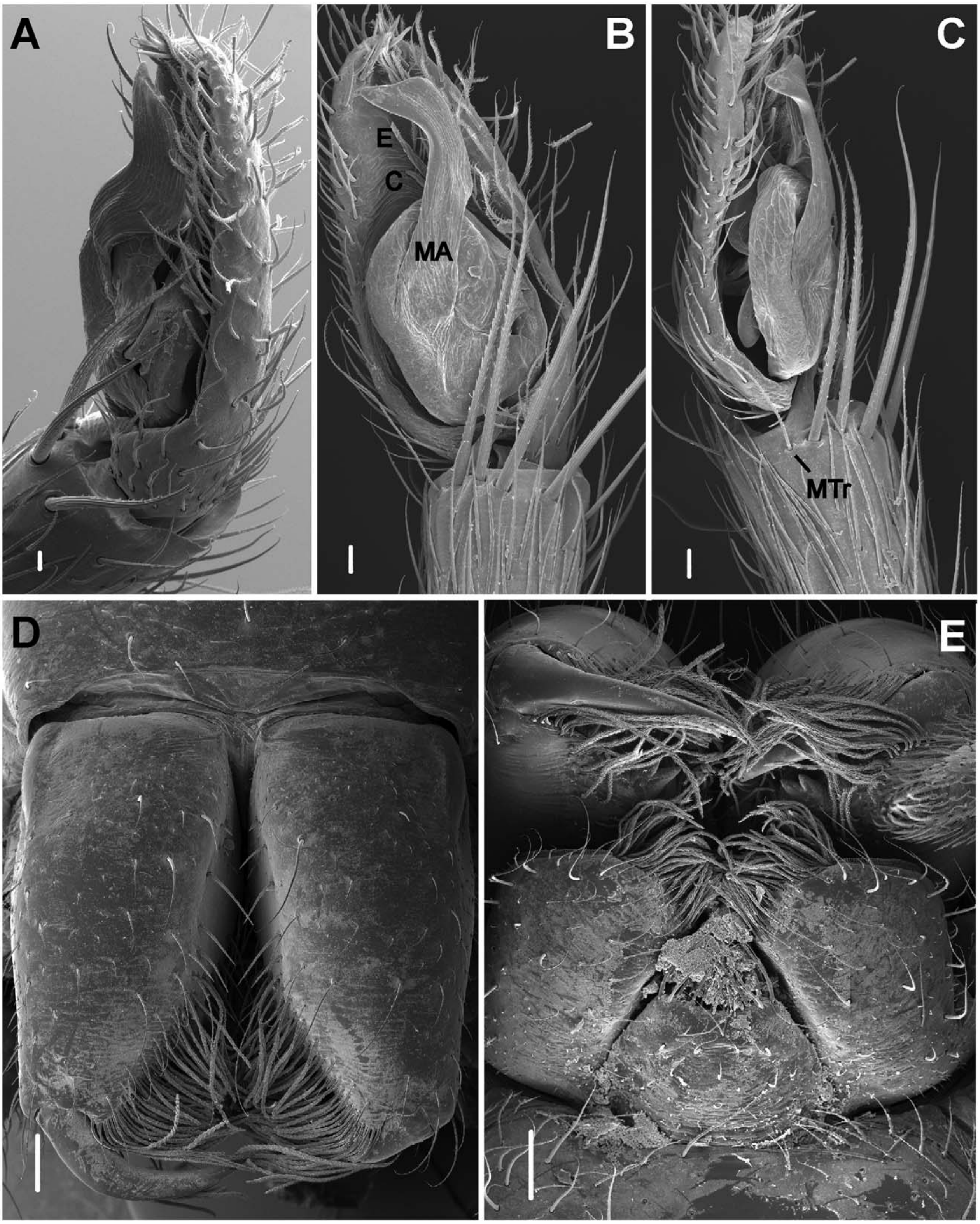

FIGURE 36. Scanning electron micrographs of *Epidius parvati* (MHNG). A–C, right male palp (A prolateral, B ventral, C retrolateral); D Chelicerae, frontal view; E labium and maxillae, ventral view. Scale bars = 10 µm (A), 20 µm (B, C), 100 µm (D, E).

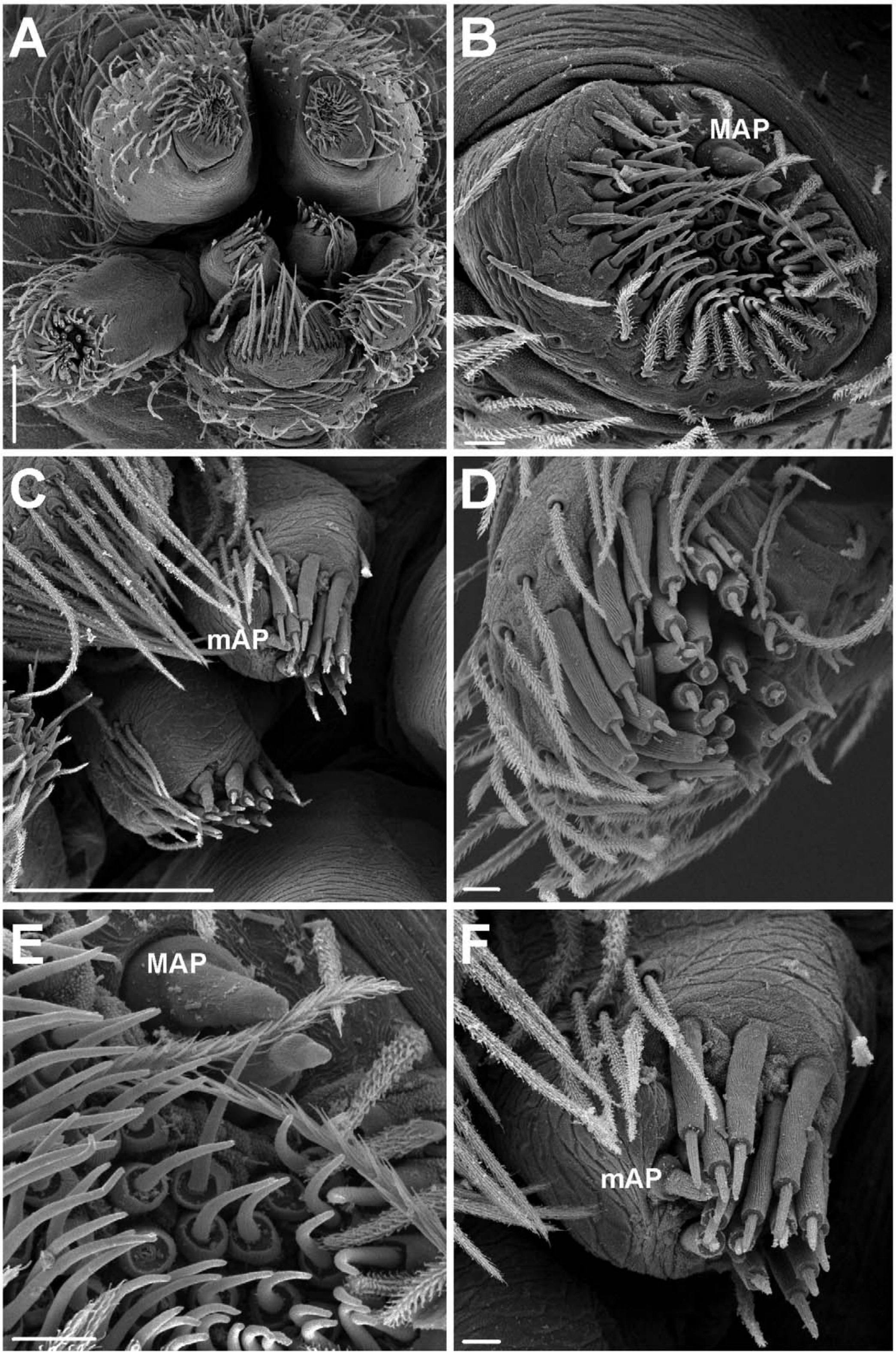

FIGURE 37. Scanning electron micrographs of female *Epidius parvati* (MHNG). A spinnerets B, E ALS; C, F PMS; D, PLS. Scale bars = 10 µm (B, D–F), 100 µm (A, C).

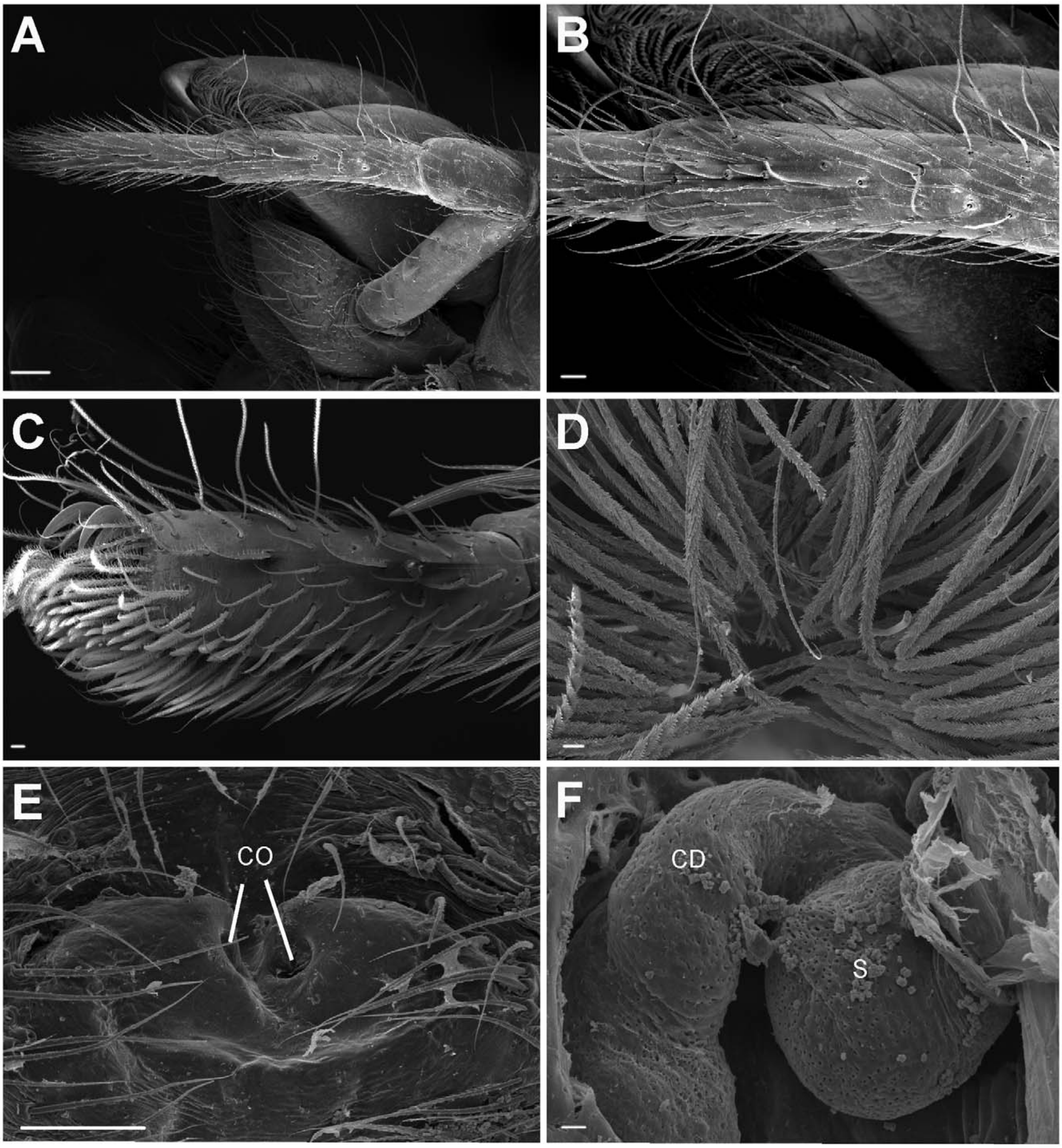

FIGURE 38. A–D *Epidius parvati* female (MHNG) (A, B palp, C Left leg 1, D setae of the promargin of the chelicerae, front view). E, F *E. binotatus* (E epigynum, ventral view, F vulva, dorsal view). Scale bars = 10 µm (C, D, F), 30 µm (B), 100 µm (A, E).

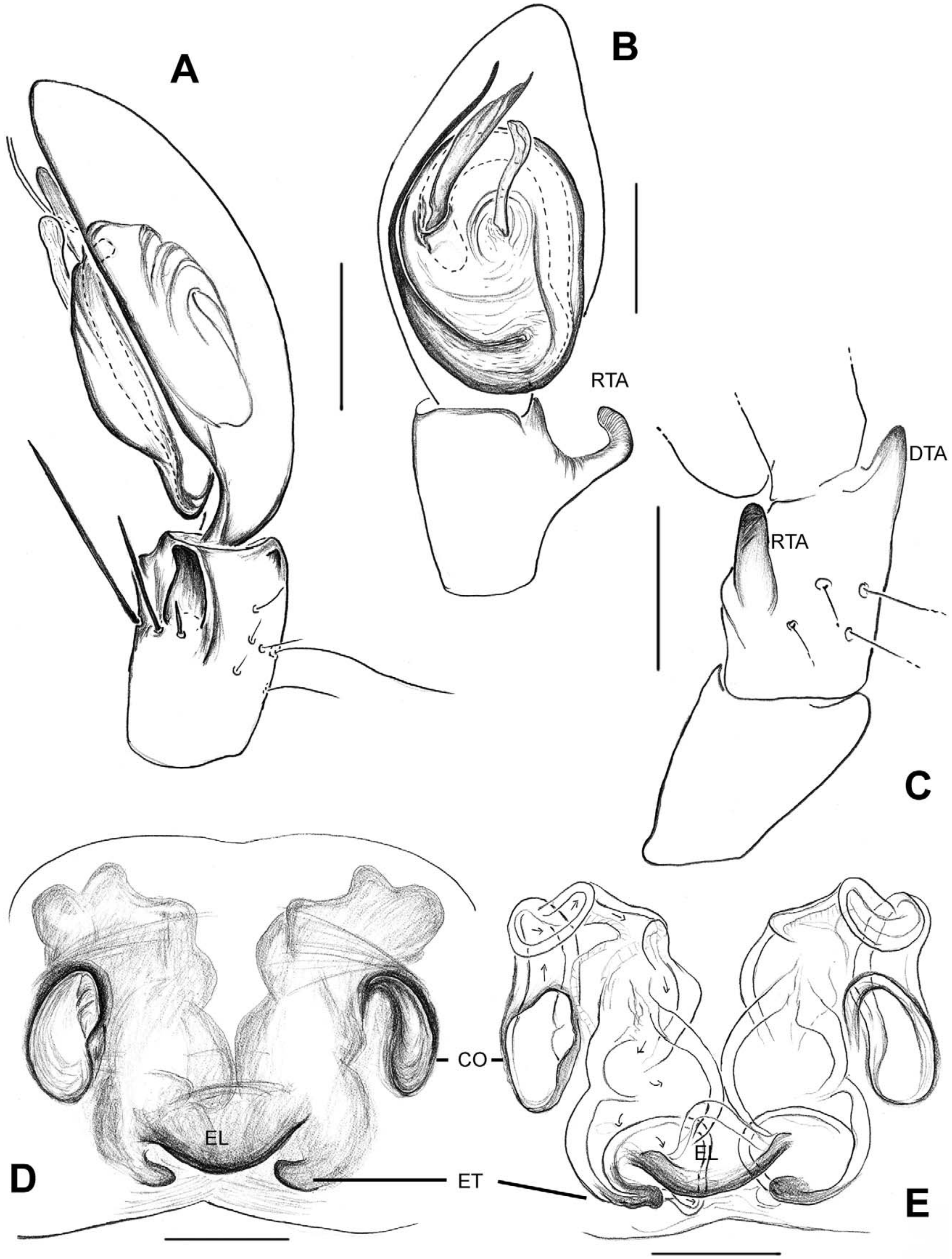

FIGURE 39. *Geraesta hirta* (USNM). A–C male palp (A, C retrolateral, B ventral); D epigynum, ventral view; E vulva, ventral view. Scale bars = 0.1 mm (D, E), 0.2 mm (A–C).

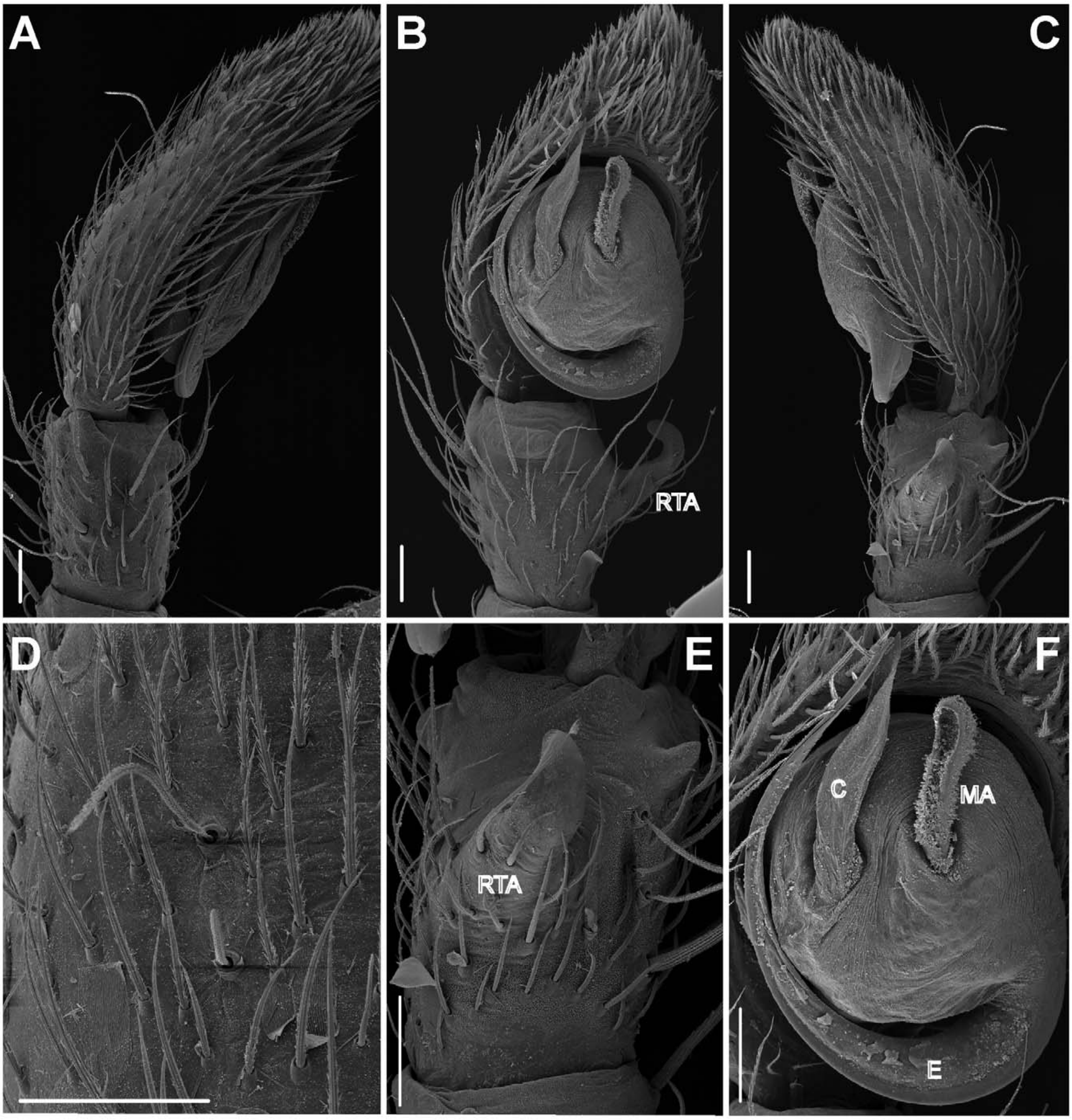

FIGURE 40. Scanning electron micrographs of *Geraesta hirta* (USNM). A–C, E–F male palp (A prolateral, B, F ventral, C, E retrolateral); D Cymbium, dorsal view. Scale bars = 100 µm.

