

Original Article

Tailor's drawer no more: a reappraisal of the spider family Dictynidae O. Pickard-Cambridge, 1871 *sensu lato*

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ABSTRACT

The mesh-web weaver family Dictynidae *s.l.* has been labelled a 'tailor's drawer' family because it contains taxonomically unorganized and often evolutionarily distant species. Previous molecular phylogenetic studies using limited taxonomic sampling and legacy target genes involving representatives of the family have been consistent in: (i) exhibiting low branch support values and (ii) the recovery of genera and species currently classified as dictynids outside of Dictynidae. The genera within the family and the relationships among dictynid genera have never been rigorously tested using genomic-scale data. Here, we use exemplar dictynid species from the most currently recognized dictynid genera and ultraconserved elements (UCEs) recovered *in silico* from low-coverage, whole-genome sequencing plus Sanger data to resolve the phylogenetic placement and relationships of genera within the family Dictynidae *s.l.* The resulting phylogeny, along with morphological evidence, supports several taxonomic updates to the group: Argyronetidae *stat. reinst.*, Lathyidae *fam. n.*, and Dictynidae *s.s.* are included in Dictynoidea. Argyronetidae *stat. reinst.* include the genera *Altella*, *Arctella*, *Argenna*, *Argyroneta*, *Chaerea*, *Devade*, *Hackmania*, *Iviella*, *Mizaga*, *Paratheuma*, *Saltonia*, *Tricholathys*. The family Lathyidae *fam. n.* is proposed to include the genera *Afrolathys* *gen. n.* (*Af. madagascariensis* *sp. n.* and *Af. tanzanica* *sp. n.*), *Analtella* *stat. reinst.* (*Analtella affinis* *comb. n.*, *Analtella dentichelis* *comb. n.*, *Analtella narbonensis* *comb. n.*, *Analtella pygmaea* *comb. n.*, and *Analtella teideensis* *comb. n.*), *Andronova* *gen. n.* (*Andronova alberta* *comb. n.*, *Andronova annulata* *comb. n.*, *Andronova arabs* *comb. n.*, *Andronova cambridgei* *comb. n.*, *Andronova dihamata* *comb. n.*, *Andronova lehtineni* *comb. n.*, *Andronova maculosa* *comb. n.*, *Andronova spasskyi* *comb. n.*, *Andronova subalberta* *comb. n.*, *Andronova subviridis* *comb. n.*, and *Andronova sylvania* *comb. n.*), *Asialathys* *gen. n.* (*As. deltoidea* *comb. n.*, *As. fibulata* *comb. n.*, *As. huangyangjieensis* *comb. n.*, *As. spiralis* *comb. n.*, and *As. zhanfengi* *comb. n.*), *Bannaella* (*B. lhasana*, *B. sexoculata* *comb. n.*, *B. sinuata*, and *B. tibialis*), *Denticulathys* *gen. n.* (*D. amaataaidoo* *sp. n.*), *Langlibaitiao* (*Langlibaitiao chishuiensis*, *Langlibaitiao inaeffectus*, *Langlibaitiao insulanus* *comb. n.*, and *Langlibaitiao zhangshun*), *Lathys* *s.s.* (*Lathys bin*, *Lathys borealis*, *Lathys brevitybialis*, *Lathys coralynae*, *Lathys dixiana*, *Lathys foxi*, *Lathys heterophthalma*, *Lathys humilis*, *Lathys humilis meridionalis*, *Lathys lepida*, *Lathys mantarota*, *Lathys sexpustulata*, *Lathys spiralis*, and *Lathys subhumilis*), *Scotolathys* *s.s.* (*S. delicatula* *stat. reinst.*, *S. immaculata* *stat. reinst.*, *S. maculina* *stat. reinst.*, *S. pallida* *stat. reinst.*, and *S. simplex*), *Tolokonniella* *gen. n.* (*Tolokonniella ankaraensis* *comb. n.*, *Tolokonniella mallorcensis* *comb. n.*, *Tolokonniella maura* *comb. n.*, *Tolokonniella stigmatisata* *comb. n.*, and *Tolokonniella truncata* *comb. n.*). Finally, Dictynidae *s.s.* are strongly supported to include the genera *Adenodictyna*, *Ajmonia* (*Aj. changtunesis* *comb. n.*) *Anaxibia*, *Arangina*, *Archaeodictyna* (*Archaeodictyna aguasverdes* *comb. n.*, *Archaeodictyna bispinosa* *comb. n.*, *Archaeodictyna fuerteventurensis* *comb. n.*, and *Archaeodictyna lanzarotensis* *comb. n.*), *Arethyna* *gen. n.* (*Arethyna coloradensis* *comb. n.*, *Arethyna idahoana* *comb. n.*, *Arethyna osceola* *comb. n.*, *Arethyna personata* *comb. n.*, *Arethyna peon* *comb. n.*, *Arethyna saltona* *comb. n.*, *Arethyna secuta* *comb. n.*, *Arethyna sierra* *comb. n.*, *Arethyna ubsunurica* *comb. n.*, *Arethyna volucripes* *comb. n.*, and *Arethyna volucripes volucripoides* *comb. n.*), *Argennina*, *Atelolathys*, *Banaidja*, *Brigittea* (*B. colona* *comb. n.*), *Califorenigma* *gen. n.* (*C. linsdalei* *comb. n.*), *Callevophthalmus*, *Dictyna* (*D. abundans*, *D. alaskae*, *D. albicoma*, *D. albivittata*, *D. alyceae*, *D. apachea*, *D. arundinacea*, *D. bostoniensis*, *D. brevitarisus*, *D. cafayate*, *D. chandrai*,

D. cofete, *D. columbiana*, *D. cronebergi*, *D. crosbyi*, *D. dauna*, *D. ectrapela*, *D. fluminensis*, *D. guineensis*, *D. hamifera*, *D. kosiorowiczii*, *D. laeviceps*, *D. linzhiensis*, *D. livida*, *D. marilina*, *D. moctezuma*, *D. namulinensis*, *D. navajoa*, *D. pictella*, *D. procerula*, *D. pusilla*, *D. quadrispinosa*, *D. ranchograndei*, *D. saepi*, *D. similis*, *D. simoni*, *D. sinaloa*, *D. siniloanensis*, *D. tarda*, *D. togata*, *D. tristis*, *D. trivirgata*, *D. tullgreni*, *D. turbida*, *D. uncinata*, *D. uvs*, *D. vittata*, *D. vultuosa*, and *D. yongshun*), *Dictynomorpha*, *Emblyna* (*E. acoreensis*, *E. aiko*, *E. altamira*, *E. ampla*, *E. angulata*, *E. annulipes*, *E. ardea*, *E. artemisia*, *E. borealis*, *E. borealis cavernosa*, *E. branchi*, *E. brevidens*, *E. budarini*, *E. burjatica*, *E. callida*, *E. capens*, *E. cavata* comb. n., *E. chitina*, *E. completa*, *E. completoides*, *E. consulta*, *E. cornupeta*, *E. coweta*, *E. crocana*, *E. decapriini*, *E. evicta*, *E. florens*, *E. formicaria*, *E. hentzi*, *E. horta*, *E. hoya*, *E. joaquina*, *E. lina*, *E. linda*, *E. manitoba*, *E. marissa*, *E. melva*, *E. nanda*, *E. oasa*, *E. palomara*, *E. pinalia*, *E. piratica*, *E. peragrata*, *E. reticulata*, *E. roscida*, *E. saylori*, *E. scotta*, *E. seminola*, *E. shasta*, *E. shoshonea*, *E. stulta*, *E. sublatoides*, *E. suwaneana*, and *E. zaba*), *Eriena* gen. n. (*Er. minuta* comb. n. and *Er. mora* comb. n.), *Helenactyna*, *Khalotyna* gen. n. (*K. calcarata* comb. n.), *Kharitonovia*, *Mallos*, *Marilynia*, *Mashimo*, *Mexitlia*, *Myanmardictyna*, *Nigma*, *Nopalityna* gen. n. (*N. francisca* comb. n., *N. jonesae* comb. n., *N. orbiculata* comb. n., *N. sublata* comb. n., *N. suprenans* comb. n., and *N. uintana* comb. n.), *Pangunus* gen. n. (*Pa. kaszabi* comb. n., *Pa. umai* comb. n., and *Pa. xizangensis* comb. n.), *Paradictyna*, *Penangodyna*, *Phantyna*, (*Ph. agressa* comb. n. and *Ph. formidolosa* comb. n.), *Purplecorna* gen. n. (*Pu. gloria* comb. n., *Pu. guerrenensis* comb. n., *Pu. incredula* comb. n., *Pu. lecta* comb. n., *Pu. meditata* comb. n., *Pu. miniata* comb. n., and *Pu. terrestris* comb. n.), *Rhion*, *Shango*, *Shikibutyna* gen. n. (*Sh. felis* comb. n., *Sh. follicola* comb. n., *Sh. guanchae* comb. n., *Sh. mongolica* comb. n., *Sh. procerula* comb. n., *Sh. schmidti* comb. n., *Sh. szaboi* comb. n., *Sh. wangi* comb. n., *Sh. xizangensis* comb. n., and *Sh. zherikhini* comb. n.), *Simziella* gen. n. (*Si. annexa* comb. n., *Si. cebolla* comb. n., *Si. dunini* comb. n., *Si. major* comb. n., *Si. palmgreni* comb. n., *Si. paramajor* comb. n., *Si. sancta* comb. n., *Si. sotnik* comb. n., *Si. sylvania* comb. n., *Si. tridentata* comb. n., *Si. tucsona* comb. n., *Si. tyshchenkoi* comb. n., *Si. tyshchenkoi wrangeliana* comb. n., *Si. canadas* comb. n., and *Si. teideensis* comb. n.), *Spagnius* gen. n. (*Sp. albopilosa* comb. n., *Sp. foliacea* comb. n., *Sp. jacalana* comb. n., and *Sp. nebraska* comb. n.), *Sudesna*, *Tahuantina*, *Thallumetus*, *Tivyna* (*Ti. sonora* comb. n.), *Tolkienus* gen. n. (*Tolkienus armatus* comb. n., *Tolkienus bellans* comb. n., *Tolkienus bellans hatchi* comb. n., *Tolkienus estoc* sp. n., *Tolkienus otto* comb. n., and *Tolkienus longispina* comb. n.), and *Viridictyna*. This study begins to remedy the dearth of systematic knowledge about this incredibly diverse spider group and fills knowledge gaps in the tree of life for little brown spiders.

Keywords: arachnology; genome subsampling; marronoid; new families; new genera; phylogenomics; ultraconserved elements

INTRODUCTION

Assembling the spider tree of life is an opportunity to better understand why spiders are such an evolutionarily successful group and to gain insights into how they have evolved and adapted through time (Wheeler et al. 2017, Kulkarni et al. 2023). Wheeler et al. (2017) greatly advanced the knowledge of the spider tree of life and, importantly, illuminated areas where additional work is required. One area of concern noted in this seminal work is the ‘marronoid clade’ (Wheeler et al. 2017, Crews et al. 2020, Gorneau et al. 2023a, Kulkarni et al. 2023)—a clade initially defined solely on the basis of weakly supported Sanger data (Wheeler et al. 2017) but more recently strongly supported by Gorneau et al. (2023a) and Kulkarni et al. (2023) using a combination of genomic (ultraconserved elements, UCEs) and Sanger data. This group, as defined by Wheeler et al. (2017), comprises brown or grey spiders with few explicit characters and is host to ‘tailor’s drawer’ families, including Dictynidae O. Pickard-Cambridge, 1871, which represent a ‘dumping ground for a diverse array of cribellate and ecribellate three-clawed Entelegynae’. This study also concluded that ‘Dictynidae are clearly in need of a major overhaul which was begun by Spagna et al. (2010) and Zamani et al. (2016)’.

Diverse, dazzling Dictynidae

The marronoid family Dictynidae is commonly known as the mesh-web spiders because cribellate dictynid webs are constructed in a close-knit lattice that are often found on plants (Chamberlin and Gertsch 1958). Despite being one of the oldest of the 136 families presently described, relationships within the family remain elusive (Wheeler et al. 2017, Crews et al. 2020, Gorneau et al. 2023). Dictynids are globally distributed, with 461 extant species in 52 genera (World Spider Catalog 2024), in addition to more than 50 fossil species in 30 genera (Dunlop et al. 2023). They typically have complex genitalia, of which many have not been illustrated, as well as striking secondary sexual characteristics. While generalized as small and

brown or grey, many Dictynidae species are quite colourful (e.g. *Nigma* Lehtinen, 1967) and are perhaps most notable for their intriguing distributional patterns and fascinating ecological characteristics.

Among dictynid species is an extreme diversity of adaptations to a wide range of habitats and life histories—species can be found from 81°N latitude (Leech 1966, Marusik et al. 2006a) to 55°S latitude (Dupérré and Harms 2018), in temperatures ranging from −71°C (Marusik et al. 2008) to 56.7°C (air temperature) and 93.9°C (ground temperature) (Kubecka 2001, Mammola et al. 2017). Some species are endemic to very small areas, whereas others are some of the most widespread of all spider species (Marusik and Koponen 1998, Marusik et al. 2000). Markedly prolonged cohabitation with relatively non-aggressive mating has been noted in dictynids as a whole: Bristowe (1976) pondered ‘the unusual friendship which seems to exist between the males and females’ of Dictynidae. Some species are even known to exhibit sociality, e.g. *Mallos gregalis* (Simon, 1909), which lives in arboreal communal webs (Chamberlin and Gertsch 1958). In another unusual niche, *Archaeodictyna ulova* Griswold and Meikle-Griswold, 1987 lives as an inquiline in the nests of two species of communal eresid spiders (Griswold and Meikle-Griswold 1987). Additionally, the family contains members in which a semi-aquatic lifestyle appears to have independently arisen several times (Spagna et al. 2010, Crews et al. 2020). The diving bell spider *Argyroneta aquatica* (Clerck, 1757) makes an air bubble that allows it to live nearly its entire life underwater. *Emblyna borealis* (O. Pickard-Cambridge, 1877) is found as far north as Arctic Greenland (GBIF). *Saltonia incerta* (Banks 1898) lives in salt flats in the deserts of south-western North America, including Death Valley, one of the hottest places on Earth (Crews and Gillespie 2014). The presence of this level of variation within a single family of spiders shows considerable potential as a system for answering a huge range of evolutionary and ecological questions, especially examining the evolution of specific characteristics or behaviours.

Taxonomy of Dictynidae s.l.

Dictynidae was informally designated as 'Lauerspinnen' (lurking spiders) by Menge (1866). The genus *Dictyna* Sundevall, 1833 was divided by Simon (1870) into three groups [Group 1: Ergatis (consisting of what are now *Nigma* and *Marilynia* Lehtinen, 1967); Group 2: *Dictyna* (*Brigittea* Lehtinen, 1967); Group 3: no name provided for this group (now all in the family Titanoecidae Lehtinen, 1967)]. O. Pickard-Cambridge (1871) then moved the genus into its own family, Dictynidae. Adding to taxonomic confusion, Thorell (1869) contemporaneously described the family Argyronetidae, consisting only of the genus *Argyroneta* Latreille, 1804. Ever since, the family has been a revolving door for small, brown spiders found the world over, with many genera being added and removed multiple times. The history of phylogenetic work on the family is summarized in Table 1. For most of its existence, the family only comprised members with a cribellum, or a spinning plate anterior to the spinnerets from which the silk is extruded and combed with a calamistrum, or a comb, on the fourth leg (Lehtinen 1967). The resulting silk is mechanically 'sticky' rather than sticky from glue droplets, as in the silk of ecribellate spiders (Opell 2012). The presiding paradigm of spider evolution was that all cribellates formed a clade, while all ecribellates formed a separate clade. However, in 1967, Lehtinen published a monograph that placed cribellates and ecribellates in the same families, causing much controversy in the arachnology community (Lehtinen 1967). Without using any cladistic analysis, just careful observation, he moved ecribellate genera into Dictynidae, but many of his proposed taxonomic changes were disregarded for several years. Eventually, and with the advent of molecular systematics, many of Lehtinen's hypotheses have been supported (see: Crews et al. 2020 and references therein).

Early revisionary work of the group used morphological characters to define the family and the placement of genera (Chamberlin and Gertsch 1958, Lehtinen 1967). Phylogenetic studies based on morphology and behavioural traits determined the family to be monophyletic (Griswold et al. 1999, 2005). In 2010, Spagna et al. used molecular data derived from three nuclear genes to examine 'dictynoid' relationships, finding that aquatic and semi-aquatic spider genera from different families [*Saltonia* Chamberlin and Ivie, 1942 (at the time placed in Dictynidae), *Paratheuma* Bryant, 1940 (at the time placed in

Desidae Pocock, 1895), and *Argyroneta* (at the time placed in Cybaeidae Banks, 1892)] formed a single clade and supported Lehtinen's (1967) proposed subfamilies of Dictynidae (see below). Spagna et al. (2010) made no taxonomic changes at the time, but subsequent publications have formally transferred both *Paratheuma* (Zamani et al. 2016) and *Argyroneta* (Wheeler et al. 2017) to Dictynidae. In a molecular phylogeny of nearly all extant spider families based on multi-locus Sanger data, Wheeler et al. (2017) included seven representative genera, recovering Dictynidae as monophyletic with weak support (maximum likelihood bootstrap for trimmed alignments, constrained by a transcriptomic skeleton, CMLT BS = 11). However, this support was much higher (CMLT BS = 99) with the exclusion of *Lathys* Simon, 1885 and the transfer of *Argyroneta* to Dictynidae, indicating that Dictynidae was both polyphyletic and paraphyletic. Similarly, Crews et al. (2020), using expanded sampling with Sanger data, also recovered dictynids as monophyletic to the exclusion of both *Brommella* Tullgren, 1948 and *Lathys*. Most recently, using genomic subsampling, both Kulkarni et al. (2023) and Gorneau et al. (2023a) recovered Dictynidae (excluding *Lathys*) as monophyletic. Gorneau et al. (2023a) further recovered new placements for genera previously considered to be dicytnids, resulting in the transfer of *Brommella* to Cicuriniidae F.O. Pickard-Cambridge, 1893 and *Funny valentine* Lin and Li, 2022 to Macrobnunidae Bonnet, 1957. More data are required, however, to resolve the placement of dictynid genera with statistical support.

The phylogenetic relationships of genera within Dictynidae are morphologically confounded by the presence of both cribellate and ecribellate species within and across genera (Gorneau et al. 2023a). Adding to this taxonomic uncertainty is that few dictynid genera containing more than one or two species have been revised within the last 50 years. Lehtinen (1967) divided the family into six subfamilies: Dictyninae, Tricholathysinae, Argyronetinae, Cybaeinae, Litesidiinae, and Cicuriniinae. Half the subfamilies have been subsequently transferred to other families or elevated to family level. Cybaeinae were elevated to family as Cybaeidae by Forster (1970), synonymized with Argyronetidae by Grothendieck and Kraus (1994), but not accepted by subsequent authors who considered it a family (Murphy and Roberts 2015, Wheeler et al. 2017, Gorneau et al. 2023, among others); *Argyroneta aquatica*, the sole member of

Table 1. Summary of major phylogenetic and taxonomic works related to Dictynidae s.l. The percentage of dictynid genera represented is based on the genera that were considered dictynids at the time of publication (World Spider Catalog 2024).

Phylogenetic hypothesis	# genera incl.	% genera incl. in analysis	Data	Monophyletic?
Griswold et al. (1999)	4	7.7%	Phenotypic	Monophyletic
Griswold et al. (2005)	4	7.7%	Phenotypic	Monophyletic
Spagna and Gillespie (2008)	4	7.7%	Sanger loci	Polyphyletic
Miller et al. (2010)	6	11.5%	Sanger loci	Polyphyletic
Spagna et al. (2010)	5	9.6%	Sanger loci	Polyphyletic
Wheeler et al. (2017)	7	13.5%	Sanger loci	Polyphyletic
Crews et al. (2020)	20	38.5%	Sanger loci	Polyphyletic
Kulkarni et al. (2023)	7	13.5%	UCEs + Sanger loci	Polyphyletic
Gorneau et al. (2023a)	10	19.2%	UCEs + Sanger loci	Paraphyletic

Argyronetinae, was first elevated to family-level, then placed in Cybaeidae, and finally transferred back to Dictynidae (Wheeler *et al.* 2017). The two genera placed in the Litesediinae (*Litesedes* Oi, 1960 and *Swainsia* Marples, 1964) have been synonymized with one another as *Paratheuma*, and Cicuriniinae has been re-elevated to family (Gorneau *et al.* 2023a). The most recent and thorough phylogenetic hypotheses for the group do not support the monophyly of the remaining subfamilies (Crews *et al.* 2020, Gorneau *et al.* 2023a), clearly highlighting a need for resolving the subfamilial taxonomy of Dictynidae.

Straightening the tailor's drawer

Ultraconserved elements (UCEs) are subsamples of whole genomes that have demonstrated utility for recovering genomic-scale data, including from museum arthropod specimens (Faircloth *et al.* 2015, Van Dam *et al.* 2017, Wood *et al.* 2018, Derkarabetian *et al.* 2019, Zhang *et al.* 2019a, b, 2023, Gorneau *et al.* 2023a, Kulkarni *et al.* 2023). UCEs allow for phylogenetic hypothesis inference from highly conserved, targeted areas of the genome. Combining UCEs with Sanger loci generated over the past 30 years allows for expanded taxonomic representation in a genomic-scale analysis, adding to the evergreen utility of these legacy data (Azevedo *et al.* 2022, Li *et al.* 2022, Gorneau *et al.* 2023a, Santos and Brady 2024).

Herein, we test the monophyly of Dictynidae using: (i) expanded taxonomic sampling to encompass 63% of currently recognized dictynid genera, and (ii) a combination of UCEs recovered *in silico* from *de novo* low-coverage whole-genome sequencing (lcWGS), a technique that has widely expanded the availability of data to help elucidate evolutionary relationships, and Sanger loci fragments to allow for the inclusion of legacy data from previous studies. While we integrate morphology to verify our clade delimitations and describe new genera and species, our combined molecular and bioinformatics approach to generating UCEs with phylogenetic utility continues a growing practice of maximizing the effectiveness of museum samples and enduring datasets. Our study provides a backbone hypothesis for further investigation of the remarkable adaptations exhibited by various members of Dictynidae *s.l.*

MATERIALS AND METHODS

Taxon sampling

To build the most representative phylogeny, we gathered as many museum specimens of Dictynidae *s.l.* as possible from collections around the world. 'Museum specimens' refers to a combination of samples preserved in 75% EtOH at room temperature and those frozen at 95% EtOH; preservation methods for each sample can be found in the Supporting Information, Table S1. Utilizing these and existing genomic data, our study sampled a total of 33 genera (63% of Dictynidae *s.l.*): *Adenodictyna* Ono, 2008; *Ajmonia* Caporiacco, 1934; *Altella* Simon, 1885; *Anaxibia* Thorell, 1898; *Arangina* Lehtinen, 1967; *Archaeodictyna* Caporiacco, 1928; *Arctella* Holm, 1945; *Argenna* Thorell, 1870; *Argyroneta*; *Bannaella* Zhang and Li, 2011; *Brigittea*; *Callevophthalmus* Simon, 1906; *Chaerea* Simon, 1885; *Devade* Simon, 1885; *Dictyna*; *Emblyna* Chamberlin, 1948; *Hackmania* Lehtinen, 1967; *Iviella* Lehtinen, 1967;

Lathys; *Mallos* O.Pickard-Cambridge, 1902; *Mashimo* Lehtinen, 1967; *Mexitlia* Lehtinen, 1967; *Mizaga* Simon, 1898; *Nigma*; *Paradictyna* Forster, 1970; *Paratheuma*; *Phantyna* Chamberlin, 1948; *Saltonia*; *Sudesna* Lehtinen, 1967; *Tahuantina* Lehtinen, 1967; *Thallumetus* Simon, 1893; *Tivyna* Chamberlin, 1948; *Tricholathys* Chamberlin and Ivie, 1935; and *Viridictyna* Forster, 1970. We had specimens or existing genomes of 91 species (20% of Dictynidae *s.l.*). A total of 30 outgroup exemplars from the related families Desidae, Macrobnidae, Hahniidae Bertkau, 1878, Cybaeidae, Cicuriniidae, and Toxopidae Hickman, 1940 were also included based on the results of Gorneau *et al.* (2023a) (Supporting Information, Table S2).

Genomic extractions were performed using the QIAamp DNA Micro kit (Qiagen, USA), modifying the manufacturer's protocol by adding 60 μ L of proteinase K (rather than 20 μ L) and 1 μ L of dissolved carrier RNA at the Buffer AL step. The proteinase K + Buffer ATL soak was placed on a thermomixer for 6 to 18 h at 56°C at 900 rpm. The samples were then eluted to 55 μ L. Following extraction, we quality-checked our extractions using an Agilent TapeStation 4150, and sheared high-quality samples with intact DNA to 350 bp using a Covaris M220 focused-ultrasonicator. We did not attempt shearing on those extractions with peaks at fragment lengths of less than 200 bp. The NEBNext UltraII DNaseq kit (New England Biolabs, Ipswich, MA) with 8 bp indices was used for library preparation. Samples underwent adaptor ligation, a 1.5X New England Biolabs NEBNext Sample Purification SPRI Beads cleanup, PCR enrichment for 10–12 cycles, and another 1.5X SPRI bead cleanup. Some samples were dual-indexed and others were single-indexed. Libraries that showed adaptor-dimer on a TapeStation read underwent another 0.8–0.9X bead wash. Libraries that had adaptor-dimer and Invitrogen Qubit 4 fluorometer concentration values under 1 ng/ μ L underwent polymerase chain reaction (PCR) enrichment for 12 additional cycles and another 0.8–0.9X bead wash. Libraries were sequenced on an Illumina NovaSeq S4 platform via 150 bp paired-end reads to produce 10X-coverage whole genomes. Without a reference genome, we estimated our target 10X coverage using an average of the known genome size estimates for araneomorph spiders (average estimate 2.35 gigabases (Gb) [= 2.4 picograms (pg) multiplied by ~0.978 Gb/1 pg], Gregory and Shorthouse 2003).

Ultraconserved elements

To generate our UCE matrices, we followed the bioinformatic pipeline outlined in Gorneau *et al.* (2023a). Raw sequences were cleaned using fastp (Chen *et al.* 2018), and contigs were assembled with SPAdes (Bankevich *et al.* 2012). After converting the resulting fasta files to 2bit files using faToTwoBit (UCSC), we harvested UCEs with PHYLUCE v.1.7 (Faircloth 2016) *in silico* using the RTA clade probes developed by Zhang *et al.* (2023). To locate the contigs for UCE extraction, we used *phyluce_probe_run_multiple_lastzs_sqlite* then *phyluce_probe_slice_sequence_from_genomes*, followed by *phyluce_assembly_match_contigs_to_probes*. We counted UCEs recovered as we harvested via *phyluce_assembly_get_match_counts* and compiled them using *phyluce_assembly_get_fastas_from_match_counts*. We aligned our UCE matrix using *phyluce_align_seqcap_align*, which uses MAFFT v.7, and then edge-trimmed the matrix with

GBlocks v.0.91b (Castresana 2000, Talavera and Castresana 2007) using *phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed*. We performed edge trimming rather than internal trimming as is recommended in the PHYLUCE manual for phylogenetic divergences <50 MY. We defined a 50% occupancy matrix via *phyluce_align_get_only_loci_with_min_taxa* and concatenated our alignments with *phyluce_align_concatenate_alignments* exemplars from the families. With a few duplicates of species represented from different localities, our UCE-only phylogeny was built from an alignment of 666 UCE loci and included 98 terminals. Information on the number of reads per sample before filtering with *fastp*, as well as read coverage information for the UCEs can be found on Table S1. The latter was calculated via a script using BWA and SAMtools (Li and Durbin 2009, Danecek et al. 2021).

Sanger loci

To incorporate legacy data and increase taxonomic representation, we harvested Sanger loci (cytochrome *c* oxidase subunit I: *COI*; histone H3: *H3*; 12S ribosomal RNA: 12S rRNA; 16S ribosomal RNA: 16S rRNA; 18S ribosomal RNA: 18S rRNA; and 28S ribosomal RNA: 28S rRNA) from our low-coverage genomes. In GENEIOUS PRIME v.2023.0.4, we searched for and isolated Sanger loci from our low-coverage genomes using the *Map to Reference* function. We used *Agelenopsis pennsylvanica* (C.L. Koch, 1843) as our reference: *COI* (accession number KY017545), *H3* (accession number KY018083), 12S rRNA (accession number KY015266), 16S rRNA (accession number KY01569), 18S rRNA (accession number KY016263), and 28S rRNA (accession number KY016881). In addition to adding Sanger loci retrieved from the low-coverage genomes that we sequenced, we included Sanger loci from GenBank (Supporting Information, Table S3). These consisted of species of all additional Dictynidae *s.l.* that were available on GenBank and not already represented in our phylogeny; when more than one individual of a species was available on GenBank, we chose the one with the most data. Gaps were treated as missing for *COI* and *H3* alignments but retained for rRNA genes (12S, 16S, 18S, and 28S). A single concatenated matrix of 164 terminals, 672 loci, and 229 689 bp incorporating both Sanger and UCE loci was used for a subsequent IQ-TREE2 phylogenetic analysis. Adding Sanger loci increased the number of terminals to 134, representing 107 species (22% species representation).

Phylogenetic analysis

We conducted analyses using the UCE-only dataset and the UCEs + Sanger loci dataset. Additionally, to investigate generic relationships between *Dictyna* and *Emblyna*, the most species-rich dictynid genera, we built a phylogeny using only taxa in the clade that contains the aforementioned genera and *Argyroneta aquatica*, *Lathys dentichelis* (Simon, 1883), and *L. delicatula* (Gertsch and Mulaik, 1936) as outgroups. We inferred maximum likelihood phylogenies in IQ-TREE v.2.1 with 10 000 ultrafast bootstraps (Nguyen et al. 2015, Hoang et al. 2018, Minh et al. 2020b) incorporating the SH-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010). Also, for the three alignments, we inferred coalescent-based phylogenies using the coalescent gene tree-species tree reconciliation program ASTRAL

v.5.7.8 (Zhang et al. 2018). For the UCEs + Sanger loci alignment, we also inferred maximum likelihood phylogenies that incorporated support value tests of gene and site concordance factors (gCF and sCF, respectively; Minh et al. 2020a, Mo et al. 2023).

Morphology

Morphology was studied in detail using light microscopy and SEM photography. SEM photographs were taken using a Hitachi SU3500 SEM Microscope in the Scanning Electron Microscopy Laboratory at the California Academy of Sciences, California, USA. Samples were examined using a LEICA M125 stereomicroscope and LEICA DM 4000M microscope. Photographs of the habitus, palp, and epigyne were taken using various microscopes and cameras: KEYENCE VHX-7000N digital microscope (California Academy of Sciences, California, USA), KEYENCE VHX-6000 digital microscope (Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA), Nikon SMZ18 microscope and an OMAX A35180U3 attached camera (American Museum of Natural History, New York, USA), and AIMSCOPE MU1603 attached camera (Muséum National d'Histoire Naturelle, Paris, France). Male palpi were expanded with KOH according to Shear (1967). Both male and female genitalia were cleared using a pancreatin solution (Álvarez-Padilla and Hormiga 2008) and illustrated using bitmap graphics in Autodesk SketchBook (<https://sketchbook.com>; see: Cala-Riquelme 2021). For illustrations of the male palp, the left palp was used. If the left palp was not present, the right palp was illustrated, photographed, and/or scanned, and the position of the image was subsequently mirrored. The description of coloration follows Syme (2018), and the description of spinnerets follows Murphy and Roberts (2015). All measurements (in millimeters) were taken using a scale grid. In this study, we use terminology standardized by Marusik and Penney (2010), Marusik and Fritzén (2011), Ramírez (2014), and Cala-Riquelme et al. (2022). This standardization allowed us to propose a hypothesis of homology between structures.

Anatomical abbreviations

AC, aciniform gland spigot; ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; BG, Bennett's gland; BH, basal hematodochae; Ca, calamistrum; CC, cheliceral lateral condyle; CD, copulatory duct; CdC, cavity of dorsal extension of the cymbium; Cl, colulus; CLA, conductor lower arm; Cm, conductor locking mechanism; CO, copulatory opening; Cr, cribellum; CSt, conductor scaly tip; CUA, conductor upper arm; Cx, conductor; CY, cylindrical gland spigots; Cy, cymbium; DH, distal hematodochae; Dp, dictynid process (dorsal tibial process with ctenidia); DTA, dorsal tibial apophysis; E, embolus; FD, fertilization duct; HTA, hook-shaped tibial process; Ju, jugum; MA, major ampullate spigot; mA, minor ampullate gland spigot; MA + n, major ampullate gland spigot, including nubbin; MH, medial hematodochae; Ms, membranous sac; MsO, membranous sac opening; Mx, medial apophysis; PC, paracribellar spigots; Pi, piriform spigot; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; PMS, posterior median spinnerets; Pp, patellar process; PS, primary spermatheca; PTA, prolateral tibial apophysis; Pxp,

paraconductor process; RTA, retrolateral tibial apophysis; S, spermophor; SL, spermophor loop; SS/AG, secondary spermatheca/opening of accessory gland; STe, subtegulum; Te, tegulum; Tp, trochanter process; Xt, ctenidia.

Type material examined

Our research aims to address confusion among spiders presently aggregated in the family Dictynidae. To address this, we prioritized reviewing as many type species/genera as possible. Given the morphological diversity observed in *Dictyna*, *Emblyna*, and *Lathys*, we concentrated efforts on these genera, examining the largest feasible number of type specimens. When type material access was challenging, or if holotypes were missing, we employed alternative strategies such as reviewing (i) paratypes, (ii) syntypes, (iii) additional material cited in original publications (e.g. Chamberlin and Gertsch 1958, Lehtinen 1967, Dupérré and Harms 2018), (iv) original descriptions of the type species, (v) photos, and/ or (vi) illustrations of the type species.

We examined specimens of the types and/or paratypes of *Adenodictyna kudoae* Ono, 2009 (NMST7953), *Aebutina binotata* Simon, 1892 (MNHN-AR-AR159), *Ajmonia marakata* (Sherriffs, 1927) (NHMUK1635133), *Aj. smaragdula* (Simon, 1905) (MNHN-AR-AR714), *Aj. velifera* (Simon, 1906) (MNHN-AR-AR713), *Anaxibia difficilis* (Kraus, 1960) (MNHN-AR-AR477), *Arangina cornigera* (Dalmas, 1917) (MNHN-AR-AR715, MNHN-AR-AR703), *Archaeodictyna anguinceps* (Simon, 1899) (NHMUK1635121), *Archaeodictyna ulova* (NHMUK1635102), *Argenna obesa* Emerton, 1911 (MCZ-IZ22345), *Argenna prominula* Tullgren, 1948 (MCZ-IZ24836), *Banaidja bifasciata* (L. Koch, 1872) (NHMUK 1635122), *Callevophthalmus albus* (Keyserling, 1890) (NHMUK1635107), *C. maculatus* (Keyserling, 1890) (NHMUK 1635108), *Chaerea maritimus* Simon, 1885 (MNHN-AR-AR446), *Chelicirrum stridulans* Wunderlich, 2004 (SMFBe586, SMFBe587), *Copaldictyna madagascariensis* Wunderlich, 2004 (SMFBe691), *Devade indistincta* (O. Pickard-Cambridge, 1872) (MNHN-AR-AR483), *Dictyna abundans* Chamberlin and Ivie, 1941 (CASENT9129301, CASENT9129314), *D. agressa* Ivie, 1947 (MNHN-AR-AR688, CASENT9129275), *D. alyceae* Chickering, 1950 (MCZ-IZ20244), *D. apachea* Chamberlin and Ivie, 1935 (MNHN-AR-AR671, CASENT9129548), *Dictyna bellans* Chamberlin 1919 (MCZ-IZ15152), *D. bellans hatchi* Jones, 1948 (MCZ-IZ24764, MCZ-IZ21526), *D. bostoniensis* Emerton, 1888 (MCZ-IZ15971, MCZ-IZ20564), *D. brevitarsus* Emerton, 1915 (MCZ-IZ20588), *Dictyna calcarata* Banks, 1904 (MCZ-IZ20638), *D. cavata* Jones, 1947 (MCZ-IZ24758, MCZ-IZ20740, MCZ-IZ24759, MCZ-IZ24760), *D. cebolla* Ivie, 1947 (CASENT9129444), *D. coloradensis* Chamberlin, 1919 (MCZ-IZ15151), *D. crosbyi* Gertsch and Mulaik, 1940 (CASENT9129379), *D. denisi* (Lehtinen, 1967) (MNHN-AR-AR683), *D. donaldi* Chickering, 1950 (MCZ-IZ44000, MCZ-IZ21112, MCZ-IZ24320, MCZ-IZ24318), *D. foliacea* (Hentz, 1850) (MCZ-IZ21350), *D. formidolosa* Gertsch and Ivie, 1936 (MCZ-IZ20351), *D. juno* Ivie, 1947 (CASENT9129353), *D. lecta* Chickering, 1952 (MCZ-IZ21815), *D. longispina* Emerton, 1888 (MCZ-IZ151459), *D. marilina* Chamberlin, 1948 (CASENT9129288), *D. minuta* Emerton, 1888 (MCZ-IZ22095),

D. nebraska Gertsch, 1946 (CASENT9129366), *D. pictella* Chamberlin and Gertsch, 1958 (CASENT9129431), *D. secuta* Chamberlin, 1924 (MCZ-IZ15594), *D. segregata* Gertsch and Mulaik, 1936 (MCZ-IZ22549), *D. terrestris* Emerton, 1911 (MCZ-IZ23261), *D. vittata* Keyserling, 1883 (NHMUK1635146), *Emblyna altamira* (Gertsch and Davis, 1942) (CASENT9129340, CASENT9129457), *E. andesiana* (Berland, 1913) (MNHN-AR-AR5292), *E. angulata* (Emerton, 1915) (MCZ-IZ20279), *E. borealis cavernosa* (Jones, 1947) (MCZ-IZ20743), *E. completa* (Chamberlin and Gertsch, 1929) (CASENT9129392), *E. completoides* (Ivie, 1947) (CASENT9129470), *E. cruciata* (Emerton, 1888) (MCZ-IZ151460), *E. nanda* (Chamberlin and Gertsch, 1958), *E. olympiana* (Chamberlin, 1919) (MCZ-IZ29975), *E. osceola* (Chamberlin and Gertsch, 1958) (CASENT9129457, CASENT9129483), *E. palomara* Chamberlin, 1948 (CASENT9129327), *E. sublata* (Hentz, 1850) (MCZ-IZ23186), *E. suwaneae* (Gertsch, 1946) (CASENT9129496), *E. uintana* (Chamberlin, 1919) (MCZ-IZ15154), *Eocryphoeca electrina* Wunderlich, 2004 (SMFBe740), *Eo. gracilipes* C.L.Koch and Berendt, 1854 (SMFBe2066), *Eo. mammilla* Wunderlich, 2004 (SMFBe744), *Eo. splendens* Wunderlich, 2004 (SMFBe745), *Eo. communis* Wunderlich, 2004 (SMFBe746, SMFBe750, SMFBe753, SMFBe878), *Lathys alberta* Gertsch, 1946, *L. arabs* Simon, 1910 (MNHN-AR-AR396), *L. humilis* (Blackwall, 1855) (NHMUK1635149), *L. maculina* Gertsch, 1946 (MCZ-IZ21934), *L. subviridis* Denis, 1937 (MNHN-AR-AR429), *L. sylvania* Chamberlin and Gertsch, 1958 (MCZ-IZ24838), *Mexitilia trivittata* (Banks, 1901) (MCZ-IZ23355), *Mizagalla quattuor* Wunderlich, 2004 (SMFBe1398), *Nigma longipes* (Berland, 1914) (MNHN-AR-AR586, MNHN-AR-AR5291, MNHN-AR-AR5302), *Palaeodictyna intermedia* Wunderlich, 1988 (SMFBe933, SMFBe902), *Palaeodictyna singularis* Wunderlich, 1988 (SMFBe855), *Palaeodictyna termitophila* Wunderlich, 1988 (SMFBe869, SMFBe877), *Palaeodictyna unispina* Wunderlich, 1988 (SMFBe925), *Palaeolathys* Wunderlich, 1986 (SMFBe910, SMFBe917), *Palaeolathys mulegensis* (Chamberlin, 1924) (CASTYPE1366), *Phantyna terranea* (Ivie, 1947) (CASENT9129522), *Ph. varyna* (Chamberlin and Gertsch, 1958), *Ph. varyna miranda* (Chamberlin and Gertsch, 1958) (CASENT9129392), *Saltonia incerta* (MCZ-IZ21615), *Succinya* Wunderlich, 1988 (SMFBe862, SMFBe870, SMFBe878), *Tivyna moaba* (Ivie, 1947) (CASENT9129418), *Ti. pallida* (Keyserling, 1887) (NHMUK1635136, MCZ-IZ21329), and *Tricholathys hirsutipes* (Banks, 1921) (CASTYPE738, MCZ-IZ21553).