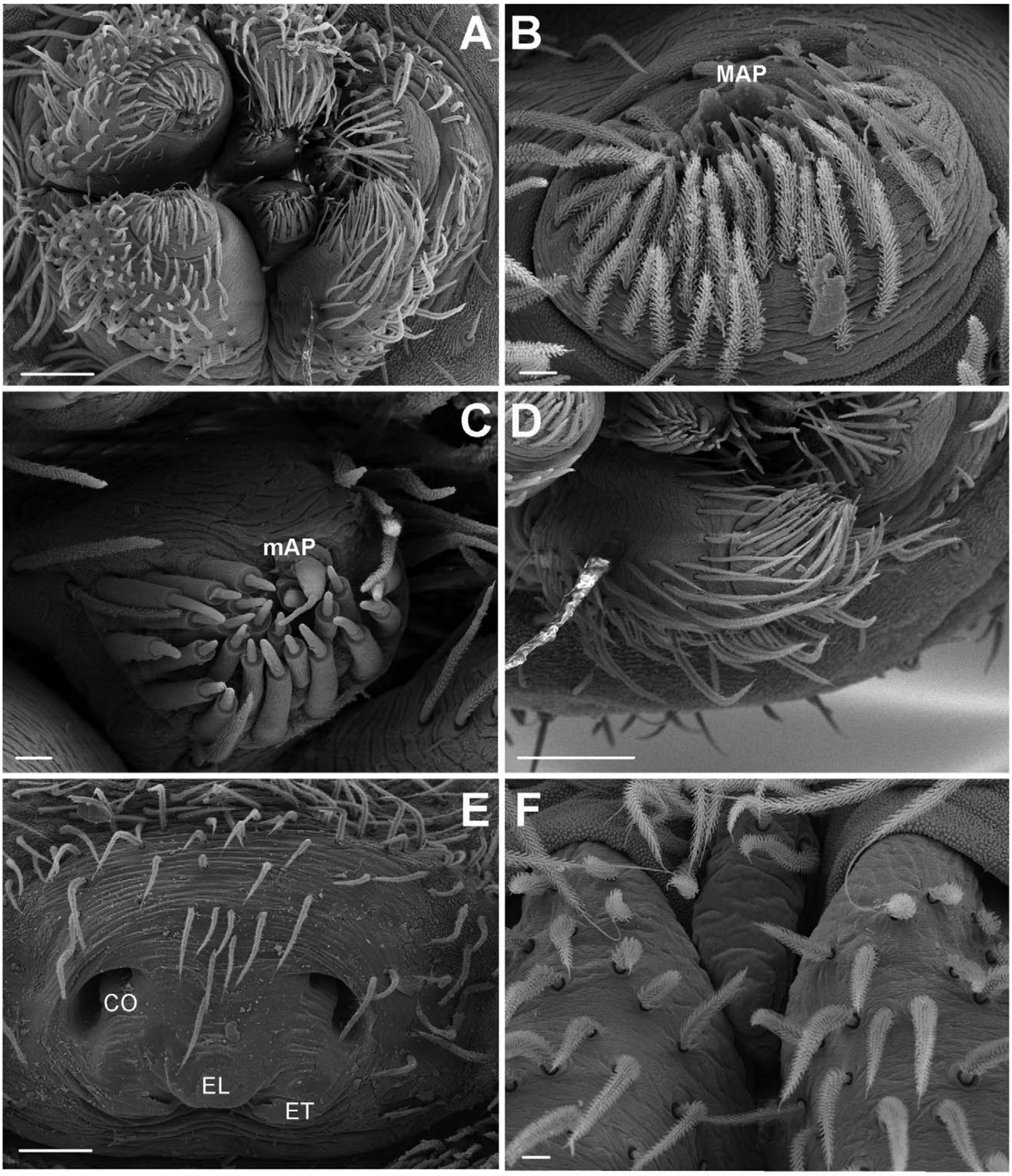

FIGURE 41. Scanning electron micrographs of *Geraesta hirta* (USNM). A spinnerets; B ALS; C PMS; D PLS; E epigynum; F colulus, ventral view. Scale bars = 10 µm (B, C, F), 100 µm (A, D, E).

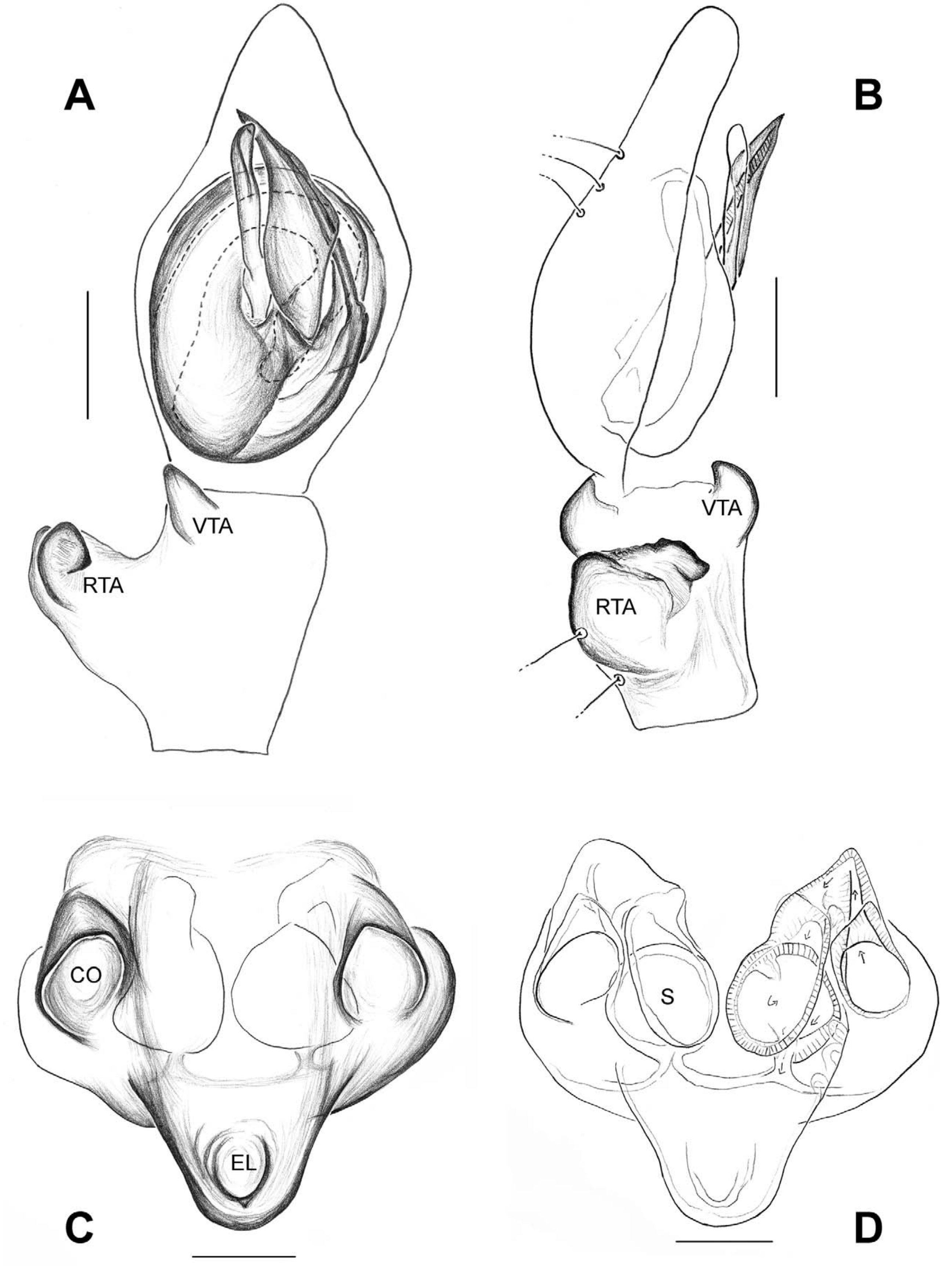

FIGURE 42. *Geraesta lehtineni* **sp. nov.** (CASENT 9015689). A–B right male palp (A ventral, B retrolateral); C epigynum, ventral view; D vulva, ventral view. Scale bars = 0.1 mm (D, E), 0.2 mm (A–C).

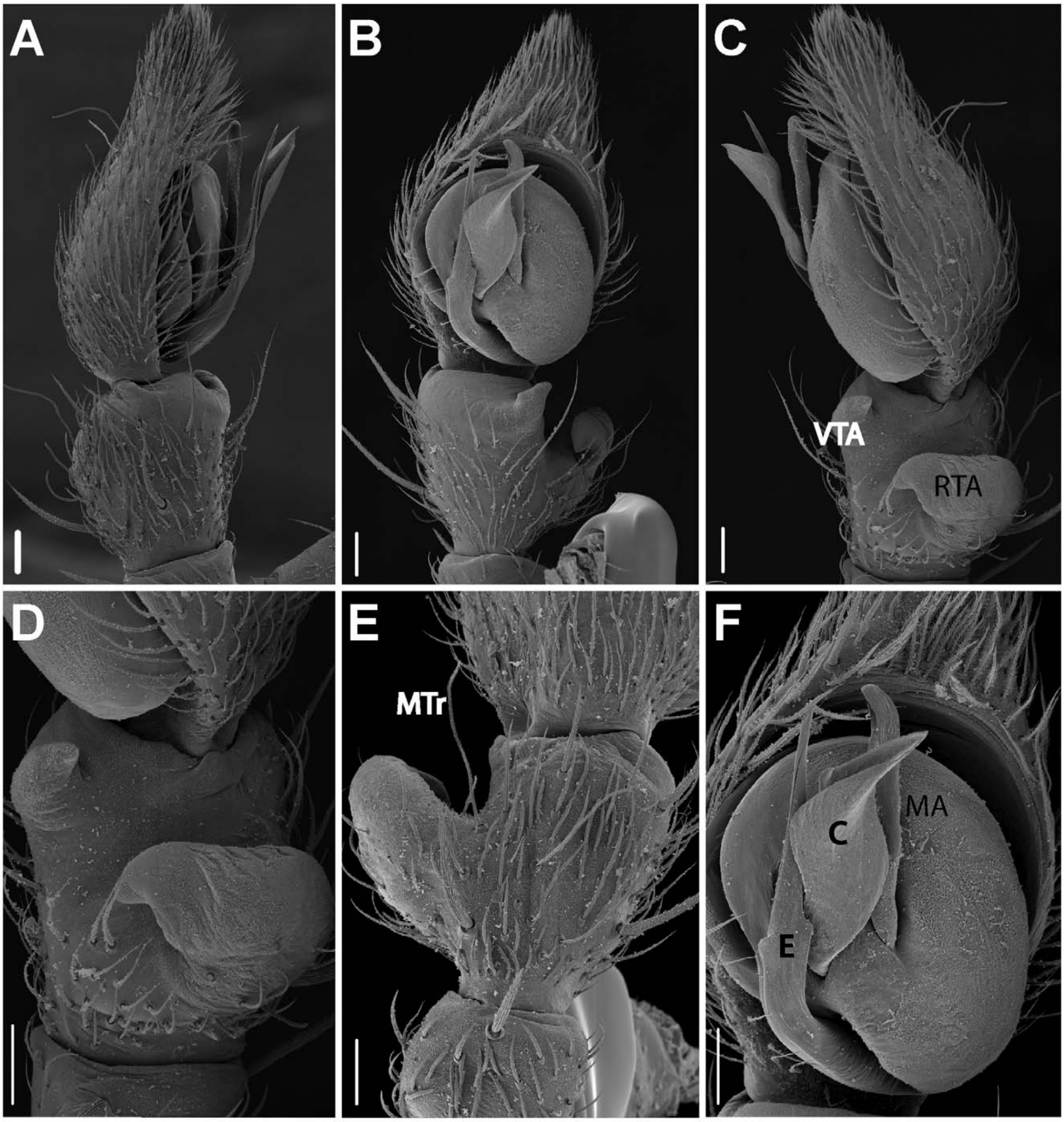

FIGURE 43. Scanning electron micrographs of *Geraesta lehtineni* **sp. nov.** (CASENT 9013883). A–F male palp (A prolateral, B, F ventral, C, D retrolateral dorsal). Scale bars = 100 µm.

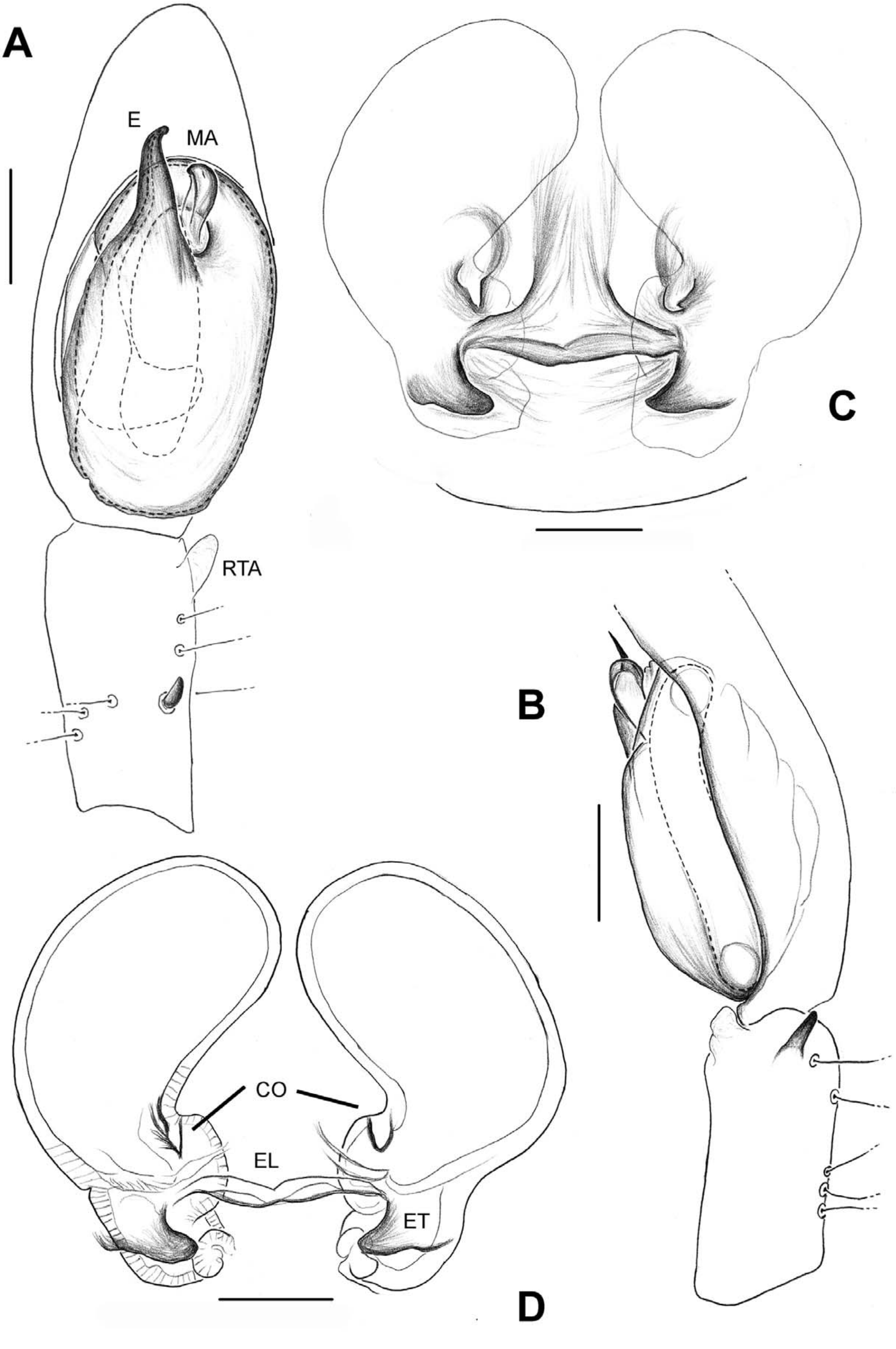

FIGURE 44. *Geraesta mkwawa* **sp. nov.** (USNM). A–B right male palp (A ventral, B retrolateral); C female epigynum, ventral view; D vulva, ventral view. Scale bars = 0.1 mm (C, D), 0.2 mm (A, B).

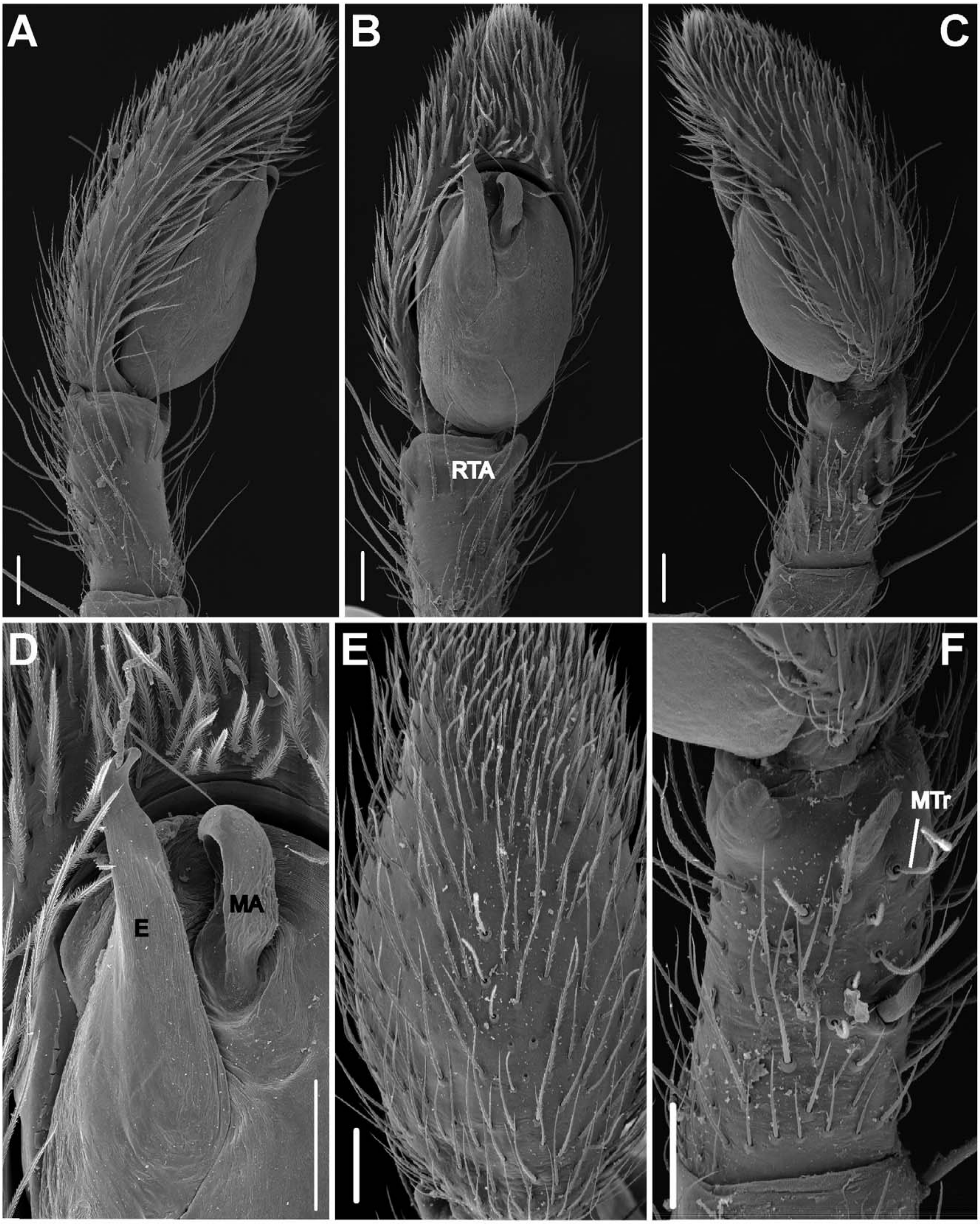

FIGURE 45. Scanning electron micrographs of *Geraesta mkwawa* **sp. nov.** (USNM). A–D, F male palp (A prolateral, B, D ventral, C, F retrolateral); E cymbium, dorsal view. Scale bars = 100 µm.

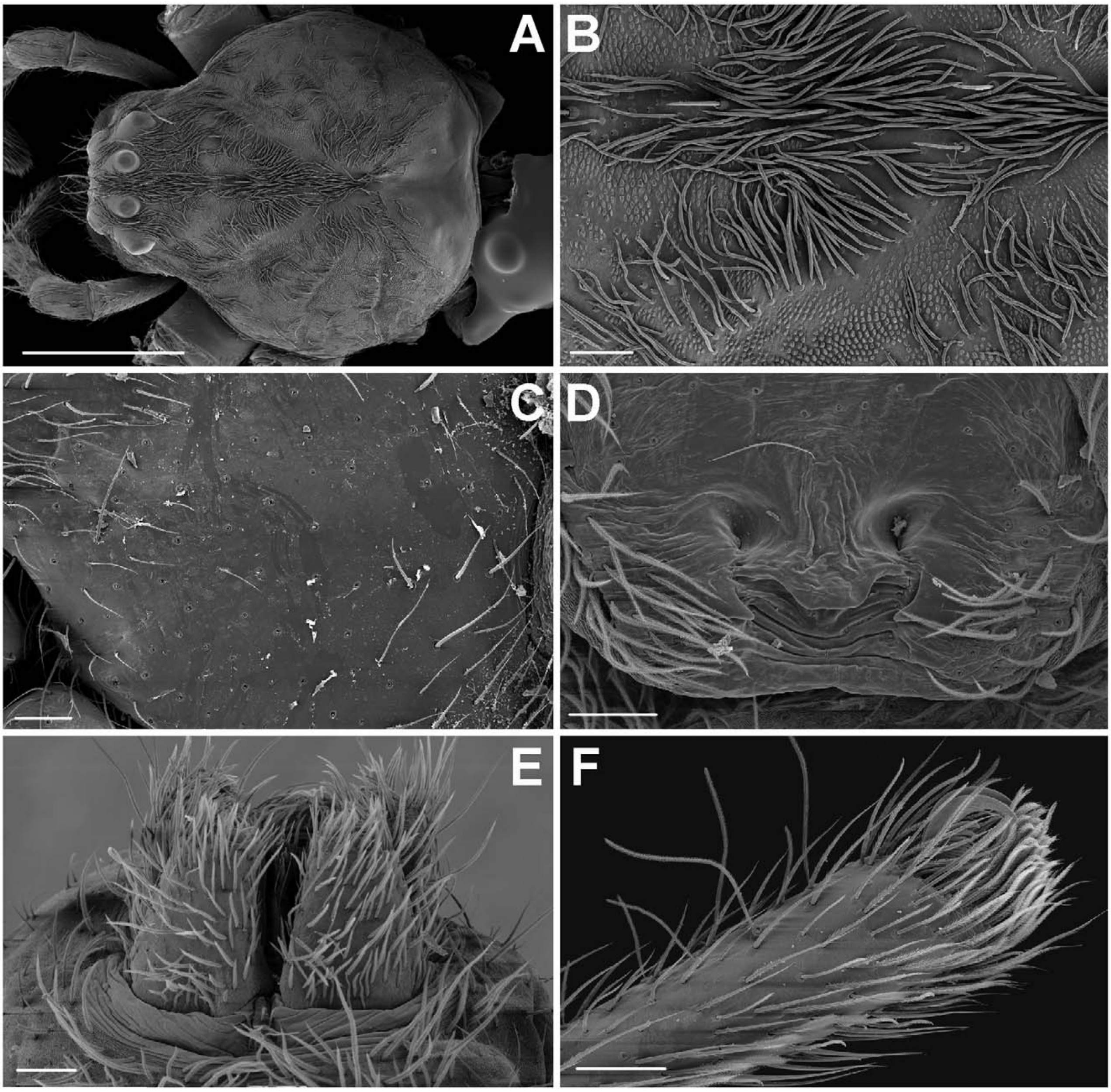

FIGURE 46. Scanning electron micrographs of *Geraesta mkwawa* **sp. nov.** (USNM). A female prosoma, dorsal view; B ditto, detail; C sternum, ventral view; D epigynum, ventral view; E colulus, ventral view; F left leg 1, lateral view. Scale bars = 100 µm (B–F), 1 mm (A).

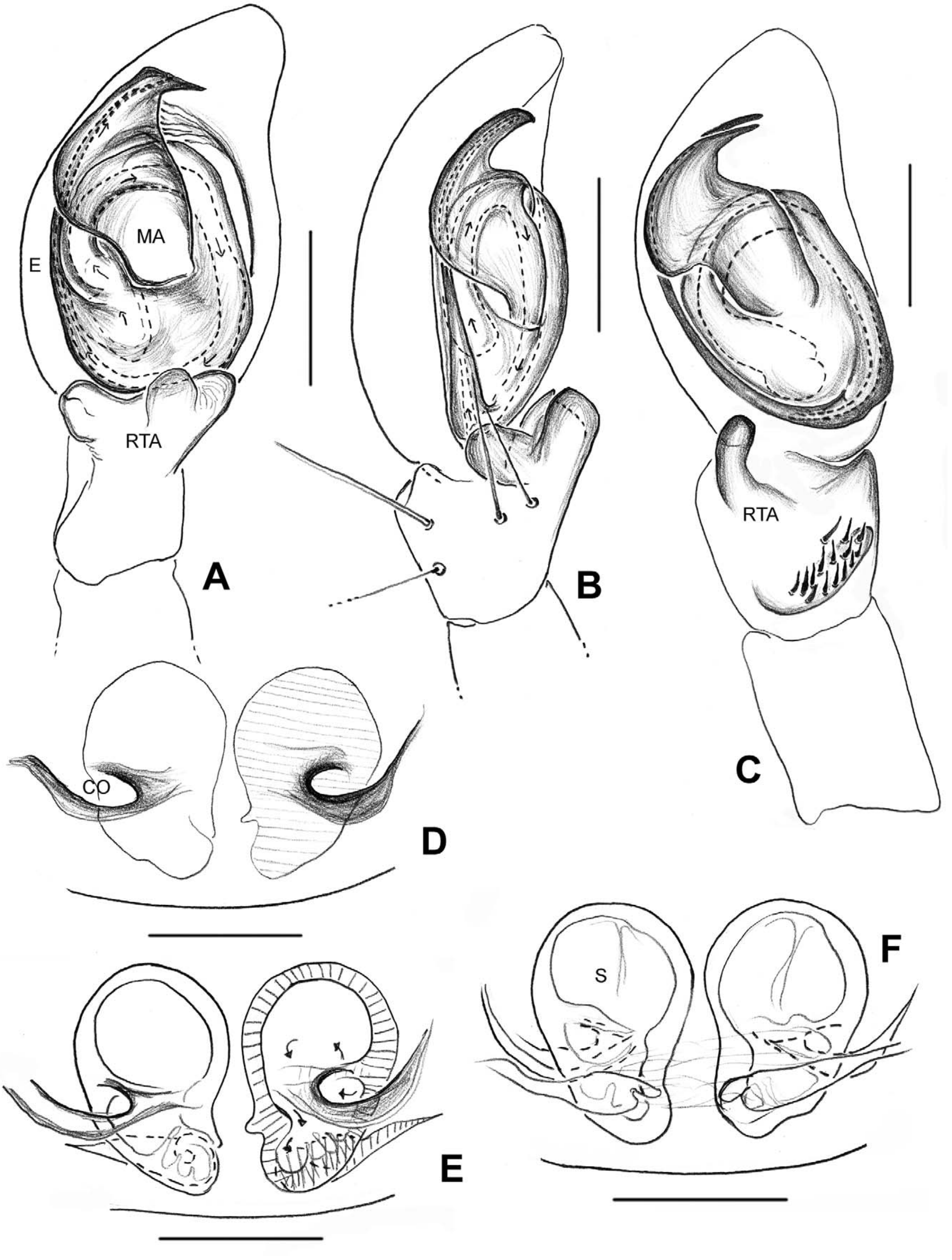

FIGURE 47. A, B, D–F *Pharta gongshan*. C, *P. brevipalpus* (MNHN 22113/1574). A–C male palp (A, C ventral, B retrolateral); D epigynum, ventral view; E–F vulva (E ventral, F dorsal). Scale bars = 0.1 mm (D–F), 0.2 mm (A–C).

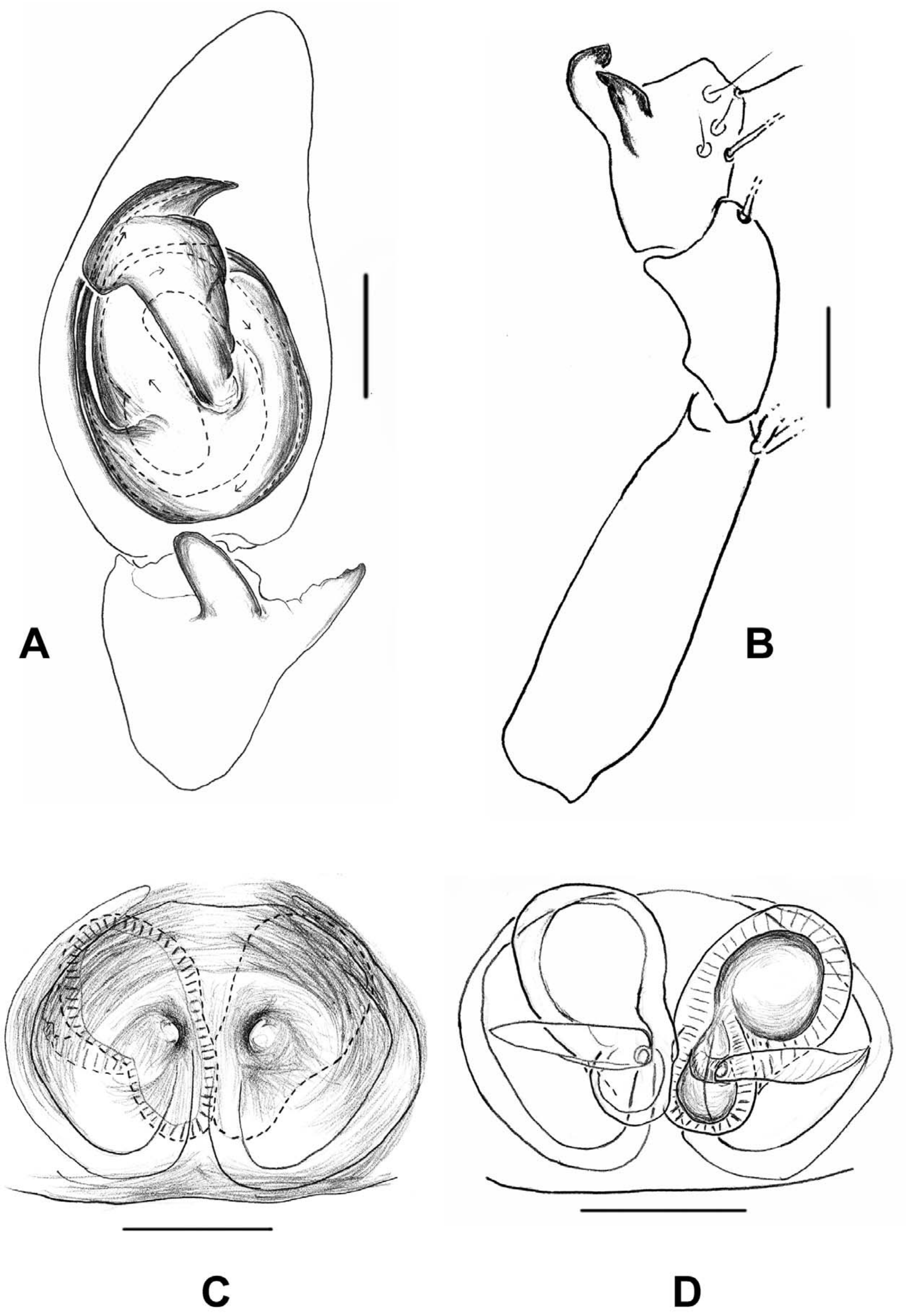

FIGURE 48. *Pharta bimaculata* (USNM). A–B male palp (A ventral, B retrolateral); C epigynum, ventral view; D vulva, dorsal view. Scale bars = 0.1 mm (A, C, D), 0.2 mm (B).

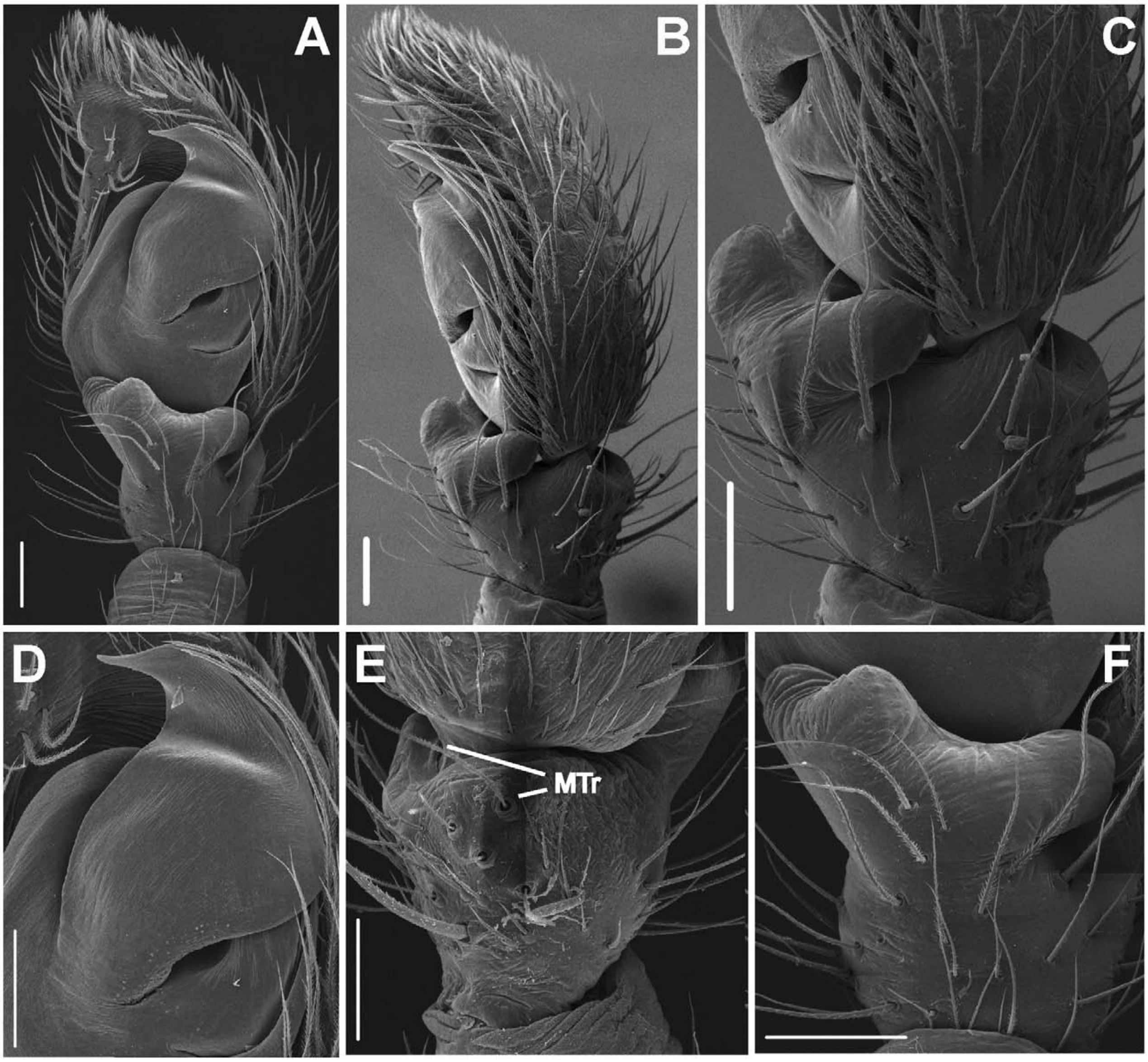

FIGURE 49. *Pharta gongshan.* A–F male palp (A, D, F ventral, B, C retrolateral, D dorsal). Scale bars = 100 µm.

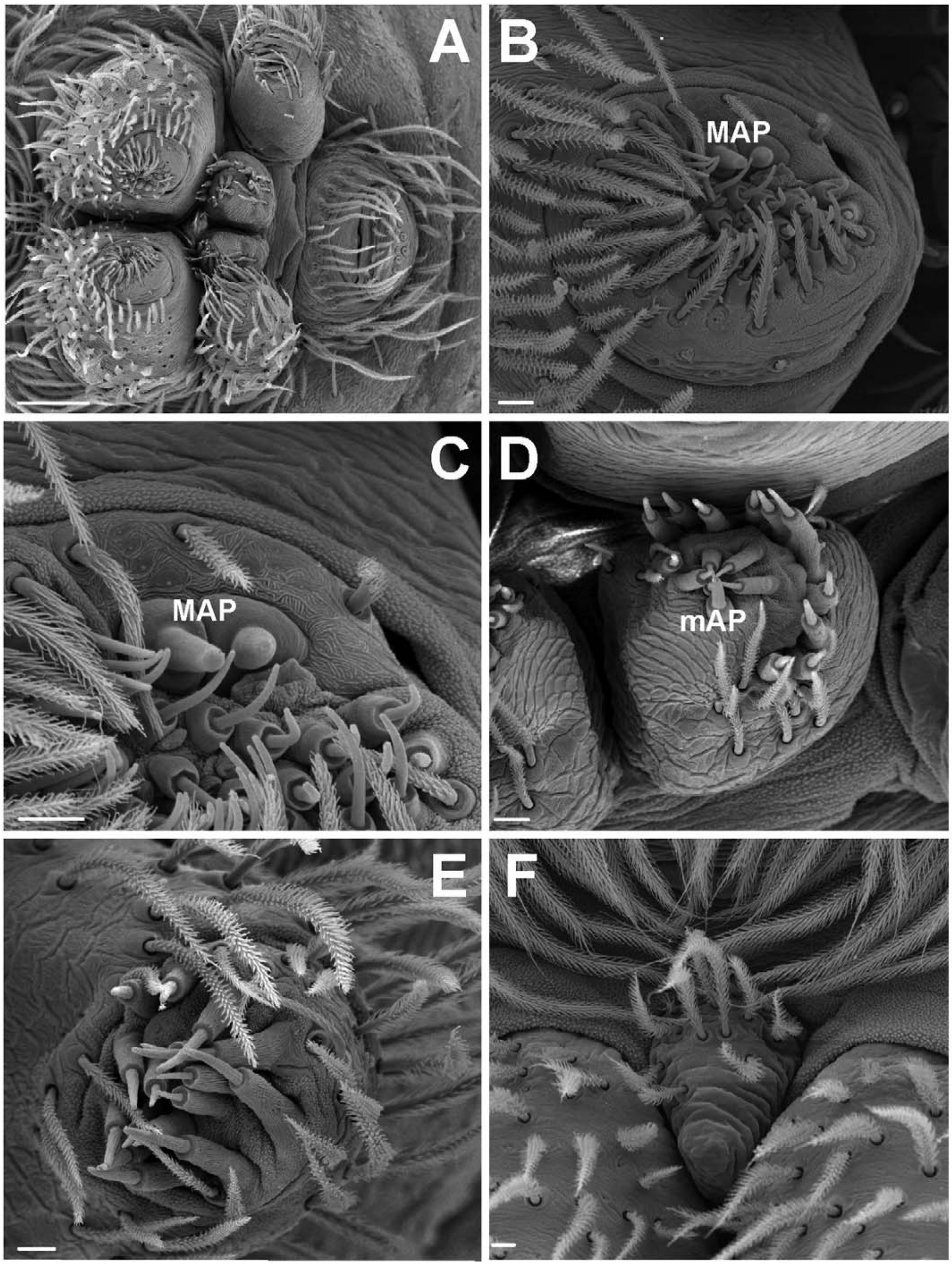

FIGURE 50. Scanning electron micrographs female *Pharta gongshan*. A spinnerets; B, C ALS; D PMS; E PLS; F colulus, ventral view. Scale bars = 10 µm (B–F), 100 µm (A).