The monotypic genera *Kharitonovia* Eshyulin et al. 2017, *Mashimo*, *Myanmardictyna* Wunderlich, 2017, *Penangodyna* Wunderlich, 1995, *Qiyunia* Song and Xu, 1989, *Shango* Lehtinen, 1967, *Scotolathys* Simon, 1885, and the type species of *Ajmonia gratiosa* (Simon, 1881) (MNHN-AR-AR600) were reviewed in the literature or from photographs. The holotypes of *Atelolathys varia* Simon, 1892, *Mizaga chevreuxi* Simon, 1898, *Tahuantina zapfeae* Lehtinen, 1967, and *Thallumetus salax* Simon, 1893 were not located in the collection.

Finally, non-type material corresponding to Simon collections (MNHN-AR) [*Ajmonia gratiosa* (MNHN-AR-AR600),

- Aj. numidica* (Denis, 1937) (MNHN-AR-AR657), *Altella lucida* (Simon, 1874) (MNHN-AR-AR441), *Anaxibia nigricauda* (Simon, 1905) (MNHN-AR-AR716), *Archaeodictyna ammophila* (Menge, 1871) (MNHN-AR-AR527), *Ar. anguiniceps* (Simon, 1899) (MNHN-AR-AR609), *Ar. consecuta* (O. Pickard-Cambridge, 1872) (MNHN-AR-AR518), *Ar. sexnotata* (Simon, 1890) (MNHN-AR-AR581), *Ar. suedicola* (Simon, 1890) (MNHN-AR-AR585, MNHN-AR-AR582), *Argyroneta aquatica* (Clerck 1757) (CASENT9021356), *Brigittea latens* (Fabricius, 1775) (MNHN-AR-AR514), *Callevophthalmus albus* (MNHN-AR-AR368), *Dictyna arundinacea* (Linnaeus, 1758) (MNHN-AR-AR706), *D. bispinosa* Simon, 1906 (MNHN-AR-AR708), *D. colona* Simon, 1906 (MNHN-AR-AR717), *D. foliacea* (Hentz, 1850) (NHMUK1635147), *D. meditata* Gertsch, 1936 (MNHN-AR-AR590, MNHN-AR-AR680, MNHN-AR-AR691), *D. turbida* Simon, 1905 (MNHN-AR-AR699, MNHN-AR-AR700), *Emblyna sublata* (NHMUK1635140), *Marilynia bicolor* (Simon, 1870) (MNHN-AR-AR597), *Nigma conducens* (O. Pickard-Cambridge, 1876) (MNHN-AR-AR586), *N. hortensis* (Simon, 1870) (MNHN-AR-AR561), *N. puella* (Simon, 1870) (MNHN-AR-AR570), *N. walckenaeri* (Roewer, 1951) (MNHN-AR-AR5315), *Phantyna micro* (Chamberlin and Ivie, 1944) (MNHN-AR-AR678), *Rhion pallidum* O. Pickard-Cambridge, 1871, (MNHN-AR-AR378), *Scotolathys simplex* Simon, 1885 (MNHN-AR-AR438), *Sudсна grossa* (Simon, 1906) (MNHN-AR-AR710), *Tahuantina zapfeae* (MNHN-AR-AR699, MNHN-AR-AR5291)], and Gertsch collections (CASENT) [*Dictyna abundans* (CASENT9129719), *D. agressa* (CASENT9129421), *D. alaskae* Chamberlin and Ivie, 1947 (CASENT9129420), *D. annexa* Gertsch and Mulaik, 1936 (CASENT9129717), *D. arundinacea* (CASENT9129316), *D. bellans* (CASENT9129330, CASENT9129381, CASENT9129665), *D. bostoniensis* (CASENT9129680, CASENT9129693), *D. brevitarisus* (CASENT9129498, CASENT9129511, CASENT9129524), *D. calcarata* (CASENT9129303), *D. cholla* Gertsch and Davis, 1942 (CASENT9129602, CASENT9129615), *D. coloradensis* (CASENT9129445, CASENT9129536), *D. foliacea* (Hentz, 1850) (CASENT9129290, CASENT9129652), *D. formidolosa* (CASENT9129654, CASENT9129667), *D. gloria* Chamberlin and Ivie, 1944 (CASENT9129278, CASENT9129304), *D. idahoana* Chamberlin and Ivie, 1933 (CASENT9129264, CASENT9129561), *D. incredula* Gertsch and Davis, 1937 (CASENT9129382), *D. juno* (CASENT9129432), *D. longispina* (CASENT9129459, CASENT9129472, CASENT9129485), *D. major* Menge, 1869 (CASENT9129252, CASENT9129369), *D. marilina* (CASENT9129614, CASENT9129627), *D. minuta* (CASENT9129433, CASENT9129446), *D. peon* Chamberlin and Gertsch, 1958 (CASENT9129575), *D. personata* Gertsch and Mulaik, 1936 (CASENT9129471, CASENT9129640, CASENT9129666, CASENT9129679, CASENT9129692, CASENT9129653), *D. quadrispinosa* Emerton, 1919 (CASENT9129276), *D. saepei* Chamberlin and Ivie, 1941 (CASENT9129317), *D. sancta* Gertsch, 1946 (CASENT9129291), *D. secuta* (CASENT9129705, CASENT9129718), *D. sierra* Chamberlin, 1948 (CASENT9129678), *D. subpinicola* Ivie, 1947 (CASENT9129367), *D. terrestris* (CASENT9129537, CASENT9129550), *D. tridentata* Bishop and Ruderman, 1946 (CASENT9129600), *D. volucripes* Keyserling, 1881 (CASENT9129393, CASENT9129394, CASENT9129407), *Emblyna altamira* (CASENT9129250, CASENT9129626), *E. ampla* Chamberlin, 1948 (CASENT9129342, CASENT9129510), *E. callida* (Gertsch and Ivie, 1936) (CASENT9129315), *E. capens* Chamberlin, 1948 (CASENT9129328), *E. completa* (CASENT9129628, CASENT9129641), *E. completoides* (CASENT9129343), *E. consulta* (Gertsch and Ivie, 1936) (CASENT9129563, CASENT9129576, CASENT9129589), *E. cruciata* (CASENT9129354, CASENT9129380), *E. francisca* (Bishop and Ruderman, 1946) (CASENT9129549), *E. hoya* (Chamberlin and Ivie, 1941) (CASENT9129497), *E. manitoba* (Ivie, 1947) (CASENT9129265, CASENT9129406), *E. marissa* (Chamberlin and Gertsch, 1958) (CASENT9129484), *E. maxima* (Banks, 1892) (CASENT9129691), *E. nanda* (CASENT9129408), *E. oasa* (Ivie, 1947) (CASENT9129523), *E. orbiculata* (Jones, 1947) (CASENT9129458, CASENT9129587), *E. piratica* (Ivie, 1947) (CASENT9129706), *E. reticulata* (Gertsch and Ivie, 1936) (CASENT9129419), *E. saylori* (Chamberlin and Ivie, 1941) (CASENT9129302), *E. scotta* Chamberlin, 1948 (CASENT9129395), *E. serena* (Chamberlin and Gertsch, 1958) (CASENT9129447), *E. suwaneae* (CASENT9129613), *E. uintana* (CASENT9129289, CASENT9129434), *Lathys stigmatisata* (Menge, 1869) (NHMUK1635150), *Phantyna bicornis* (Emerton, 1915) (CASENT9129588, CASENT9129601), *P. micro* (CASENT9129368), *Ph. mulegensis* (Chamberlin, 1924) (CASENT9129263), *P. pixi* (Chamberlin and Gertsch, 1958) (CASENT9129574, CASENT9129704), *P. rita* (Gertsch, 1946) (CASENT9129639), *P. segregata* (Gertsch and Mulaik, 1936) (CASENT9129329, CASENT9129341), *P. terranea* (CASENT9129562), *Ph. varyna miranda* (CASENT9129251), *Tivyna petrunkevitchi* (Gertsch and Mulaik, 1940) (CASENT9129355), and *T. spatula* (Gertsch and Davis, 1937) (CASENT9129277, CASENT9129356)] were used as support material after their identification was verified.
- The examined material belongs to the following institutions (abbreviations and curators in parentheses): American Museum of Natural History, New York, USA (AMNH, L. Prendini); British Museum of Natural History, London, England (NHMUK, J. Beccaloni); California Academy of Sciences, San Francisco, California, USA (CASENT, L. Esposito); Centre for Biodiversity Genomics, University of Guelph, Guelph, ON, Canada (BIOUG, A. Brown); F. Ballarin personal collections (FBPC); Field Museum Natural History, Chicago, USA (FMNH, P. Sierwald); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN, M. Ramírez); Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG, A.B. Bonaldo); Muséum National d'Histoire Naturelle, Paris, France (MNHN, C. Rollard); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ, G. Giribet); National Museum of Nature and Science, Tsukuba, Japan (NMST, K. Okumura); Royal British Columbia Museum, Museum in Victoria, British Columbia, Canada (RBCM, J. Gibson); Senckenberg Research Institute and Museum, Frankfurt am Main, Germany (SMF, P. Jäger).

The decision to establish new genera and new combinations corresponding to species not represented in the phylogeny was based on morphological differences in the male palp and female genitalia. In cases where these characters were not verified, the species remain in their current genera and should be reviewed in future research.

RESULTS

Ultraconserved elements-only phylogenetic analysis

Our UCE-only (50% gene occupancy) maximum likelihood (ML) analysis recovers Dictynidae s.l. as monophyletic (Fig. 1, SH-aLRT > 85 / UFBoot > 95). Within Dictynidae s.l.,

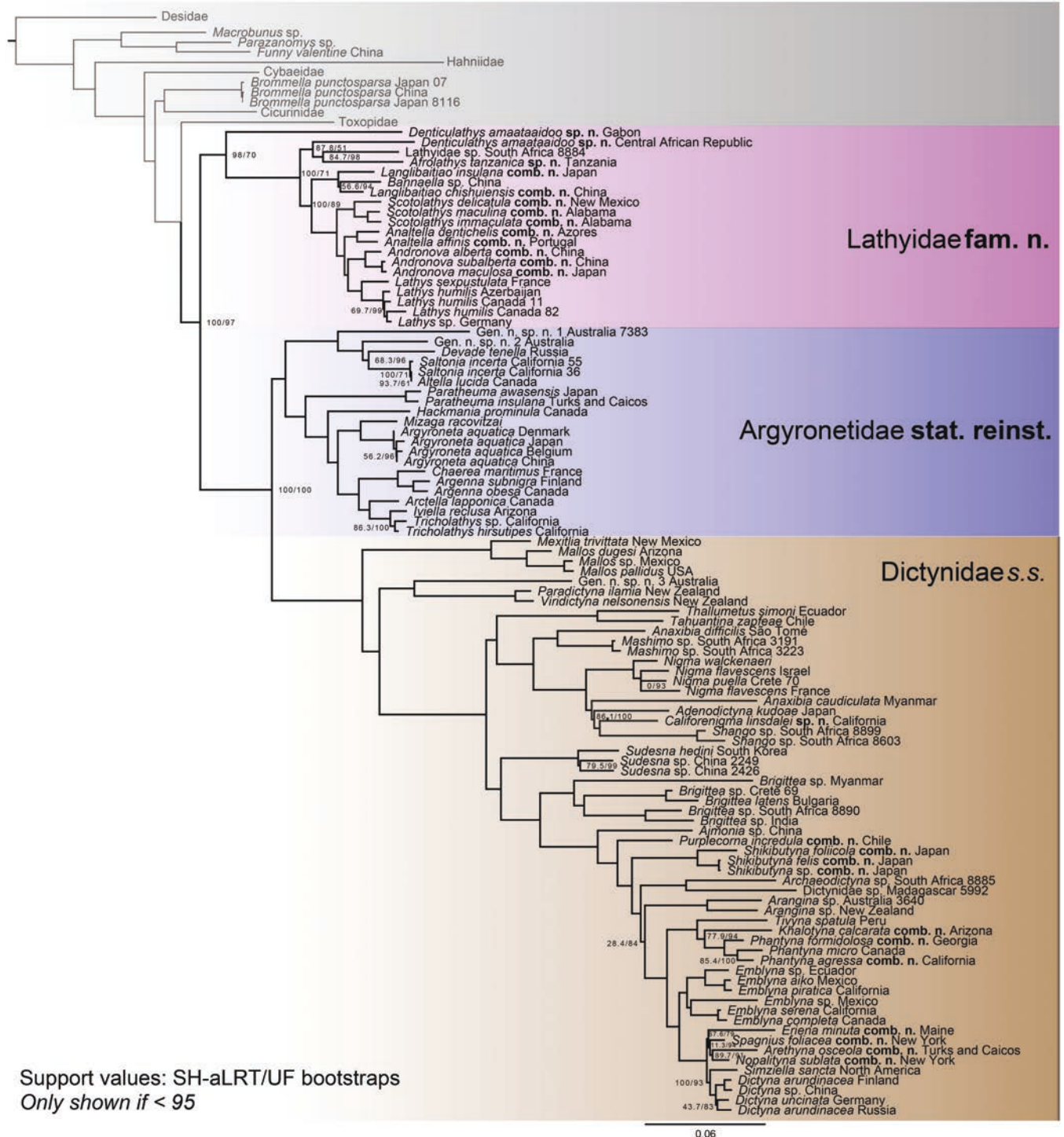


Figure 1. Maximum likelihood phylogeny of Dictynidae s.l. from UCE-only analysis showing SH-aLRT and ultrafast bootstrap support for nodes with < 95 support.

three distinct clades are recovered: the *Lathys* clade, containing *Lathys* and additional genera (*Bannaella*, *Langlibaitiao* Lin and Li, 2024, *Lathys delicatula* group, *Lathys affinis* group, *Lathys alberta* group, and *Lathys humilis* group), which is strongly supported by the SH-aLRT analyses (SH-aLRT > 85) but not by ultrafast bootstraps (UFBoot < 95); the *Argyroneta* clade, containing *Argyroneta* and other genera (*Devade*, *Saltonia*, *Altella*, *Paratheuma*, *Hackmania*, *Mizaga*, *Chaerea*, *Argenna*, *Arctella*, *Iviella*, and *Tricholathys*) (SH-aLRT > 85 / UFBoot > 95); and the *Dictyna* clade, consisting of *Dictyna* and additional genera (*Mexitlia*, *Mallos*, *Callevophthalmus*, *Paradictyna*, *Viridictyna*, *Thallumetus*, *Tahuantina*, *Anaxibia*, *Mashimo*, *Nigma*, *Anaxibia*, *Adenodictyna*, *Shango*, *Ajmonia*, *Sudesna*, *Brigittea*, *Archaeodictyna*, *Arangina*, *Tivyna*, *Phantyna*, *Emblyna*, and several new genera) (SH-aLRT > 85 / UFBoot > 95). An ASTRAL analysis produced a UCE-only phylogeny largely consistent with our maximum-likelihood phylogeny but with a polytomy at the base of the *Lathys* clade (Supporting Information, Fig. S1), and all basal nodes are supported.

The *Lathys* clade: The clade is recovered as sister to all other dictynids *s.l.* (SH-aLRT > 85 / UFBoot > 95). *Bannaella* is recovered nested with *Langlibaitiao* (SH-aLRT > 85 / UFBoot > 95); however, the relationship between *L. chishuiensis* (Z.S. Zhang, Yang, Y.G. Zhang, 2009) and *B. tibialis* Zhang and Li, 2011 has low support (SH-aLRT < 85 / UFBoot < 95).

The *Argyroneta* clade: The genus *Saltonia* is recovered as closely related to *Altella* (SH-aLRT > 85 / UFBoot > 95). *Paratheuma* is basal to *Hackmania*, *Mizaga*, *Chaerea*, *Argenna*, *Arctella*, *Iviella*, and *Tricholathys* (SH-aLRT > 85 / UFBoot > 95). *Mizaga* is recovered as sister to *Argyroneta* (SH-aLRT > 85 / UFBoot > 95), while *Chaerea* + *Argenna* (SH-aLRT > 85 / UFBoot > 95) is sister to *Arctella* + (*Iviella* + *Tricholathys*) (SH-aLRT > 85 / UFBoot > 95).

The Dictynidae *s.s.* clade: *Mallos* and *Mexitlia* are recovered as sister taxa and are basal to the rest of Dictynidae *s.s.* (SH-aLRT > 85 / UFBoot > 95). A new genus from Australia is sister to *Paradictyna* + *Viridictyna* from New Zealand (SH-aLRT > 85 / UFBoot > 95). The Neotropical *Thallumetus* + *Tahuantina* (SH-aLRT > 85 / UFBoot > 95) are basal to Old World *Anaxibia*, *Mashimo*, *Nigma*, *Adenodictyna*, and *Shango* (SH-aLRT > 85 / UFBoot > 95). *Anaxibia difficilis* is sister to *Mashimo*, while *An. caudiculata* Thorell, 1898 is sister to *Adenodictyna*, *Nigma linsdalei* Chamberlin and Gertsch, 1958, and *Shango* (SH-aLRT > 85 / UFBoot > 95). *Nigma* (excluding *N. linsdalei*) is monophyletic (SH-aLRT > 85 / UFBoot > 95) and sister to *Anaxibia caudiculata* + (*Adenodictyna* + (*N. linsdalei* + *Shango*)) (SH-aLRT > 85 / UFBoot > 95). Our results indicate that the genus *Dictyna s.l.* is polyphyletic (see Supporting Information, Fig. S2 for the phylogeny before we changed the taxonomy of terminals in this clade), found throughout the phylogeny, mainly with *Emblyna s.l.*, while the group that contains both *Dictyna s.l.* and *Emblyna s.l.* is monophyletic (SH-aLRT > 85 / UFBoot > 95). The *D. foliicola* group comprising Japanese species is strongly supported (SH-aLRT > 85 / UFBoot > 95). *Phantyna* is monophyletic (SH-aLRT > 85 / UFBoot > 95). *Emblyna s.s.* (excluding *E. osceola* and *E. sublata*) are recovered as monophyletic (SH-aLRT > 85 / UFBoot > 95).

Integrated ultraconserved elements and Sanger tree inference

The matrix integrating the 50% gene occupancy of UCEs with Sanger data resulted in a topology largely congruent with that of the UCE-only trees but with higher support values at many nodes (Fig. 2; Supporting Information, Fig. S2). The intergeneric relationships are summarized in Figure 3. The results of the major clades found in our UCE + Sanger loci phylogeny are summarized in Figure 4, including favourable support values assessed in our ASTRAL, gCF, and sCF analyses. The results of the ASTRAL UCE + Sanger loci, including all Dictynidae *s.l.* taxa, can be found in the Supporting Information, Figure S3.

The results of the UCE + Sanger loci maximum likelihood analysis of Dictynidae *s.s.*, collapsed to show just the clade that contained all taxa formerly classified as *Dictyna* and *Emblyna*, show that *Dictyna s.l.* relationships are similar to those found in the Dictynidae *s.l.* results (Supporting Information, Fig. S4)—polyphyly unless taxonomic changes are made. Many of the necessary changes are made by this study, but Sanger terminals retain *Dictyna* as polyphyletic in the Supporting Information, Figure S4, since we could not analyse the specimens from GenBank. Because Supporting Information, Fig. 4 shows the results of a unique analysis of Dictynidae *s.s.*, it includes fewer taxa than the analyses shown in Figures 1 and 2 and, thus, fewer data, which affects the topology. At the node following the branching of *Archaeodictyna*, this phylogeny has much higher support than the Dictynidae *s.l.* UCE-only phylogeny (SH-aLRT = 28.4 / UFBoot = 84), but this node in the Dictynidae *s.l.* UCE + Sanger loci phylogeny has a different topology, with *Arangina* in the same clade as *Archaeodictyna* and Dictynidae sp. Madagascar 5992 with even lower support (SH-aLRT = 15.5 / UFBoot = 75). A full ASTRAL phylogeny of Dictynidae *s.s.* can be found in the Supporting Information, Figure S5.

Taxonomy

Superfamily Dictynoidea O. Pickard-Cambridge, 1871

Diagnosis: Small to large spiders with a conspicuous lateral condyle (Figs 5E, F, 6E, 7C) on the chelicerae that may have a horn (Figs 6F, 7A–C, E); male palpus without a median apophysis and with the conductor articulating and usually resembling an expansive sheath, comprising distal hematodochae (Fig. 57A–D), a sclerotized area, and upper and lower conductor arms (Figs 19C, D, 20D, 22A) [male bulb configuration in Amaurobiidae Thorell, 1869 (Fig. 17A, B), Agelenidae C.L.Koch, 1837 (Fig. 17C–F), Stiphidiidae Dalmat, 1917 (Fig. 18A, B), Desidae (Fig. 18C), Macrobonidae (Figs 18D–F, 19A); Hahniidae (Fig. 19B)]; epigyne (Figs 13A–F, 14A–F, 15A–F, 16A–F) usually with a pair of membranous sacs (Figs 15A, B, 16E, F, 33E, 37D).

List of included families. Argyronetidae Thorell, 1869 stat. reinst., Cicuriniidae F.O. Pickard-Cambridge, 1893, Cybaeidae Banks, 1892, Dictynidae O. Pickard-Cambridge, 1871 *s.s.*, **Lathyidae fam. n.**, Toxopidae Hickman, 1940.

Family Argyronetidae Thorell, 1869, stat. reinst.

Type genus: *Argyroneta* Latreille, 1804: *Araneus aquaticus* Clerck, 1757, currently *Argyroneta aquatica* (Clerck, 1757).

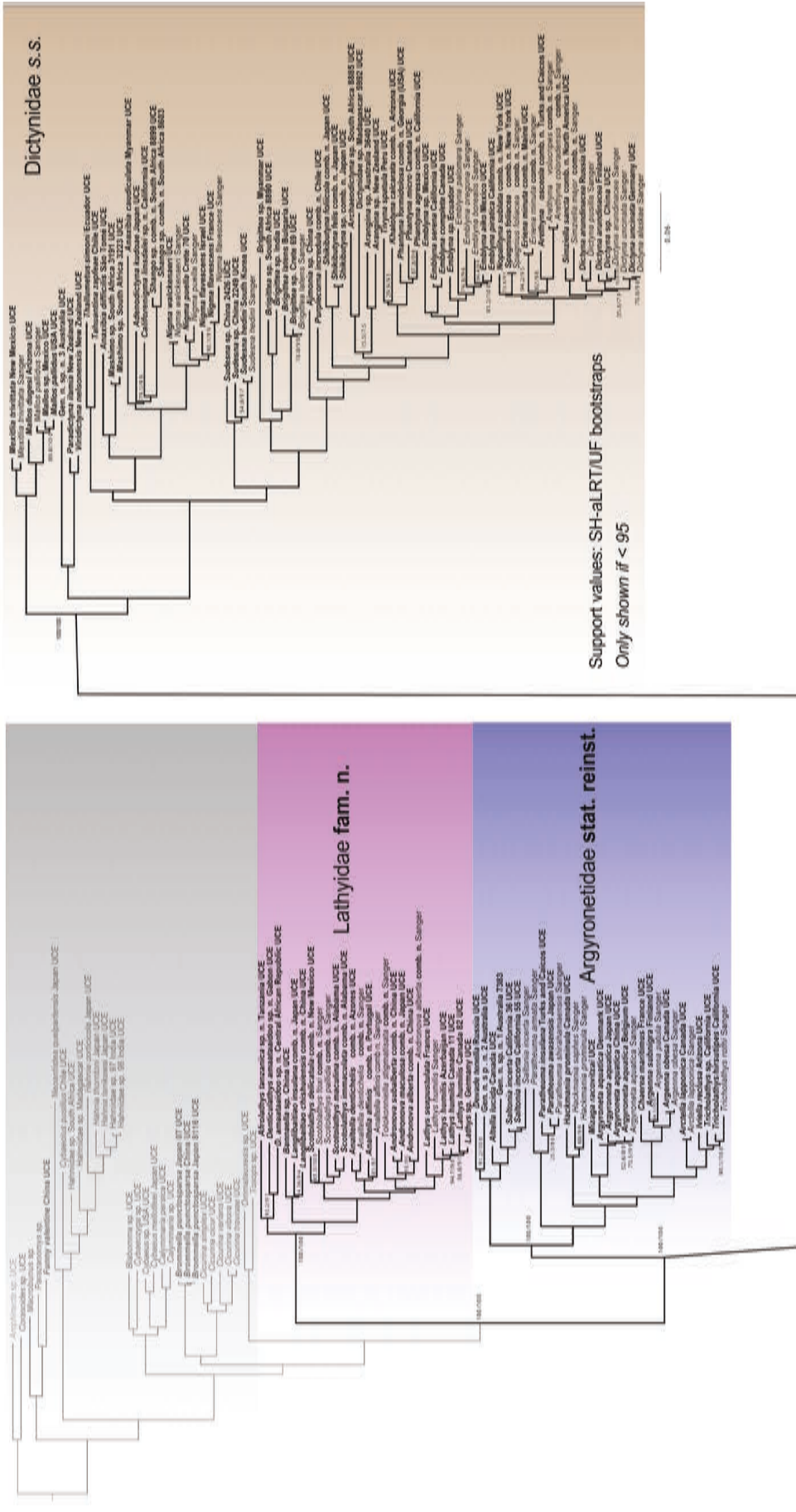


Figure 2. Maximum likelihood phylogeny of Dictynidae s.l. from UCE + Sanger loci showing SH-aLRT and ultrafast bootstrap support values for all nodes with >95 support. Nomenclature is updated.

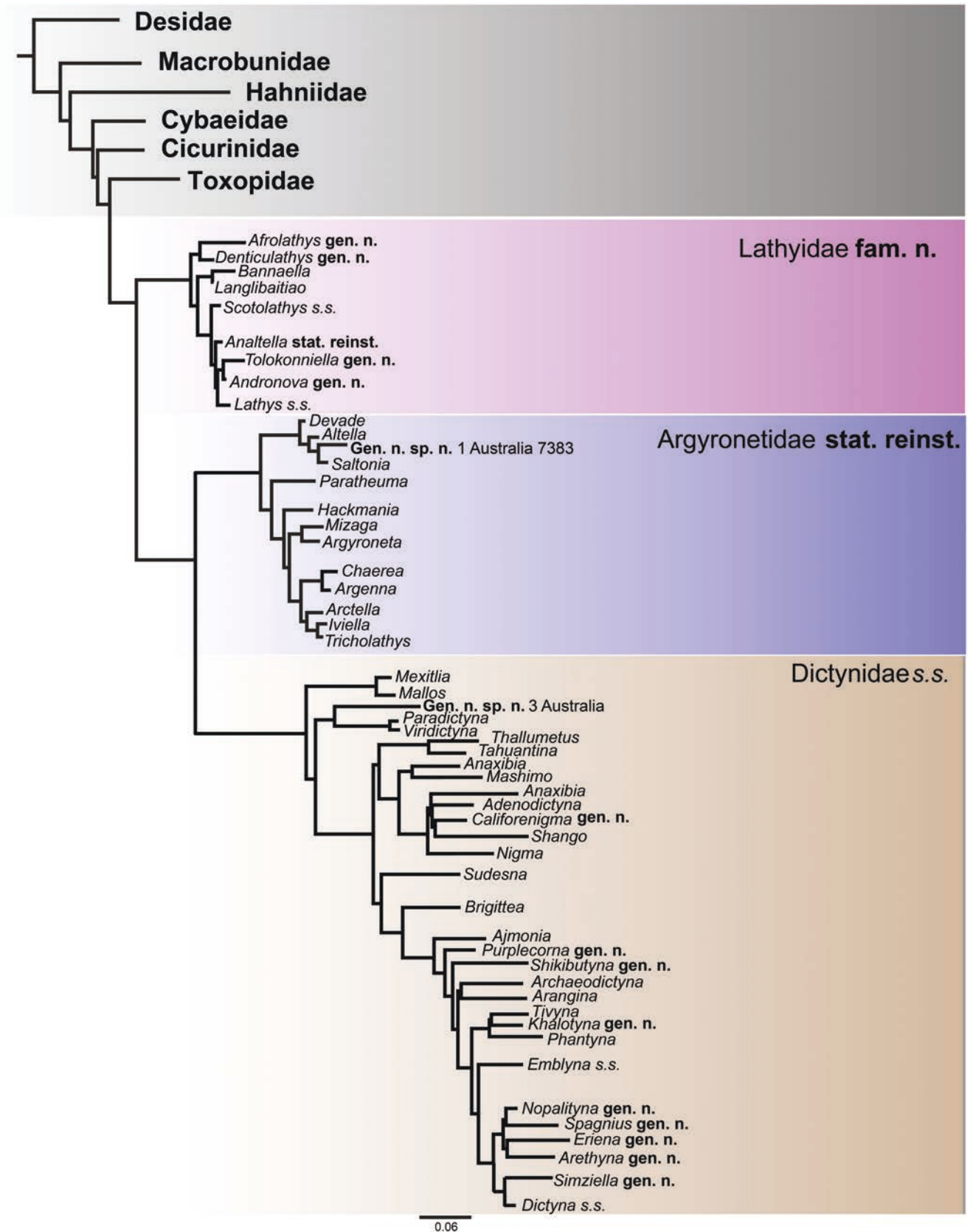


Figure 3. UCEs + Sanger loci maximum likelihood phylogeny of Dictynoidea genera, summarized from Figure 2.

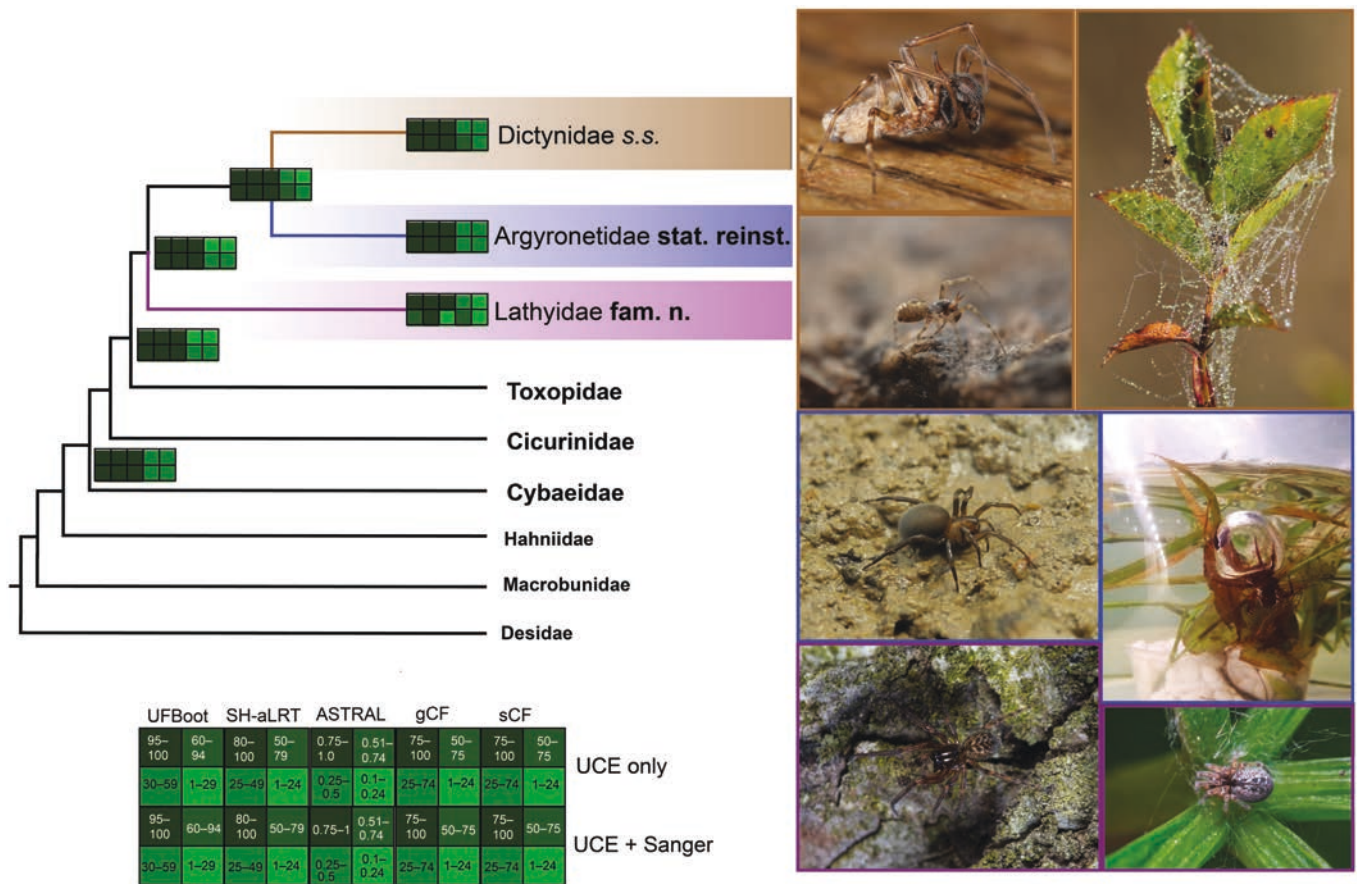


Figure 4. Summary tree of all the analyses for the UCE-only and UCE + Sanger loci Dictynidae s.l. phylogenies: SH-aLRT, UF bootstraps, ASTRAL, gene concordance factor (gCF), and site concordance factor (sCF). Images to the right of the phylogeny are of Dictynidae s.s., Argyronetidae stat. reinst., and Lathyidae fam. n. spiders observed on iNaturalist. First column, top to bottom: *Dictyna calcarata* by Paul G. Johnson (CC BY-NC-SA), *Dictyna arundinacea* by ajott (CC-BY), *Dictyna calcarata* by Toby (CC BY-NC), *Argyroneta aquatica* by Daniele Seglie (CC-BY-NC), *Argyroneta aquatica* by insect ID (CC-BY-NC), *Lathys truncata* by Anatoliy Ozernoy (CC-BY-SA), and *Lathys humilis* by Óscar Mendez (CC BY-NC).

Material examined: *Altella lucida*: Gallia (1 male, 3 females, MNHN-AR-AR441). *Argenna obesa*: USA, Massachusetts, Essex Co., Ipswich. (1 male, 2 females, MNHN-AR-AR450). USA, Alaska, Lake at Explorer Glacier near portage, 22.vii.1978, Coll. P.H. Arnaud (1 female CASENT8413341). USA, Arkansas, Mississippi Co., 15.i.1966, Coll. MX (1 female, CASENT8413351). USA, Massachusetts, Plum Island, pre-1911 publication date, Coll. James H. Emerton (Syntype, 1 female, MCZ-IZ22345). *Argenna prominula*: USA, Colorado, Virginia Basin, Elk Mts., 11 500–12 000 ft., 3.vii.1957, Coll. Herbert W. Levi, Lorna R. Levi (Paratype, 1 female, MCZ-IZ24836). *Arctella lapponica* Holm, 1945: Russia, Yakutia, North Yakutia, Yana River downflow, Kular Vill., 1.vii.1996, Coll. N.N. Vinokurov (1 male, CASENT8413348). *Chaerea maritimus*: Spain, Murcia, Cartagena, Coll. E. Simon (Syntypes, 1 male, 1 female, MNHN-AR-AR446). France, Var Department, Giens, Plage de L'Aiguade, 15.ii.2020, Coll. L. Crespo, P. Ponel (2 males, 2 females, CASENT9081477). *Devade indistincta*: Sudan, Suakin Island (Long Island), 1956.ii.20, Coll. P. Strinati (Holotype, 1 female, MNHN-AR-AR483). *Saltonia incerta*: USA, California, Salton, iii.1897, Coll. Henry G. Hubbard, Nathan Banks (Holotype, 1 female, MCZ-IZ21615). *Tricholathys hirsutipes*: USA, California,

Lassen Co., Susanville, 2.vii.1940, Coll. W.J. Gertsch (2 females, MNHN-AR-AR427). USA, California, Sacramento, 27.v.1918, Coll. Helen Van Duzee (Paratype, 2 males, MCZ-IZ21553).

Diagnosis: (Figs. 40A–C, 41A–D, 42A–F) Small to large spiders [only tiny in Lathyidae fam. n. and Dictynidae s.s.] with the carapace usually longer than wide, and wider than high (flattened) (Fig. 6A, D) [as wide as high or higher than wide in Dictynidae s.s.; Figs 6E, 7B]; AME, ALE, PLE, and PME similar in size (Fig. 6A–C, 40F) [AME usually absent (Fig. 5D, E) or considerably smaller (Fig. 5A, B) in Lathyidae fam. n.]; legs of both sexes, female palp, and male palpal cymbium usually with well-defined macrosetae (Figs 23A, 24A, F) [macrosetae absent or strongly reduced (Figs 25A, C, E, C, 26E, 27A, E, 32F) in Lathyidae fam. n. and Dictynidae s.s.]; male palp with the conductor upper arm shorter than the lower arm, the lower conductor arm uncoiled at the tip, and with the tip usually smooth (lacking a scaly appearance) (Figs 23B, C, F, 24A, B, E, F, 40D–F) [conductor upper arm longer than lower arm (Figs 20A, D, 22A, C, E) and with a scaly tip (Figs 20F) in Lathyidae fam. n.; conductor lower arm usually coiled and with scaly tip (Figs 25B, 26C, 28C, 30A, B, 31A, 57A–D, 58A–F) in Dictynidae s.s.].