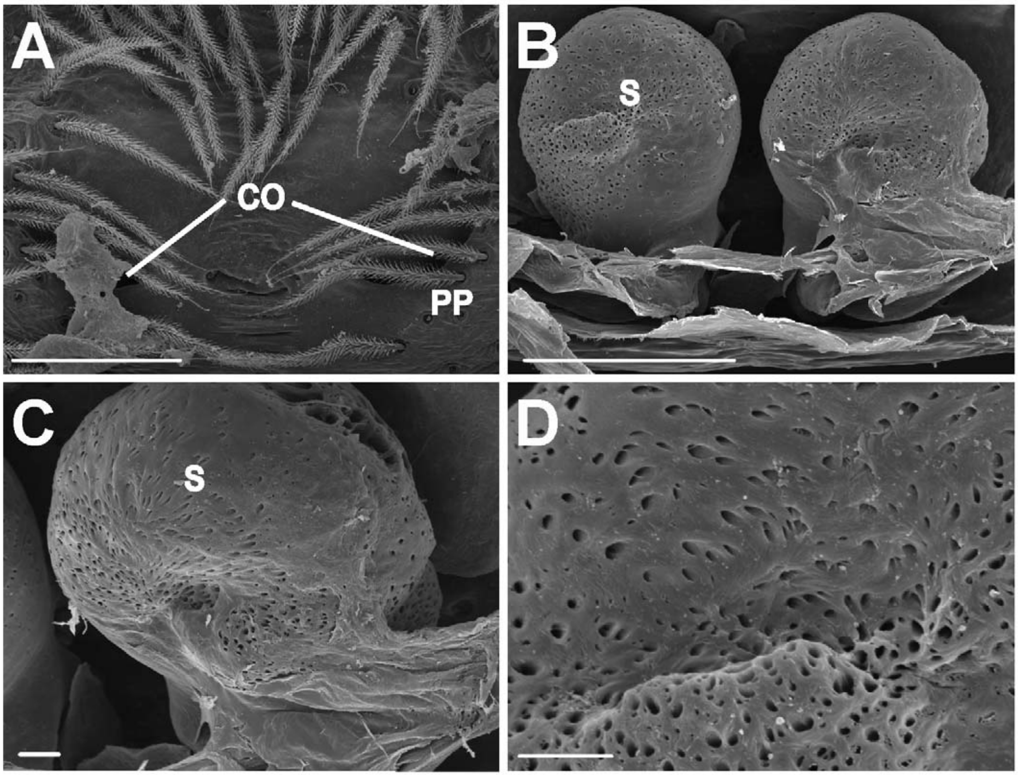

FIGURE 51. Scanning electron micrographs female *Pharta gongshan*. A Epigynum, ventral view; B vulva, dorsal view; C, spermatheca, dorsal view; D ditto, detail. Scale bars = 10 µm (C, D), 100 µm (A, B).

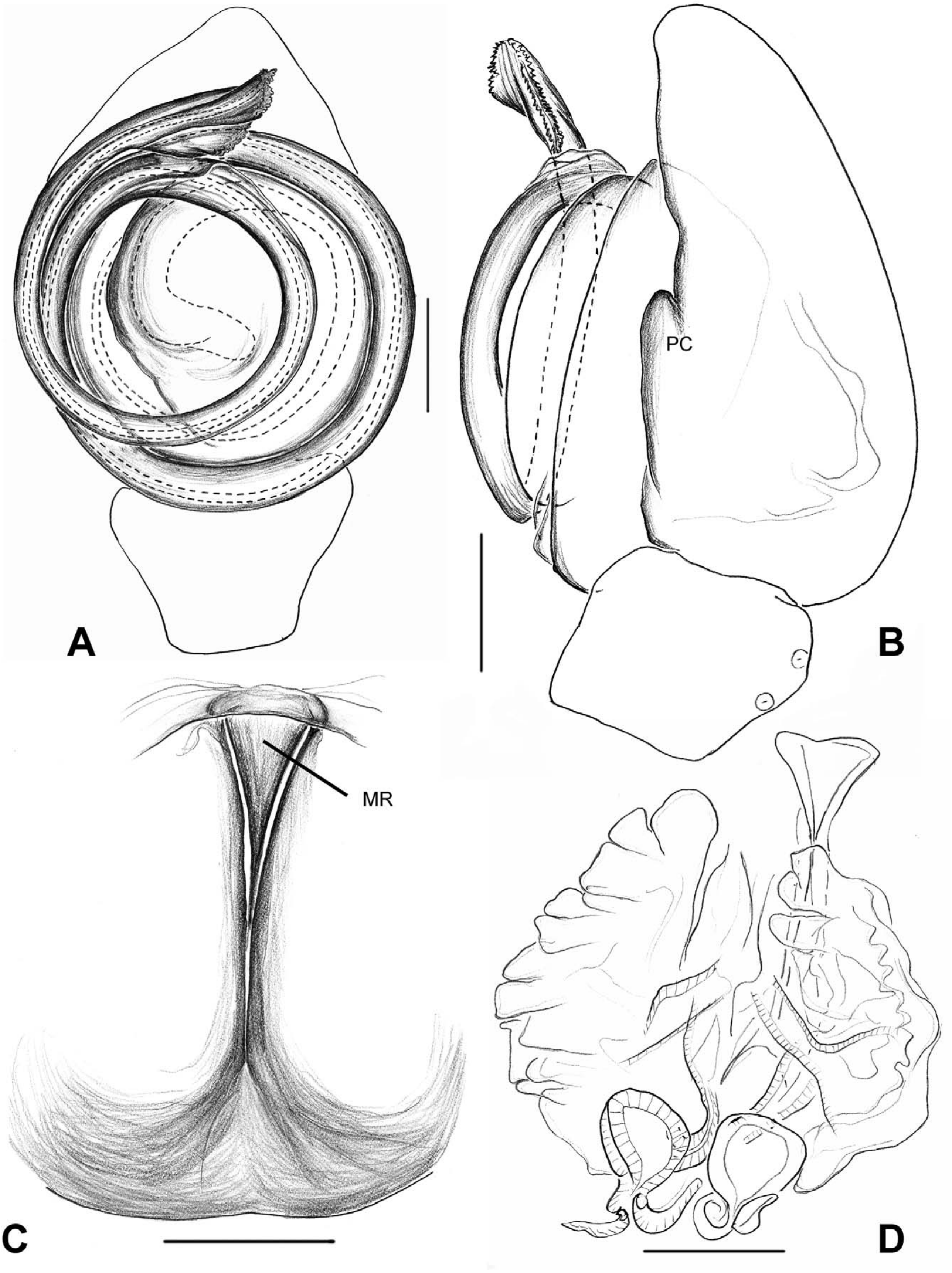

Figure 52. *Apyretina* sp. A–B male palp (A ventral, B retrolateral); C epigynum, ventral view; D vulva, dorsal view. Scale bars = 0.1 mm.

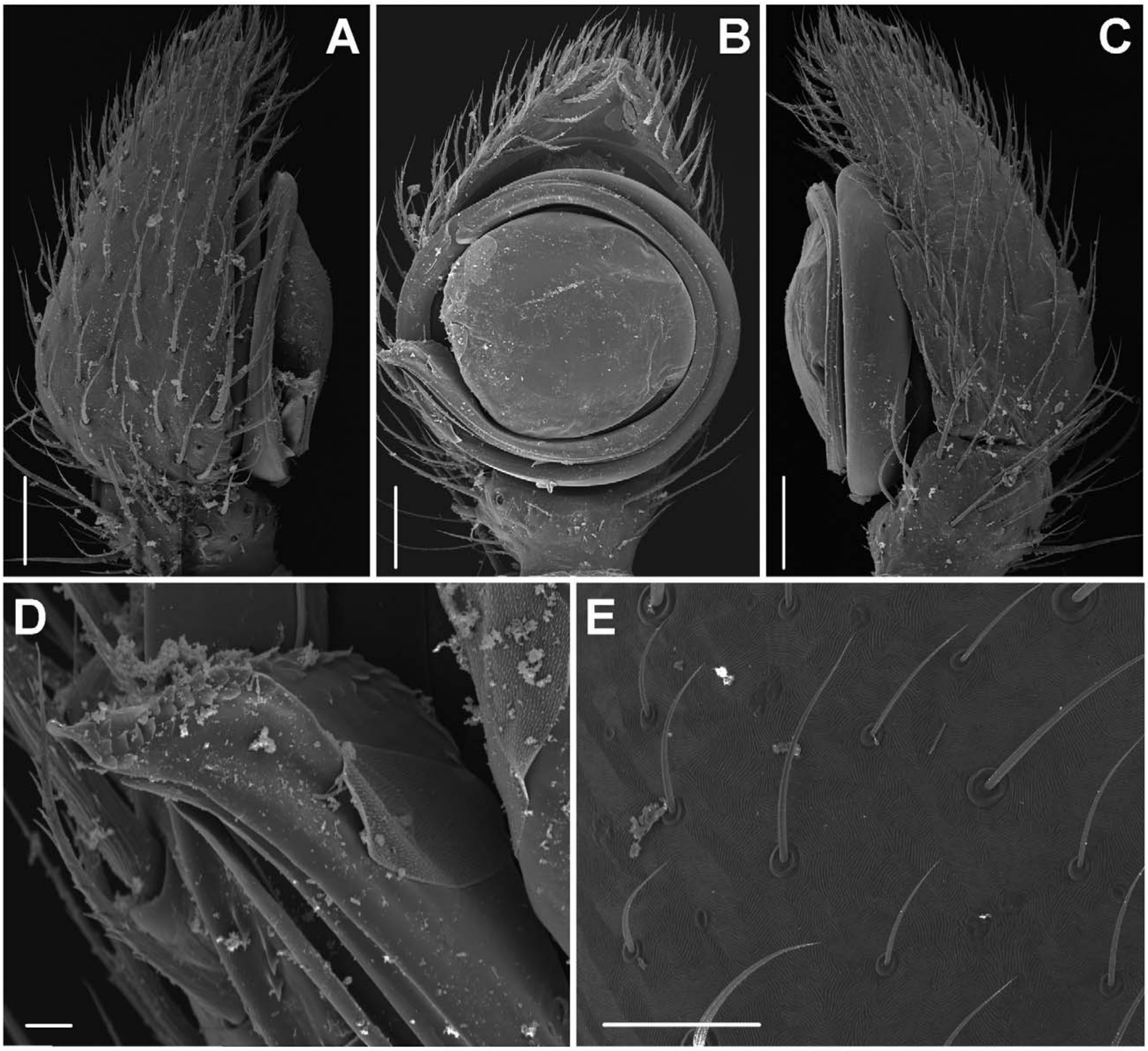

FIGURE 53. Scanning electron micrographs of *Apyretina* sp. A–D male palp (A prolateral, B ventral, C retrolateral, D tip of embolus, prolateral); E female opisthosoma, ventral view. Scale bars = 10 µm (D), 100 µm (A–C, E).

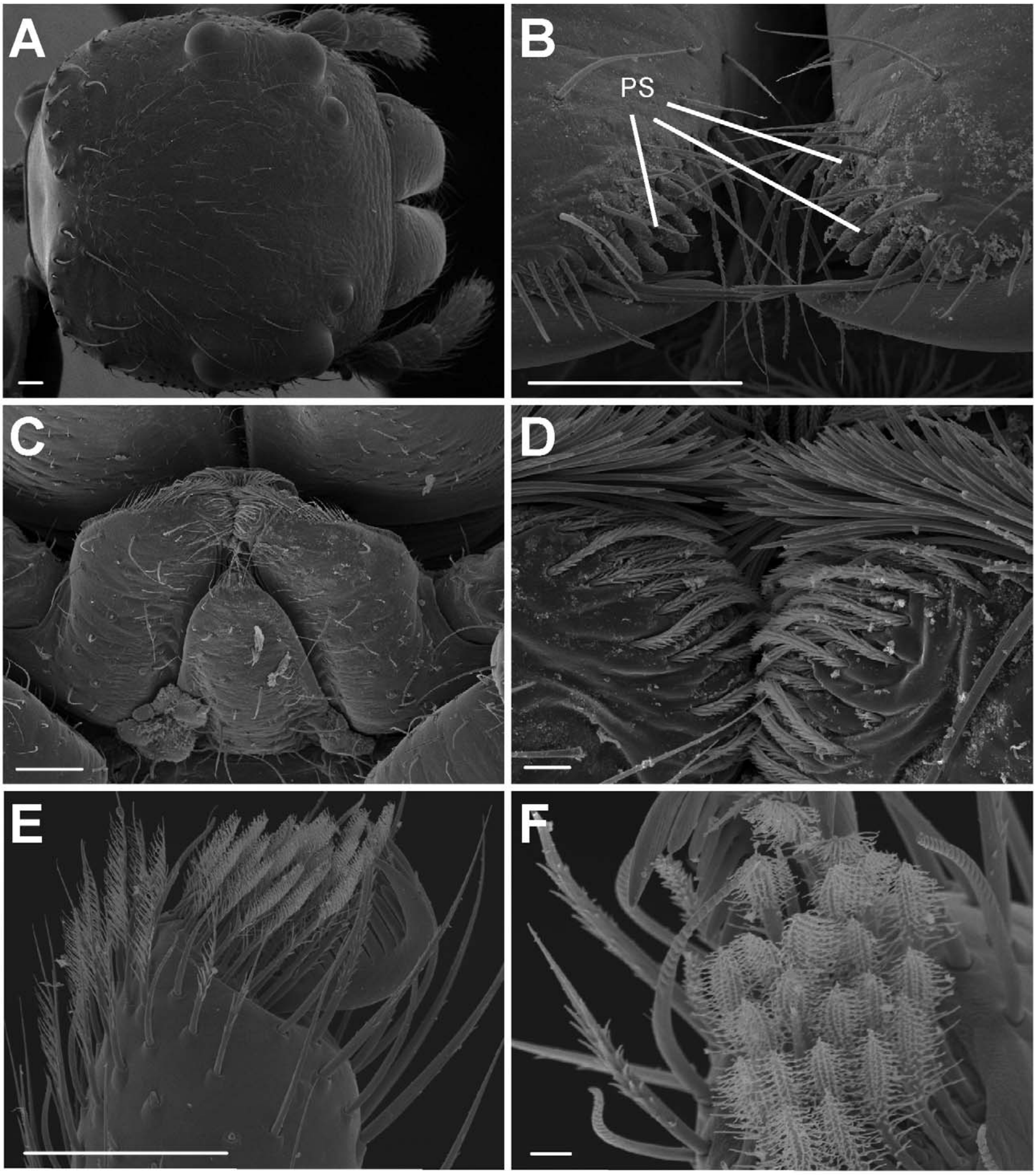

FIGURE 54. Scanning electron micrographs of *Apyretina* sp. A prosoma dorsal view; B chelicerae, front view; C endites and labium, ventral view; D detail of C; E left leg 1, lateral view; F scopula, lateral view. Scale bars = 10 µm (D, F), 100 µm (A–C, E).

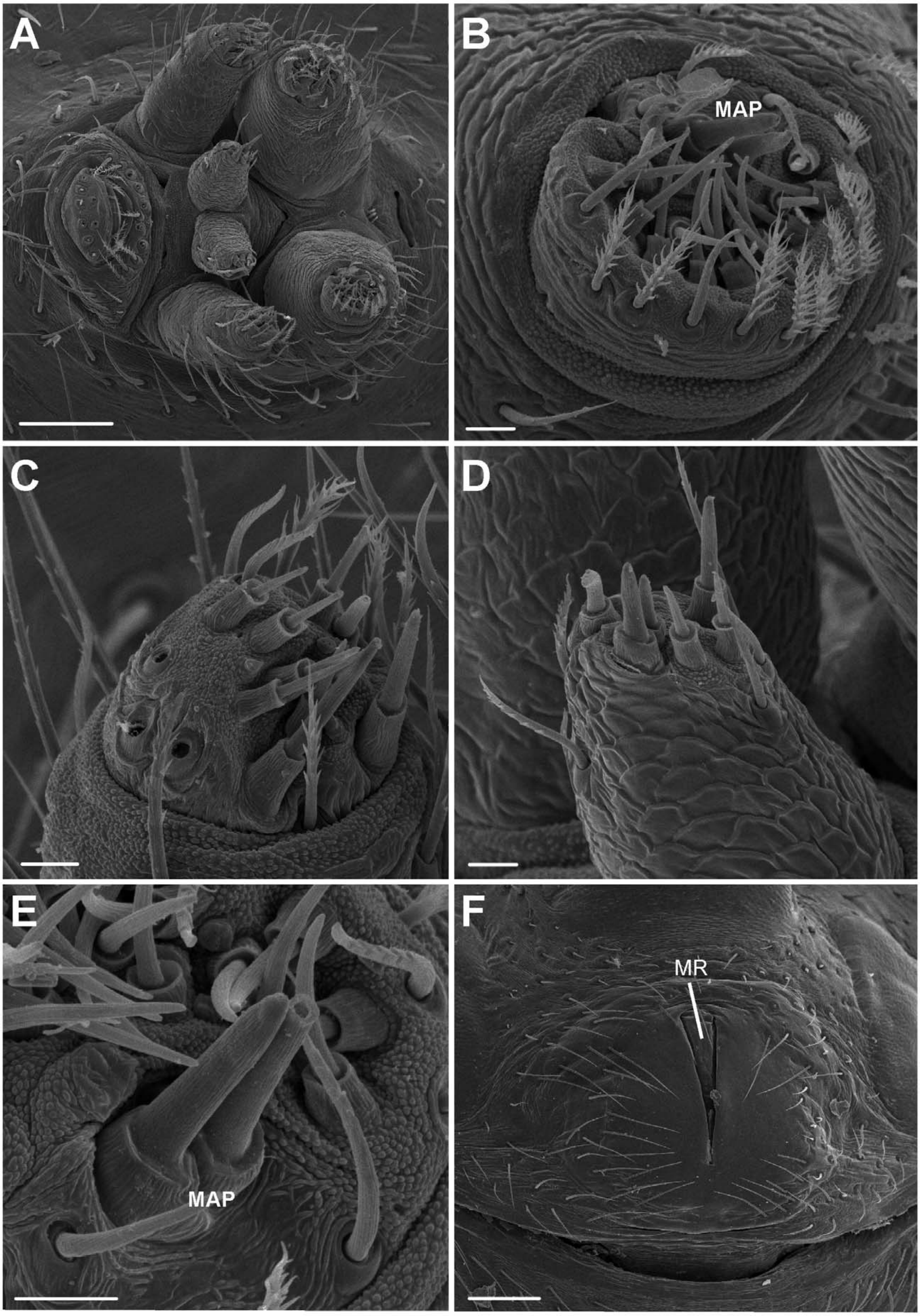

FIGURE 55. Scanning electron micrographs of *Apyretina* sp., female. A spinnerets; B, E ALS; C PLS; D PMS; F epigynum. Scale bars = 10 µm (B–D, E), 100 µm (A, F).

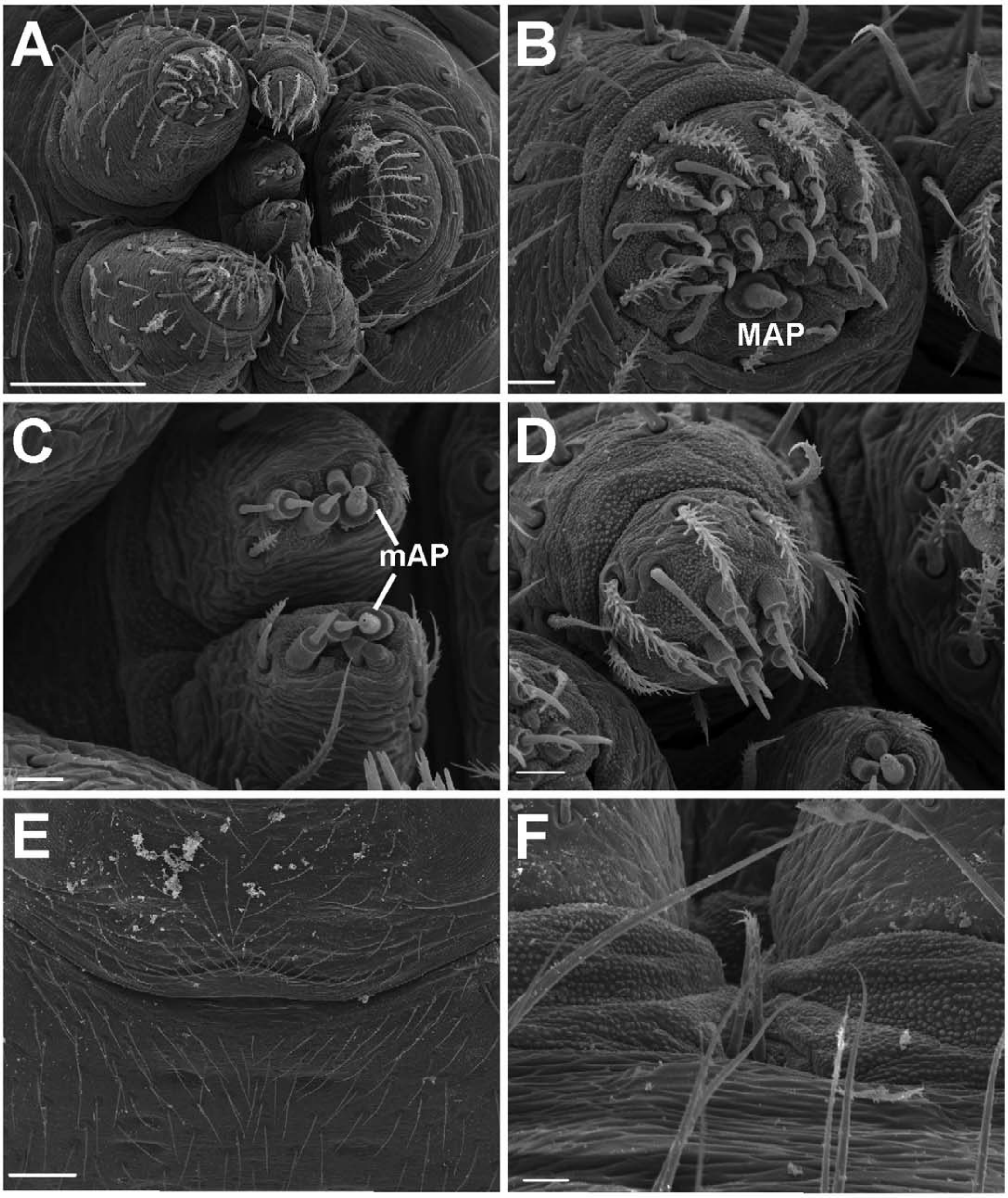

FIGURE 56. Scanning electron micrographs of *Apyretina* sp., male. A spinnerets; B ALS; C PMS; D PLS; E epigastric furrow, ventral view; F colulus, ventral view. Scale bars = 10 µm (A–D, F), 100 µm (E).

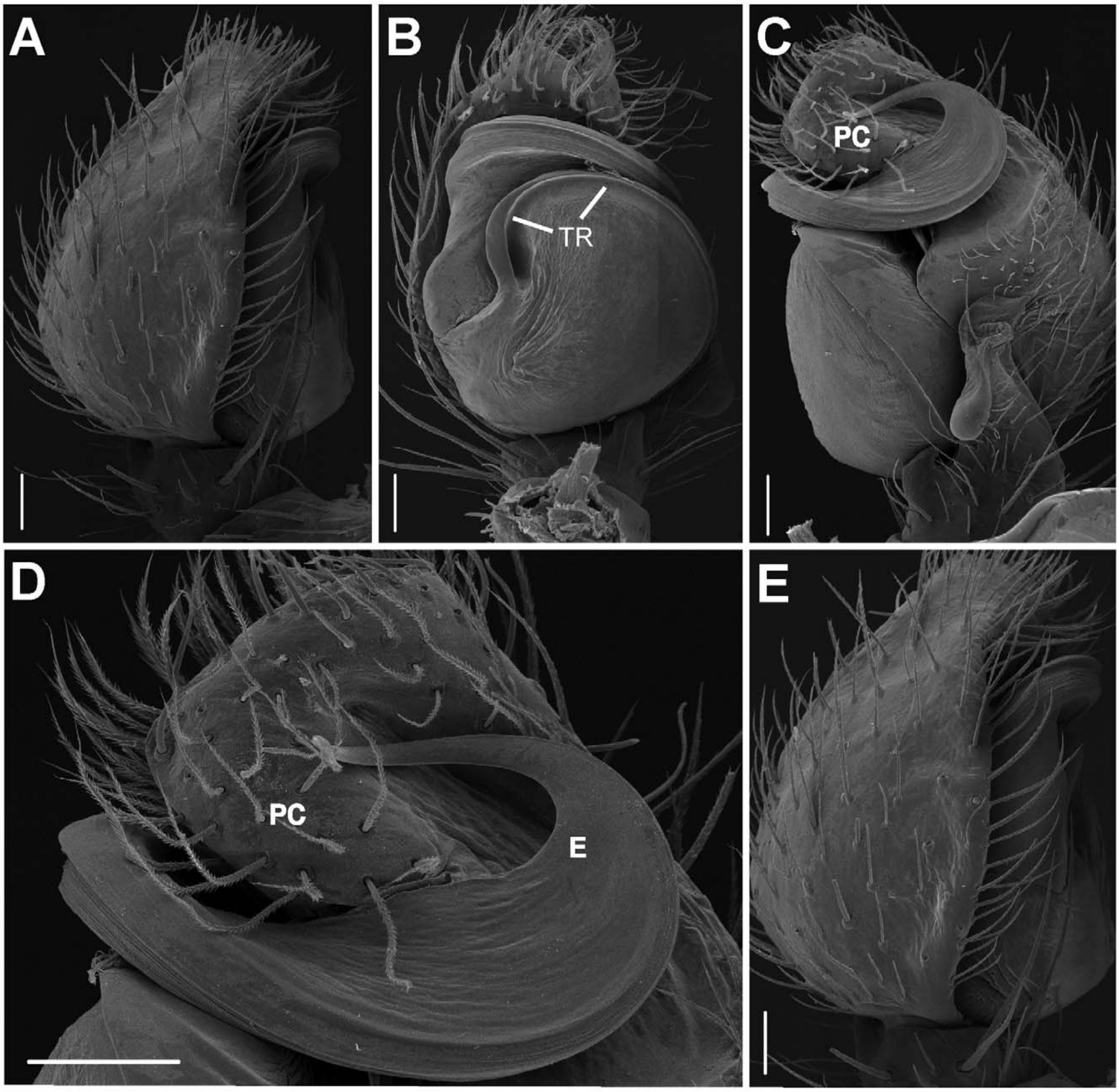

FIGURE 57. Scanning electron micrographs of *Mecaphesa asperata*. A–E male palp (A, E prolateral, B ventral, C, D retrolateral). Scale bars = 100 µm.

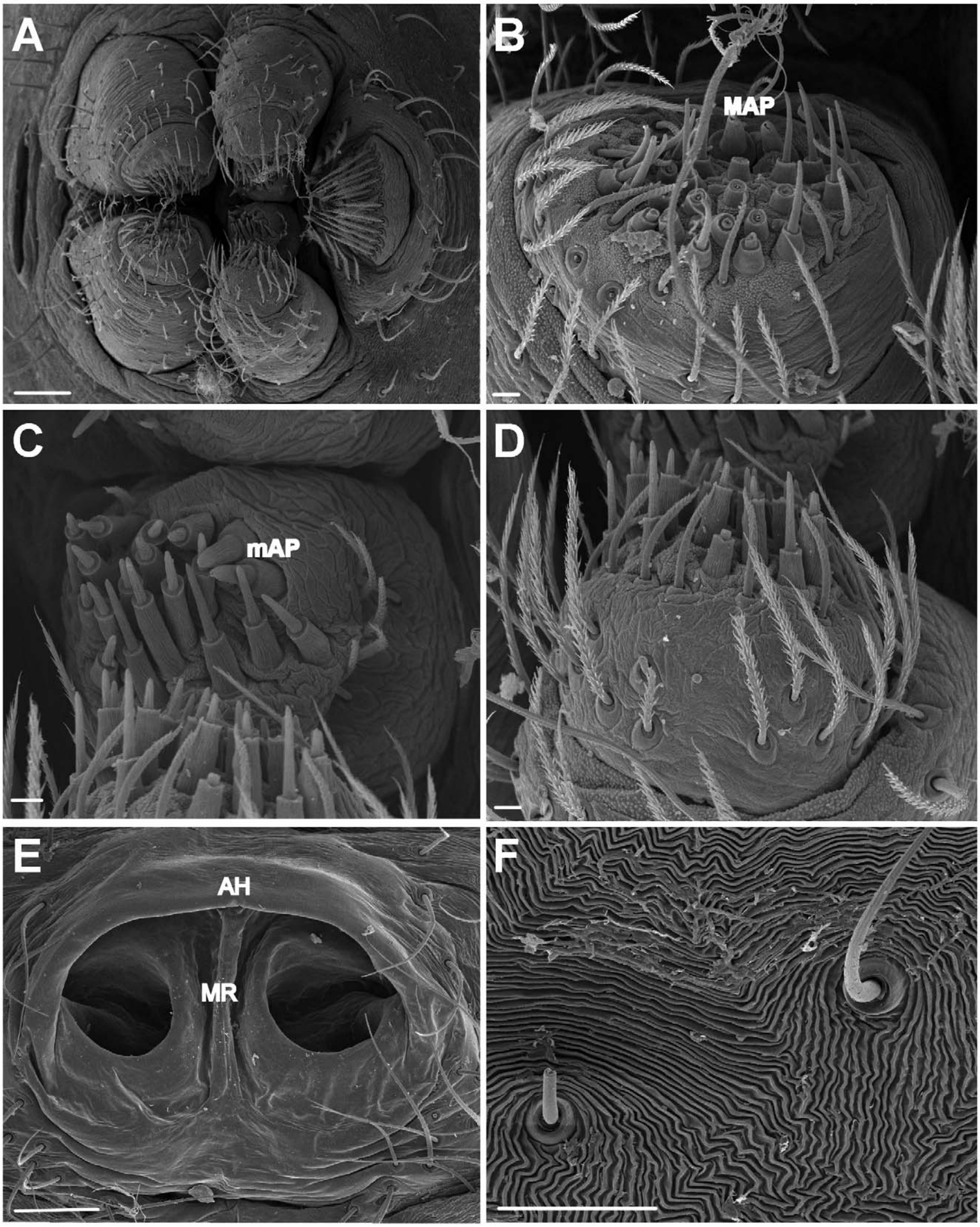

FIGURE 58. Scanning electron micrographs of *Mecaphesa asperata*. A spinnerets; B ALS; C PMS; D PLS; E epigynum, ventral view; F opisthosoma detail, dorsal view. Scale bars = 10 µm (B–D), 100 µm (A, E, F).

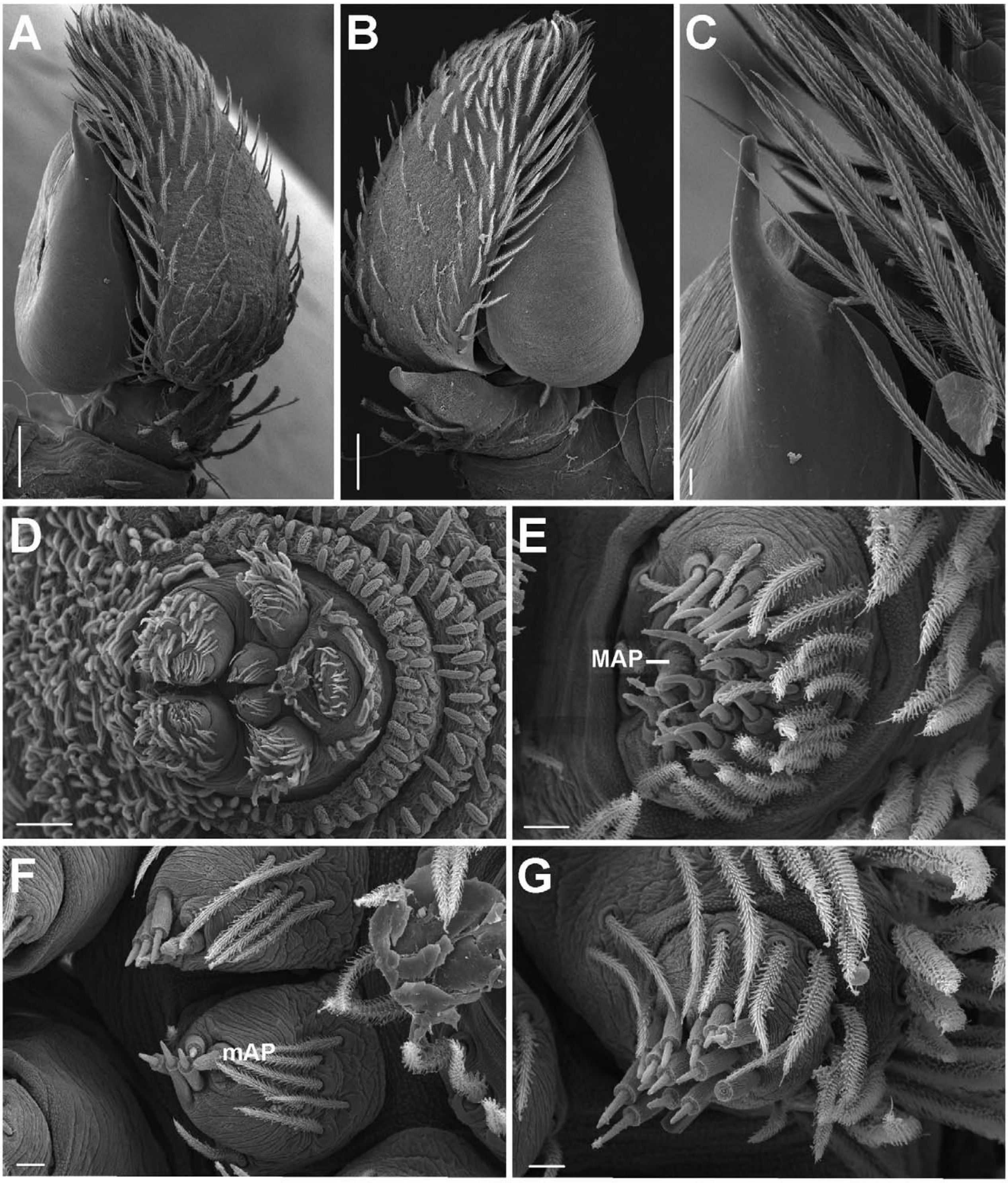

FIGURE 59. Scanning electron micrographs of male *Onocolus* sp. from Ecuador. A–C male palp (A, C prolateral, B retrolateral); D spinnerets, ventral view; E ALS; F PMS; G PLS. Scale bars = 10 µm (C, E–G), 100 µm (A, B, D).

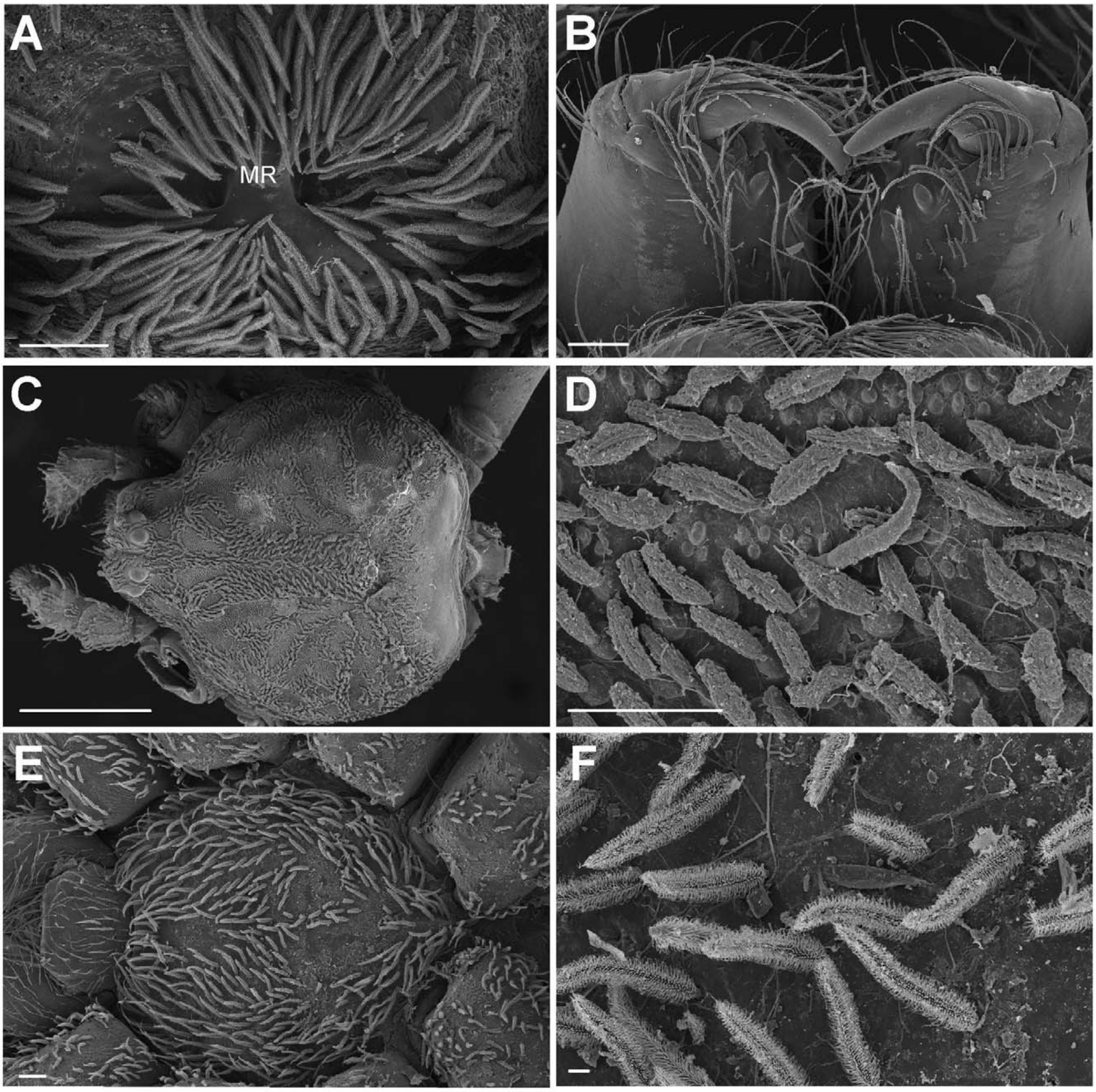

FIGURE 60. Scanning electron micrographs of female *Onocolus* sp. from Ecuador. A epigynum, ventral view; B chelicerae, ventral view; C prosoma, dorsal view; D detail of C; E sternum, ventral view; F detail of E. Scale bars = 10 µm (F), 100 µm (A, B, D, E), 1 mm (C).