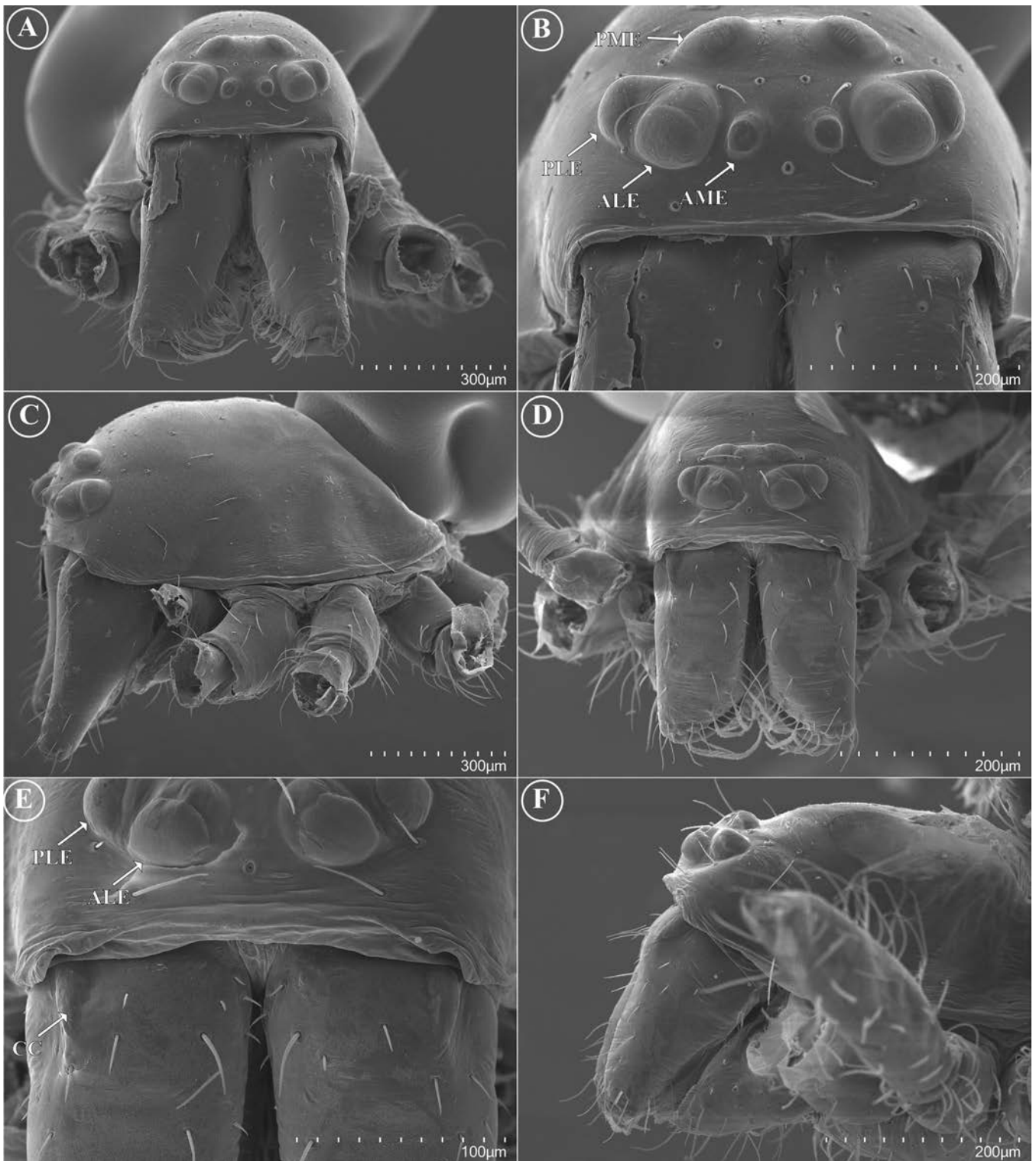


Figure 5. Scanning electron micrograph images of the prosoma of male Lathyidae fam. n.: A, B, *Lathys humilis* (Blackwall, 1855), frontal view; C, lateral view; D, E, *Scotolathys immaculata* Chamberlin and Ivie, 1944 stat. reinst., frontal view; F, lateral view. Abbreviations: ALE, anterior lateral eye; AME, anterior median eye; CC, cheliceral lateral condyle; PME, posterior median eye; PLE, posterior lateral eye.

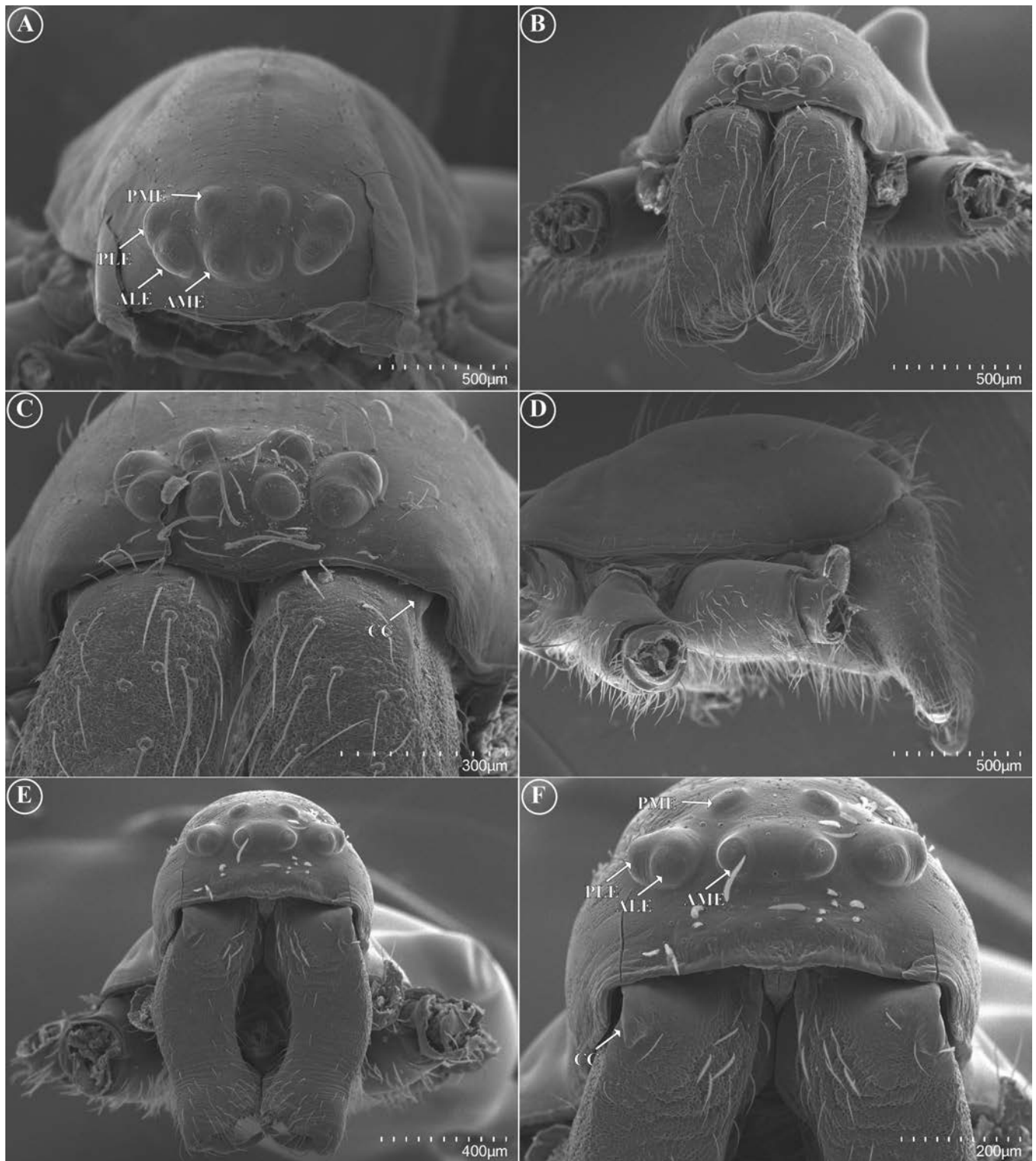


Figure 6. Scanning electron micrograph images of the prosoma of male Argynronetidae stat. reinst. and Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, *Argyroneta aquatica* (Clerck, 1757), frontal view; B, C, *Tricholathys spiralis* Chamberlin and Ivie, 1935, frontal view; D, lateral view; E, F, *Dictyna arundinacea* (Linnaeus, 1758), frontal view. Abbreviations: ALE, anterior lateral eye; AME, anterior median eye; CC, cheliceral lateral condyle; PME, posterior median eye; PLE, posterior lateral eye.

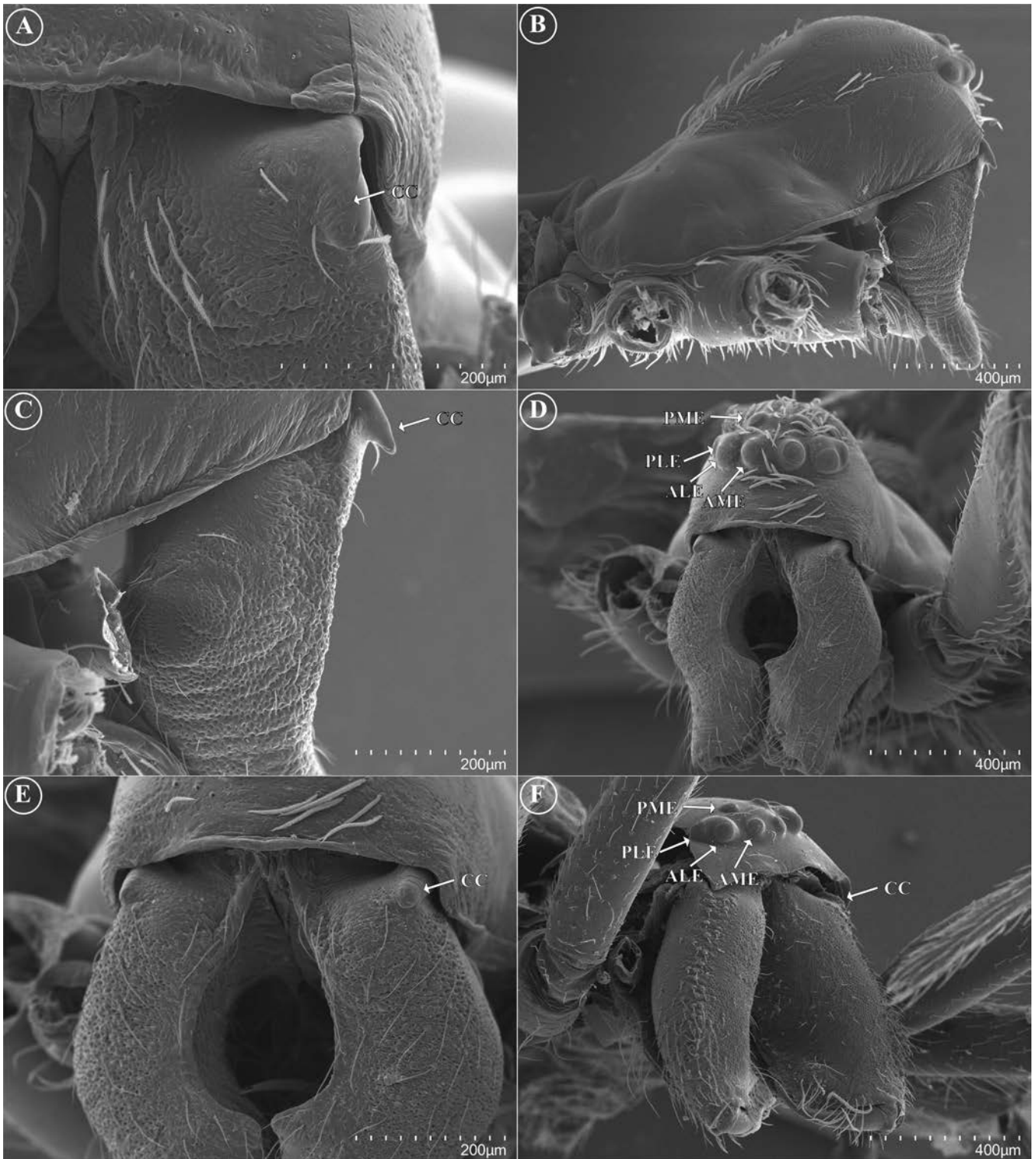


Figure 7. Scanning electron micrograph images of the prosoma of male Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, *Dictyna arundinacea* (Linnaeus, 1758), frontal view; B, C, lateral view; D, E, F, *Emblyna maxima* (Banks, 1892), frontal lateral view. Abbreviations: ALE, anterior lateral eye; AME, anterior median eye; CC, cheliceral lateral condyle; PLE, posterior lateral eye; PLE, posterior lateral eye.

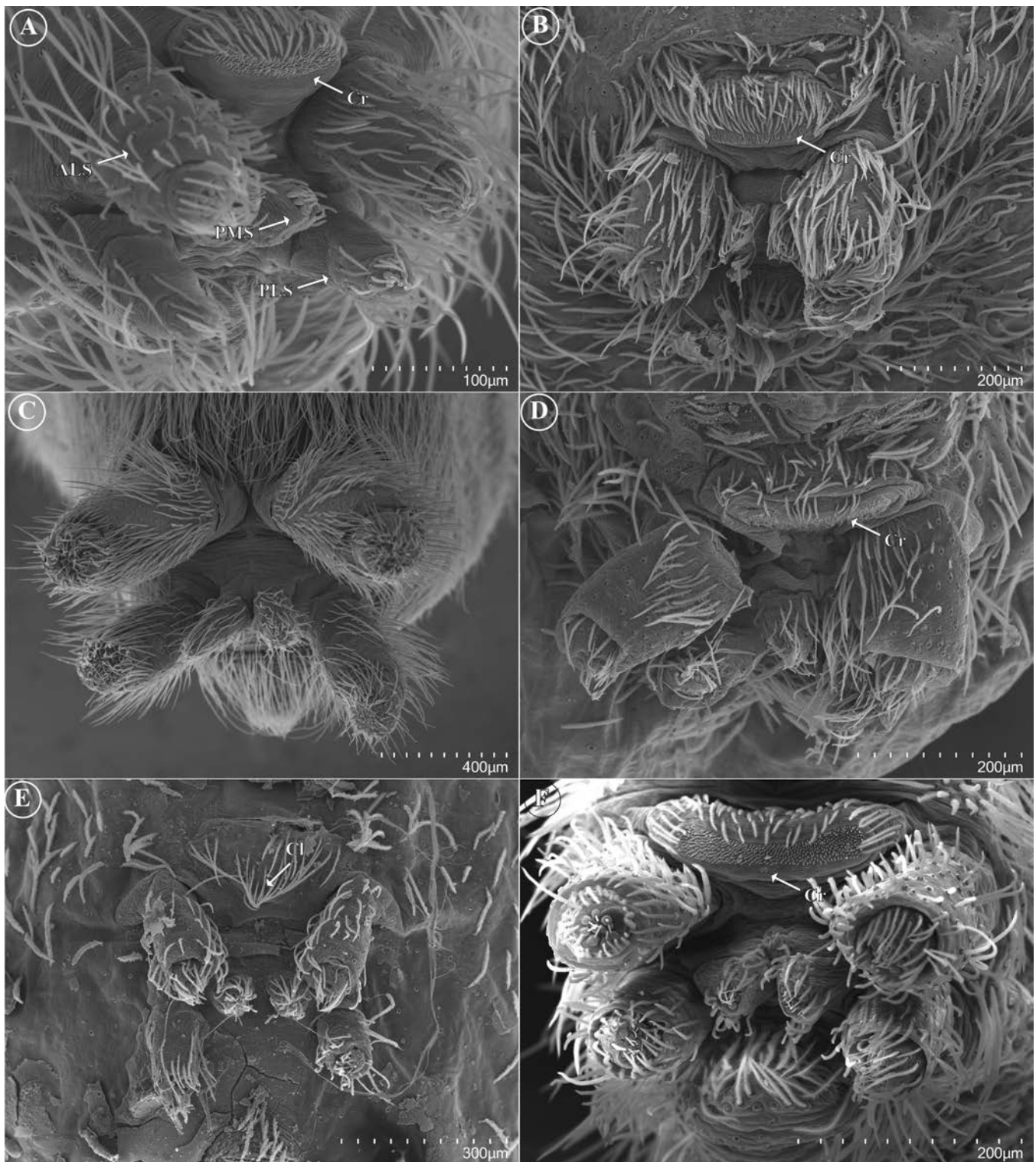


Figure 8. Scanning electron micrograph images of the spinnerets of female Lathyidae fam. n. and Argyronetidae Thorell, 1869 stat. reinst.: A, *Lathys humilis* (Blackwall, 1855), frontal lateral view; B, *Argenna pallida* L. Koch, 1881, frontal view; C, *Argyroneta aquatica* (Clerck, 1757), frontal view; D, *Devade* sp., frontal view; E, *Saltonia incerta* (Banks, 1898), frontal view; F, *Tricholathys spiralis* Chamberlin and Ivie, 1935, frontal lateral view. Abbreviations: ALS, anterior lateral spinneret; Cl, colulus; Cr, cribellum; PLS, posterior lateral spinneret; PMS, posterior median spinneret.

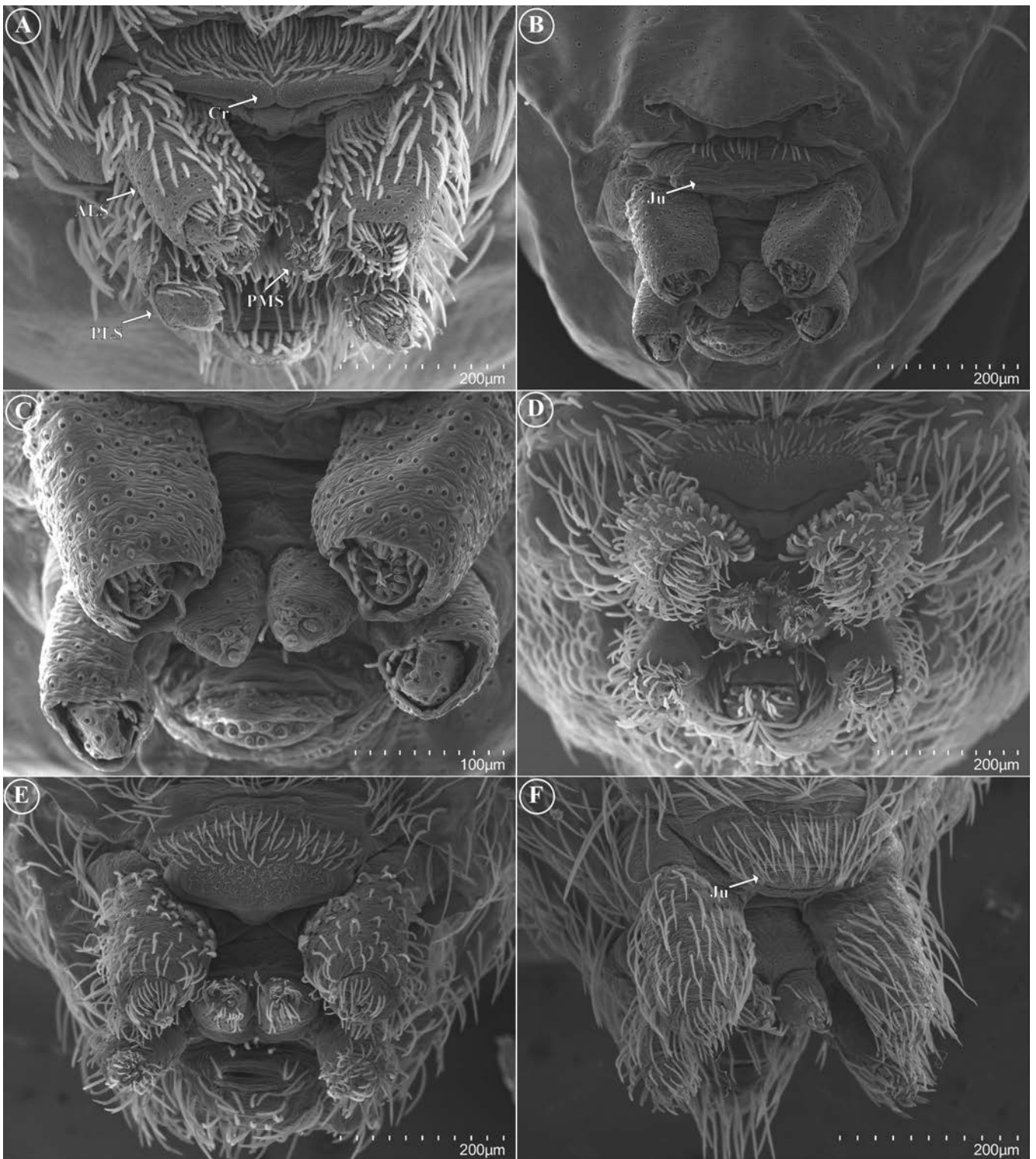


Figure 9. Scanning electron micrograph images of the spinnerets of male and female Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, female of *Brigittea latens* (Fabricius, 1775), frontal lateral view; B, C, male, frontal view; D, female of *Mallos niveus* O. Pickard-Cambridge, 1902, frontal view; E, female of *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n., frontal view; F, male, frontal lateral view. Abbreviations: ALS, anterior lateral spinneret; Cr, cribellum; Ju, Jugum; PLS, posterior lateral spinneret; PMS, posterior median spinneret.

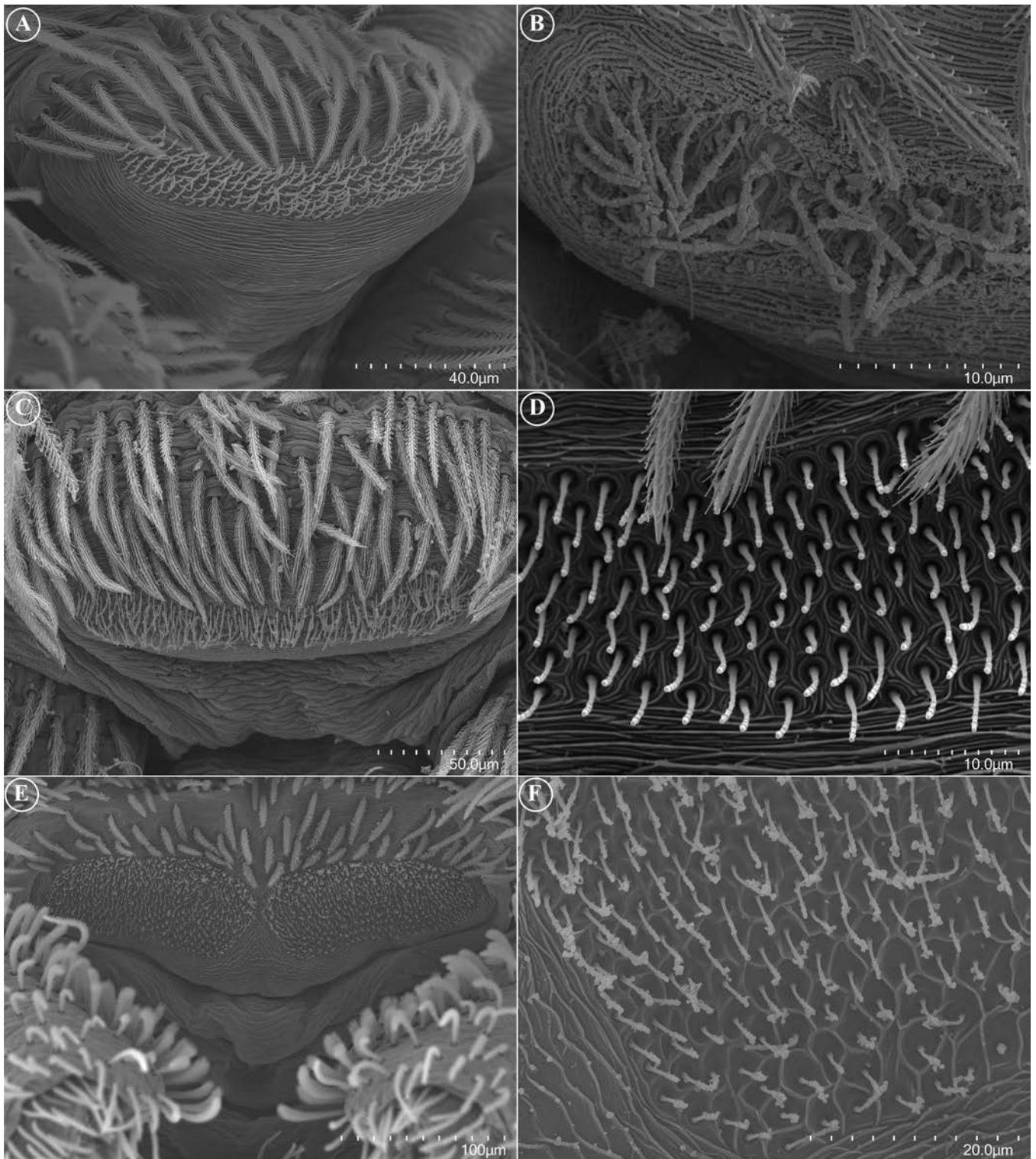


Figure 10. Scanning electron micrograph images of the cribellum of female Lathyidae fam. n., Argyronetidae stat. reinst. and Dictynidae O. Pickard-Cambridge s.s.: A, B, *Lathys humilis* (Blackwall, 1855); C, *Argenna pallida* L. Koch, 1881; D, *Tricholathys spiralis* Chamberlin and Ivie, 1935; E, F, *Mallos niveus* O. Pickard-Cambridge, 1902.

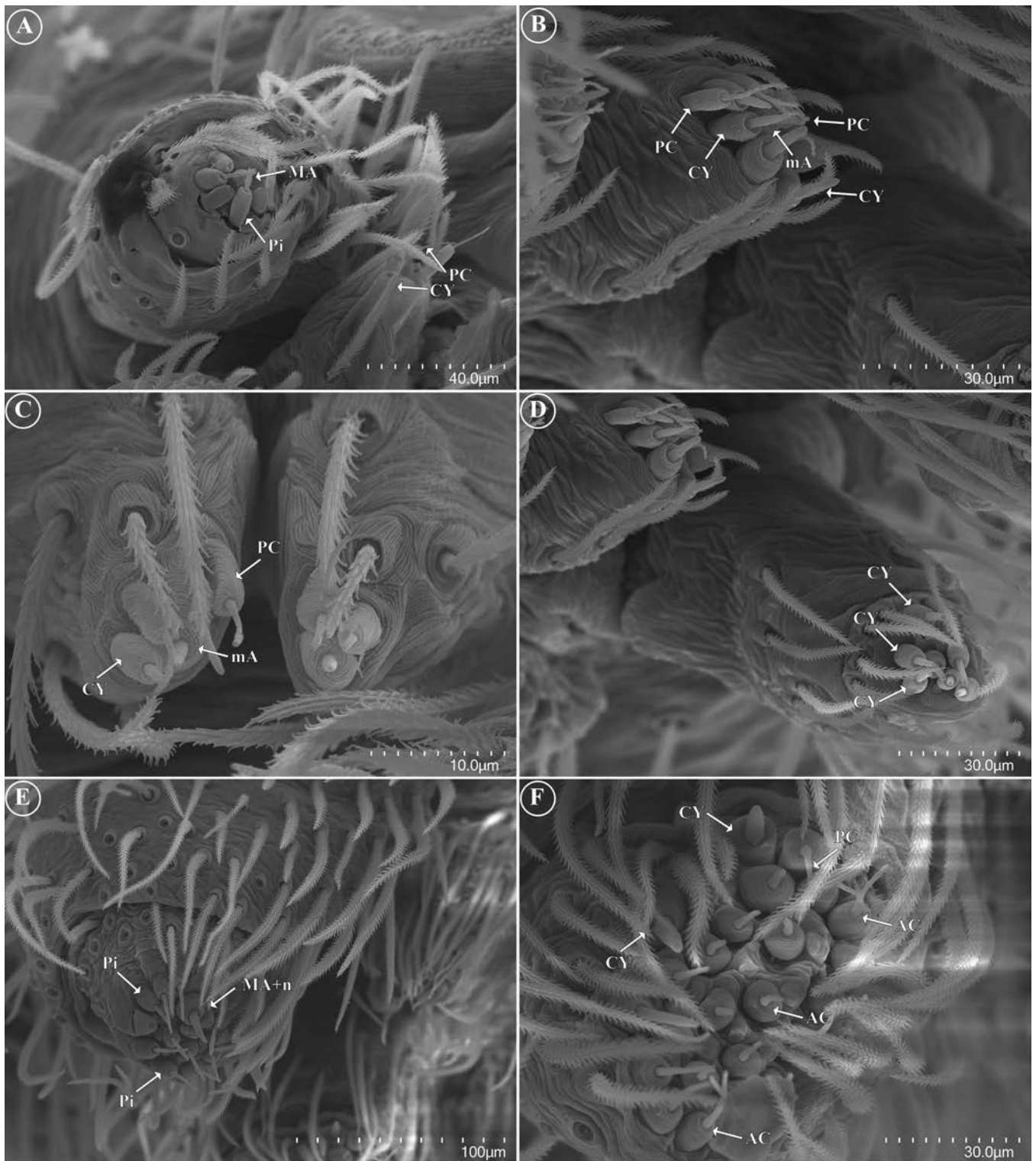


Figure 11. Scanning electron micrograph images of the spinnerets of female Lathyidae fam. n. and Argyronetidae stat. reinst.: A, *Lathys humilis* (Blackwall, 1855), anterior lateral spinneret; B, C, posterior median spinneret; D, posterior lateral spinneret; E, *Tricholathys spiralis* Chamberlin and Ivie, 1935, anterior lateral spinneret; F, posterior lateral spinneret. Abbreviations: AC, aciniform gland spigot; CY, cylindrical spigot; MA, major ampullate gland spigot; mA, minor ampullate gland spigot; MA + n, major ampullate gland plus nubbin spigot; PC, paracribellar spigots; Pi, piriform gland spigot.

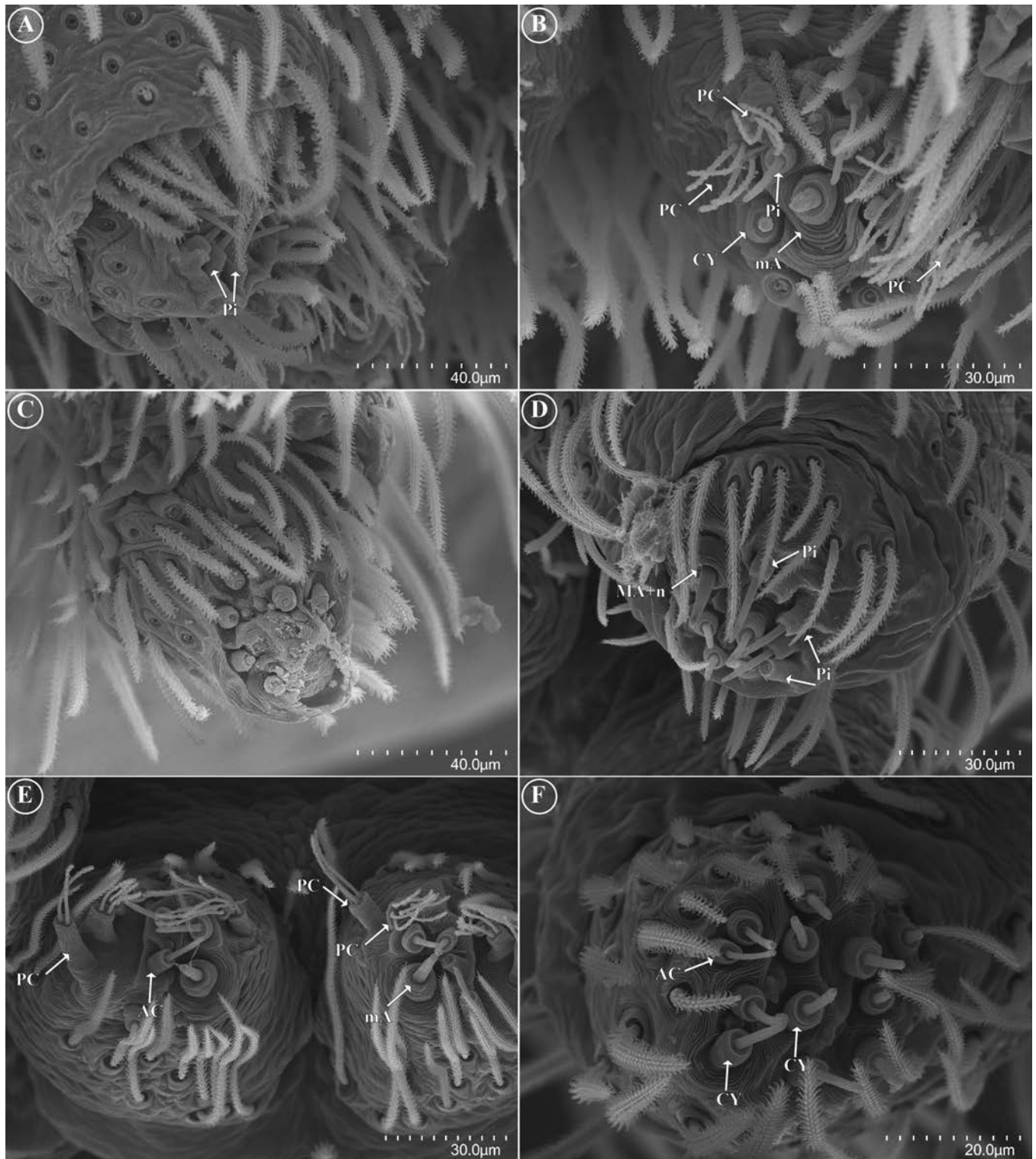


Figure 12. Scanning electron micrograph images of the spinnerets of female Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, *Brigittea latens* (Fabricius, 1775), anterior lateral spinneret; B, posterior median spinneret; C, posterior lateral spinneret; D, *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n., anterior lateral spinneret; E, posterior median spinneret; F, posterior lateral spinneret. Abbreviations: AC, aciniform gland spigot; CY, cylindrical gland spigot; mA, minor ampullate gland spigot; MA + n, major ampullate gland plus nubbin spigot; PC, paracribellar gland spigot; Pi, piriform gland spigot.

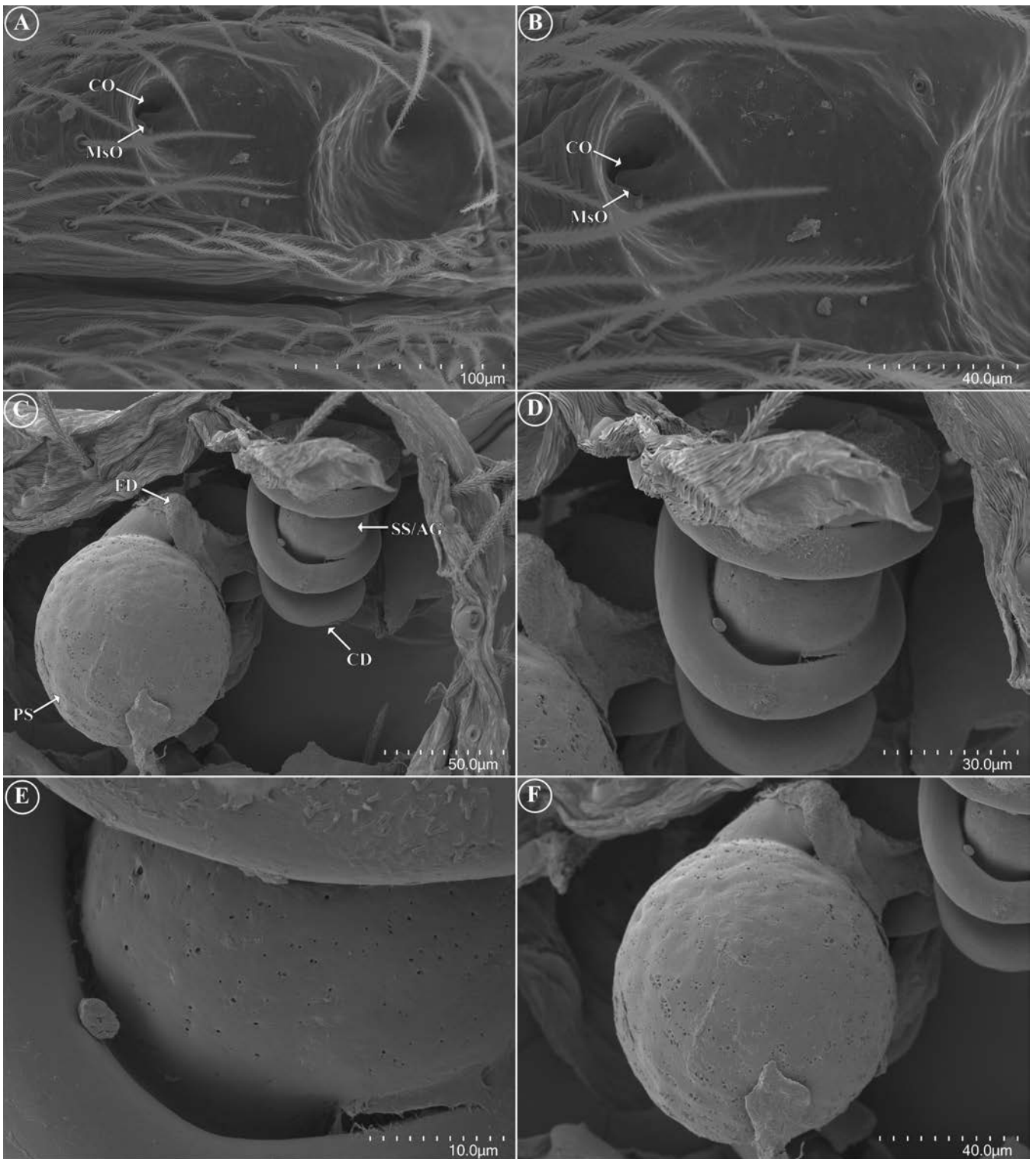


Figure 13. Scanning electron micrograph images of the epigyne of Lathyidae fam. n.: A, B, *Lathys humilis* (Blackwall, 1855), ventral view; C–F, *Analtella affinis* (Blackwall, 1862) comb. n., cleared epigyne, dorsal view. Abbreviations: CD, copulatory duct; CO, copulatory opening; FD, fertilization duct; MsO, membranous sac opening; PS, primary spermathecal; SS/AG, secondary spermatheca/opening of accessory gland.

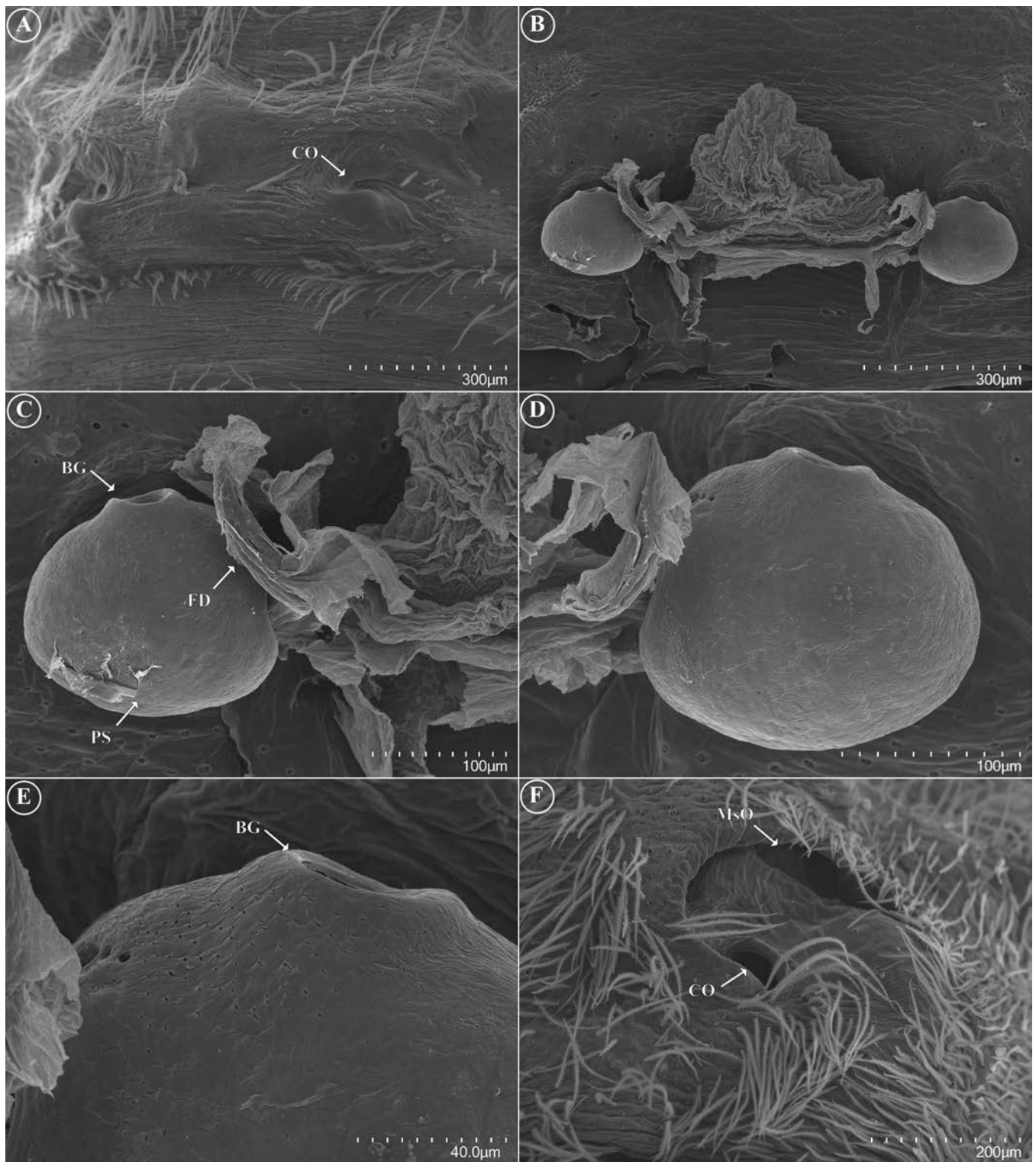


Figure 14. Scanning electron micrograph images of the epigyne of Argyronetidae stat. reinst.: A, *Argyroneta aquatica* (Clerck, 1757), dorsal view; B–E, cleared epigyne, dorsal view; F, *Tricholathys spiralis* Chamberlin and Ivie, 1935, ventral view. Abbreviations: BG, Bennett's gland; CO, copulatory opening; FD, fertilization duct; MsO, membranous sac opening; PS, primary spermatheca.