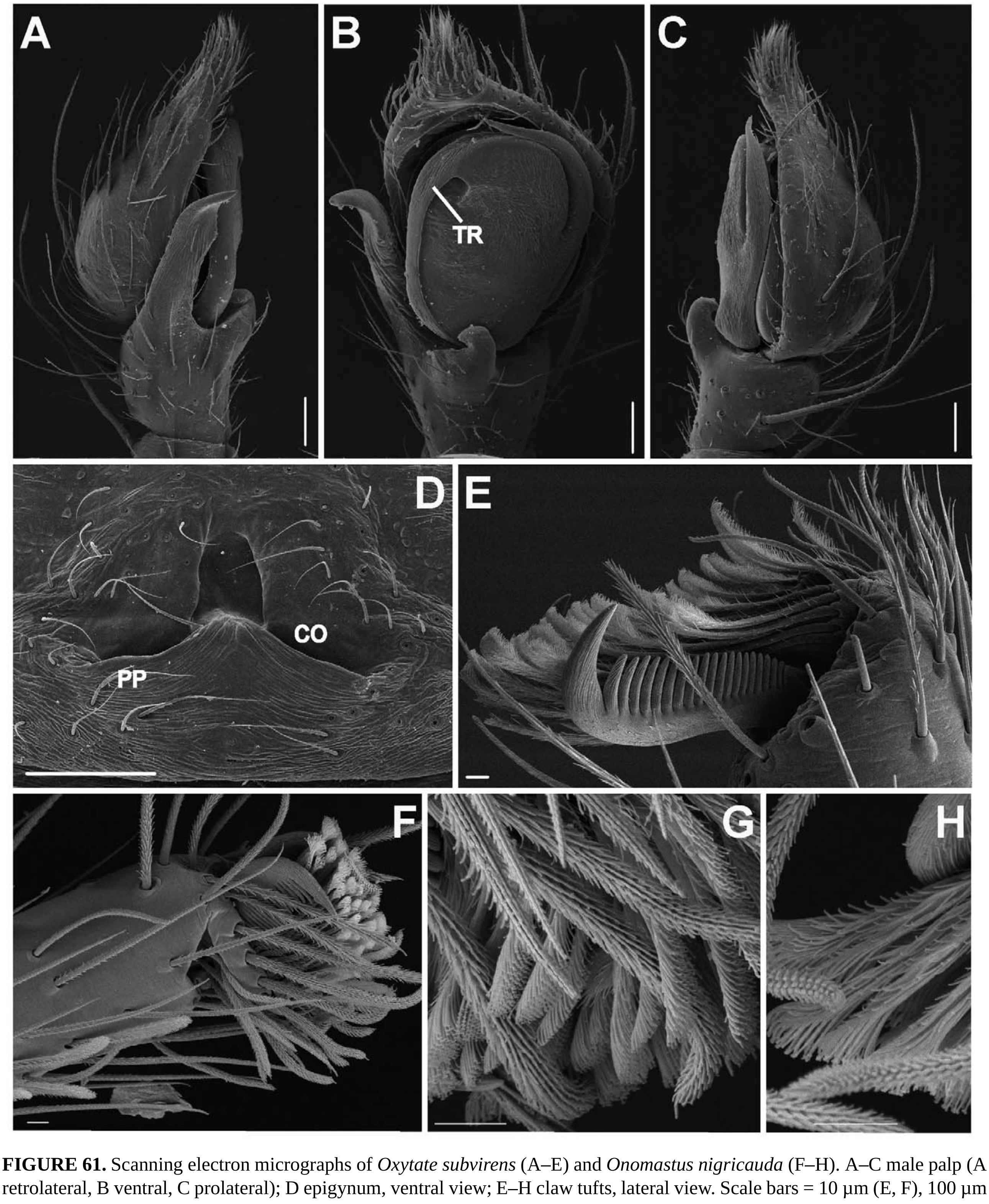

FIGURE 61. Scanning electron micrographs of *Oxytate subvirens* (A–E) and *Onomastus nigricauda* (F–H). A–C male palp (A retrolateral, B ventral, C prolateral); D epigynum, ventral view; E–H claw tufts, lateral view. Scale bars = 10 µm (E, F), 100 µm (A–D, G, H).

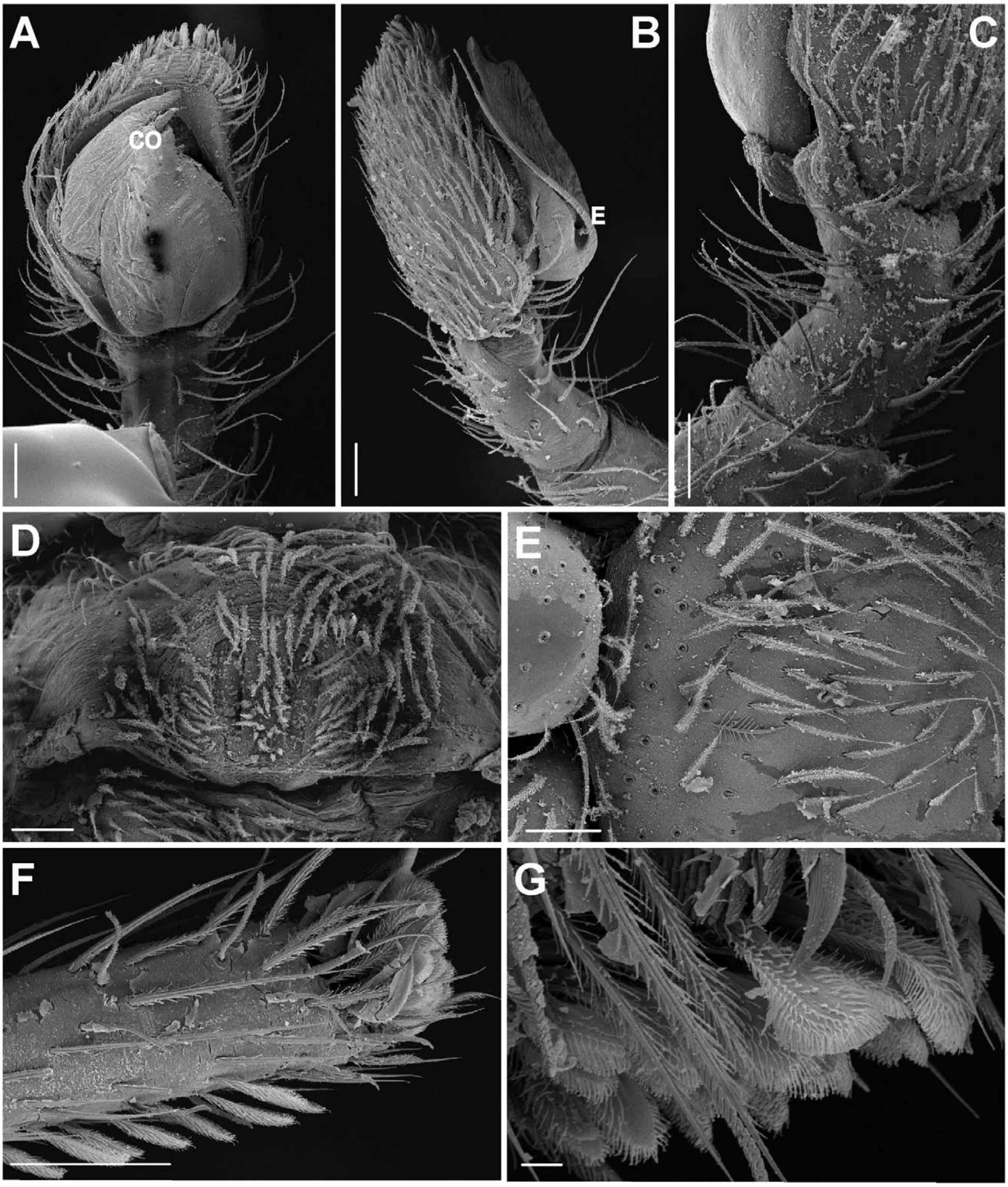

FIGURE 62. Scanning electron micrographs of *Philodromus rufus* (USNM). A–B male palp (A ventral, B prolateral); C RTA, retrolateral view; D epigynum, ventral view; E sternum, ventral view; F, female, left leg I, lateral view; G ditto, detail. Scale bars = 10 µm (G), 100 µm (A–F).

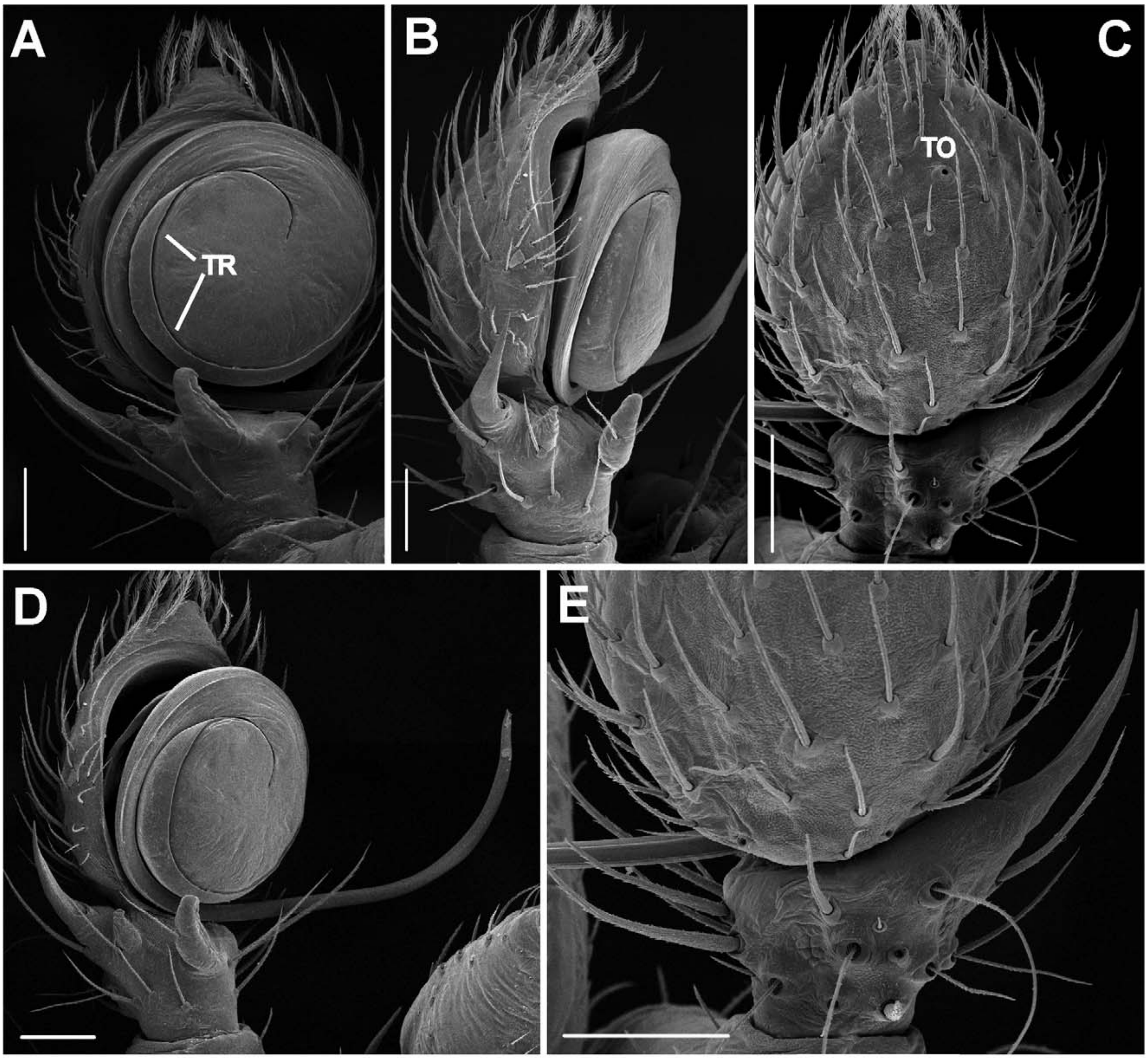

FIGURE 63. Scanning electron micrographs of *Phrynarachne* sp. (CAS). A–D male palp (A ventral, B, D retrolateral, C, E dorsal). Scale bars = 100 µm.

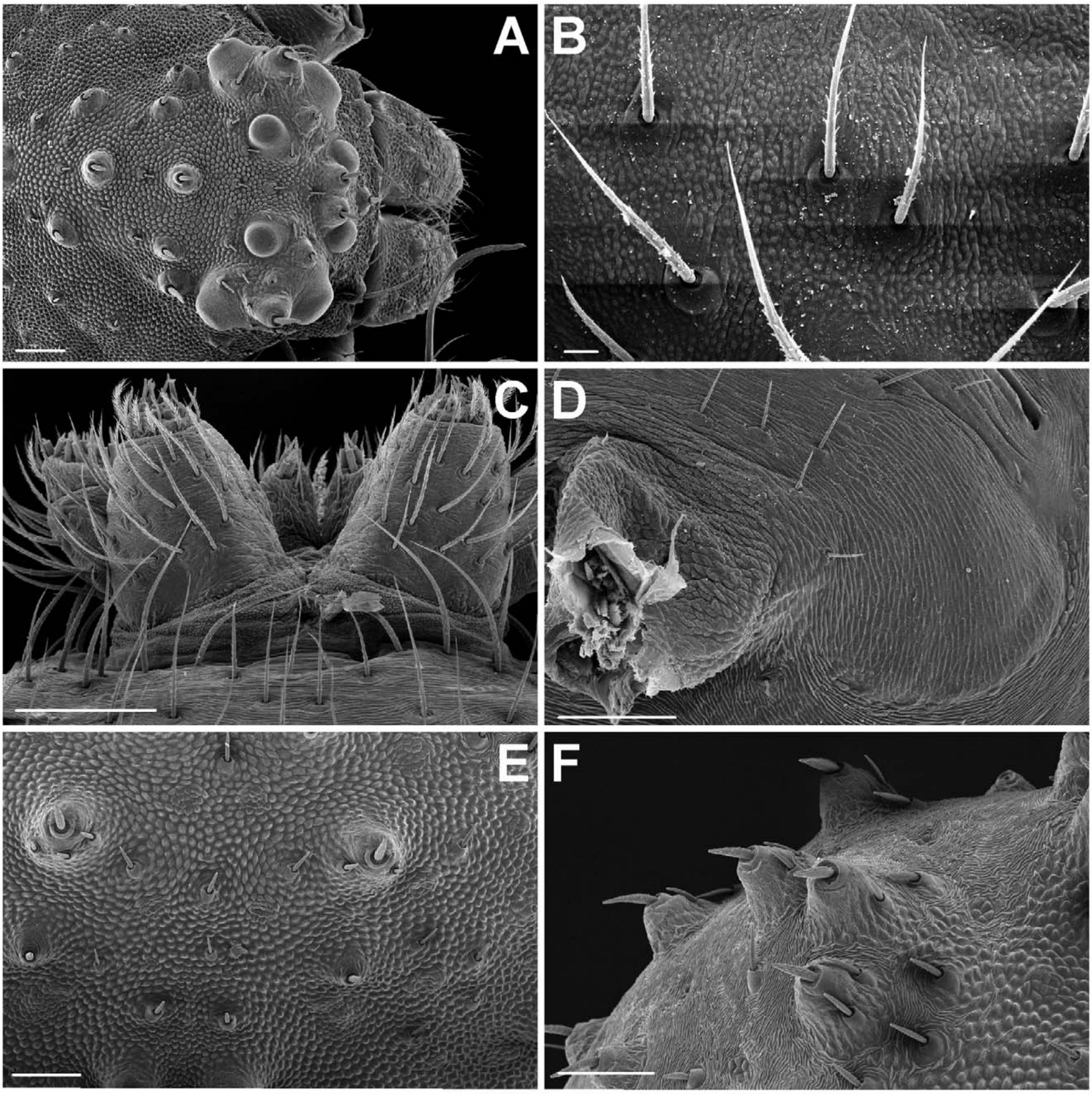

FIGURE 64. Scanning electron micrographs of *Phrynarachne* sp. male (CAS). A prosoma, dorsal view; B sternum, ventral view; C colulus, ventral view; D book lung cover, ventral view; E, F opisthosoma, dorsal view. Scale bars = 10 µm (B), 100 µm (A, C–F).

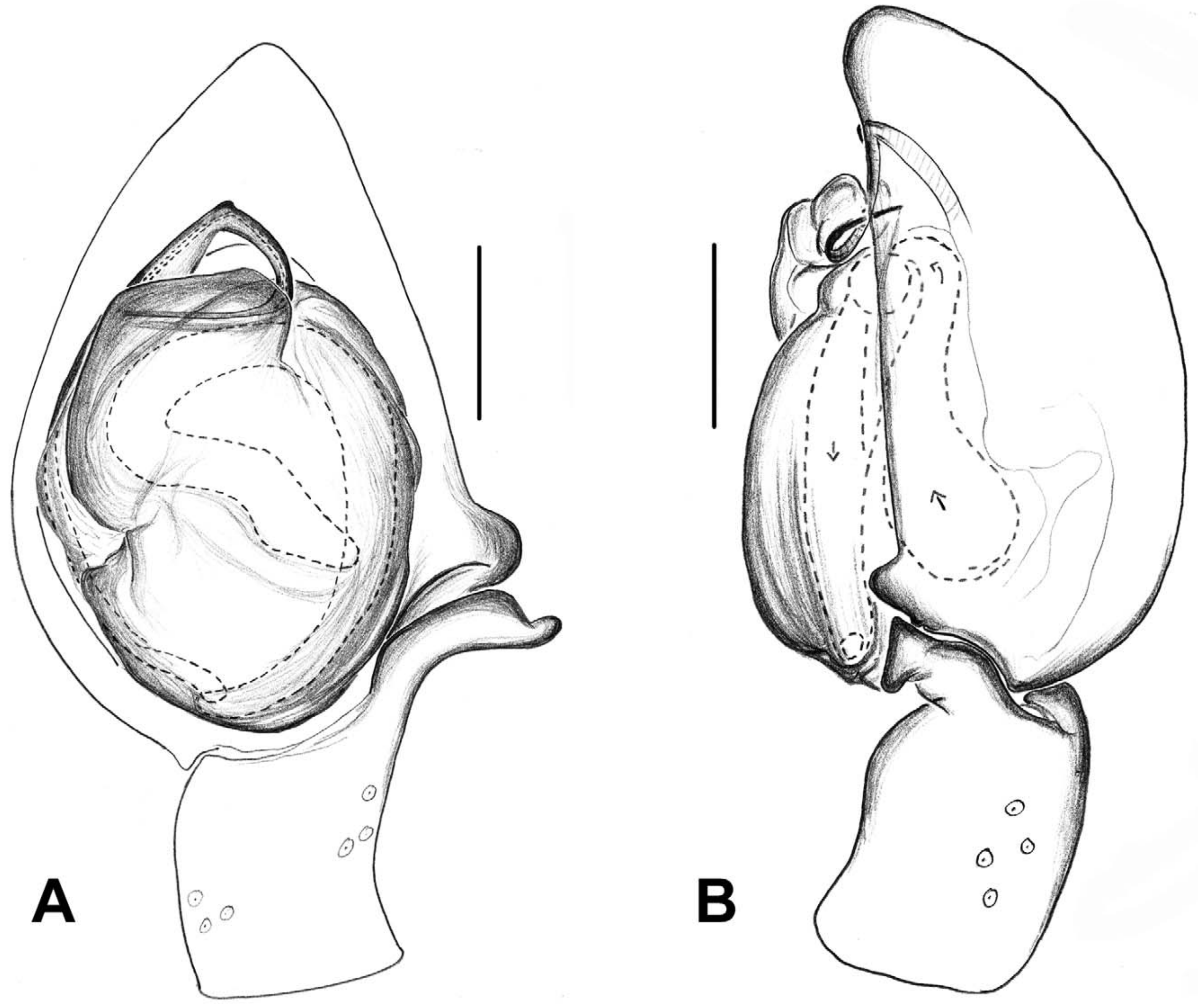

Figure 65. *Sidymella angulata* (CASENT 9023857). A–B male palp (A ventral, B retrolateral). Scale bars = 0.2 mm.

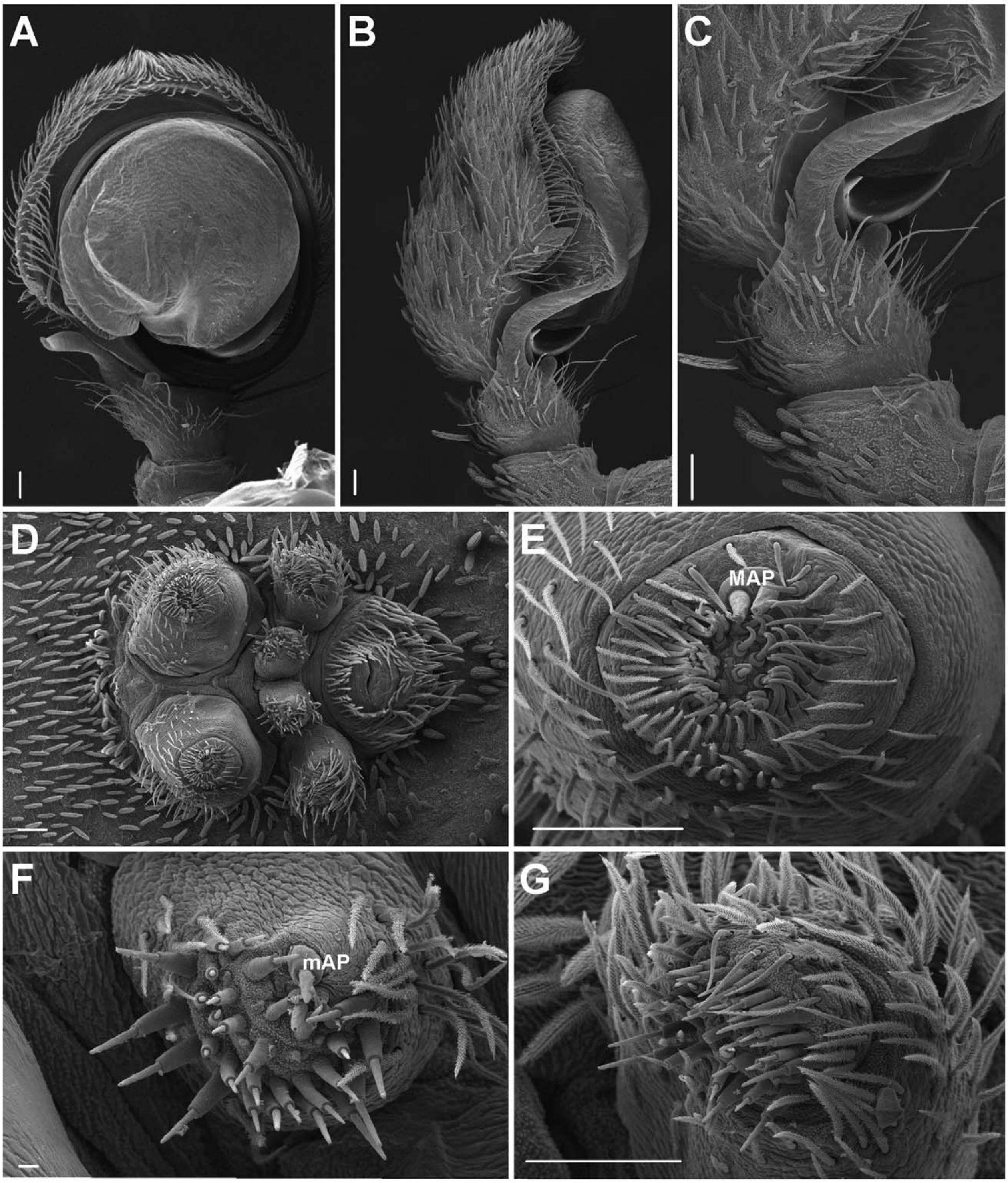

Figure 66. Scanning electron micrographs of *Stephanopis cambridgei* (USNM). A–C right male palp (A ventral, B, C retrolateral); D spinnerets, ventral view; E ALS; F PMS; G PLS. Scale bars = 10 µm (F), 100 µm (A–E, G).

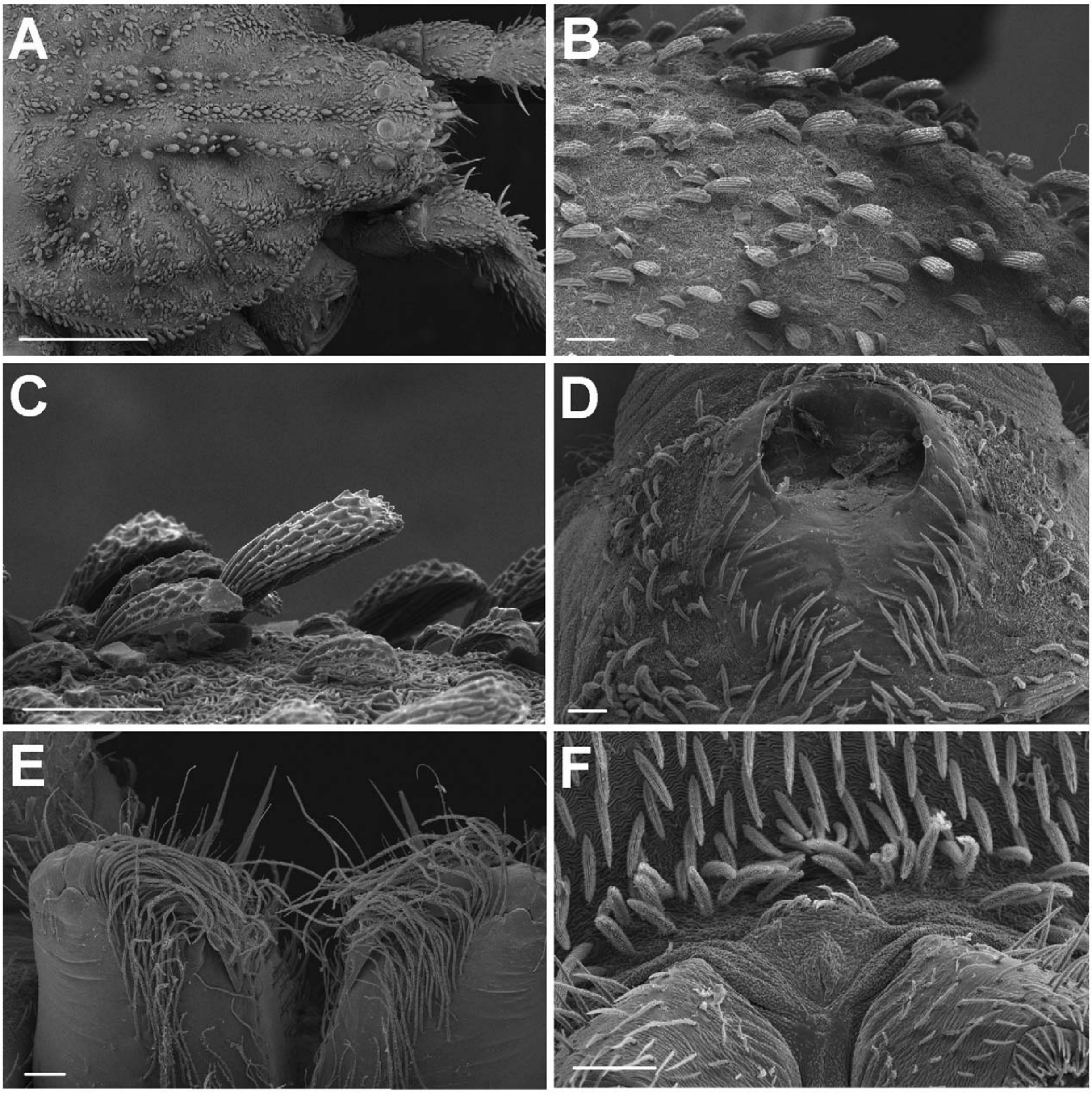

FIGURE 67. Scanning electron micrographs of *Stephanopis cambridgei* (USNM). A prosoma, dorsal view; B, C prosomal setae; D epigynum, ventral view; E chelicerae; F colulus. Scale bars = 100 µm (B, C–F), 1 mm (A).

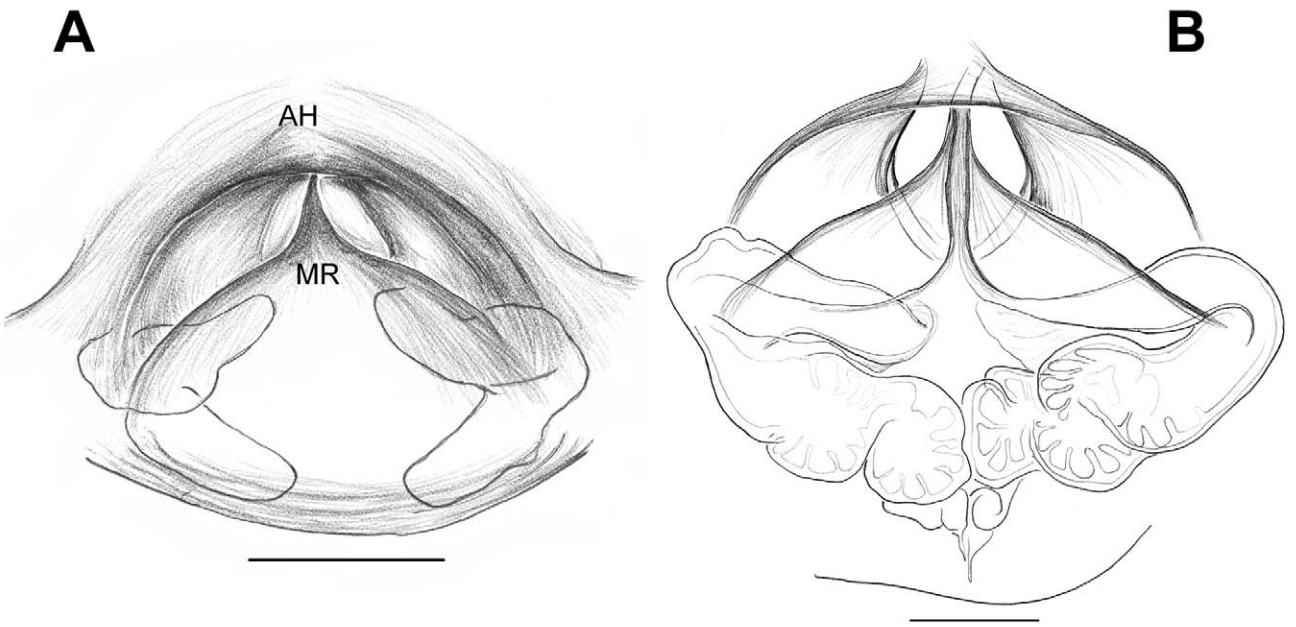

FIGURE 68. *Stephanopis* sp. from Chile (USNM). A epigynum, ventral view; B vulva, ventral view. Scale bars = 0.2 mm.

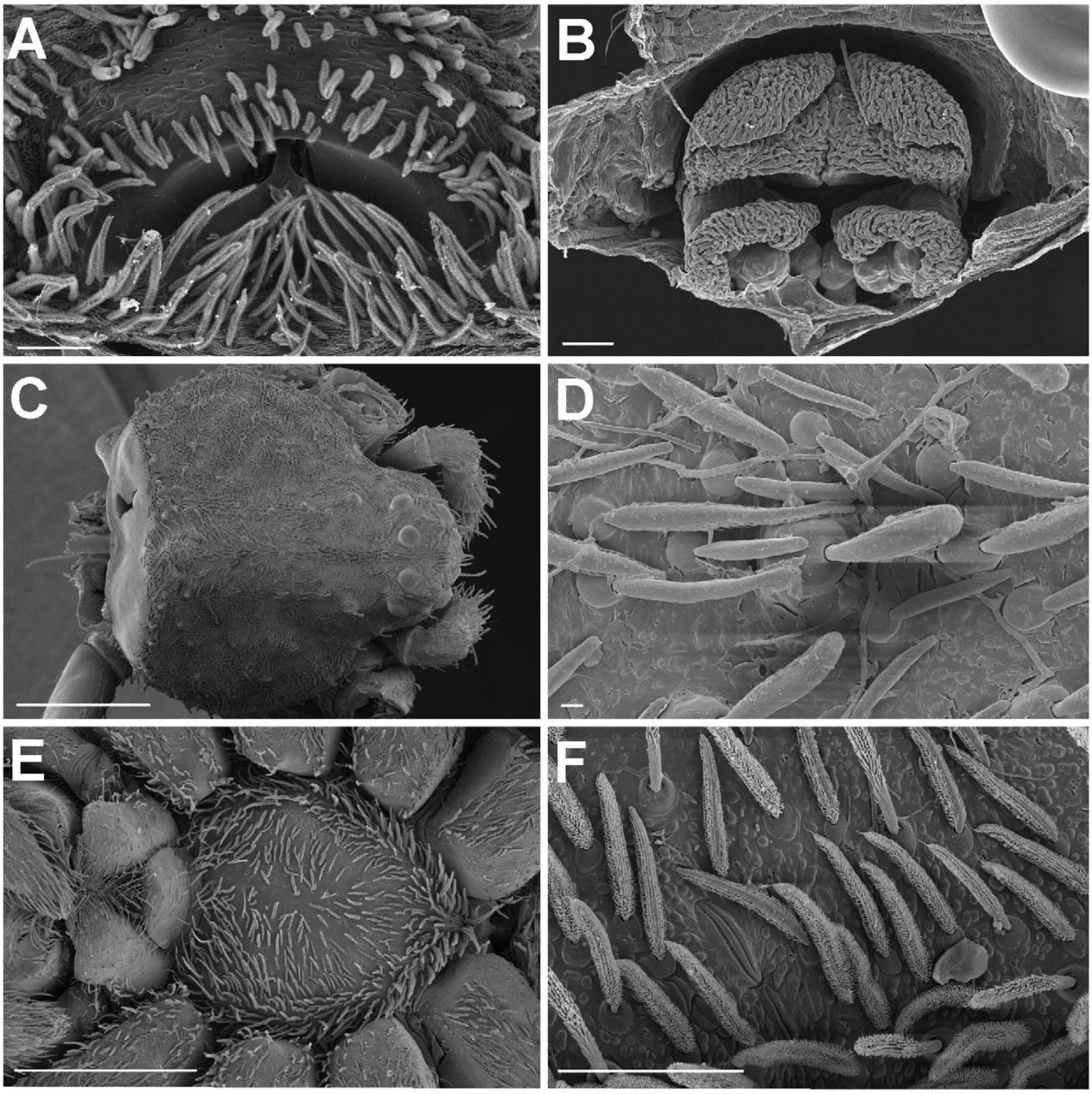

FIGURE 69. Scanning electron micrographs of *Stephanopis* sp. female from Chile (USNM). A epigynum, ventral view; B vulva, ventral view; C prosoma, dorsal view; D detail of setae, dorsal view; E sternum, ventral view; F detail of setae, ventral view. Scale bars = 10 µm (D), 100 µm (A, B, F), 1 mm (C, E, F).

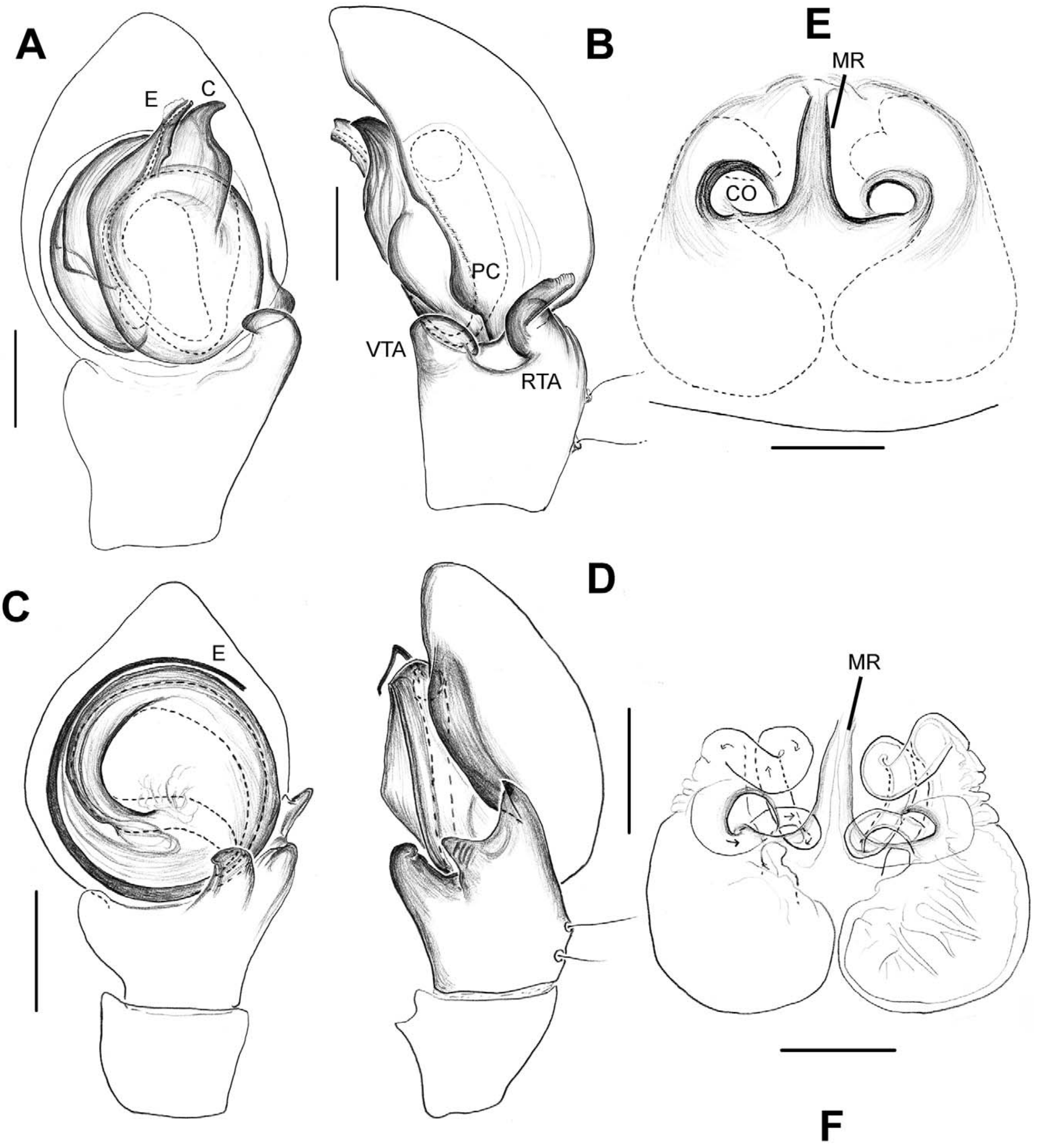

FIGURE 70. A, B *Stiphropus lugubris* (USNM). C–F *Strophius* sp. (USNM). A-D male palp (A, C ventral, C, D retrolateral); E epigynum, ventral view; F vulva, ventral view. Scale bars = 0.1 mm (A, B, E, F), 0.2 mm (C, D).