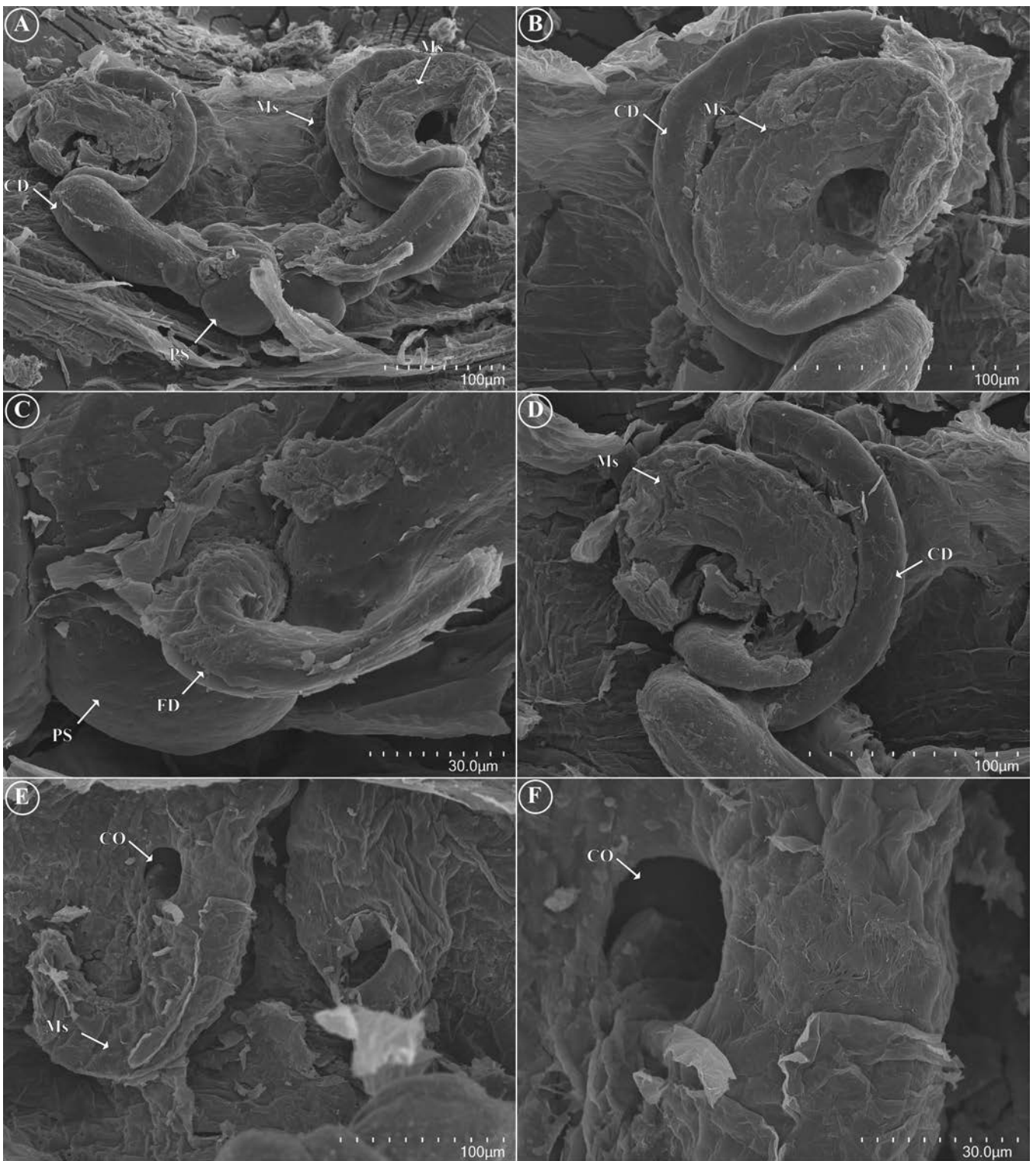


Figure 15. Scanning electron micrograph images of the epigyne of Dictynidae O. Pickard-Cambridge, 1871 s.s.: A–F, *Simziella major* (Menge, 1869) comb. n., cleared epigyne, dorsal view. Abbreviations: CD, copulatory duct; CO, copulatory opening; FD, fertilization duct; Ms, membranous sac; PS, primary spermatheca.

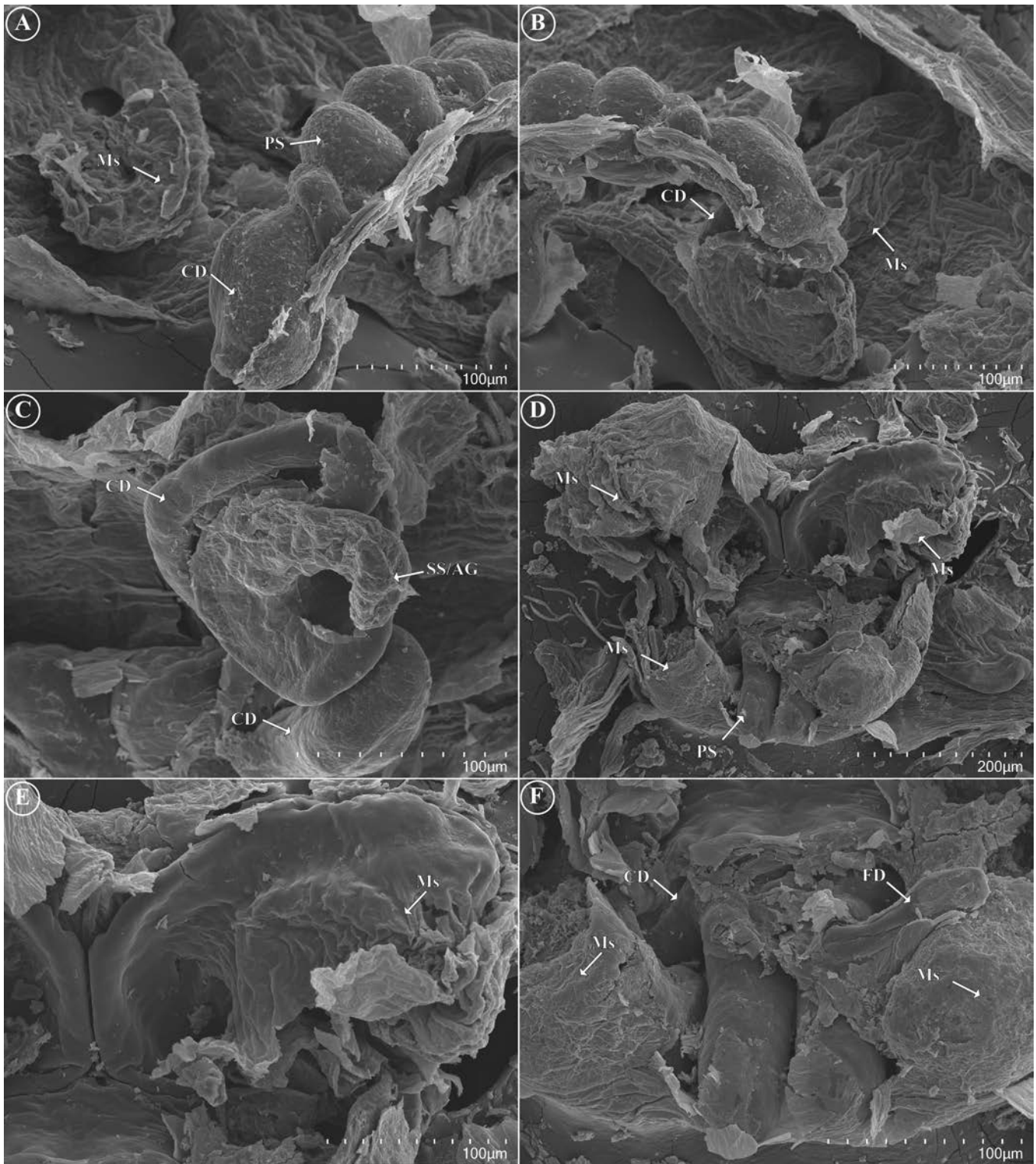


Figure 16. Scanning electron micrograph images of the epigyne of Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, B, *Simziella major* (Menge, 1869) comb. n., cleared epigyne, dorsal view; C–F, *Nopalityna sublata* (Hentz, 1850) comb. n.. Abbreviations: CD, copulatory duct; FD, fertilization duct; Ms, membranous sac; PS, primary spermathecal; SS/AG, secondary spermatheca/opening of accessory gland.

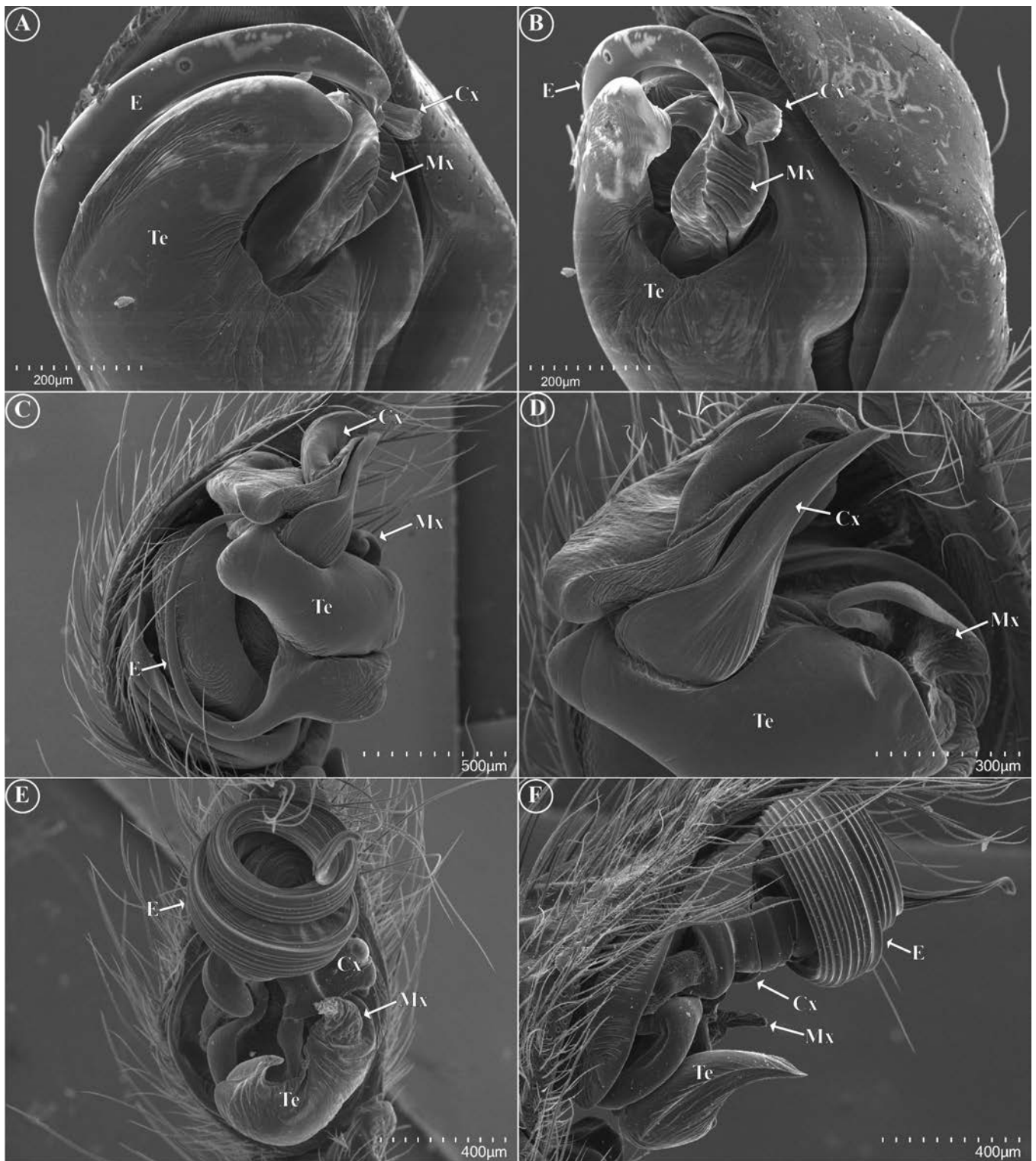


Figure 17. Scanning electron micrograph images of the male palp of members of the marronoid clade: A, *Pimus* Chamberlin, 1947 sp. (Amaurobiidae Thorell, 1869), ventral view; B, retrolateral view; C, *Coelotes lamellatus* Nishikawa, 2009 (Agelenidae C.L. Koch, 1837), prolateral ventral view; D, ventral view; E, *Barronopsis floridensis* (Roth, 1954) (Agelenidae C.L. Koch, 1837), ventral view; F, prolateral view. Abbreviations: Cx, conductor; E, embolus; Mx, median apophysis; Te, tegulum.

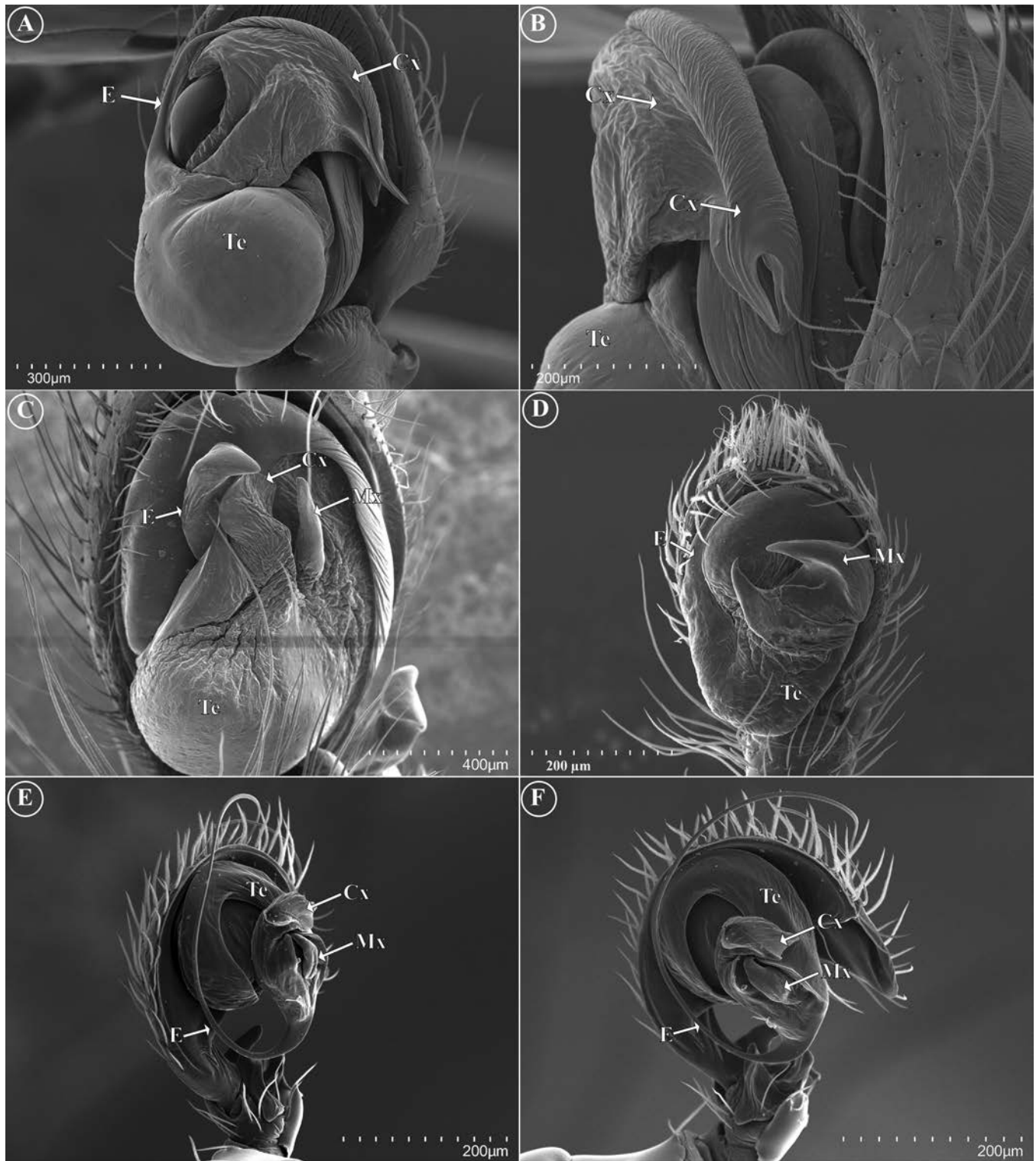


Figure 18. Scanning electron micrograph images of the male palp of members of the marronoid clade: A, *Stiphidion facetum* Simon, 1902 (Stiphidiidae Dalmas, 1917), ventral view; B, retrolateral view; C, *Cambridgea fasciata* L. Koch, 1872 (Desidae Pocock, 1895), ventral view; D, *Aebutina binotata* Simon, 1892 (Macrobnunidae Bonnet, 1957); ventral view; E, *Parazanomys thysionnes* Ubick, 2005 (Macrobnunidae Bonnet, 1957), prolateral ventral view; F, ventral view. Abbreviations: Cx, conductor; E, embolus; Mx, medial apophysis; Te, tegulum.

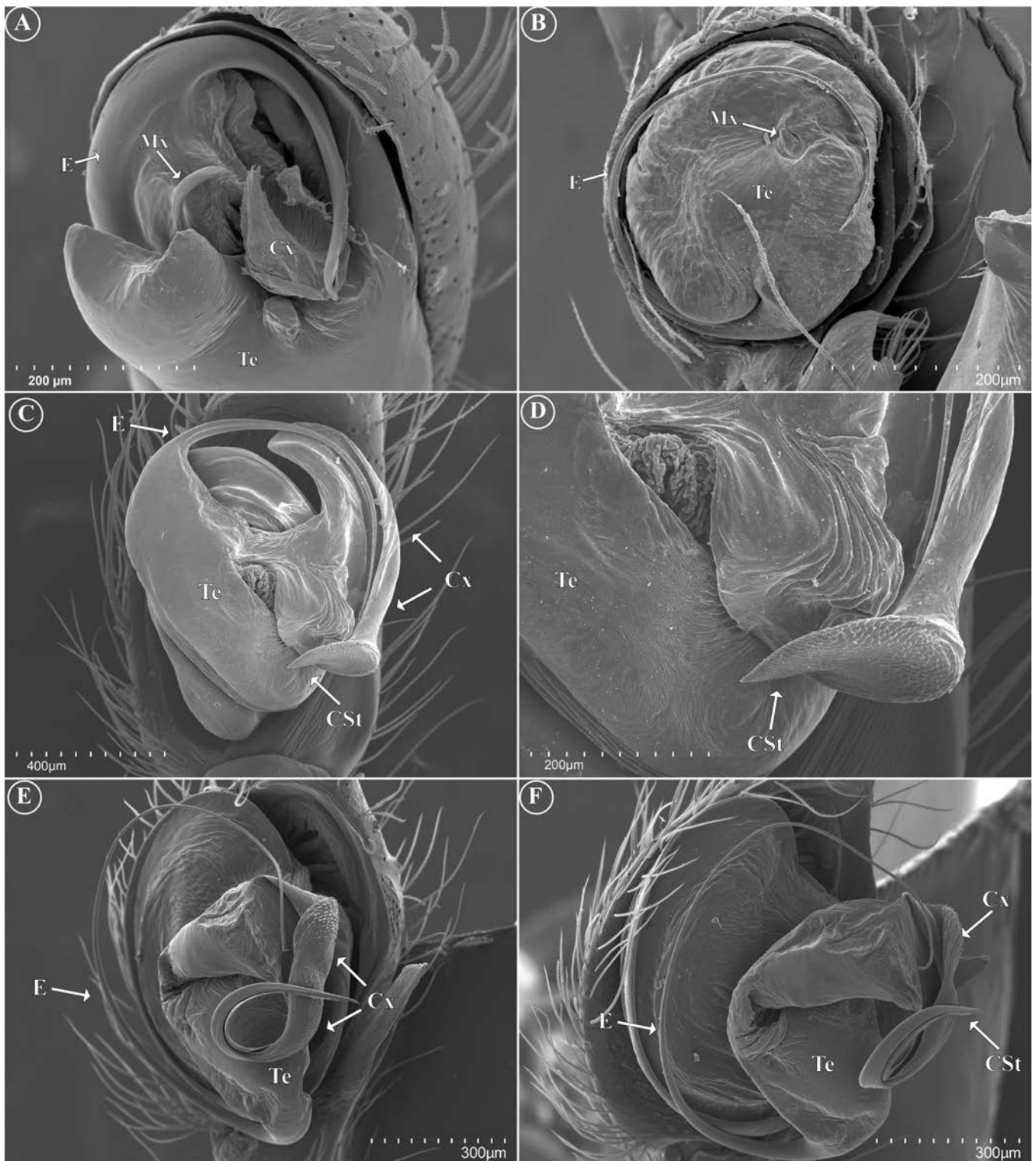


Figure 19. Scanning electron micrograph images of the male palp of members of the marronoid clade: A, *Pseudauximus pallidus* Purcell, 1904 (Macrobnidae Bonnet, 1957), ventral retrolateral view; B, *Hahnia pusilla* C.L. Koch, 1841 (Hahniidae Bertkau, 1871), ventral view; C, D, *Cybaeus* L. Koch, 1868 (Cybaeidae Banks, 1892), ventral view; E, *Cicurina cicur* (Fabricius, 1793) (Cicurinidae F.O. Pickard-Cambridge, 1893), ventral view; F, prolateral view. Abbreviations: CSt, conductor scaly tip; Cx, conductor; E, embolus; Te, tegulum; Mx, medial apophysis.

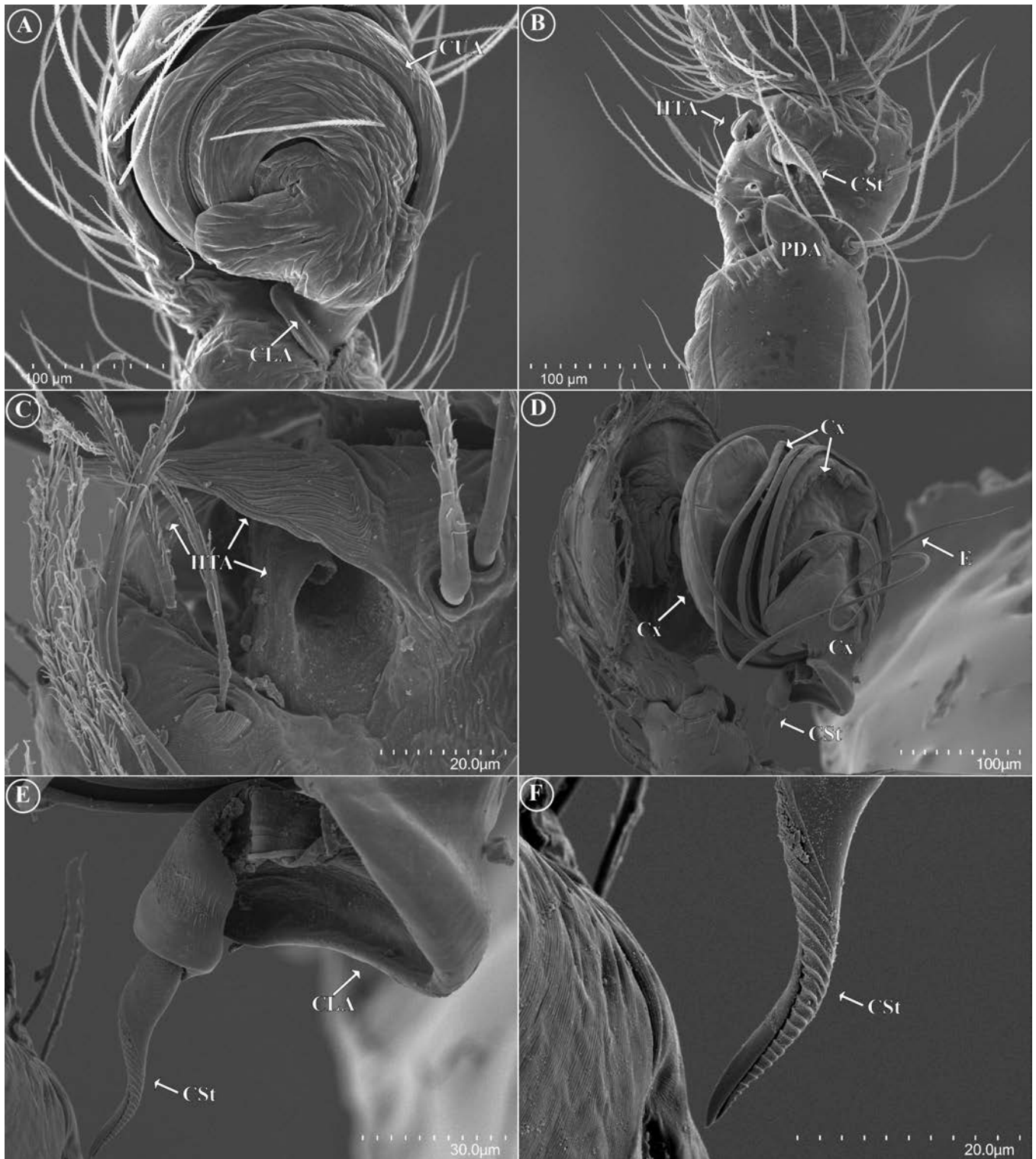


Figure 20. Scanning electron micrograph images of the male palp of *Lathys humilis* (Blackwall, 1855) (Lathyidae fam. n.): A, ventral view; B, tibia + patella, dorsal view; C, KOH expanded palp, conductor locking mechanism, dorsal view; D, KOH expanded palp, prolateral ventral view; E, KOH expanded palp, conductor scaly tip, prolateral ventral view; F, conductor scaly tip, prolateral ventral view. Abbreviations: CLA, conductor lower arm; CST, conductor scaly tip; CUA, conductor upper arm; Cx, conductor; E, embolus; HTA, hook-shaped tibial process; PDA, patellar dorsal apophysis.

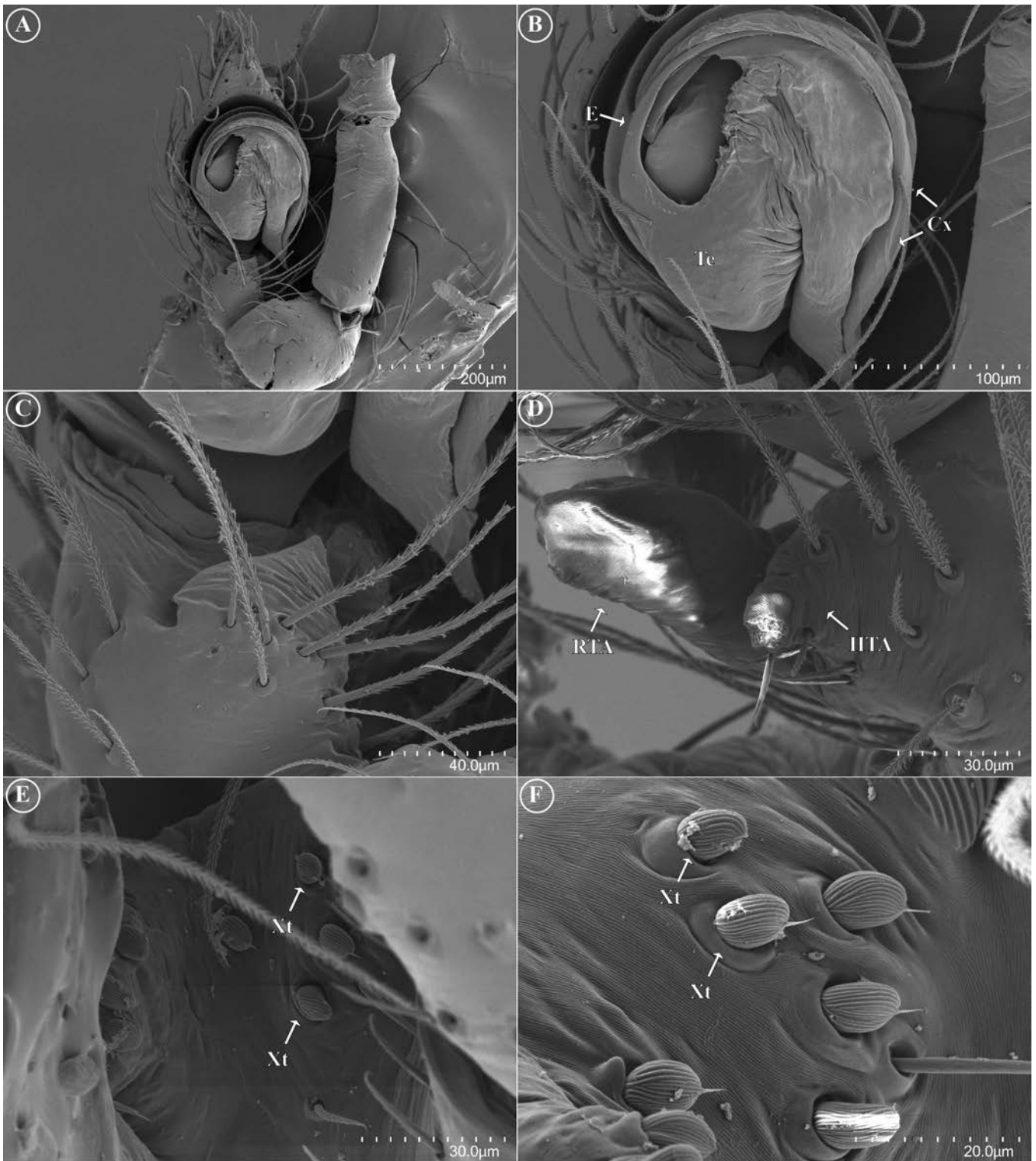


Figure 21. Scanning electron micrograph images of the male palp of *Denticulathys amaataaidoo* sp. n. (Lathyidae fam. n.): A, B, ventral view; C, tibial process and conductor scaly tip, ventral view; D, conductor locking mechanism, dorsal view; E, patella, dorsal view; F, patella, ctenidia field, dorsal view. Abbreviations: Cx, conductor; E, embolus; HTA, hook-shaped tibial process; RTA, retrolateral tibial apophysis; Te, tegulum; Xt, ctenidia.

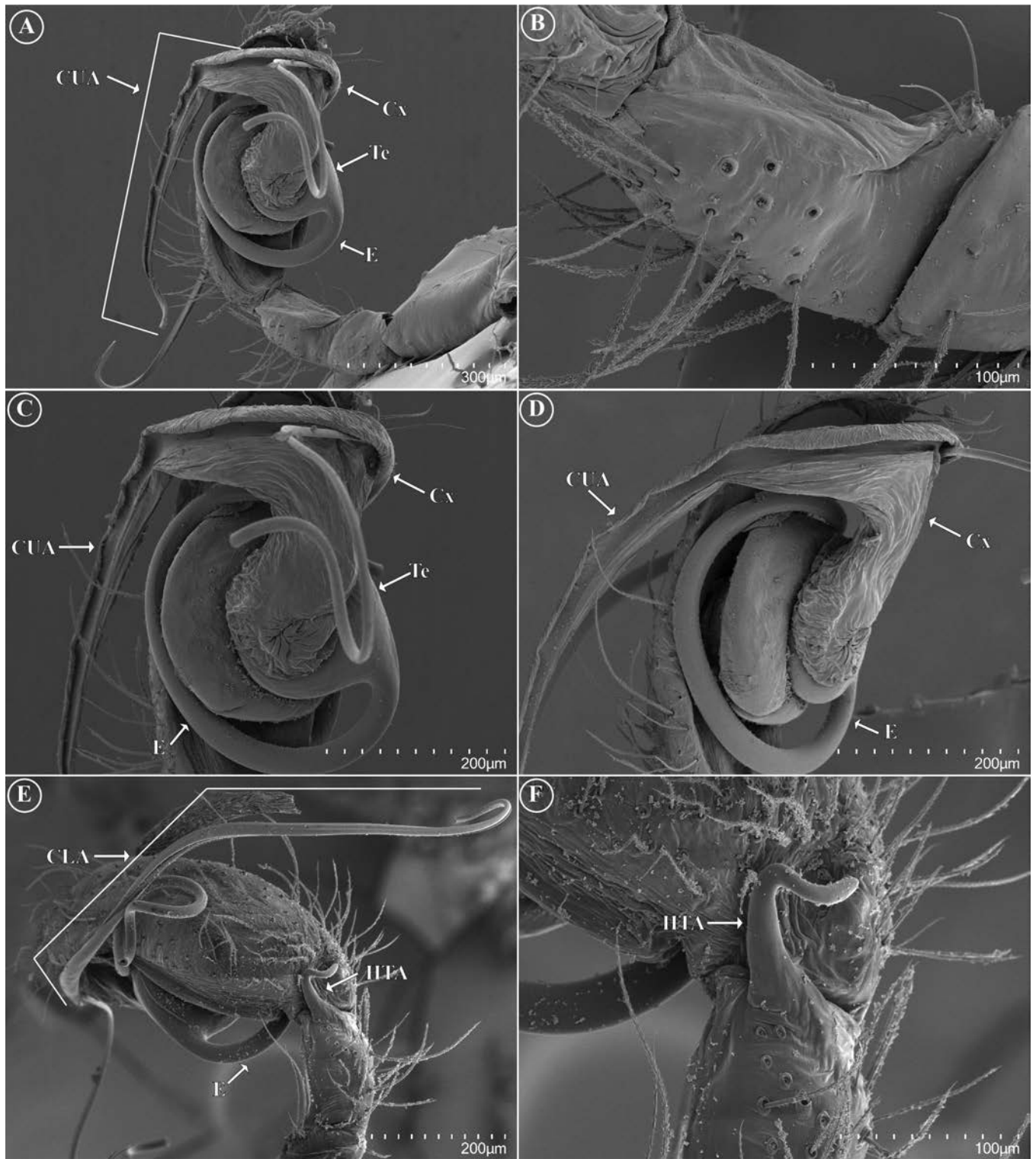


Figure 22. Scanning electron micrograph images of the male palp of *Afrolathys tanzanica* sp. n. (Lathyidae fam. n.): A, C, ventral view; B, tibia, prolateral view; D, prolateral ventral view; E, retrolateral view; F, conductor locking mechanism, dorsal view. Abbreviations: CLA, conductor lower arm; CUA, conductor upper arm; Cx, conductor; E, embolus; HTA, hook-shaped tibial process; Te, tegulum.

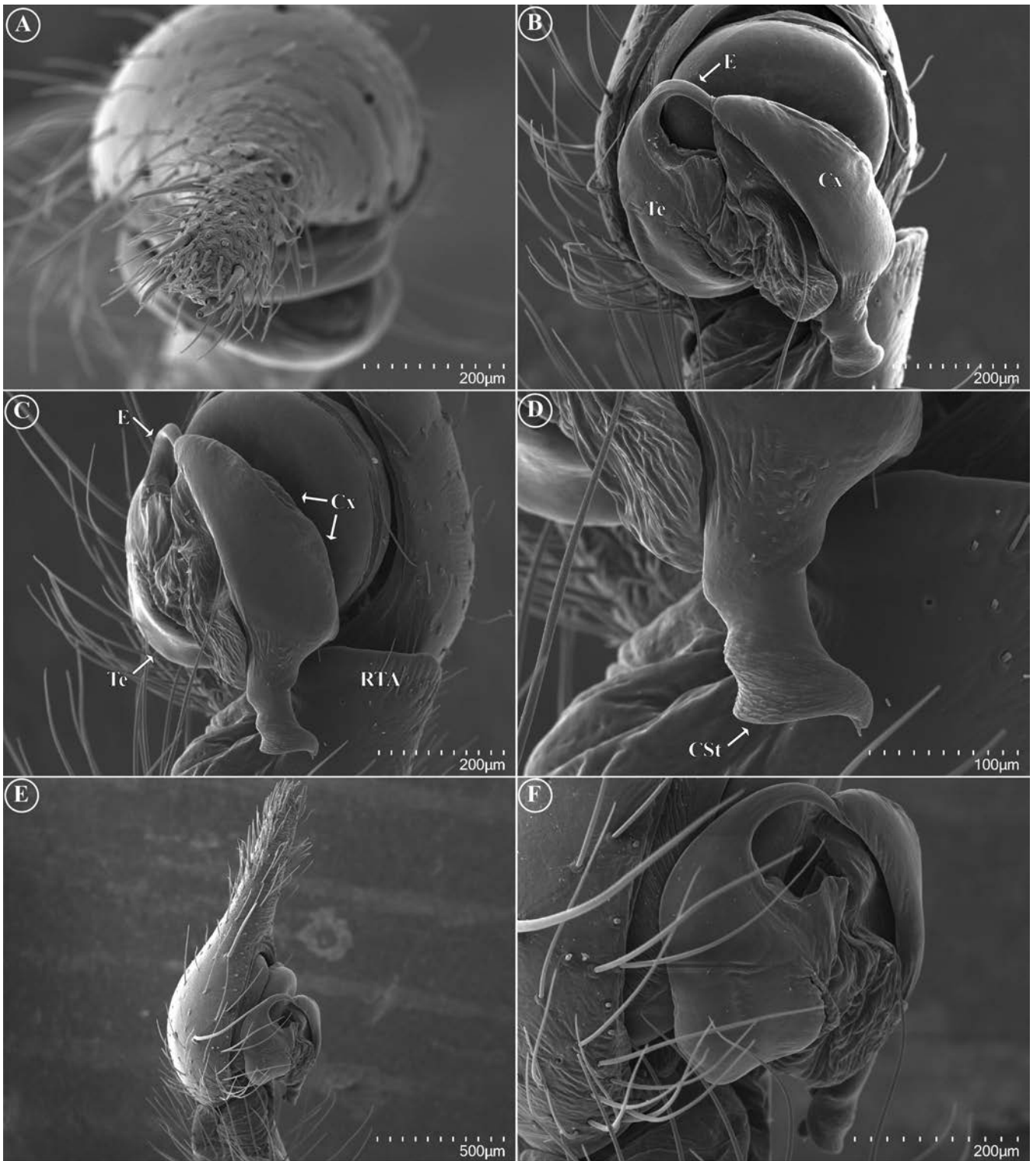


Figure 23. Scanning electron micrograph images of the male palp of *Argyroneta aquatica* (Clerck, 1757) (Argyronetidae stat. reinst.): A, cymbium, macrosetae, apical view; B, palp, ventral view; C, bulb, retrolateral view; D, conductor scaly tip, retrolateral view; E, F, prolateral view. Abbreviations: CSt, conductor scaly tip; Cx, conductor; E, embolus; Te, tegulum; RTA, retrolateral tibial apophysis.

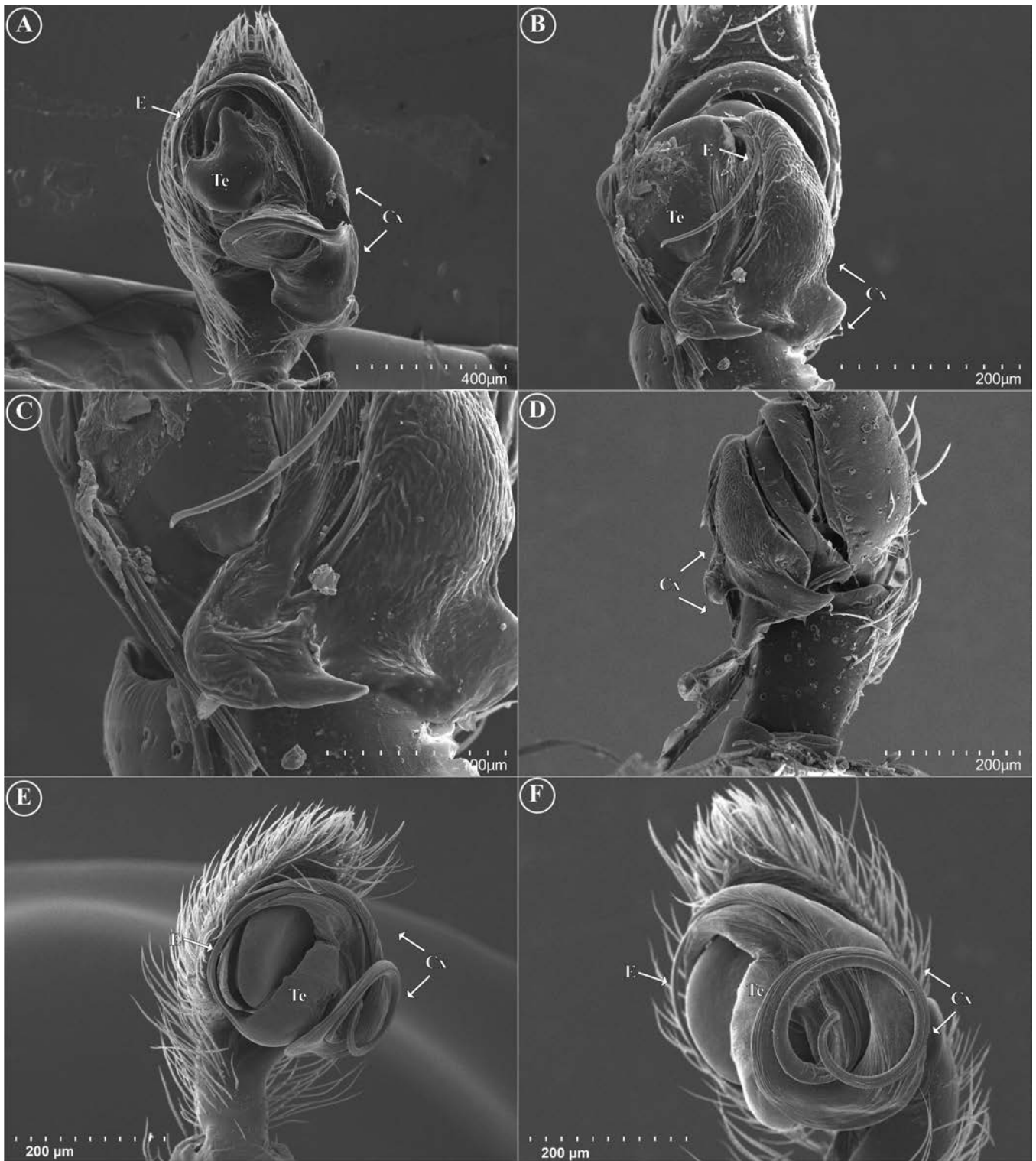


Figure 24. Scanning electron micrograph images of the male palp of Argyronetidae stat. reinst.: A, *Arctella lapponica* Holm, 1945; B, *Argenna pallida* L. Koch, 1881, ventral view; C, bulb, retrolateral view; D, bulb, retrolateral view; E, *Tricholathys spiralis* Chamberlin and Ivie, 1935, prolateral ventral view, F, bulb, retrolateral ventral view. Abbreviations: Cx, conductor; E, embolus; Te, tegulum.

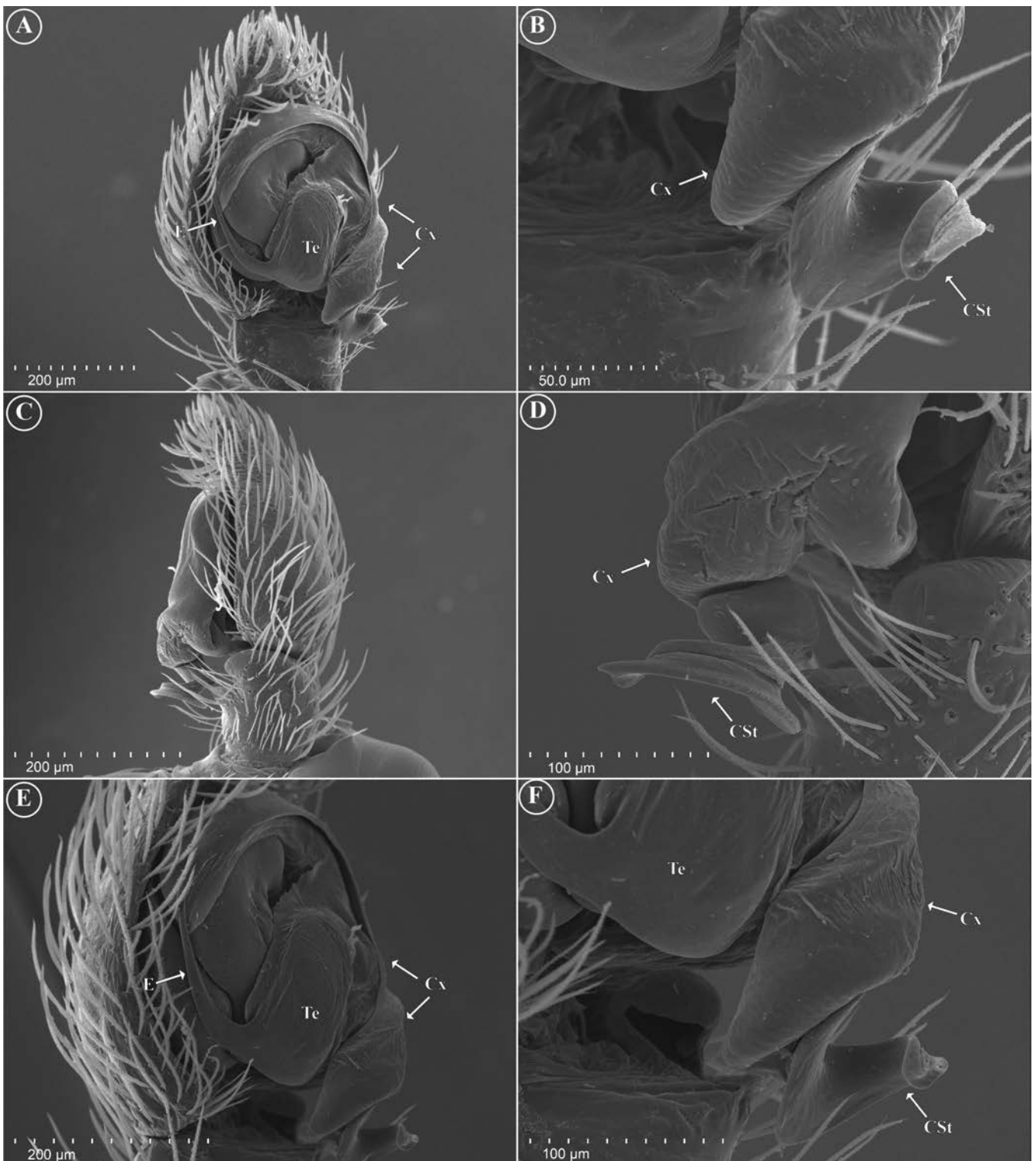


Figure 25. Scanning electron micrograph images of the male palp of *Mallos niveus* O. Pickard-Cambridge, 1902 (Dictynidae O. Pickard-Cambridge, 1871 s.s.): A, ventral prolateral view; B, conductor scaly tip, ventral prolateral view; C, retrolateral view; D, conductor scaly tip, retrolateral view; E, bulb, prolateral view; F, conductor scaly tip, prolateral view. Abbreviations: CSt, conductor scaly tip; Cx, conductor; E, embolus; Te, tegulum.

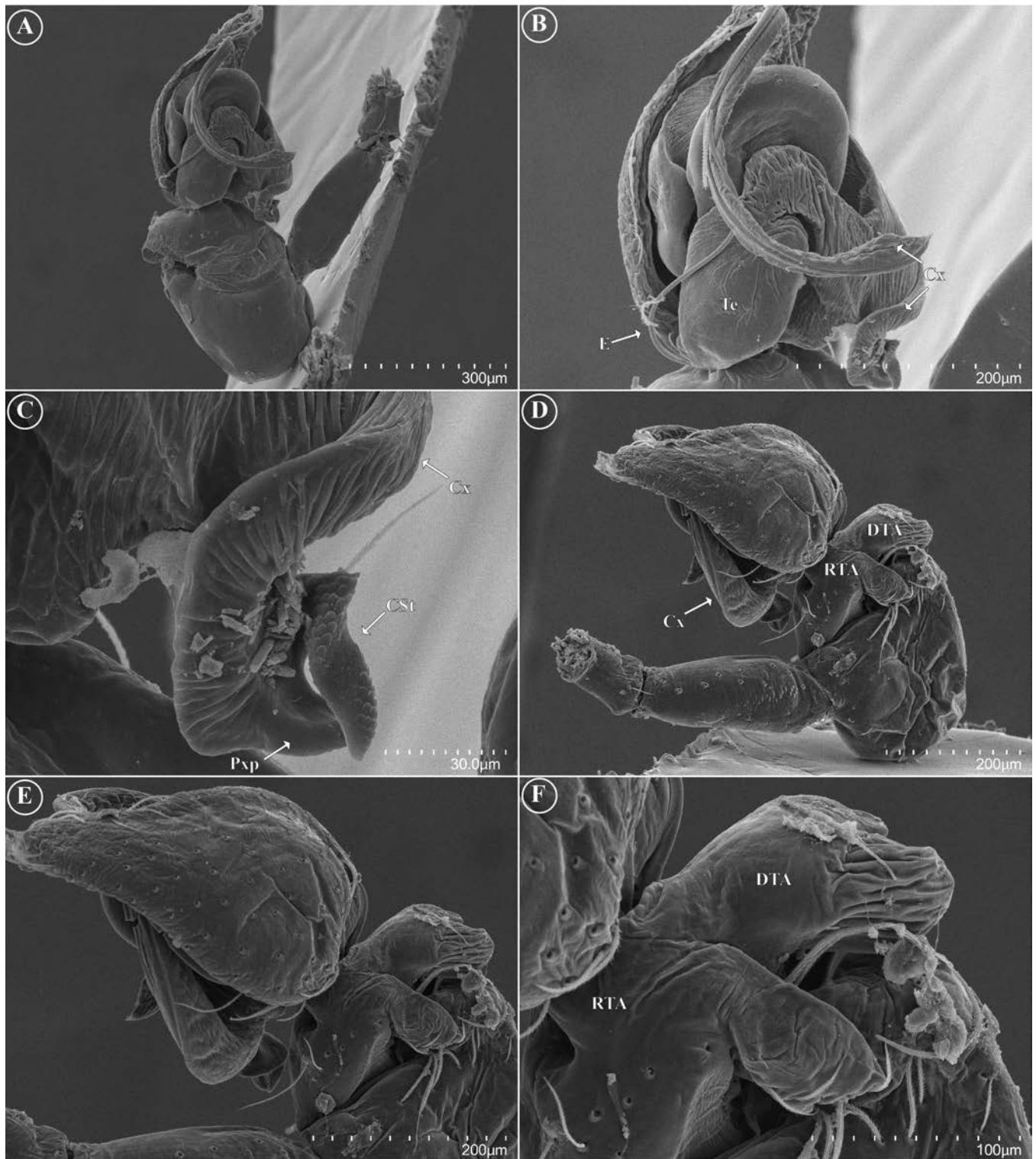


Figure 26. Scanning electron micrograph images of the male palp of *Tivyna spatula* (Gertsch and Davis, 1937) (Dictynidae O. Pickard-Cambridge, 1871 s.s.): A, ventral prolateral view; B, bulb, ventral prolateral view; C, conductor scaly tip and paraconductor process, retrolateral view; D, E, palp, retrolateral view; F, tibial process, retrolateral view. Abbreviations: DTA, dorsal tibial apophysis; CSt, conductor scaly tip; Cx, conductor; E, embolus; Te, tegulum; Pxp, paraconductor process; RTA, retrolateral tibial apophysis.

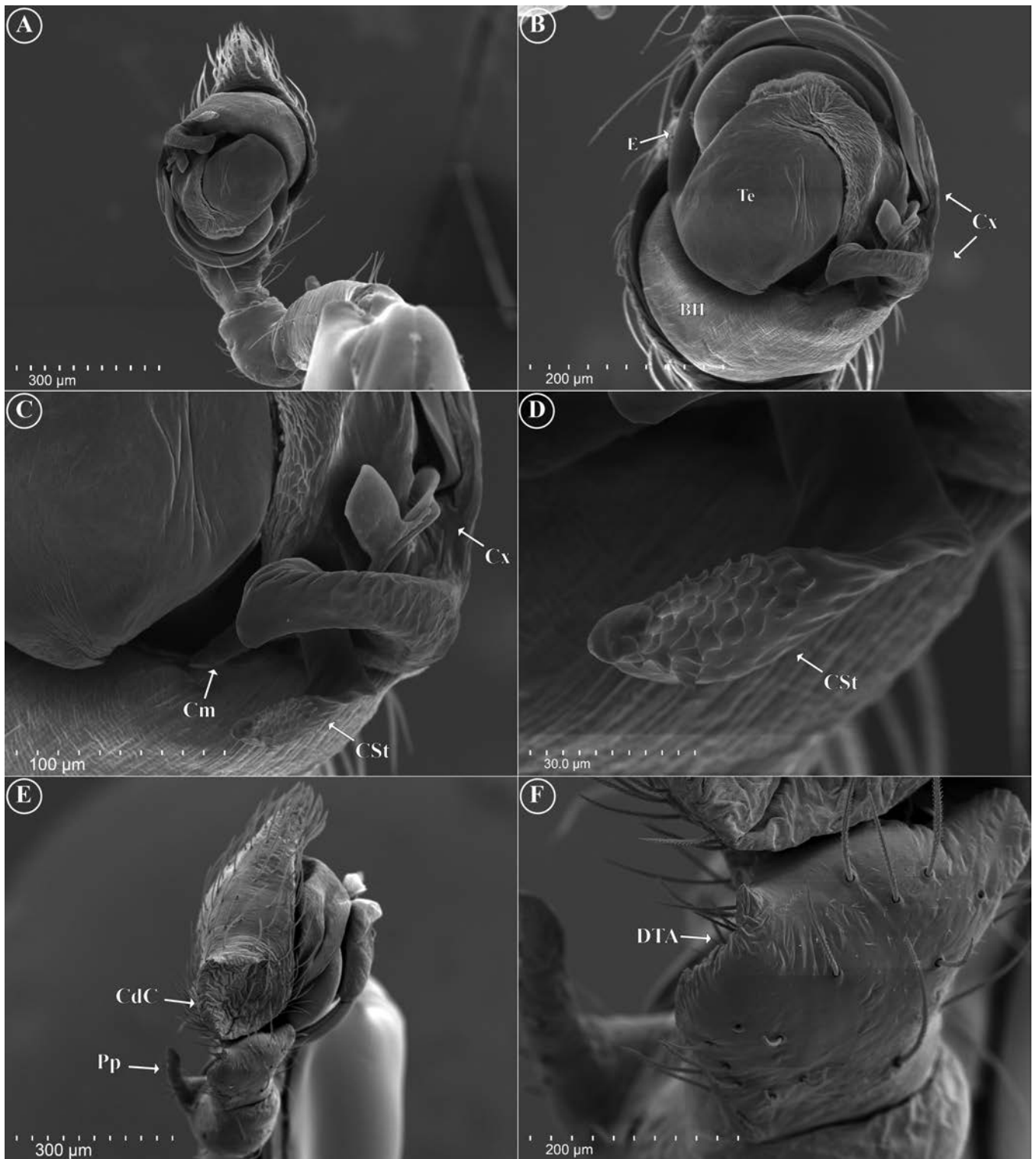


Figure 27. Scanning electron micrograph images of the male palp (KOH expanded) of *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n. (Dictynidae O. Pickard-Cambridge, 1871 s.s.): A, ventral view; B, ventral view; C, conductor lower arm, ventral view; D, conductor scaly tip, ventral view; E, palp, dorsal prolateral view; F, palpal tibia, dorsal view. Abbreviations: BH, basal hematodochae; CdC, cavity of dorsal extension of the cymbium; Cm, conductor locking mechanism; CSt, conductor scaly tip; Cx, conductor; DTA, dorsal tibial apophysis; E, embolus; Pp, patellar process; Te, tegulum.

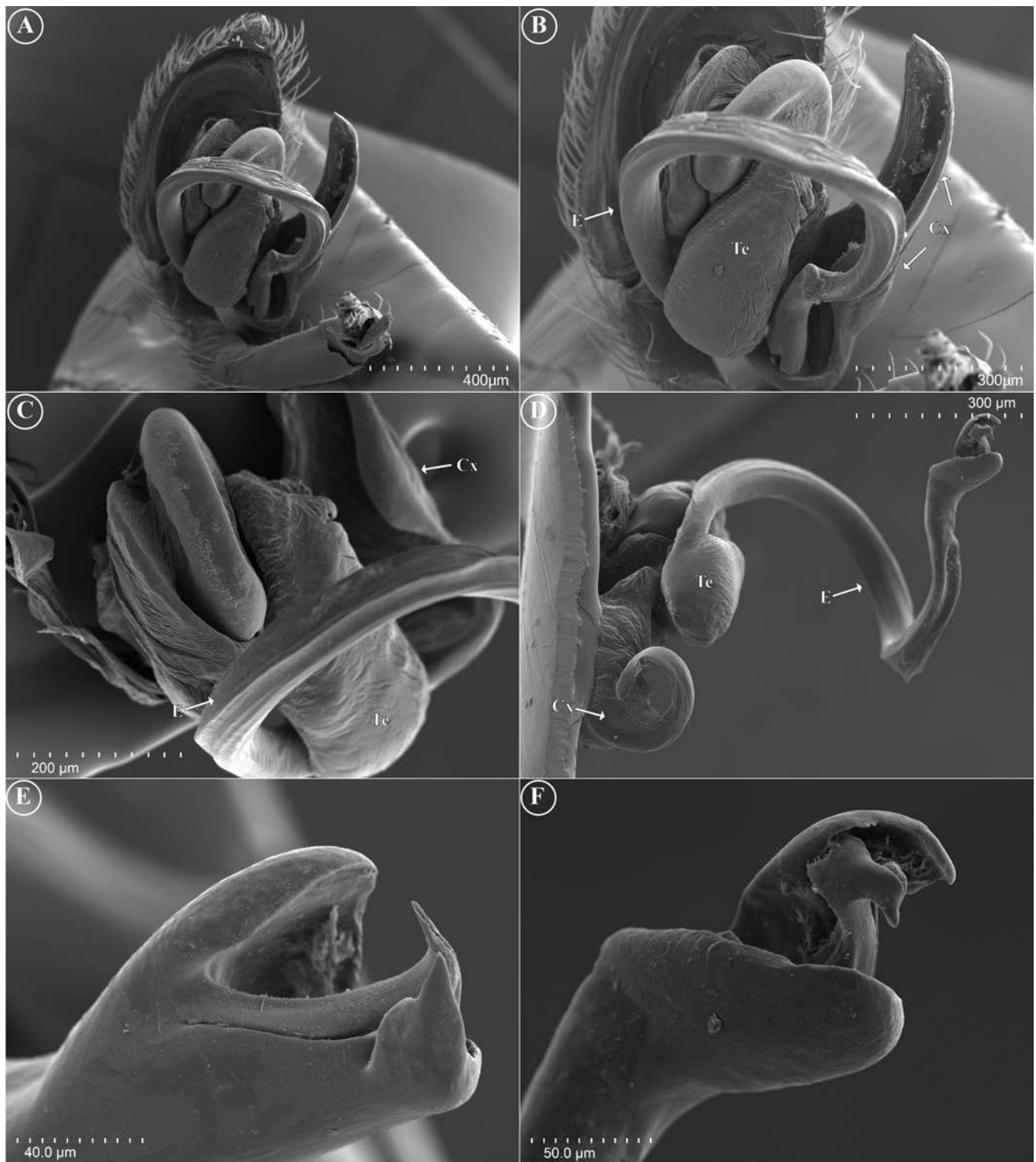


Figure 28. Scanning electron micrograph images of the male palp (KOH expanded) of *Emblyna maxima* (Banks, 1892) (Dictynidae O. Pickard-Cambridge, 1871 s.s.): A, prolateral ventral view; B, prolateral ventral view; C, apical prolateral view; D, prolateral view; E, embolus tip, prolateral view; F, embolus tip, retrolateral view. Abbreviations: Cx, conductor; E, embolus; Te, tegulum.

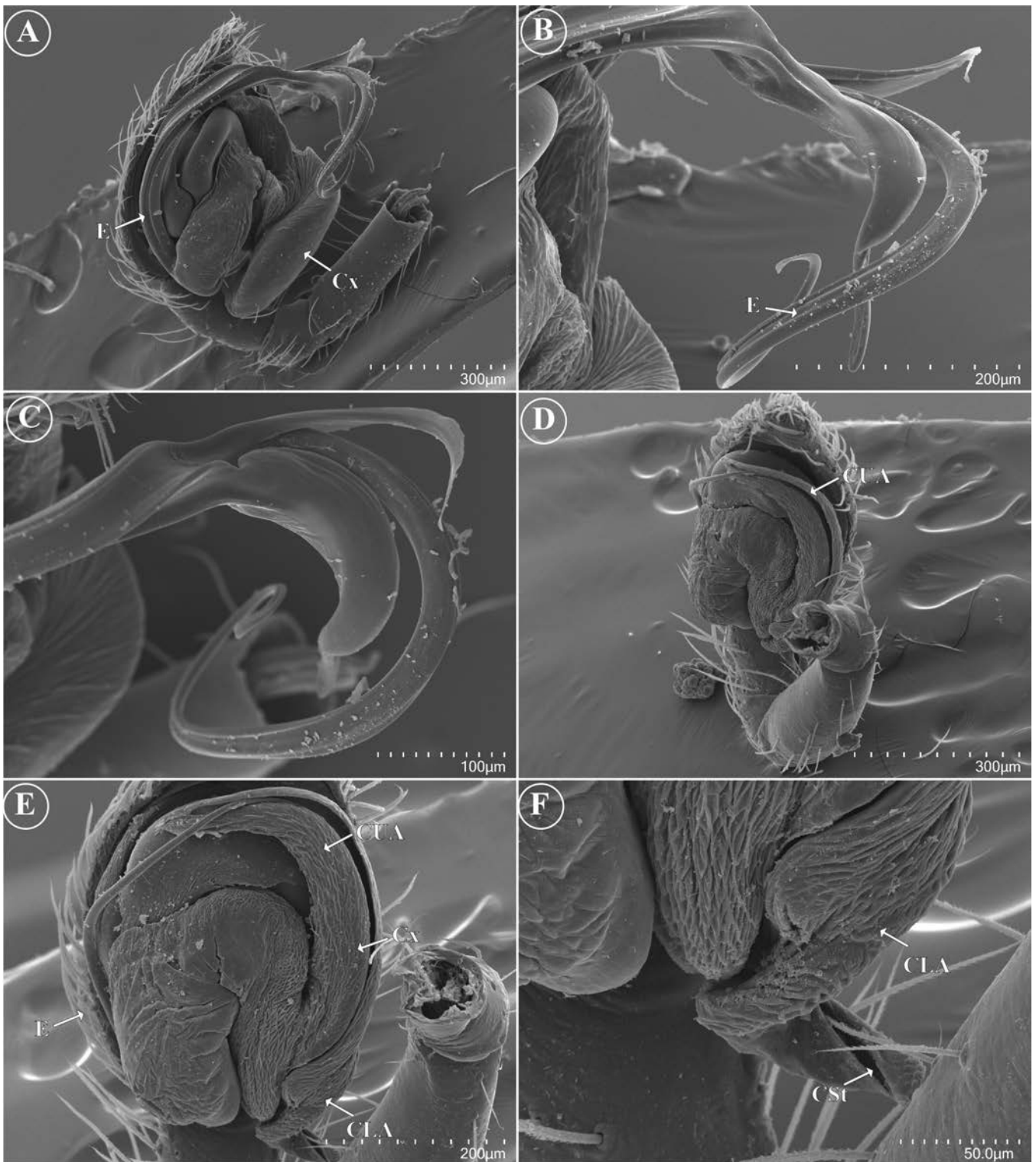


Figure 29. Scanning electron micrograph images of the male palp of Dictynidae O. Pickard-Cambridge, 1871 s.s.: A, *Nopalityna sublata* (Hentz, 1850) comb. n., prolatral ventral view; B, embolus, prolatral ventral view; C, embolus, apical prolatral view; D, *Simziella major* (Menge, 1869) comb. n., retrolateral ventral view; E, ventral view; F, conductor scaly tip, ventral view. Abbreviations: CLA, conductor lower arm; CST, conductor scaly tip; CUA, conductor upper arm; Cx, conductor; E, embolus.

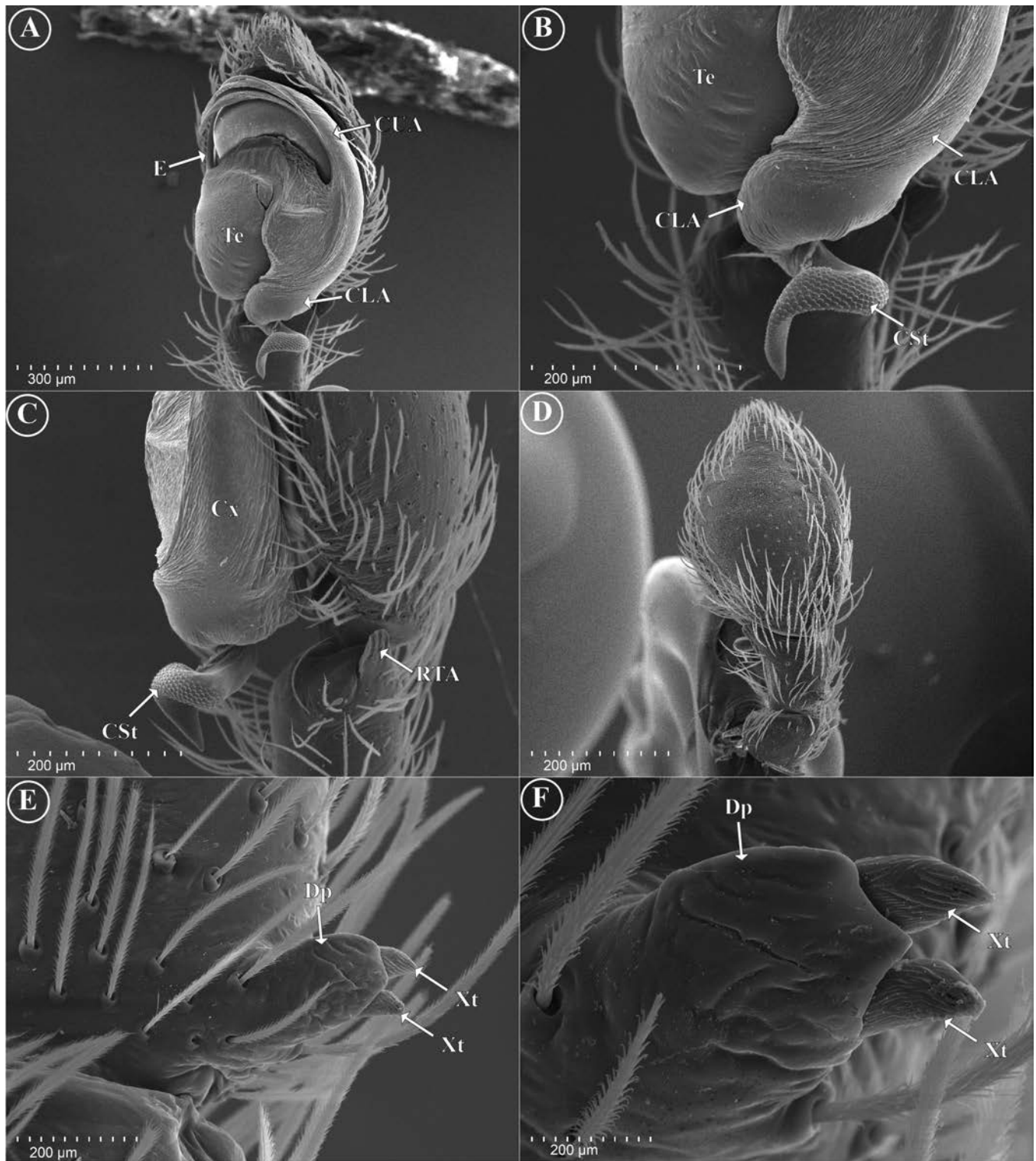


Figure 30. Scanning electron micrograph images of the male palp of *Dictyna arundinacea* (Linnaeus, 1758) (Dictynidae O. Pickard-Cambridge, 1971 s.s.): A, ventral retrolateral view; B, conductor, ventral retrolateral view; C, bulb, retrolateral view; D, dorsal view; E, F, dictynid process, retrolateral view. Abbreviations: CLA, conductor lower arm; CSt, conductor scaly tip; CUA, conductor upper arm; Cx, conductor; Dp, dictynid process (dorsal tibial process with ctenidia); E, embolus; Te, tegulum; Xt, ctenidia.

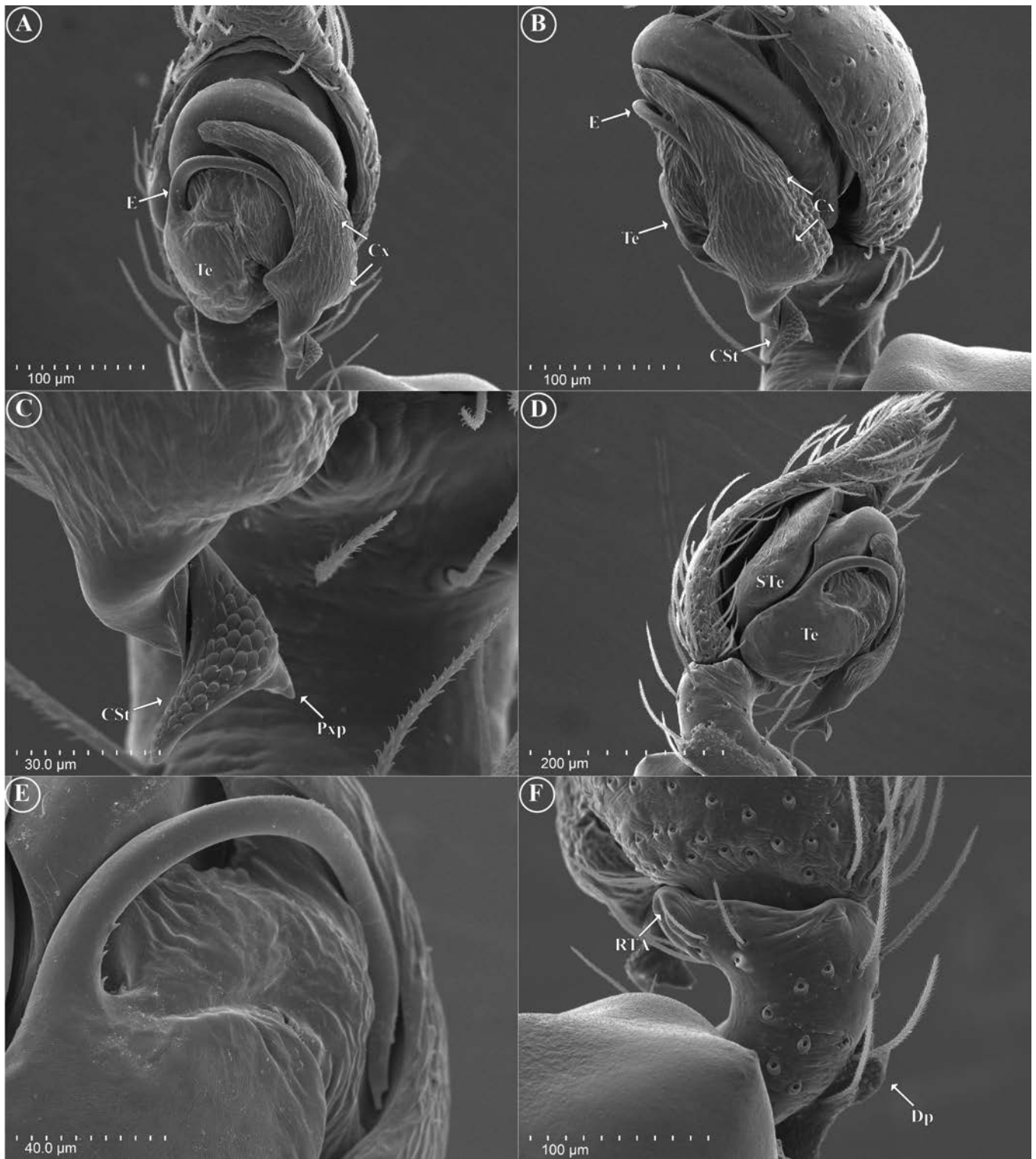


Figure 31. Scanning electron micrograph images of the male palp of *Dictyna bostoniensis* Emerton, 1888 (Dictynidae O. Pickard-Cambridge, 1871 s.s.): A, ventral view; B, retrolateral ventral view; C, conductor lower arm, retrolateral ventral view; D, proximal view; E, embolus, proximal ventral view; F, tibia, dorsal view. Abbreviations: CSt, conductor scaly tip; Cx, conductor; Dp, dictynid process (dorsal tibial process with ctenidia); E, embolus; STe, subtegulum; Te, tegulum; Pxp, paraconductor process; RTA, retrolateral tibial apophysis.

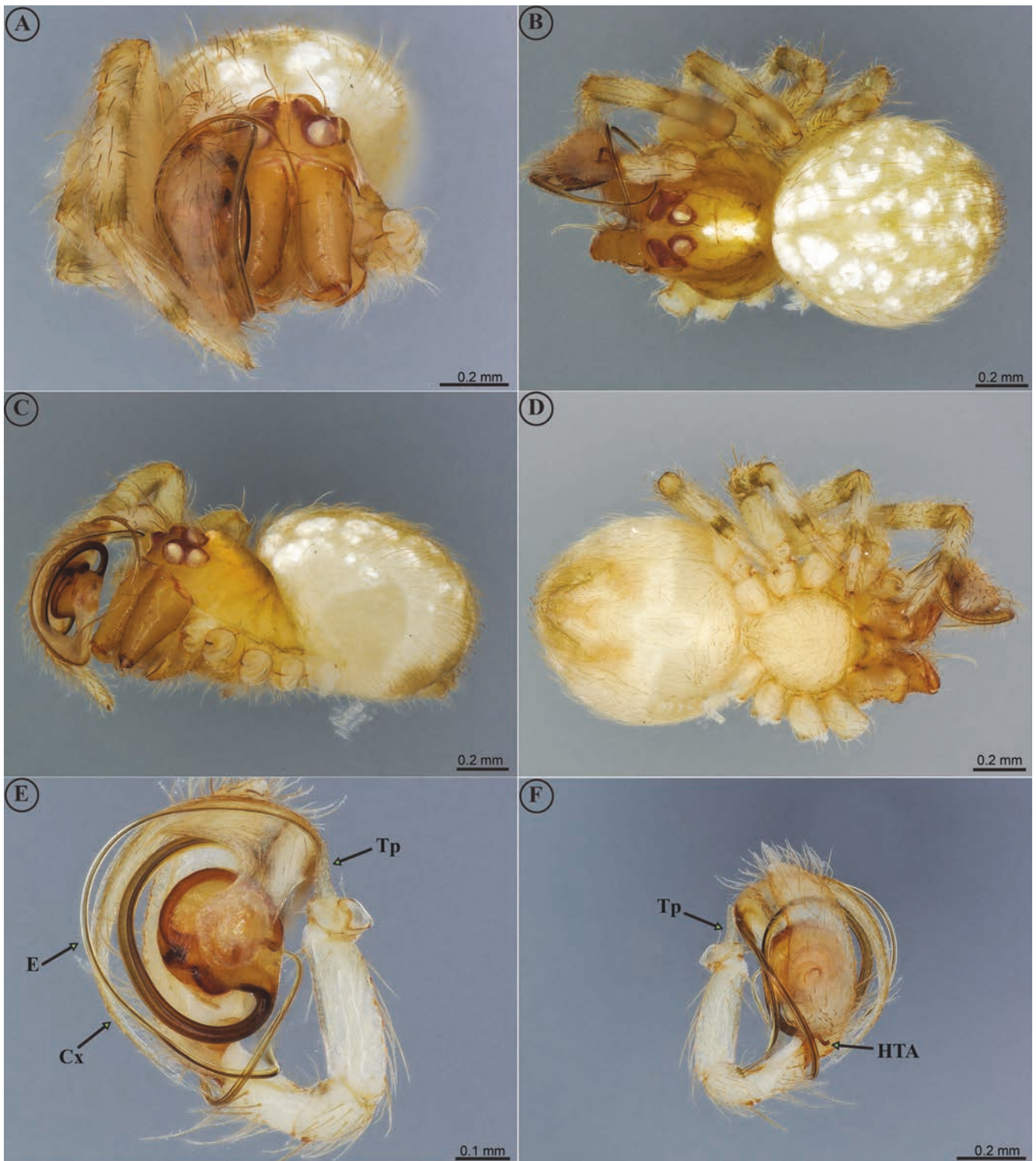


Figure 32. Habitus and palp of male *Afrolathys tanzanica* sp. n. (CASENT9118703): A, frontal view; B, dorsal view; C, lateral view; D, ventral view; E, palp, ventral view; F, palp, dorsal view. Abbreviations: Co, copulatory opening; Cx, conductor; E, embolus; HTA, hook-shaped tibial process; Tp, trochanter process.

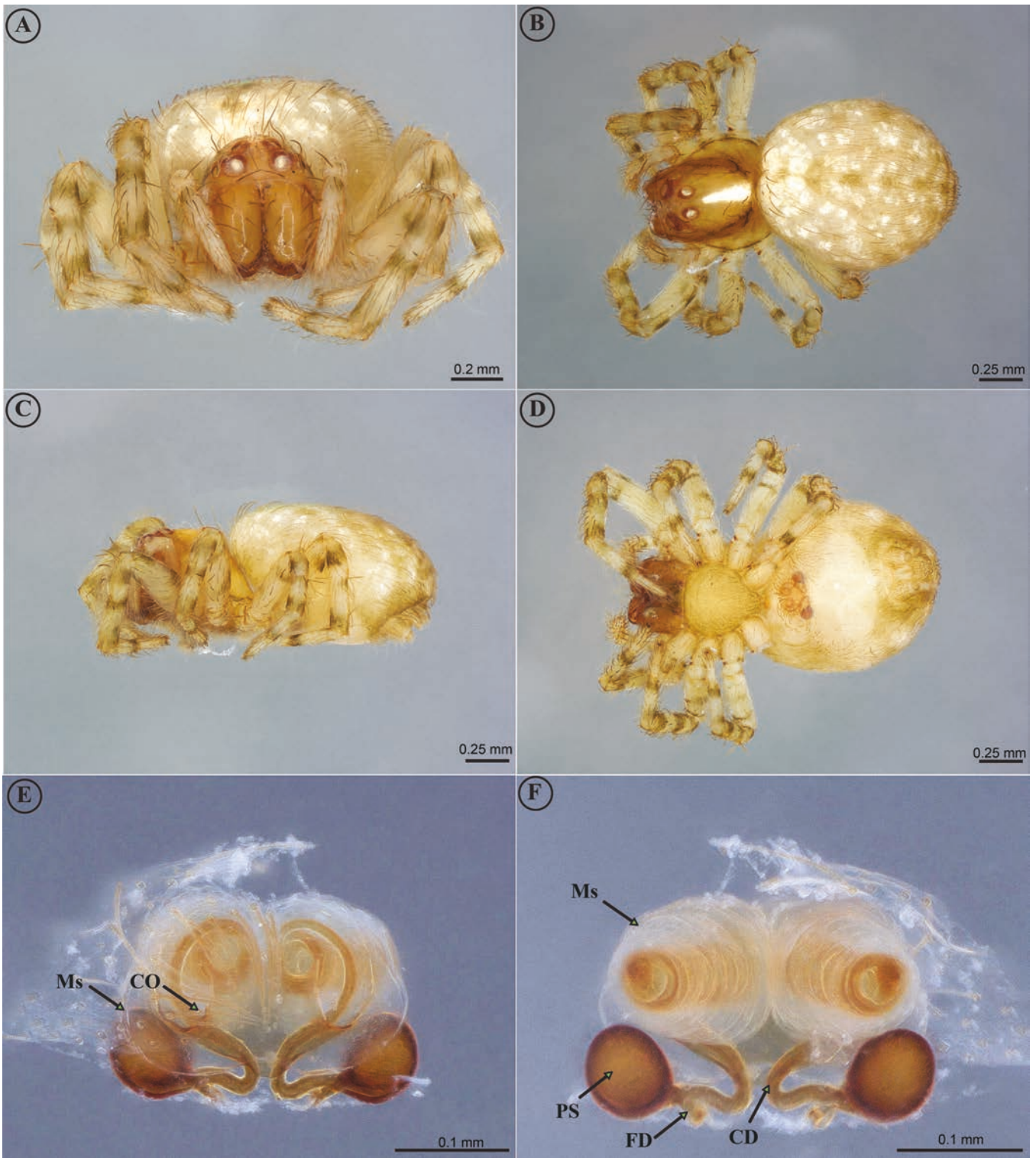


Figure 33. Habitus and epigyne of female *Afrolathys tanzanica* sp. n. (CASENT9118711): A, frontal view; B, dorsal view; C, lateral view; D, ventral view; E, cleared epigyne, ventral view; F, cleared epigyne, dorsal view. Abbreviations: CD, copulatory duct; FD, fertilization duct; Ms, membranous sac; PS, primary spermatheca.