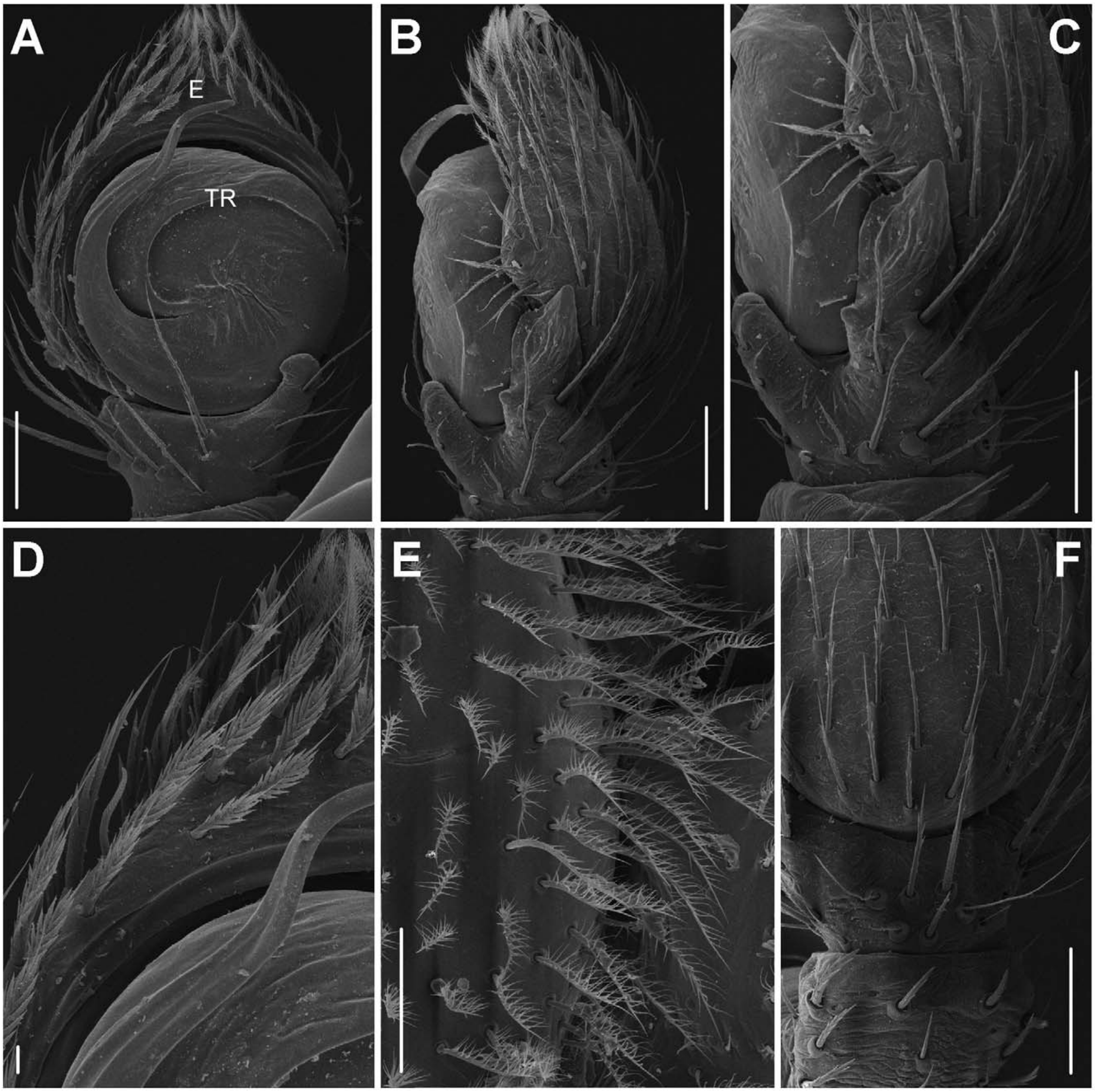

FIGURE 71. Scanning electron micrographs of *Strophius* sp. (USNM). A–D, F male palp (A, D ventral, B, C retrolateral, F dorsal); E, female sternum, ventral view. Scale bars = 10 µm (D), 100 µm (A–C, E, F).

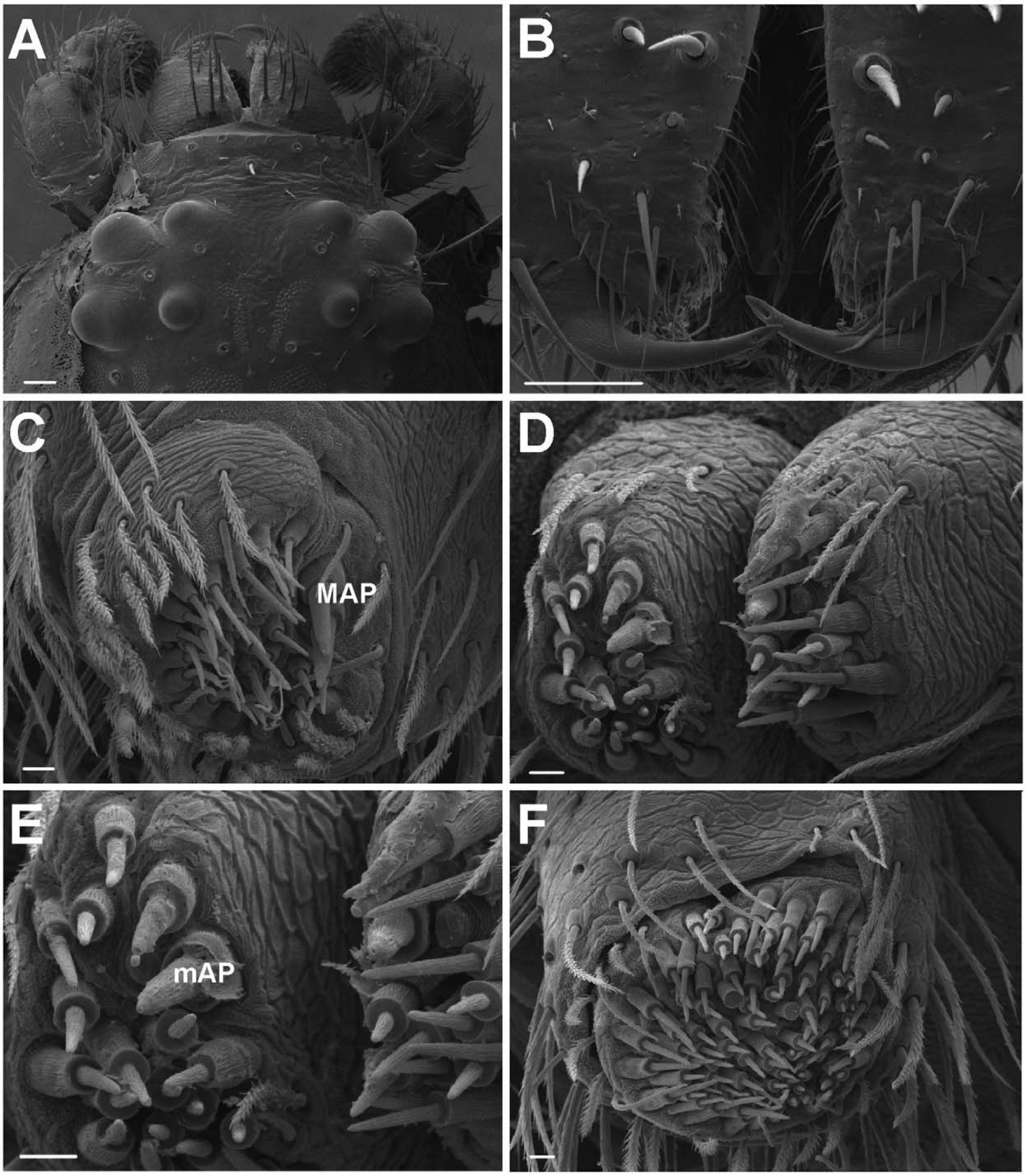

FIGURE 72. Scanning electron micrographs of *Strophius* sp., female (USNM). A prosoma, dorsal view; B; chelicerae, front view; C ALS; D, E PMS; F PLS. Scale bars = 10 µm (C–F), 100 µm (A, B).

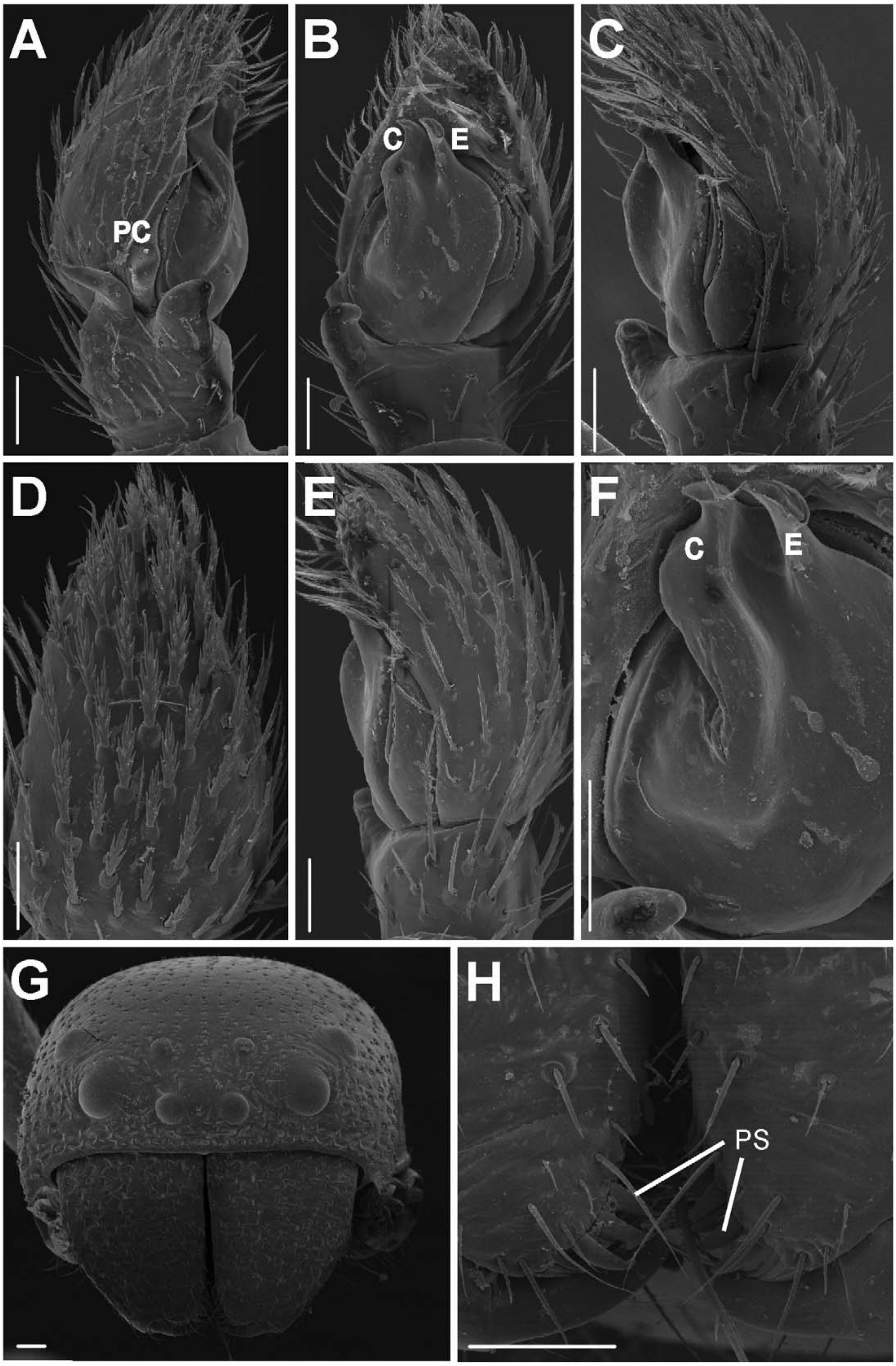

FIGURE 73. Scanning electron micrographs of *Stiphropus lugubris*, male (USNM). A–F male palp (A retrolateral, B, F ventral, C, E prolateral D dorsal); G prosoma, frontal view; H chelicerae, frontal view. Scale bars = 100 µm.

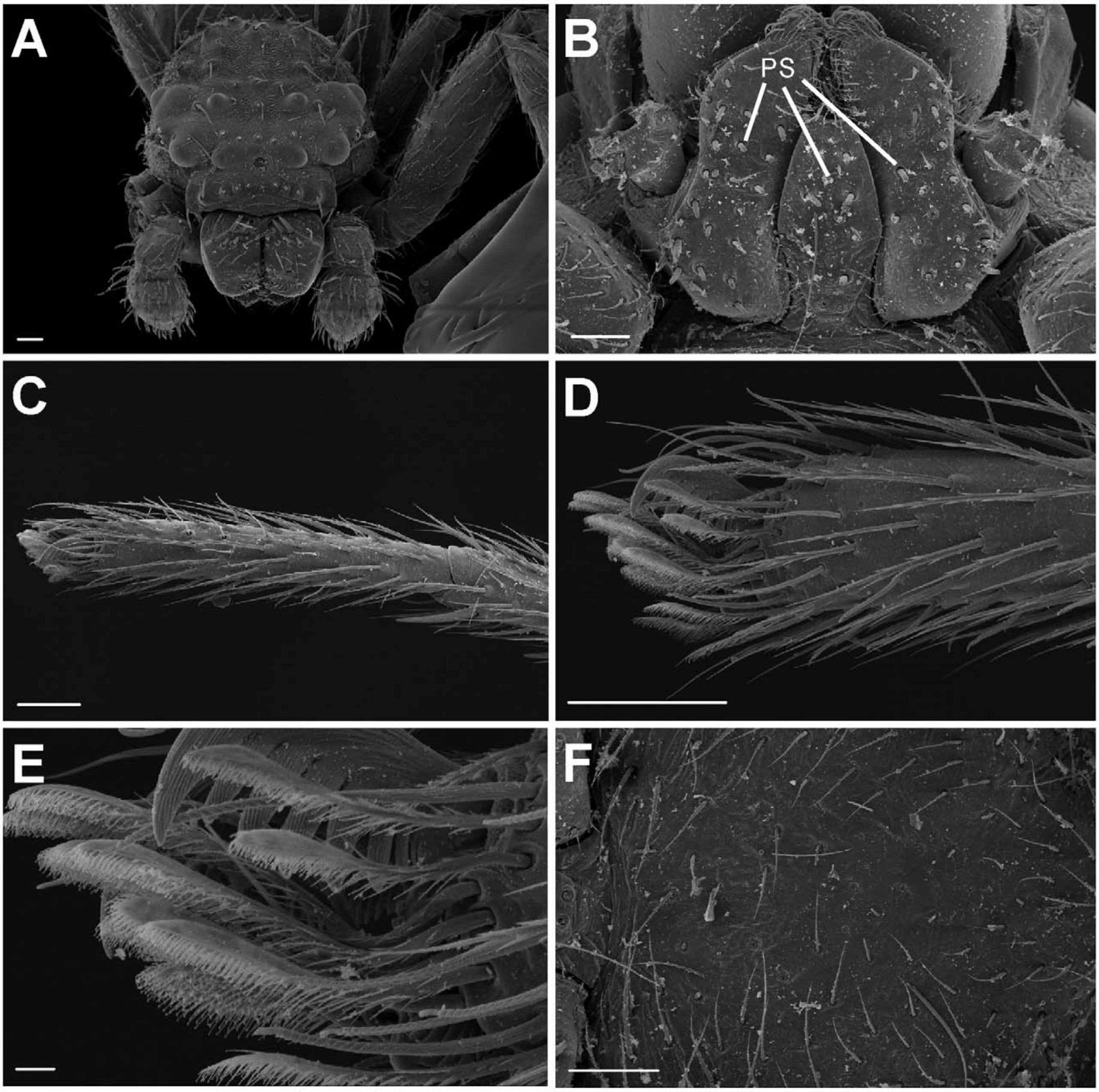

FIGURE 74. Scanning electron micrographs of *Strigoplus* sp., male. A prosoma, dorsal view; B endites and labium, ventral view; C, D left leg 1 lateral view; E scopula, lateral view; F sternum, ventral view. Scale bars = 100 µm.

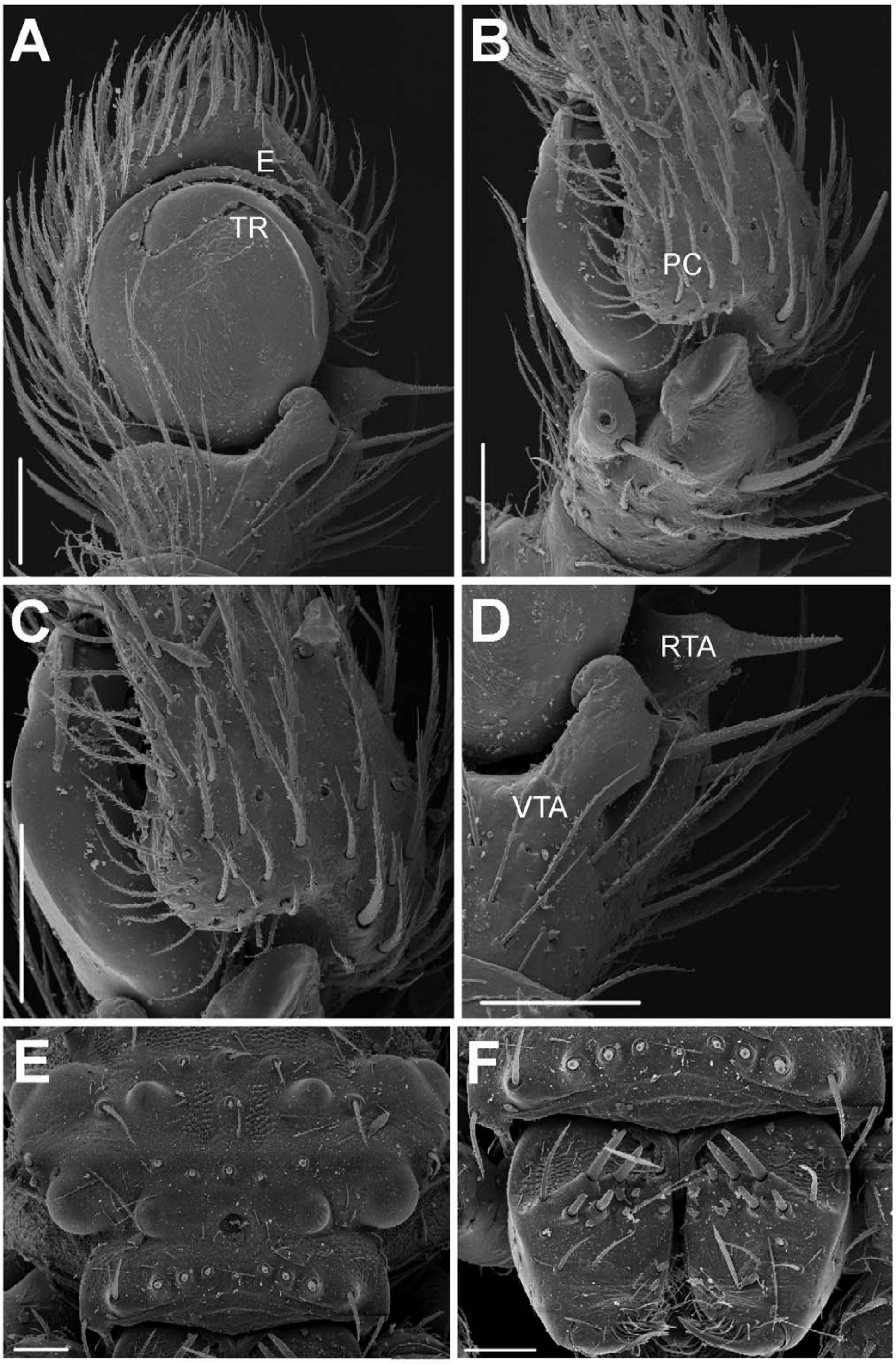

FIGURE 75. Scanning electron micrographs of *Strigoplus* sp., male. A–D male palp (A ventral, B–D retrolateral); E clypeus, front view; F chelicerae, front view. Scale bars = 100 µm.