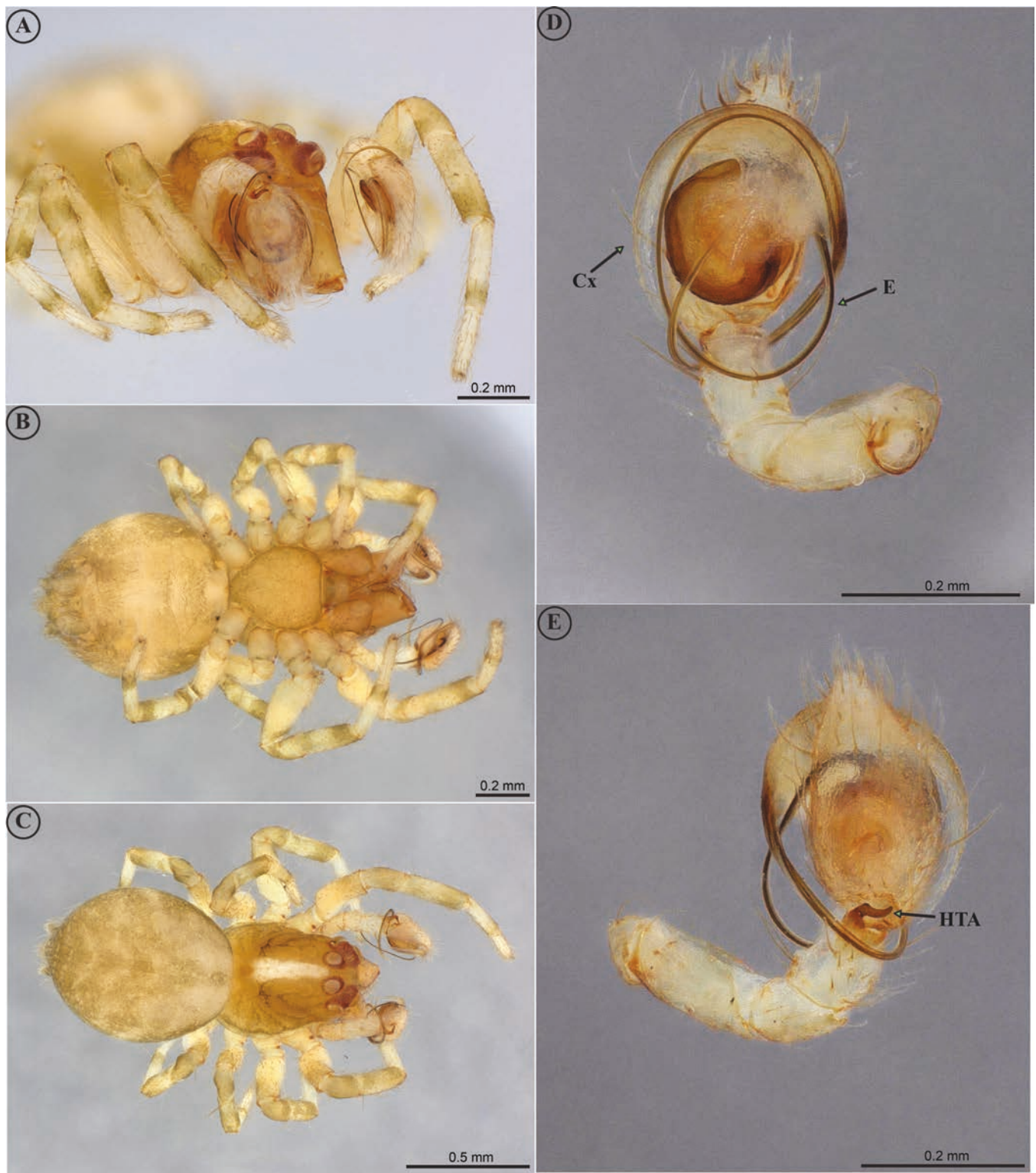


Figure 34. Habitus and palp of male *Afrolathys madagascariensis* sp. n. (CASENT9006800): A, frontal lateral view; B, ventral view; C, dorsal view; D, palp, ventral view; E, palp, retrolateral dorsal view. Abbreviations: Cx, conductor; E, embolus; HTA, hook-shaped tibial process.

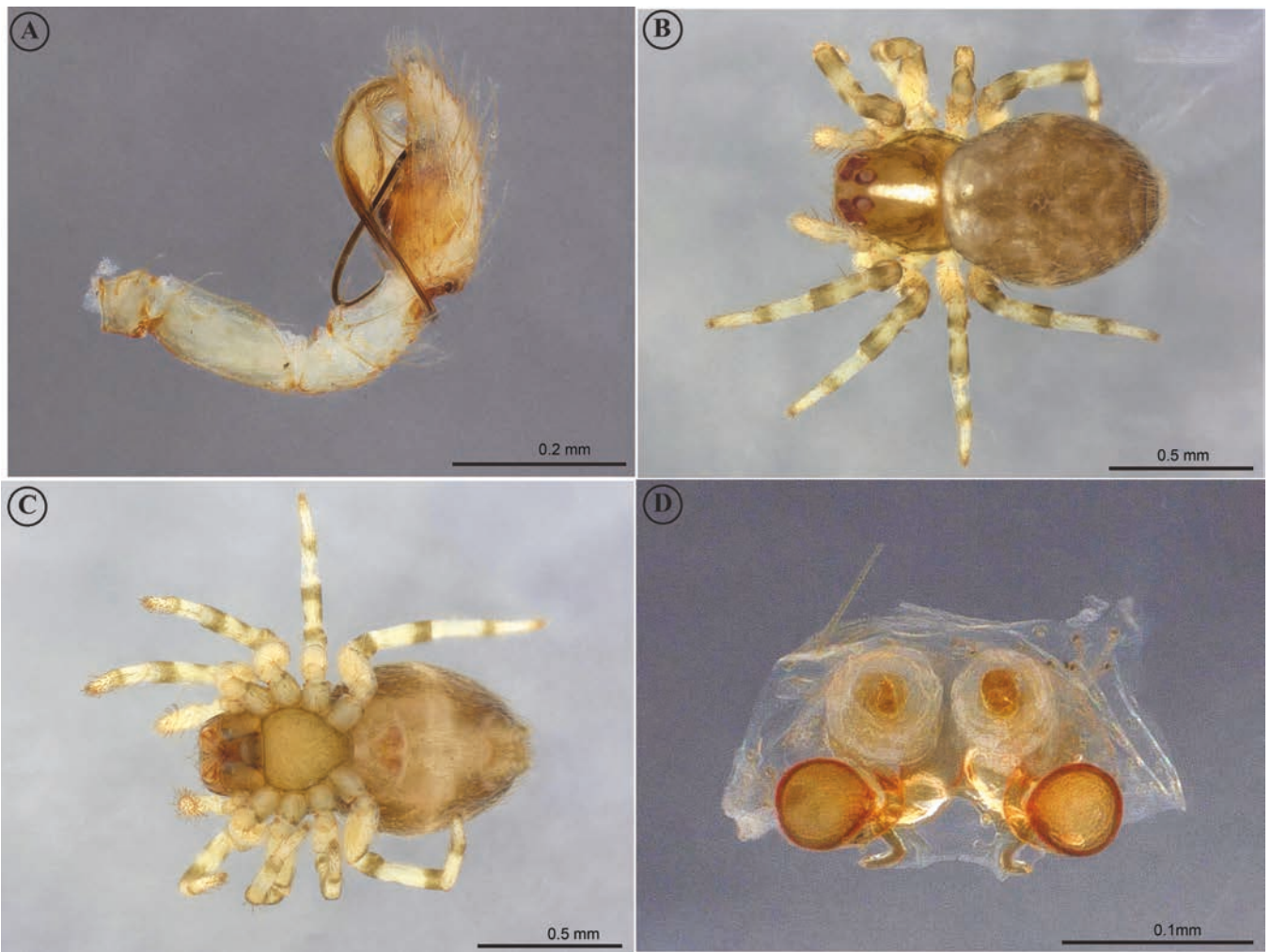


Figure 35. Habitus of female, epigyne and male palp of *Afrolathys madagascariensis* sp. n. (CASENT9006800): A, palp, retrolateral view; B, dorsal view; C, ventral view; D, cleared epigyne, dorsal view.

Remarks: Thorell (1870: 121, 136) designated the family Agalenoidae (= Agelenidae) to include the subfamilies Amaurobiinae, Agaleninae, and Argyronetinae with the genus *Argyroneta* as follows: ‘*Argyroneta aquatica* seems to me to deserve to be taken as the type of a separate sub-family, as well on account of its peculiar habits, as of the structure of its respiratory organs’. Menge (1871: 293) elevated Argyronetinae to the rank of family, with this taxonomy followed by Dahl (1937: 115–7). After, several arachnologists accepted the use of Argyronetidae (Reimoser 1919, Kishida 1930, Petrunkevitch 1939, Roewer 1942, Kaston 1948, Bonnet 1955, Yaginuma 1955, Komatsu 1961, Ono 2009, Murphy and Roberts 2015), whereas others no longer considered Argyronetidae to be a valid rank (Berland 1932, Saito 1941, Gertsch 1949, Millot 1949, Locket and Millidge 1953, Grothendieck and Kraus 1994, Wheeler *et al.* 2017). Miller *et al.* (2010), Spagna *et al.* (2010), and Wheeler *et al.* (2017) found evidence to support *Argyroneta* as a member of Dictynidae *s.l.* Crews *et al.* (2020), using Sanger loci, and Gorneau *et al.* (2023a), using UCE and Sanger data, recovered *Argyroneta* with other cribellates (Fig. 11C), resulting in a morphologically coherent group.

List of included genera: *Altella* Simon, 1884; *Arctella* Holm, 1945; *Argenna* Thorell, 1870; *Argyroneta* Latreille, 1804; *Chaerea*

Simon, 1884; *Devade* Simon, 1884; *Hackmania* Lehtinen, 1967; *Iviella* Lehtinen, 1967; *Mizaga* Simon, 1898; *Paratheuma* Bryant, 1940; *Saltonia* Chamberlin and Ivie, 1942; and *Tricholathys* Chamberlin and Ivie, 1935.

Family Lathyidae Cala-Riquelme, Montana, Crews, Esposito fam. n.

urn:lsid:zoobank.org:act:8BBD8958-0267-43EF-9FF6-3CCA9A0E6EC1.

Type genus: *Lathys* Simon, 1884; *Lethia varia* Menge, 1869, currently *Lathys humilis* (Blackwall, 1855).

Material examined: See the material examined for genera.

Diagnosis: Small, cribellate spiders (Figs 8A, 10A, B, 11B) with the carapace low or of moderate height, with the clypeus narrow (Figs 5A–E, 32A, 33A, 36A, 38A) (Chamberlin and Gertsch 1958); AME usually narrower than ALE, PME, and PLE (Fig. 5A, B) or absent (Fig. 5D, E) (present and as wide as ALE, PME, and PLE in Argyronetidae stat. reinst. and Dictynidae *s.s.*); ALE, PME, and PLE subequal in size and sub-equidistantly spaced (Figs 32A, 33A, 36A, 38A); chelicerae rather short, moderately

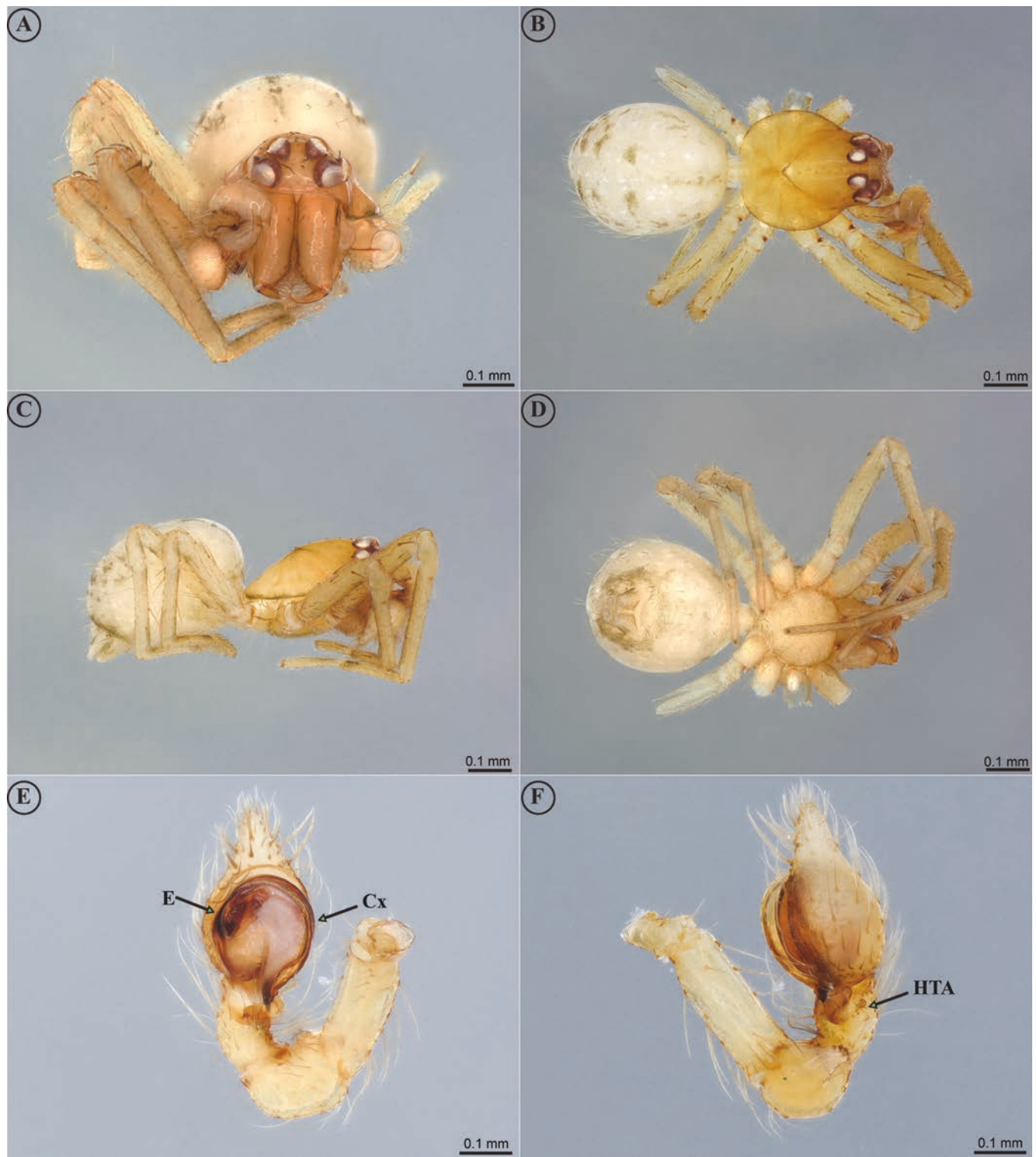


Figure 36. Habitus and palp of male *Denticulathys amaataaidoo* sp. n. (CASENT9118716): A, frontal view; B, dorsal view; C, lateral view; D, ventral view; E, palp, ventral view; F, palp, retrolateral view. Abbreviations: Cx, conductor; E, embolus; HTA, hook-shaped tibial process.

stout, without basal enlargements or spurs (Fig. 5A, C–F); male palp with the conductor upper arm usually longer than the lower arm (Figs 20A, D, 21B, 22A, C, D) (conductor upper arm shorter than lower arm in Argyronetidae stat. reinst.); conductor lower arm usually directed dorsally (Figs 20A, 32E, 34E; Marusik et al. 2009: figs 43, 45, 46) (ventrally in Argyronetidae stat. reinst. and Dictynidae s.s.), and locked by a mechanism

that comprises a longitudinal furrow, RTA, and hook-shaped tibial process (Figs 20C, 21D, 22E, F; 32F) (tibial lock mechanism absent in Argyronetidae stat. reinst. and Dictynidae s.s.); embolus coiled more than 150 degree but not more than 1200° (Figs 20D, 32E, F, 34D, E) (coiled $\leq 720^\circ$ in Argyronetidae stat. reinst. and Dictynidae s.s.); epigyne with the primary spermathecae two or more times wider than the copulatory

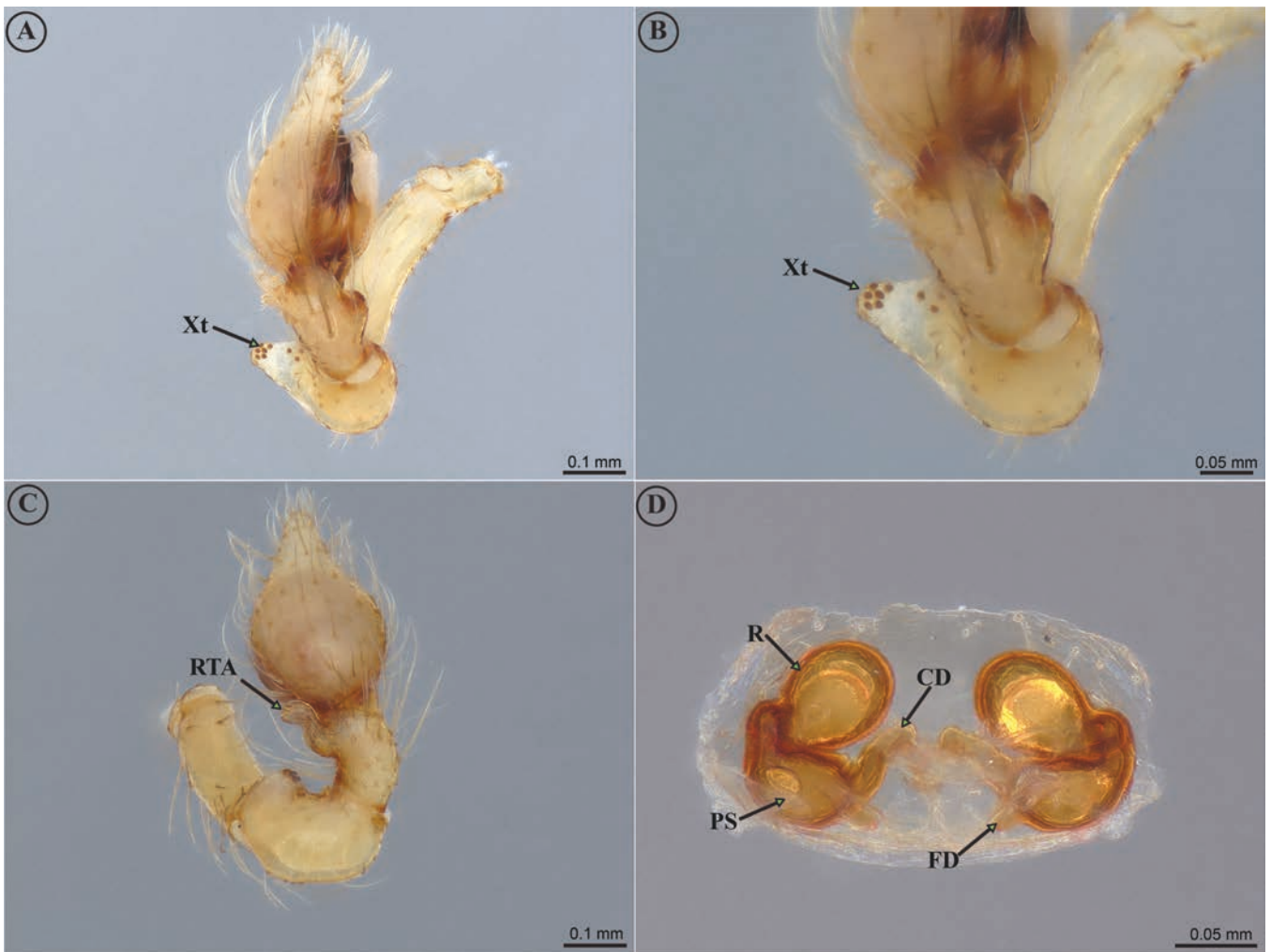


Figure 37. Male palp (CASENT9118716) and epigyne (CASENT9118606) of *Denticulathys amaataaidoo* sp. n.: A, B, prolateral view; C, dorsal view; D, cleared epigyne, dorsal view; Abbreviations: CD, copulatory duct; PS, primary spermathecae; R, receptacle; RTA, retrolateral tibial apophysis; Xt, ctenidia.

duct width (Figs 13C–F, 33E, F, 37D); copulatory duct well developed (Figs 13C–F, 33E, F), usually many times longer than the primary spermathecae width and coiled between the membranous sac and the SS/AG (Fig. 13C, D), or as long as primary spermathecae (Fig. 37D).

Remarks: Wheeler *et al.* (2017) recovered *Lathys* close to Dictynidae *s.l.* but with very low support. Crews *et al.* (2020), using denser sampling, recovered *Lathys* as more distantly related to Dictynidae *s.l.*, and as in Wheeler *et al.* (2017), the position of *Lathys* was weakly supported. Gorneau *et al.* (2023a) using UCEs + Sanger loci recovered *Lathys* as closely related to Dictynidae *s.l.* with high support; however, the deep phylogenetic divergence and observed diversity indicate that it should be treated as a separate family (see: Gorneau *et al.* 2023a). The subfamily Lathysinae proposed by Gorneau *et al.* (2023a) was unavailable following ICZN article 16 (see: ICZN 1999, article 16). We propose Lathyidae fam. n. [Type genus *Lathys* Simon, 1884: *Lethia varia* Menge, 1869 = *Lathys humilis* (Blackwall, 1855)] based on the synapomorphies of the male palp, the eye configuration, and the morphology of the epigyne.

List of included genera: *Afrolathys* gen. n. (*Af. madagascariensis* sp. n. and *Af. tanzanica* sp. n.), *Analtella* stat. reinst. [*Analtella affinis* (Blackwall, 1862) comb. n., *Analtella dentichelis* (Simon, 1883) comb. n., *Analtella narbonensis* (Simon, 1876) comb. n., *Analtella pygmaea* (Wunderlich 2011) comb. n., and *Analtella teideensis* (Wunderlich, 1992) comb. n.], *Andronova* gen. n. [*Andronova alberta* (Gertsch, 1946) comb. n., *Andronova annulata* (Bösenberg and Strand, 1906) comb. n., *Andronova arabs* (Simon, 1910) comb. n., *Andronova cambridgei* (Simon, 1874) comb. n., *Andronova dihamata* (Paik, 1979) comb. n., *Andronova lehtineni* (Kovblyuk *et al.*, 2014) comb. n., *Andronova maculosa* (Karsch, 1879) comb. n., *Andronova spasskyi* (Andreeva and Tystshenko, 1969) comb. n., *Andronova subalberta* (Z.S. Zhang, Zhang, Hu, Y.G. Zhang) comb. n., *Andronova subviridis* (Denis, 1937) comb. n., and *Andronova sylvania* (Chamberlin and Gertsch, 1958) comb. n.], *Asialathys* gen. n. [*As. deltoidea* (Liu, 2018) comb. n., *As. fibulata* (Liu, 2018) comb. n., *As. huangyangjieensis* (Liu, 2018) comb. n., *As. spiralis* (Z.S. Zhang, Hu, Y.G. Zhang, 2012) comb. n., and *As. zhanfengi* (Liu, 2018) comb. n.], *Bannaella* Zhang and Li, 2011 [*B. lhasana* (Hu, 2001), *B. sexoculata* (Seo and Sohn, 1984) comb. n., *B. sinuata* Zhang and Li, 2011, and *B. tibialis* Zhang and Li, 2011], *Denticulathys* gen. n. (*D. amaataaidoo*

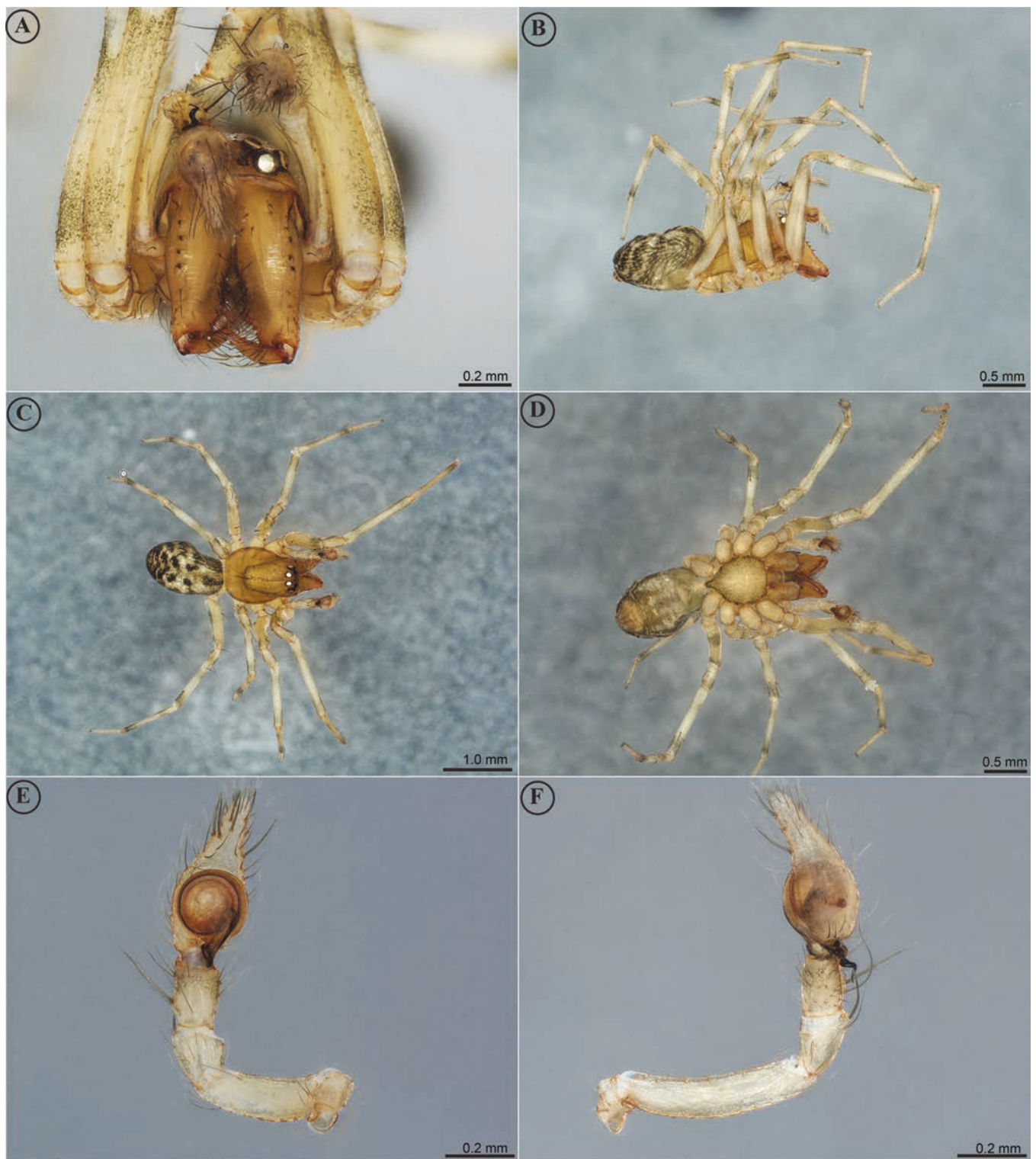


Figure 38. Habitus and palp of male *Analtella affinis* (Blackwall, 1862) comb. n. (CASENT9087229): A, frontal view; B lateral view; C, dorsal view; D, ventral view; E, palp, ventral view; F, palp, retrolateral view.

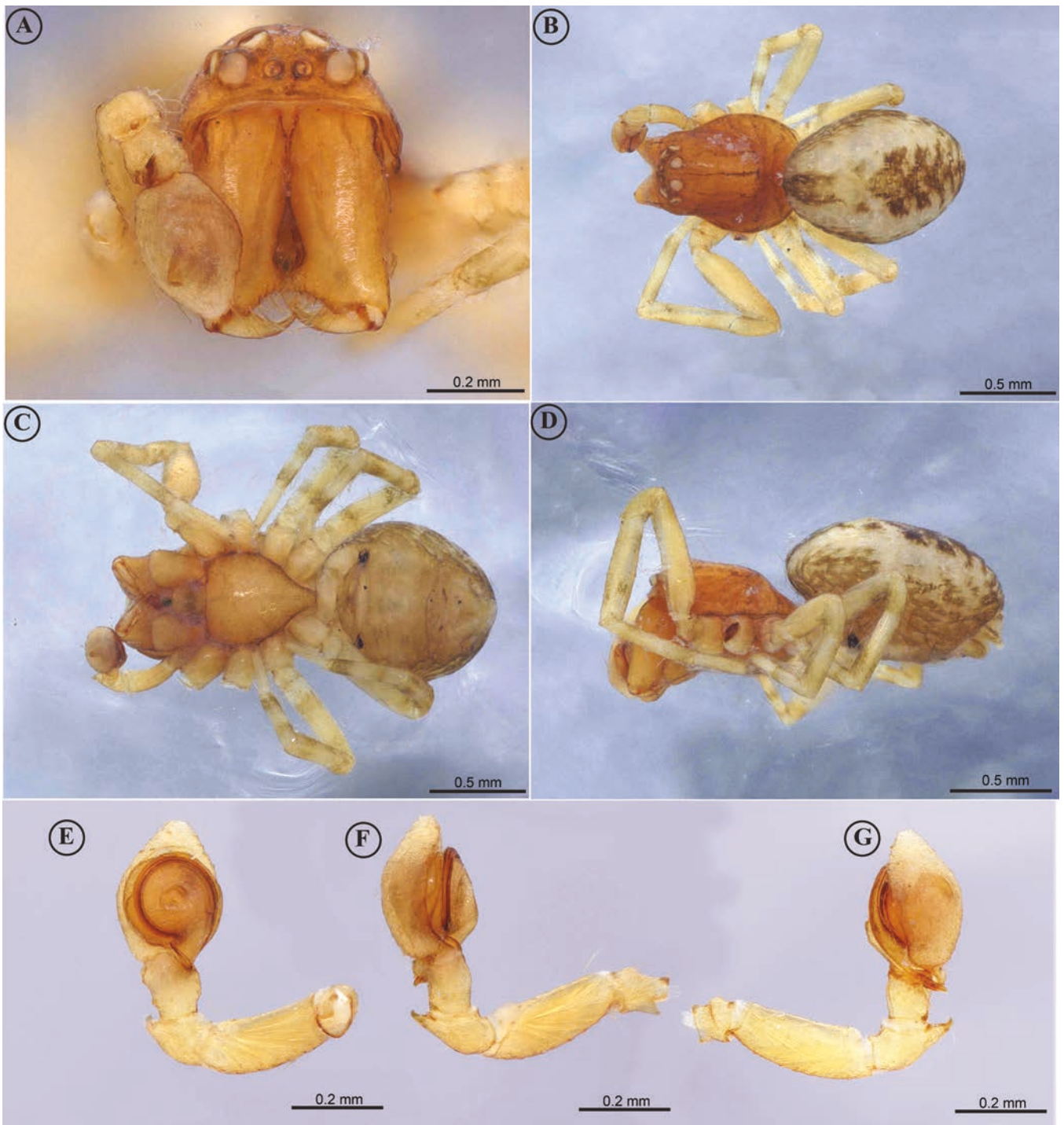


Figure 39. Habitus and palp of male *Lathys humilis* (Blackwall, 1855) (Syntype, NHMUK): A, frontal view; B dorsal view; C, ventral view; D, lateral view; E, palp, ventral view; F, palp, prolateral view; G, palp, retrolateral view.

sp. n.), *Langlibaitiao* Lin and Li 2024 [*Langlibaitiao chishuiensis* (Z.S. Zhang, Yang, Y.G. Zhang, 2009), *Langlibaitiao inaeffectus* (Li, 2017), *Langlibaitiao insulanus* (Ono, 2003) comb. n., and *Langlibaitiao zhangshun* Lin and Li, 2024], *Lathys* s.s. Simon, 1885 [*Lathys bin* Marusik and Logunov, 1991, *Lathys borealis* Z.S. Zhang Zhang, Hu, Y.G. Zhang, 2012, *Lathys brevitibialis* Denis, 1956, *Lathys coralynae* Gertsch and Davis, 1942, *Lathys dixiana* Ivie and Barrows, 1935, *Lathys foxi* (Marx, 1891), *Lathys heterophthalma* Kulczyński, 1891, *Lathys humilis* (Blackwall, 1855), *Lathys humilis meridionalis* (Simon, 1874), *Lathys lepida*

O.Pickard-Cambridge, 1909, *Lathys mantarota* Wunderlich, 2022, *Lathys sexpustulata* (Simon, 1878), and *Lathys subhumilis* Z.S. Zhang *et al.*, 2012], *Scotolathys* s.s. Simon, 1885 [*S. delicatula* Gertsch and Mulaik, 1936 stat. reinst., *S. immaculata* Chamberlin and Ivie, 1944 stat. reinst., *S. maculina* (Gertsch, 1946) stat. reinst., *S. pallida* (Marx, 1891) stat. reinst., and *S. simplex* (Simon, 1885)], and ***Tolokoniella* gen. n.** [*T. ankaraensis* (Özkütük *et al.*, 2016) comb. n., *T. mallorcensis* (Lissner, 2018) comb. n., *T. maura* (Simon, 1911) comb. n., *T. stigmatisata* (Menge, 1869) comb. n., and *T. truncata* (Danilov, 1994) comb. n.].



Figure 40. Habitus and palp of male *Argenna obesa* Emerton, 1911 (Holotype, MCZ-IZ22345): A, dorsal view; B ventral view; C, lateral view; D, palp, ventral view; E, palp, retrolateral view; F, palp, dorsal view.



Figure 41. Habitus of female *Hackmania prominula* (Tullgren, 1948) (MCZ-IZ22345): A, dorsal view; B lateral view; C, D, ventral view.

Genus *Afrolathys* Cala-Riquelme, Al-Jamal, Esposito gen. n.

Type species: Afrolathys tanzanica sp. n.

Material examined: See the material examined for *Afrolathys madagascariensis* sp. n. and *A. tanzanica* sp. n.

Etymology: The generic epithet is a combination of ‘Afro-’ referring to the locality of the type species of the genus, Africa, and *Lathys*, another member of the family; gender feminine.

Diagnosis: ***Afrolathys* gen. n.** can be distinguished from other Lathyidae fam. n. by lacking AME (Figs 32A–D; 33A–D; 34A–C; 35A, B) (AME present in *Andronova* gen. n., *Analtella* stat. reinst., *Lathys* s.s.), and the ALE are separated by a distance equal to their diameter (Figs 32A–D, 33A–D, 34A–C, 35A, B) (ALE contiguous in *Bannaella*). Additionally, the male can be distinguished by the embolus coiled twice around the tegulum (Figs 32E, F, 34D, E); the conductor connected retrolateral-distal to the tegulum, with the conductor upper arm coiled no more than 225°, and two times longer than the conductor lower arm;

and the trochanter with a distal process (Fig. 32E, F); the embolus coiled 720°, joining with the hook-shaped process in a coil around the tibia (Figs 32F, 34E). Females can be distinguished by the reduced SS/AG; the copulatory duct elongated and coiled more than 720° near the copulatory opening; and the fertilization duct located mesal proximally to the copulatory duct (Figs 33E, F, 35D).

List of included species: ***Afrolathys madagascariensis* sp. n.** and ***A. tanzanica* sp. n.**

Distribution. Madagascar, Tanzania.

Afrolathys tanzanica Cala-Riquelme, Al-Jamal, Esposito sp. n.
urn:lsid:zoobank.org:act:CDD8CDE2-3936-489A-BADF-AD680F2E7C9D.

Type material. Male holotype (CASENT9118703) from Tanzania, Tanga Prov., E Usambara Mtns., Amani Nature Reserve, 55°5'42"S, 38°37'59.99"E, Elev. 950 m, forest, 27.x–9.xi.1995, Coll. C.E. Griswold, N. Scharff, D. Ubick, 3 female paratypes (CASENT9118711), same data as holotype.

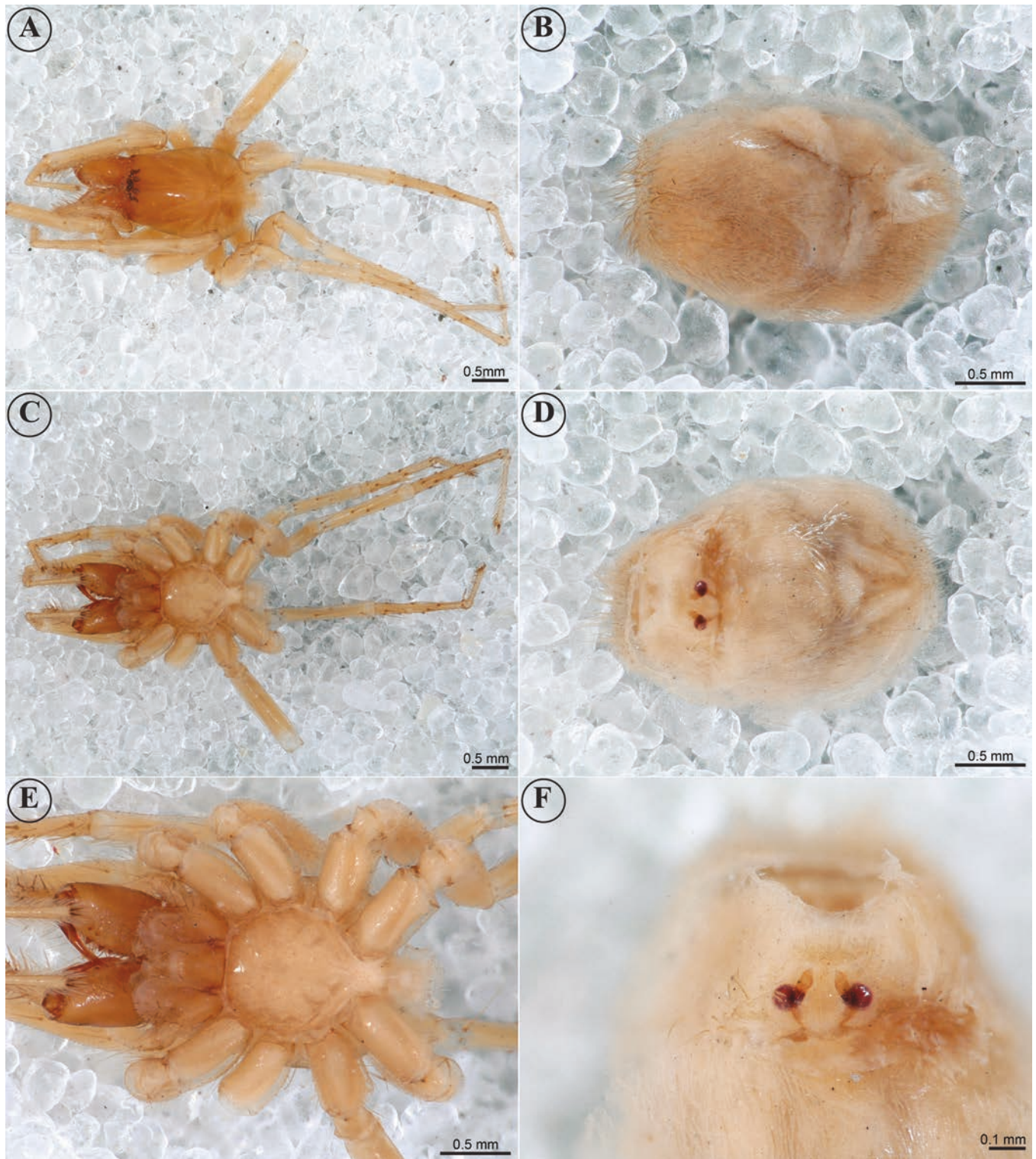


Figure 42. Habitus of female *Saltonia incerta* (Banks, 1898) (Holotype, MCZ-IZ21615): A, B, habitus, dorsal view; C–F, ventral view.

Etymology: The species epithet is an adjective referring to Tanzania where the species has been collected.

Diagnosis: The male of *Afrolathys tanzanica* sp. n. can be distinguished from *A. madagascariensis* sp. n. by the embolus connected retrolateral proximal to the tegulum (Fig. 22A, C, D, 32E) [embolus connected retrolateral distal in *A.*

madagascariensis sp. n. (Fig. 34E)]. Females can be distinguished by the copulatory duct connected ectal distally to the primary spermathecae (Fig. 33E).

Male (CASENT9118703, Tanzania): Carapace (Fig. 32A–D) pale honey-yellow, white longitudinal stripe starting at fovea and narrowing to terminate at PME. Eyes on short, hyacinth red tubercles. Chelicerae, labium, and endites pale honey yellow.



Figure 43. Male and female *Arangina cornigera* (Dalmis, 1917) (MNHN-AR715): A, male habitus, dorsal view; B, male habitus, lateral view; C, female habitus, dorsal view; D, habitus, lateral view; E, female, leg IV, calamistrum, lateral view; F, female, cribellum. Abbreviations: Ca, calamistrum; Cr, cribellum.

Legs sienna-yellow, slightly darker bands around distal half of each leg segment, excluding femur. Abdomen (Fig. 32B–D) dorsum pale sienna yellow with white guanine crystals forming pattern, venter pale sienna yellow. Sternum squared off anteriorly. Total length 1.48. Carapace length 0.60, width 0.60, height 0.28. Clypeus height 0.03, PME 0.09, ALE 0.09, PLE 0.09, PME–PME 0.04. Sternum length 0.43, width 0.40. Palp: femur

length 0.33, tibia length 0.19. Leg I: femur 0.63, patella 0.25, tibia 0.49, metatarsus 0.39, tarsus 0.36. II: 0.59, 0.20, 0.36, 0.33, 0.24. III: 0.51, 0.20, 0.24, 0.31, 0.23. IV: 0.65, 0.20, 0.33, 0.36, 0.23. Abdomen: length 0.90, width 0.80. Male palp (Figs 22A–F, 32E, F): trochanter with a distal process as long as trochanter width; femur straight, as long as patella + tibia; tibia slightly longer than patella, with a hook-shaped process, directed posteriorly;

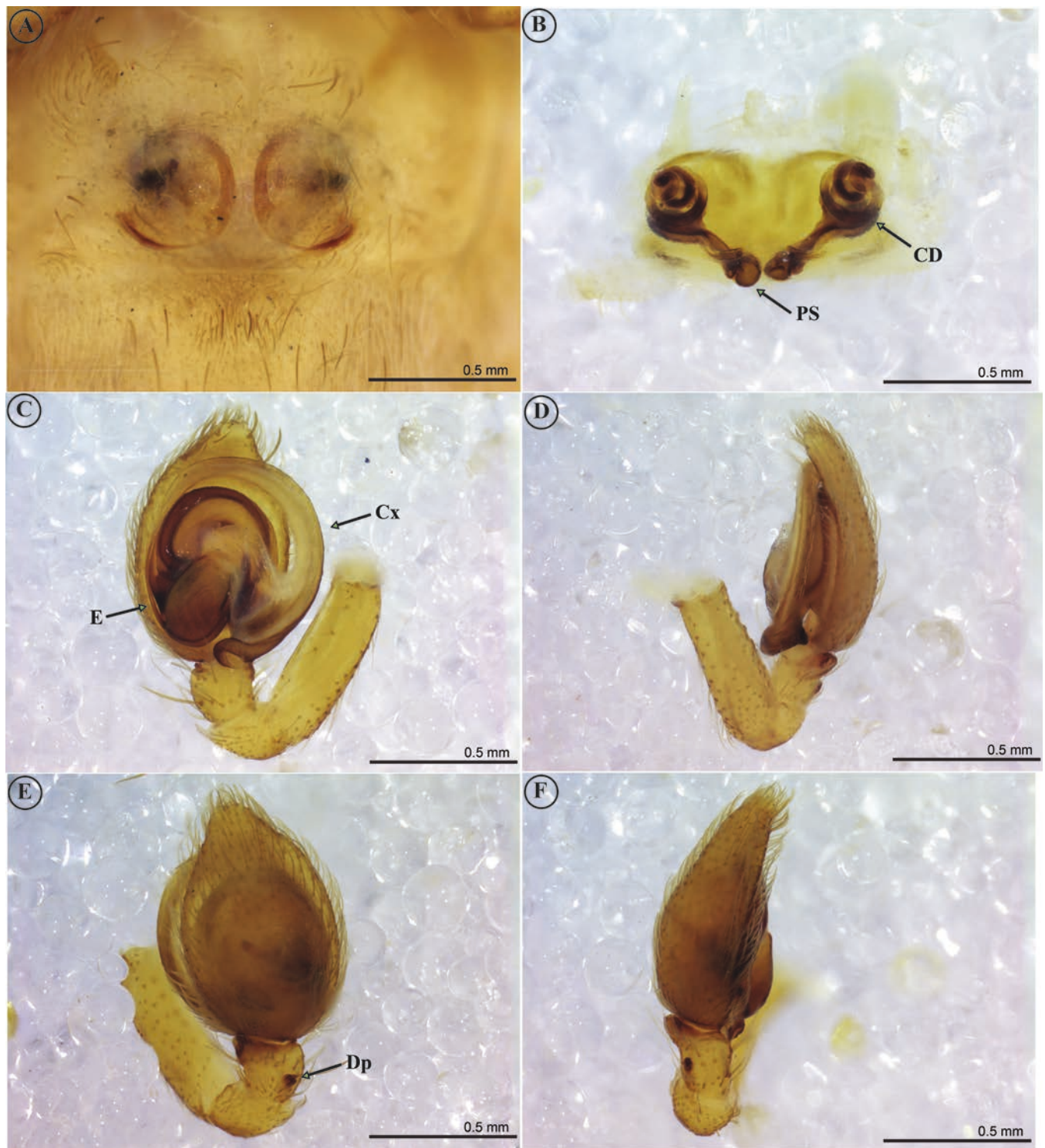


Figure 44. *Arangina cornigera* (Dalmis, 1917) (MNHN-AR715): A, epigyne, ventral view; B, epigyne, dorsal view; C, male palp, ventral view; D, retrolateral view; E, dorsal view; F, prolateral view. Abbreviations: CD, copulatory duct; Cx, conductor; Dp, dictynid process; E, embolus; PS, primary spermathecae.

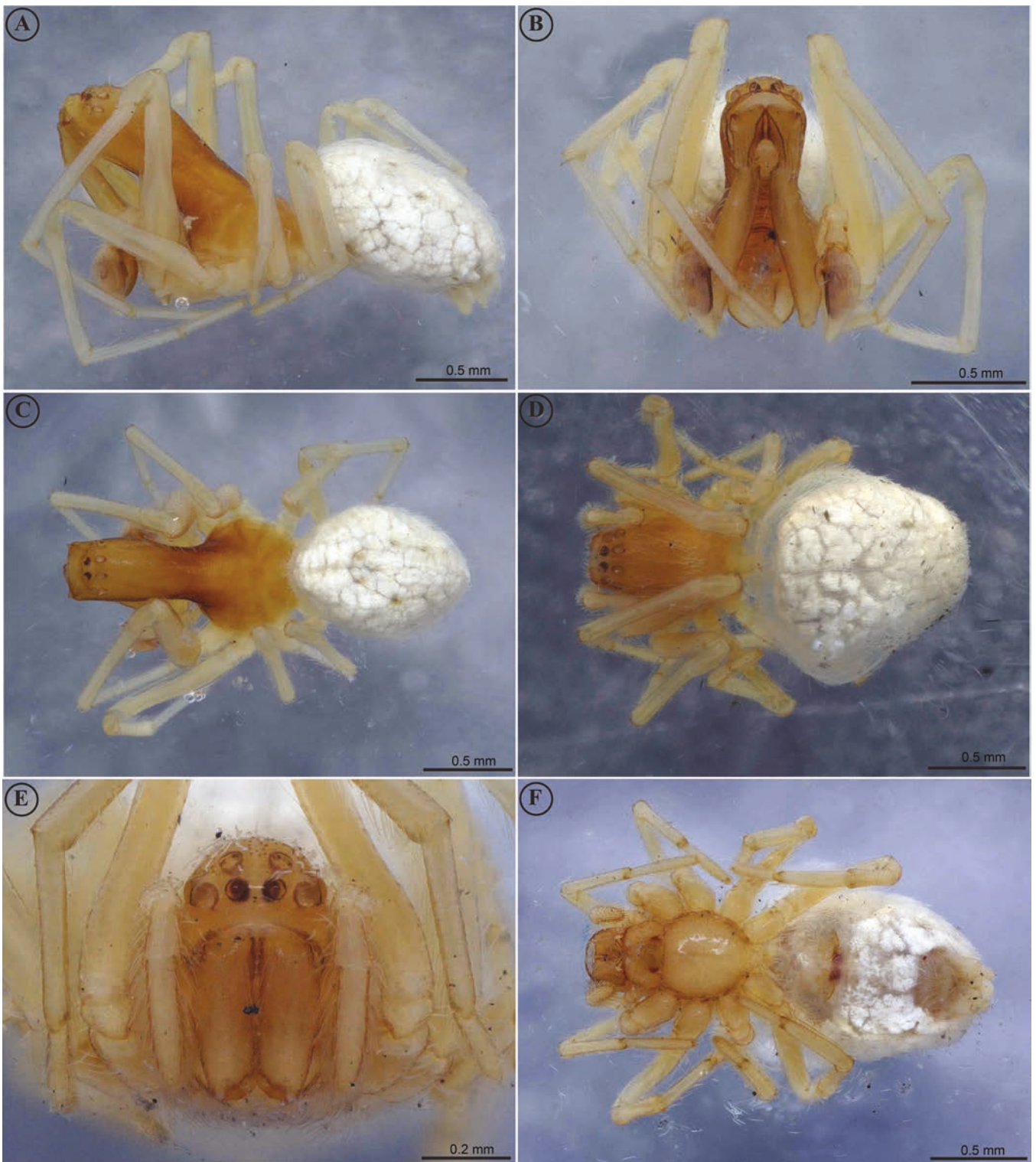


Figure 45. Male and female habitus of *Archaeodictyna anguinceps* (Simon, 1899) (Syntype, NHMUK1635121): A, male, lateral view; B, frontal view; C, dorsal view; D, female, dorsal view; E, frontal view; F, ventral view.

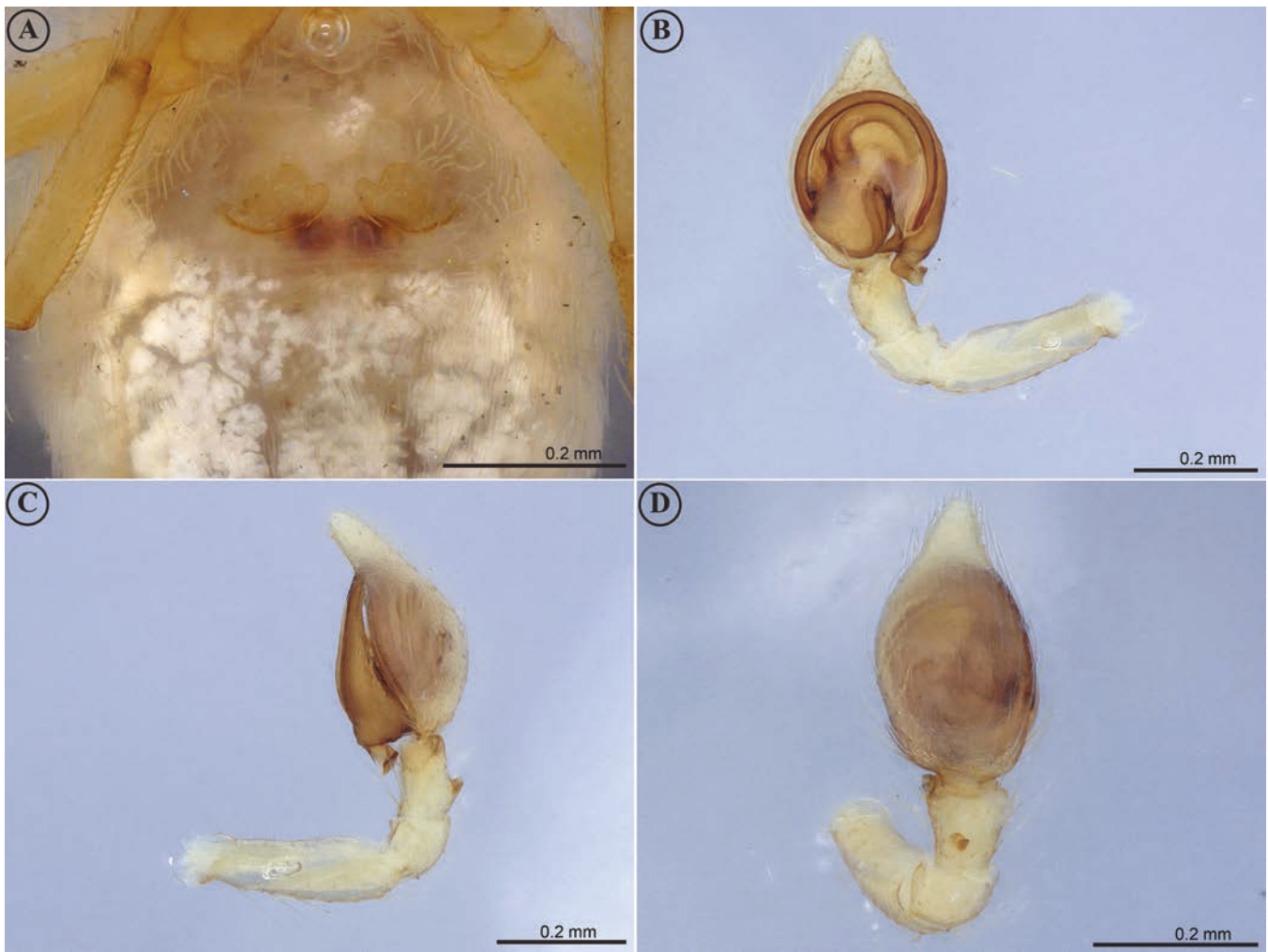


Figure 46. Epigyne and male palp of *Archaeodictyna anguiniceps* (Simon, 1899) (Syntype, NHMUK1635121): A, epigyne, ventral view; B, male palp, ventral view; C, retrolateral view; D, dorsal view.

spermophor with a wide loop near embolus base; embolus connected retrolateral proximal to the tegulum.

Female (CASENT9118711, Tanzania): Carapace (Fig. 33A–D) pale honey yellow, white longitudinal stripe starting at fovea and narrowing to terminate at PME, faint broccoli brown branching patterns on lateral surfaces of prosoma. Eyes on short, hyacinth red tubercles. Chelicerae, labium, endites, and sternum pale honey yellow. Legs sienna yellow, slightly darker bands around distal half of each leg segment after femur. Abdomen (Fig. 33B–D) dorsum pale sienna yellow with white guanine crystals with dorsal line of faint darker chevrons medially, venter pale sienna yellow. Sternum squared off anteriorly. Total length 1.88. Carapace length 0.75, width 0.68, height 0.38. Clypeus height 0.02, PME 0.06, ALE 0.08, PLE 0.08, PME–PME 0.05. Sternum length 0.48, width 0.43. Palp: femur length 0.40, tibia 0.13 length. Leg I: femur 0.61, patella 0.25, tibia 0.40, metatarsus 0.39, tarsus 0.23. II: 0.49, 0.24, 0.34, 0.34, 0.24. III: 0.45, 0.25, 0.21, 0.30, 0.23. IV: 0.59, 0.20, 0.31, 0.40, 0.23. Abdomen: length 1.28, width 0.98. Cribellum length 0.25, entire, as long as the width between the ALS, slightly curved proximally, with the spigots strobilate, grouping uniformly, arranged in a continuous field. Epigyne (Fig. 33E, F): copulatory openings

located ectally, anterior to the primary spermathecae, separated by approximately three times their diameter; membranous sac two times longer than primary spermathecae diameter; copulatory duct elongate, coiled seven or more times near the copulatory opening, uniformly wide, and connected ectal distally to the primary spermathecae; SS/AG reduced; the fertilization duct is connected mesal proximally at the copulatory duct and primary spermathecae.

Afrolathys madagascariensis Al-Jamal and Cala-Riquelme sp. n.

urn:lsid:zoobank.org:act:F8A0CCC6-EAEF-4287-AC10-135CAFECDFCE.

Type material: Male holotype (CASENT9006800) from Madagascar: Antsiranana Prov., Reserve Speciale d'Ambre, 3.5 km 235°SW Sakaramy, 12°28'8"S, 49°14'32"E, Elev. 325 m, tropical dry forest, beating low vegetation, 26–31.i.2001, Coll. B.L. Fisher, C. Griswold, *et al.* 1 male, 2 female paratypes (CASENT9006800), same data as holotype.

Etymology: The species epithet is an adjective referring to Madagascar where the species has been collected.



Figure 47. Habitus and palp of male *Thallumetus* sp. (CASENT 9118795): A, habitus, frontal view; B dorsal view; C, palp, prolateral ventral view; D, prolateral ventral view; E, prolateral view; F, retrolateral view.

Diagnosis: See the diagnosis for *A. tanzanica* sp. n.
Male (CASENT9006800, Madagascar): Carapace (Fig. 34A–C) pale honey yellow, yellowish white longitudinal stripe starting at fovea and narrowing to terminate at PME, faint broccoli brown branching patterns on lateral surfaces of prosoma. Eyes on short, hyacinth red tubercles. Chelicerae, labium, endites and sternum pale honey yellow. Legs sienna yellow, slightly darker bands

around distal half of each leg segment after femur. Abdomen (Fig. 34B, C) dorsum sienna yellow, venter sienna yellow. Sternum squared off anteriorly, slightly procurved. Total length 1.40. Carapace length 0.63, width 0.50, height 0.28. Clypeus height 0.03, PME 0.18, ALE 0.18, PLE 0.15, PME–PME 0.08. Sternum length 0.30, width 0.30. Palp: femur length 0.33, tibia length 0.18. Leg I: femur 0.39, patella 0.19, tibia 0.38, metatarsus

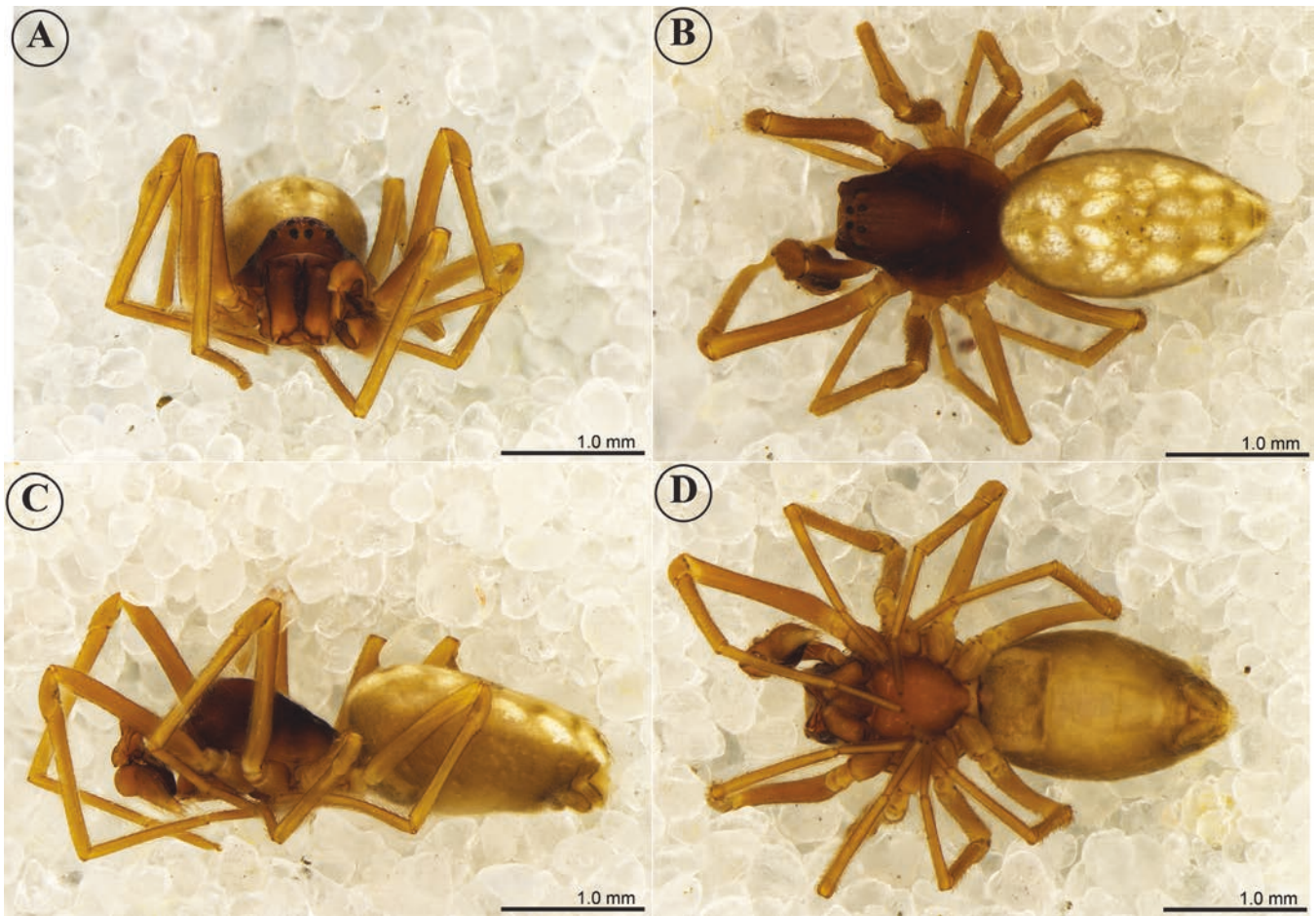


Figure 48. Habitus of male *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n. (Holotype, AMNH 769): A, frontal view; B, dorsal view; C, lateral view; D, ventral view.

0.26, tarsus 0.20. II: 0.39, 0.14, 0.26, 0.24, 0.20. III: 0.33, 0.11, 0.20, 0.24, 0.14. IV: 0.40, 0.16, 0.31, 0.15, 0.13. Abdomen: length 0.85, width 0.65. Male palp (Fig. 34D, E): trochanter with distal process shorter than trochanter width; femur straight, slightly longer than patella + tibia; tibia slightly longer than patella, with a hook-shaped process, directed posteriorly; spermophor with a wide loop close to the embolus base; embolus connected retrolateral distally to the tegulum.

Female (CASENT9006800, Madagascar): Carapace (Fig. 35A, B) pale honey yellow, snow white longitudinal stripe starting at fovea and narrowing to terminate at PME, faint broccoli brown branching patterns on lateral surfaces of prosoma. Eyes on short, hyacinth red tubercles. Chelicerae, labium, endites, and sternum pale honey yellow. Legs pale sienna yellow, darker bands around distal half of each leg segment after femur and on femora I and II. Abdomen (Fig. 35A, B) dorsum pale broccoli brown, venter sienna yellow. Sternum squared off anteriorly, slightly procurved. Total length 1.30. Carapace length 0.58, width 0.50, height 0.27. Clypeus height 0.02, PME 0.15, ALE 0.18, PLE 0.13, PME–PME 0.08. Sternum length 0.25, width 0.15. Palp: femur length 0.48, tibia length 0.18. Leg I: femur 0.35, patella 0.20, tibia 0.05, metatarsus 0.25, tarsus 0.14. II: 0.31, 0.14, 0.26, 0.21, 0.18. III: 0.33, 0.16, 0.18, 0.23, 0.20. IV: 0.38, 0.14, 0.30, 0.24, 0.18. Abdomen: length 0.90, width 0.70. Cribellum length 0.13, entire, as long as the width between the ALS, slightly curved proximally, with the

spigots strobilate, grouping uniformly, arranged in a continuous field. Epigyne (Fig. 35D): copulatory opening antero ectal to the primary spermathecae, separated by approximately three times their diameter; membranous sac two times longer than primary spermathecae diameter; copulatory duct elongate, coiled seven or more times near the copulatory opening, uniformly wide, and connected ectal distally to the primary spermathecae; SS/AG reduced; fertilization duct located mesal proximally at the copulatory duct and primary spermathecae.

Genus *Analtella* Denis, 1947, stat. reinst.

Type species: Analtella brevitarsis Denis, 1947, currently *Lathys narbonensis* (Simon, 1876).

Material examined: *Lathys affinis* (Blackwall, 1862): Portugal, Madeira, Porto Santo Island, 32°44'48.8754"N 16°42'11.052"W, iv.2017, Coll. J. Malumbres-Olarte et al. (2 females, 4 imm, CASENT9081474). Portugal, Madeira, Porto Santo, Pico do Castelo, 17.iv.2017, Coll. L. Crespo, I. Silva (1 female CASENT9081478). Portugal, Madeira, Porto Santo, Ilheu de Ferro, 18.iv.2017, Coll. L. Crespo, I. Silva (1 female, CASENT9081479). Portugal, Madeira, Deserta Grande, Planalto Sul, 11.iv.2017, Coll. L. Crespo, I. Silva (1 female, CASENT9081480). Portugal, Madeira, Deserta Grande,

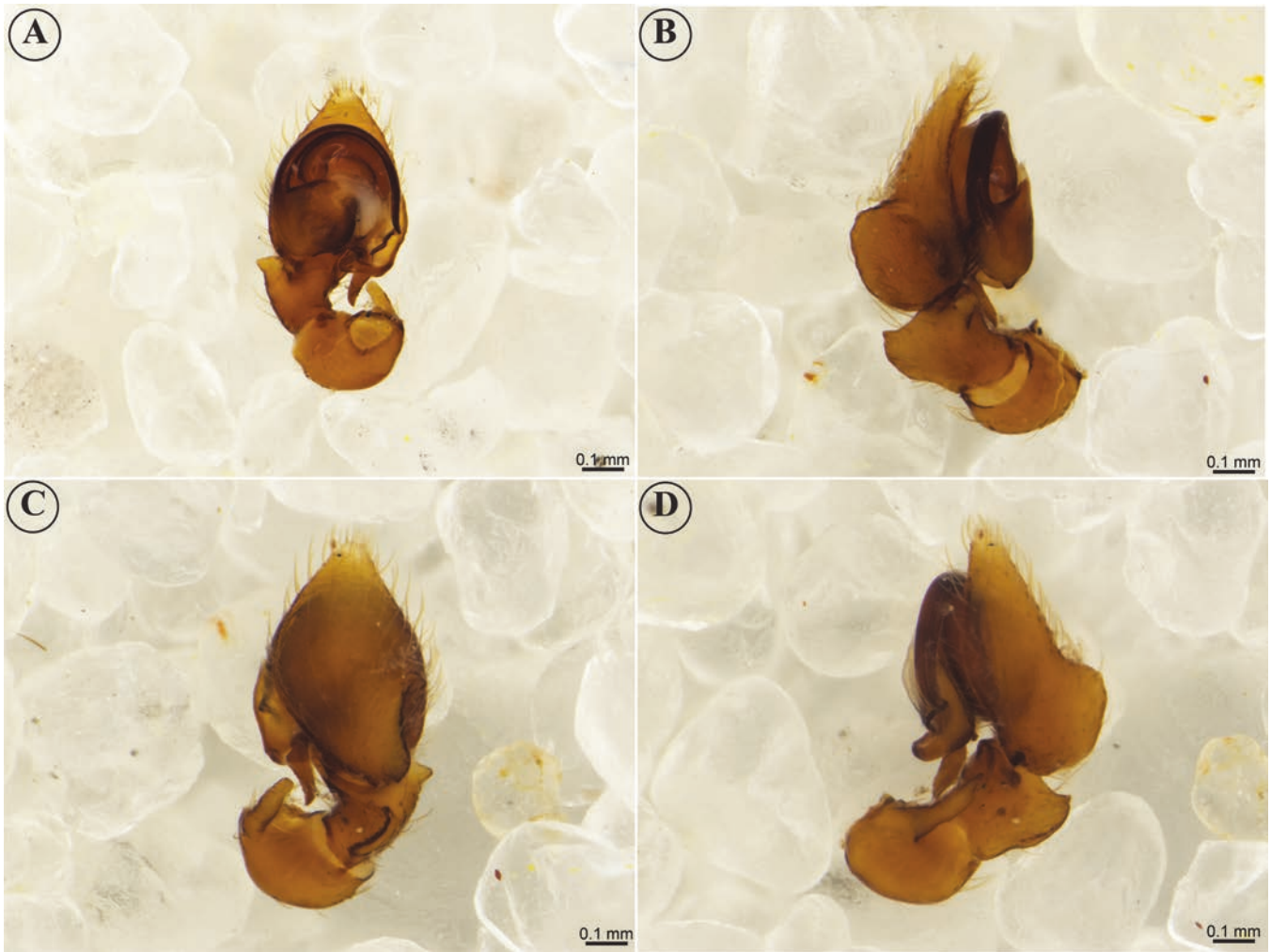


Figure 49. Male palp of *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n. (Holotype, AMNH 769): A, ventral view; B, retrolateral view; C, dorsal view; D, prolateral view.

Planalto Sul, 11.iv.2017, Coll. L. Crespo, I. Silva (1 female, CASENT9081481). Portugal, Madeira, Porto Santo, Pico do Castelo, 17.iv.2017, Coll. L. Crespo, I. Silva (1 female, CASENT9081482). Portugal, Madeira, Porto Santo, Rocha De Nossa Senhora, 21.iv.2017, Coll. L. Crespo, I. Silva (1 female, CASENT9081483). Portugal, Madeira, Porto Santo, Pico Branco, 23.iv.2017, Coll. L. Crespo, I. Silva (1 male, CASENT9087229). *Lathys dentichelis*: Portugal, Azores, Terceira Island, Lagoinha, Coll. Project BALA (1 male, 2 females, CASENT9081472; 1 female, CASENT9081473). Equatorial Guinea, Bioko, Moca, 3°21'46"N, 8°39'52"E, Elev. 1400 m, 4–9.x.1998, Coll. D.K. Dabney, D. Ubick (1 female, CASENT9118700).

Diagnosis: The male of *Analtella* stat. reinst. (Figs 13C–F, 38A–F) resembles *Andronova* gen. n. by having three apophyses that block the distal end of the conductor (Bosmans and Gavalas 2023: fig. 1E, H); however, it can be distinguished from *Andronova* gen. n. and other Lathyidae fam. n. by the chelicerae with an ectal, longitudinal row of macrosetae (Fig. 38A; Bosmans and Gavalas 2023: fig. 1B, C); the reduced AME (Fig. 38A; Bosmans and Gavalas 2023: fig. 1B) (AME absent in *Afrolathys* gen. n., *Scotolathys* s.s.) embolus usually coiled less than 1080°,

and usually with a retrolateral distal origin; palpal tibia with lamellate lateral apophysis with deep or shallow longitudinal furrow in addition to the RTA, and hook-shaped tibial process (lamellate lateral apophysis absent in *Lathys* s.s., *Scotolathys* s.s., *Bannaella*, *Afrolathys* gen. n.); the conductor tip elongated, not compressed, and coiled two or more times (Fig. 38F). Females (Fig. 13C–F; Bosmans and Gavalas 2023: fig. 1I, J) can be distinguished by the SS/AG, usually shorter than the primary spermathecae; copulatory duct elongated and coiled more than 720° around itself and the SS/AG, and bent 90° or less around the primary spermatheca; the fertilization duct is located mesal distally.

Remarks: *Analtella* was described by Denis (1947: 145) based on females of *Analtella jubata* Denis, 1947 (1947:146) and *Analtella brevitarsis* Denis, 1947 (1947: 148) in a comparison with species of *Altella*. Denis (1947) did not designate a type species, so Lehtinen (1967: 243) designated *A. brevitarsis* as the type of *Analtella*. In the same paper, Lehtinen (1967: 243) considered *A. brevitarsis* a junior synonym of *Lathys narbonensis* Simon, 1914 and placed *Analtella* and *Scotolathys* within the *narbonensis* group, while *A. jubata* (= *Lathys jubata*) became part of the *puta* group with *L. stigmatisata*. Here, we reinstate the status of *Analtella* to include *L. narbonensis* Simon, 1914 based on the morphology of

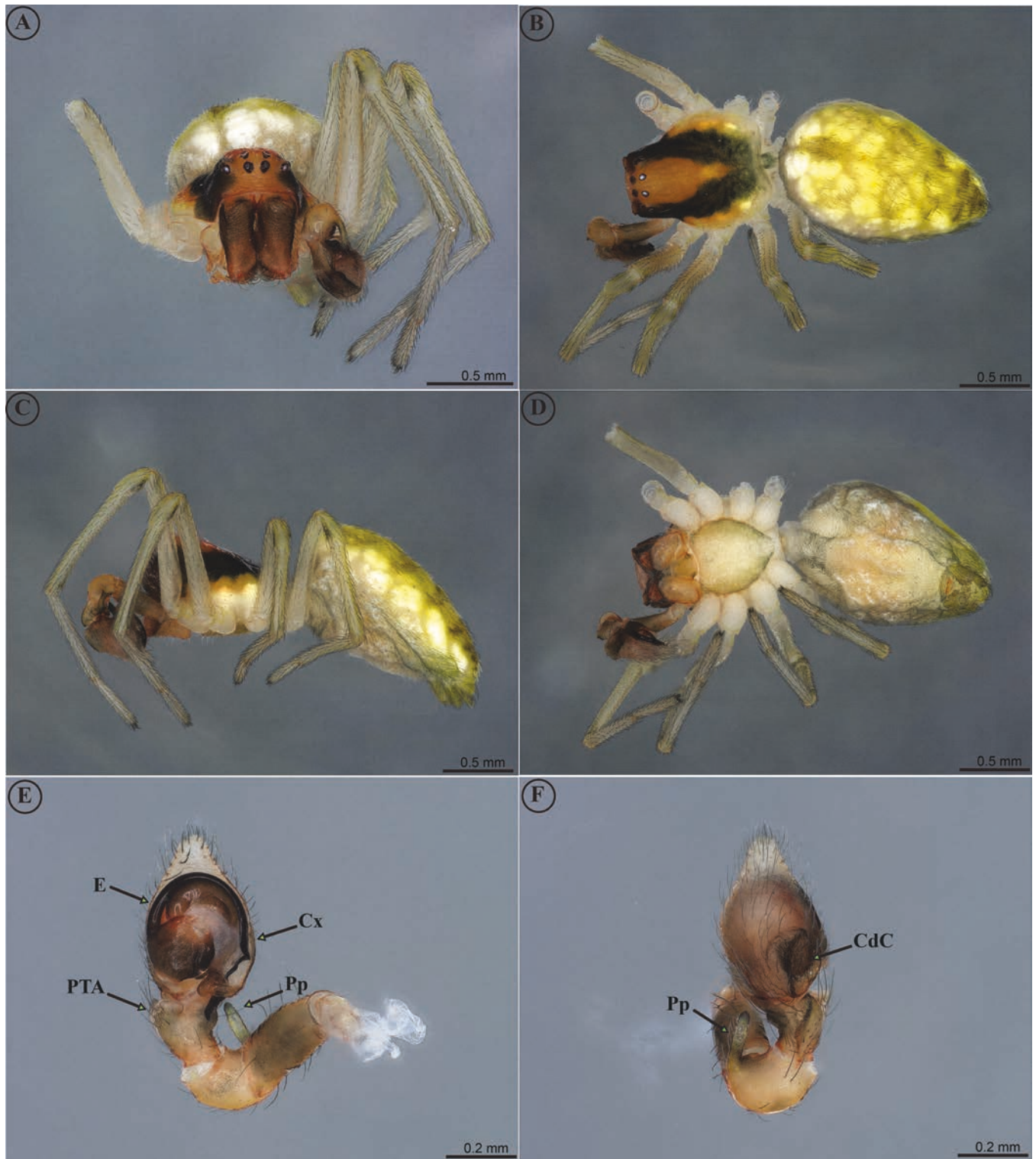


Figure 50. Habitus and palp of male *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n. (CASENT9112276): A, habitus, frontal view; B, dorsal view; C, lateral view; D, ventral view; E, palp, ventral view; F, dorsal view. Abbreviations: CdC, cavity of dorsal extension of the cymbium; Cx, conductor; E, embolus; Pp, patellar process; PTA, prolateral tibial apophysis.

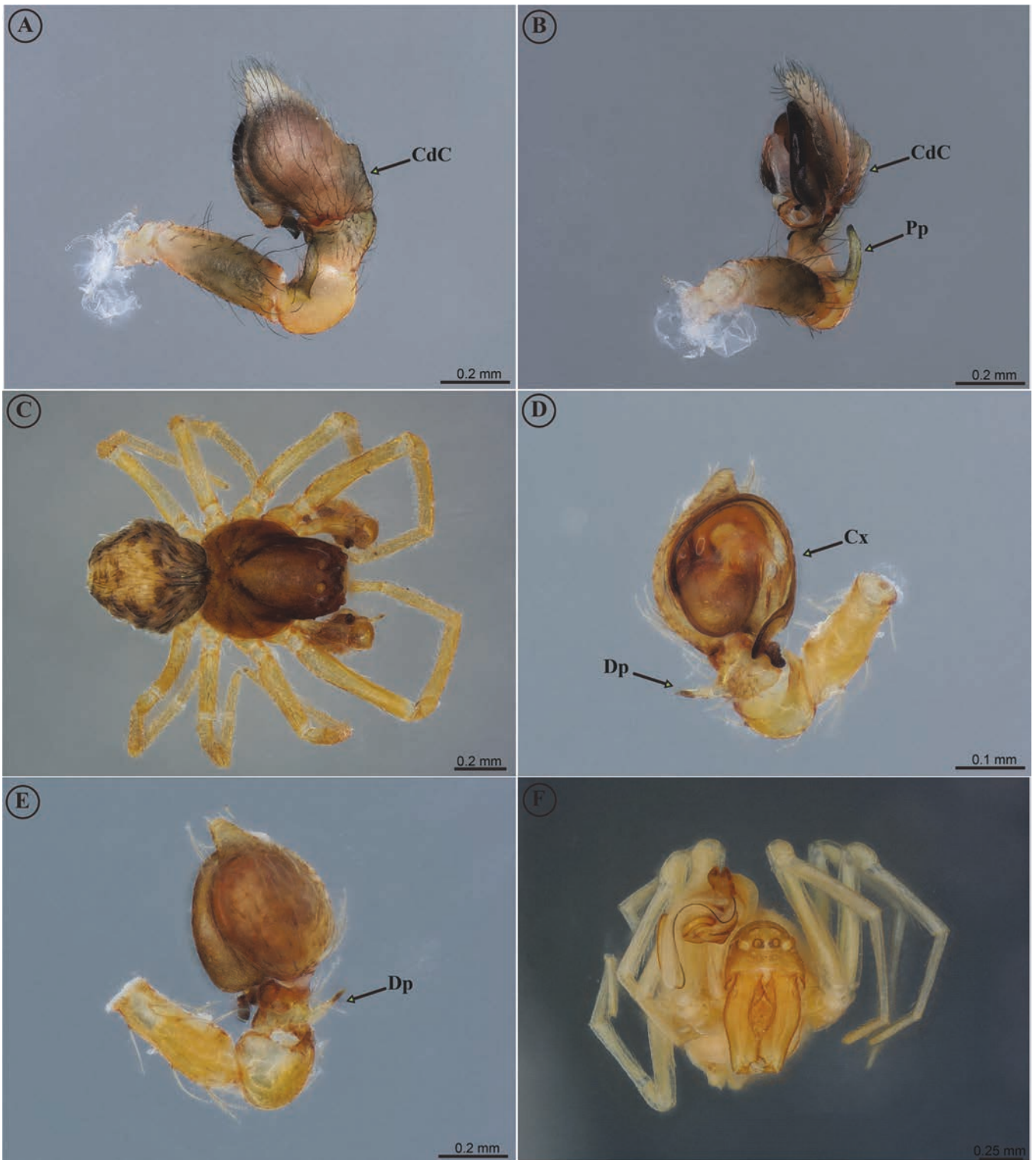


Figure 51. Palp of male *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n. (CASENT9112276): A, retrolateral dorsal view; B, retrolateral view. Habitus and palp of *Phantyna cf. micro* (Chamberlin and Ivie, 1944) (CASENT9129368): C, habitus, dorsal view; D, palp, ventral view; E, palp, dorsal view. Male of *Tivyna pallida* (Keyserling, 1887) (Syntype, MCZ-IZ 21329): F, habitus, frontal view. Abbreviations: CdC, cavity of dorsal extension of the cymbium; Cx, conductor; Dp, dictynid process; Pp, patellar process.

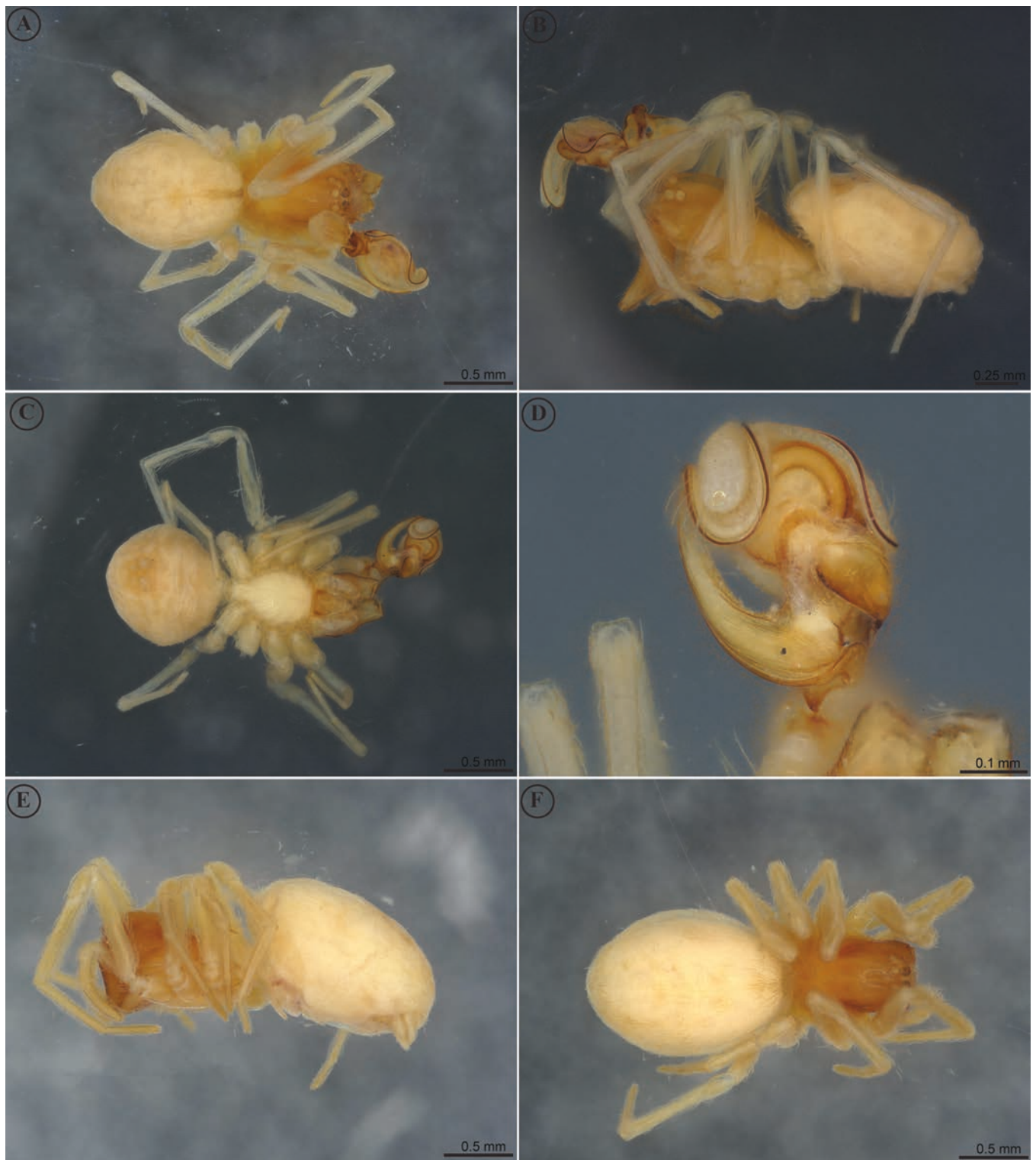


Figure 52. Habitus of male and female *Tivyna pallida* (Keyserling, 1887) (Syntype, MCZ-IZ 21329): A, male, dorsal view; B, lateral view. C, ventral view; D, palp, ventral view; E, female, lateral view; F, dorsal view.

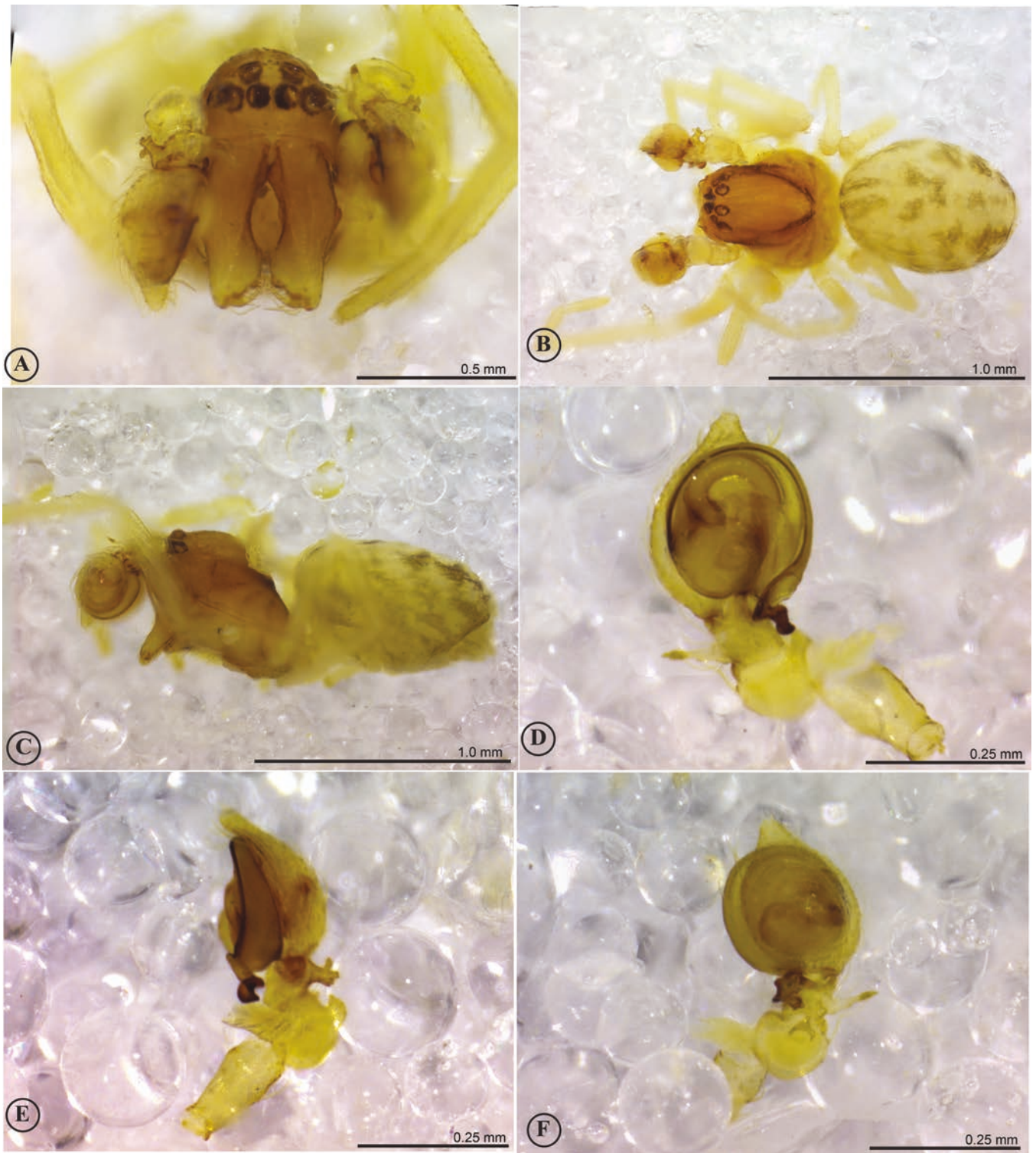


Figure 53. Male habitus and palp of *Phantyna micro* (Holotype, MNHN-AR-AR678): A, habitus, frontal view; B dorsal view; C, lateral view; D palp, ventral view; E, retrolateral view; F, dorsal view.



Figure 54. Habitus and palp of male *Purplecorna incredula* (Gertsch and Davis, 1937) comb. n. (CASENT9129382): A, frontal view; B, C, dorsal view; D, palp, ventral view; E, prolateral view; F, ventral retrolateral view. Abbreviations: Cx, conductor; E, embolus.

the male palp and the female genitalia. Additionally, we consider *L. jubata* a junior synonym of *L. stigmatisata* (= *Tolokonniella stigmatisata* comb. n.) based on the morphology of the epigynum with reduced SS/AG, the copulatory duct elongated and coiled 720° around itself, and 180° around the primary spermathecae.

List of included species: *Analtella affinis* (Blackwall, 1862) comb. n., *A. denticelis* (Simon, 1883) comb. n., *A. narbonensis* (Simon,

1876) comb. n., *A. pygmaea* (Wunderlich, 2011) comb. n., and *A. teideensis* (Wunderlich, 1992) comb. n.

Genus *Andronova* Cala-Riquelme, Montana, Esposito gen. n.

Type species: *Lathys alberta* Gertsch, 1946.

Type material: *Lathys alberta*: Canada, Laggan (publication: Rocky Mts., near Laggan), pre-1894 publication date,



Figure 55. Habitus and palp of male *Purplecornia terrestris* (Emerton, 1911) comb. n. (CASENT9129537): A, frontal view; B, dorsal view; C, palp, ventral view; D, prolateral view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.

Coll. J.H. Bean (J.H. Emerton Coll.), (Syntype, 1 male, MCZ-IZ22474).

Material examined: *Lathys annulata* Bösenberg and Strand 1906: Japan, Tokyo Pref., Hachijo-jima Is., Hachijo city, Okago, on arboreal vegetation, 33°06'11.3"N 139°47'58.7"E, 03.v.2021, Coll. F. Ballarin (1 male, FBPC). *Lathys arabs* Simon, 1910: Algeria, 'Ain Ograb, Djebel Messaad (Syntype, 2 females, MNHN-AR-AR403). Tunisia, Nefzaoua, Coll. Vibert (Syntype, 2 females, MNHN-AR-AR420). *Lathys cambridgei* (Simon, 1874): Syria, Coll. C.B. (Holotype, 1 female, MNHN-AR-AR401). *Lathys dihamata* Paik, 1979: Japan, Shizuoka Pref., Tagata Distr., Izu city (former Amagi-yugashima), Ichiyama, 2.vi.1984, Coll. K. Kamada (1 female, NMST17797). *Lathys sylvania*: USA, Florida, Edgewater, 18.ii.1939, Coll. Charles A. Frost (Paratype, 1 female, MCZ-IZ24837). USA, Florida, Dunedin, iii.1927, Coll. Willis S. Blatchley (Paratype, 5 females, MCZ-IZ24838).

Etymology: The generic name refers to the Andronovo, a collection of late Bronze Age cultures (c. 2000–1150 BC) from Central Asia; gender feminine.

Diagnosis: The male of *Andronova* gen. n. can be distinguished from other Lathyidae genera by having narrower AME than ALE (AME absent in *Scotolathys* s.s., *Bannaella*, and *Afrolathys* gen. n.) embolus usually coiled 1080° or less, and usually with a medial retrolateral origin (Marusik et al. 2006b: figs 13–15, 17–18, 20–21); the palpal patella without an apophysis (Marusik et al. 2006b: fig. 17) (palpal patellar apophysis present in *Lathys* s.s.); palpal tibia with lamellate lateral apophysis with deep or shallow longitudinal furrow (Marusik et al. 2006b: figs 10–12, 16A–C) in addition to an RTA and hook-shaped tibial process (lamellate lateral apophysis absent in *Lathys* s.s., *Scotolathys* s.s., *Bannaella*, and *Afrolathys* gen. n.). Females (Marusik et al. 2006b: figs 22, 23) can be distinguished by the reduced SS/AG, copulatory duct elongated and coiled more than 720° around itself, and 520° around the primary spermathecae; the fertilization duct located mesal distally between the copulatory duct and primary spermathecae.

List of included species: *Andronova alberta* (Gertsch, 1946) comb. n., *A. annulata* (Bösenberg and Strand, 1906) comb. n., *A. arabs* (Simon, 1910) comb. n., *A. cambridgei* (Simon, 1874) comb. n., *A. dihamata* (Paik, 1979) comb. n., *A. lehtineni* (Kovblyuk et al.,

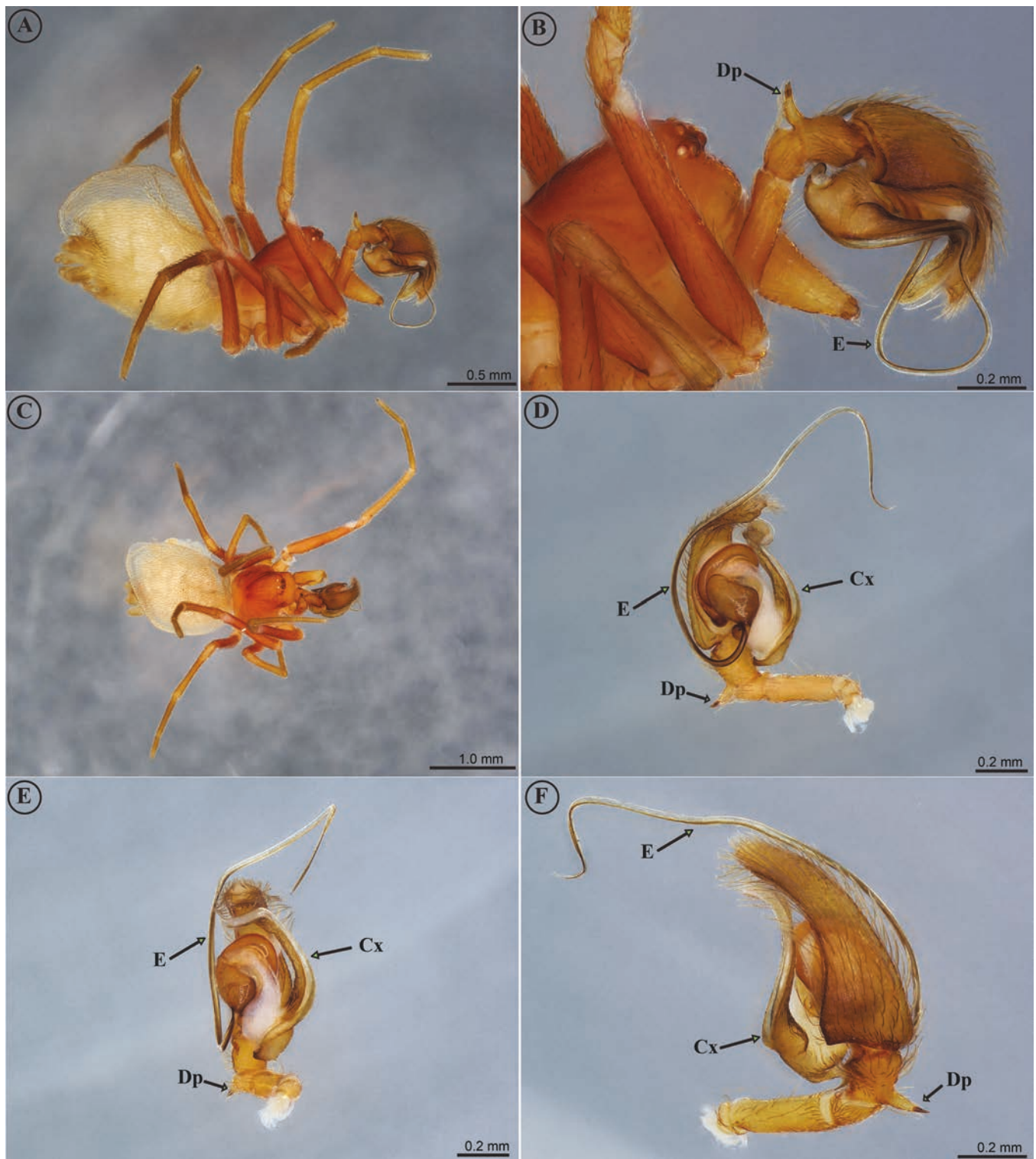


Figure 56. Habitus and palp of male *Shikibutyna foliicola* (Bösenberg and Strand, 1906) comb. n. (CASENT9118689): A, B, lateral view; C, dorsal view; D, palp, prolateral view; E, ventral retrolateral view. F, retrolateral view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.

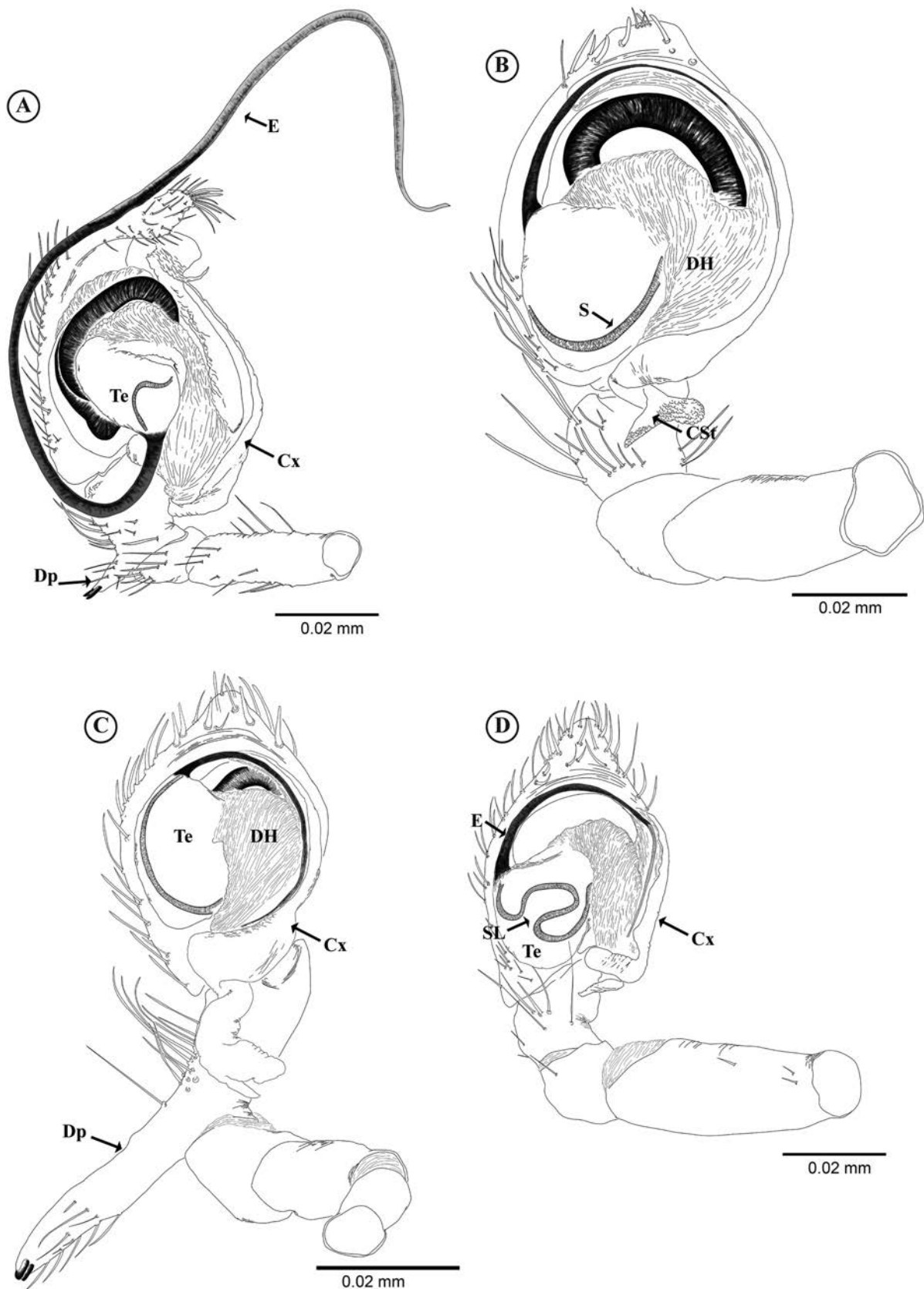


Figure 57. Male palp, ventral view: A, *Shikibutyna foliicola* (Bösenberg and Strand, 1906) comb. n. (CASENT 9118689); B, *Dictyna arundinacea* (Linnaeus, 1758) (CASENT9129316); C, *Tolkienus estoc* sp. n. (CASENT 9118702); D, *Shango* Lehtinen, 1967 sp. (CASENT9118603): Abbreviations: CSt, conductor scaly tip; Cx, conductor; DH, distal hematodochae; Dp, dictynid process; E, embolus; S, spermophor; SL, spermophor loop; Te, tegulum.

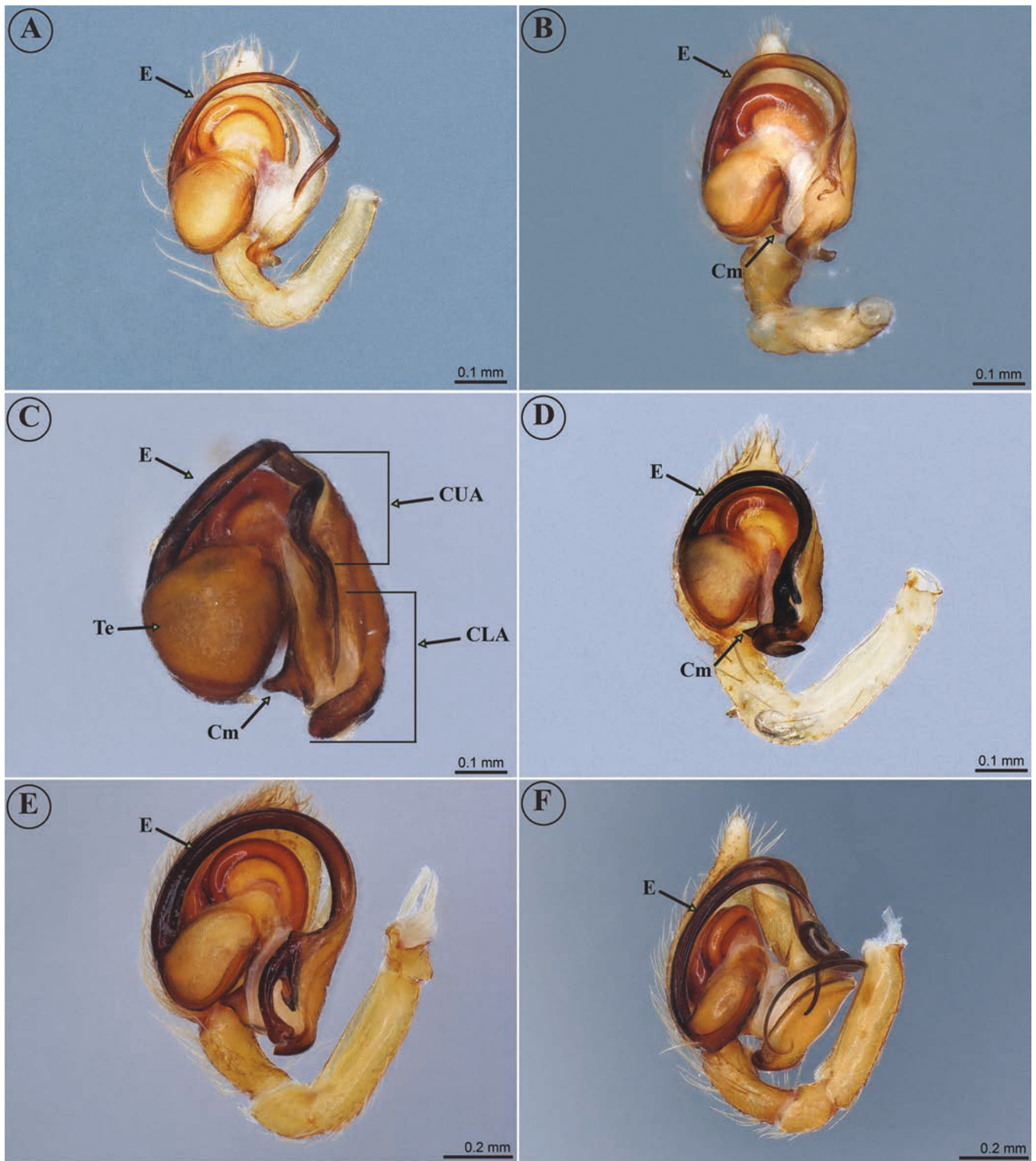


Figure 58. Male palp, ventral view: A, *Arethyna cruciata* (Emerton, 1888) comb. n. (CASENT 9129380); B, *Emblyna hentzi* (Kaston, 1945) (CASENT9122395); C, *E. palomara* Chamberlin, 1948 (CASENT9118624); D, *E. completa* (Chamberlin and Gertsch, 1929) (AMNH); E, *E. aiko* (Chamberlin and Gertsch, 1958) (CASENT9118653); F, *Nopalityna sublata* (Hentz, 1850) comb. n. (CASENT 9103497). Abbreviations: CSt, conductor scaly tip; Cx, conductor; DH, distal hematodochae; Dp, dictynid process; E, embolus; S, spermophor; SL, spermophor loop; Te, tegulum.



Figure 59. Habitus and palp of male *Emblyna completoides* (Ivie, 1947) (CASENT9129628): A, frontal view; B, lateral view; C, dorsal view; D, ventral view; E, palp, ventral view; F, dorsal view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.



Figure 60. Habitus of male *Tolkienus estoc* sp. n. (CASENT 9118702): A, dorsal view; B, lateral view; C, ventral view; D, frontal view; E, abdomen and right leg IV, lateral view; F, abdomen, ventral view.



Figure 61. Habitus and epigyne of female *Tolkienua estoc* sp. n. (CASENT9118702): A, frontal view; B, dorsal view; C, lateral view; D, ventral view; E, epigyne, ventral view; F, dorsal view.

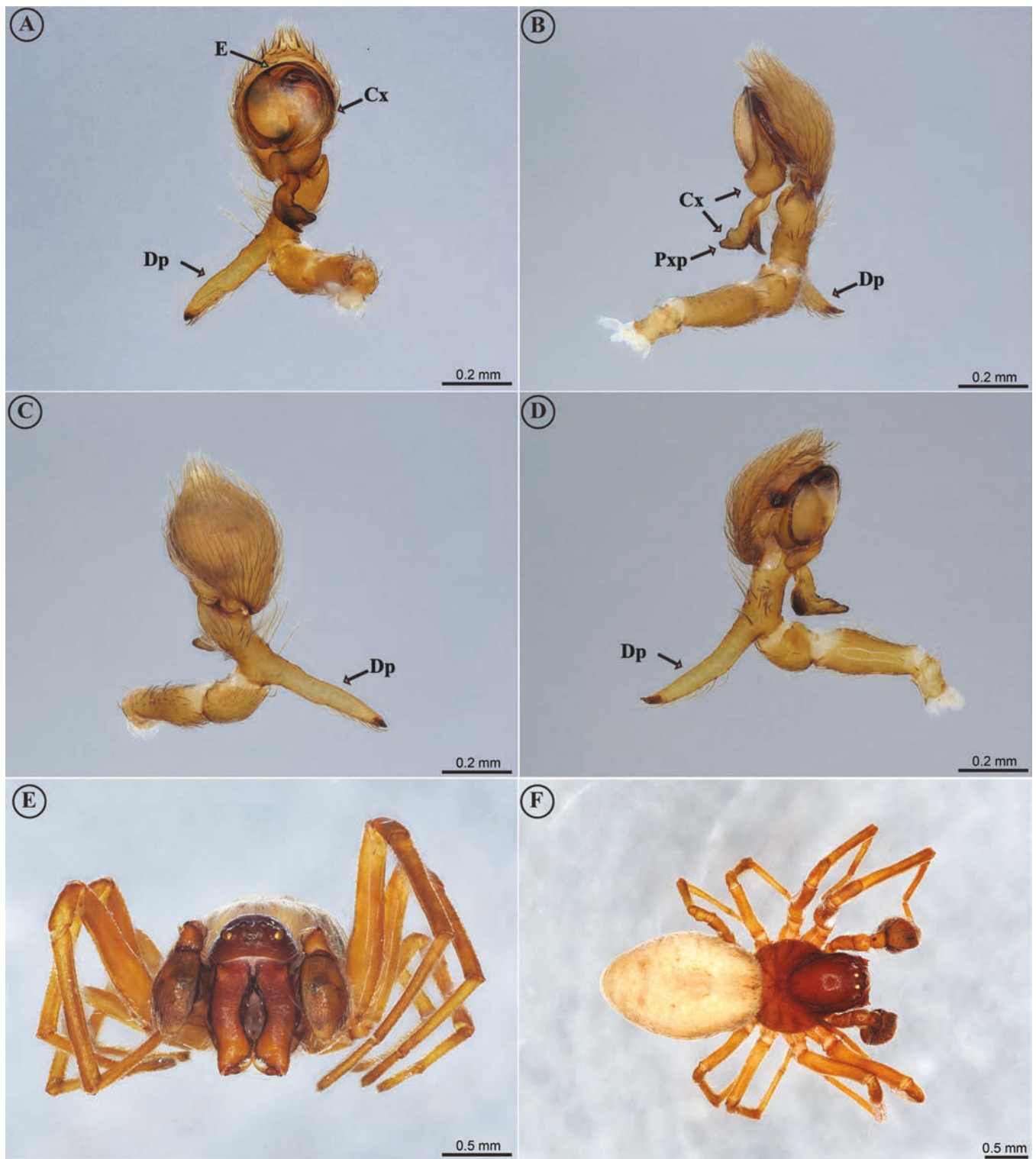


Figure 62. Male palp of *Tolkienus estoc* sp. n. (CASENT9118702) and habitus of male *Dictyna arundinacea* (Linnaeus, 1758) (CASENT9129316): A, ventral view; B, retrolateral view; C, retrolateral dorsal view; D, prolateral view; E, frontal view; F, dorsal view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus; Pxp, paraconductor process.

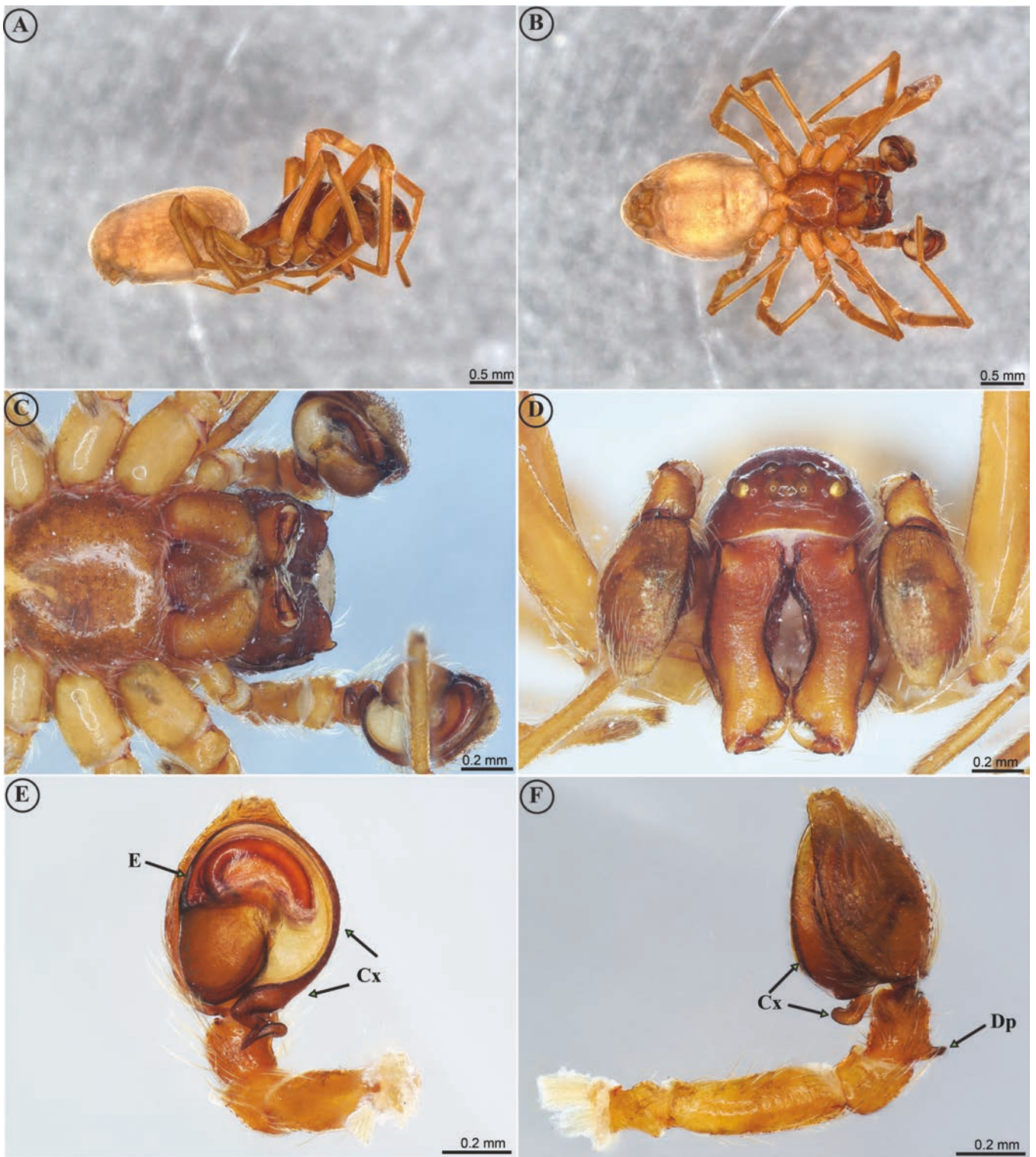


Figure 63. Habitus and palp of male *Dictyna arundinacea* (Linnaeus, 1758) (CASENT9129316): A, lateral view; B, C, ventral view; D, frontal view; E, palp, dorsal view; F, retrolateral view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.

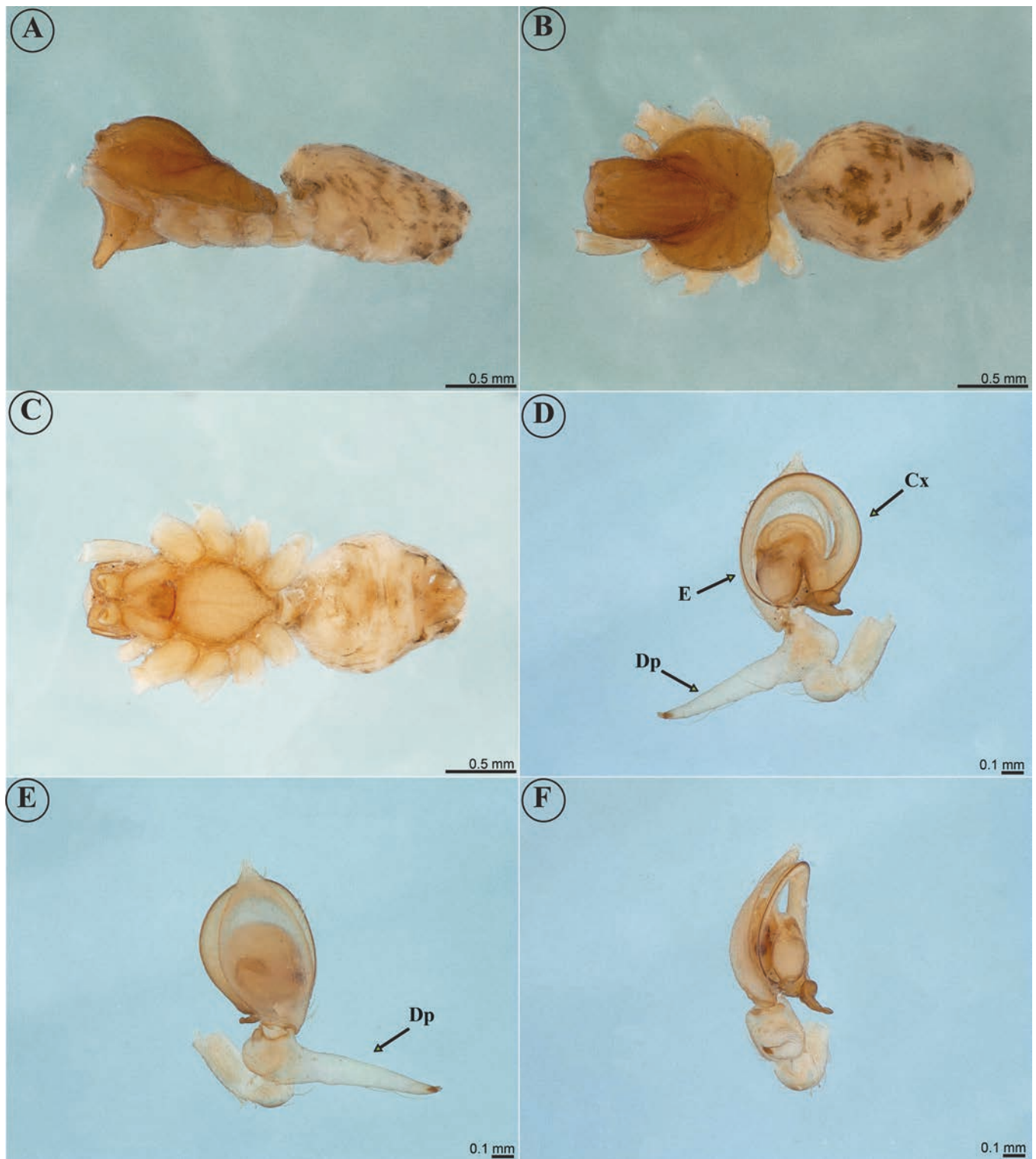


Figure 64. Habitus and palp of male *Khalotyia calcarata* (Banks, 1904) comb. n. (MCZ-IZ20638): A, lateral view; B, dorsal view; C, ventral view; D, palp, ventral view; E, dorsal view; F, retrolateral view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.

2014) comb. n., *A. maculosa* (Karsch, 1879) comb. n., *A. spasskyi* (Andreeva and Tystshenko, 1969) comb. n., *A. subalbata* (Z.S. Zhang, Hu, Y.G. Zhang, 2012) comb. n., *A. subviridis* (Denis, 1937) comb. n., and *A. sylvania* (Chamberlin and Gertsch, 1958) comb. n.

Genus *Asialathys* Cala-Riquelme and Crews gen. n.

urn:lsid:zoobank.org:act:AD6EA29A-2CAC-4AF5-82F0-D512FC0E8219.

Type species: Lathys spiralis Zhang, Hu, Y.G. Zhang, 2012.

Material examined: Lathys deltoidea: China, Jiangxi Prov., Ji'an City, Jinggangshan County Level City, Huang'ao Town, Menxiandong Village, broad-leaf forest, 26°28'30.0"N 114°14'52.8"E, 462 m

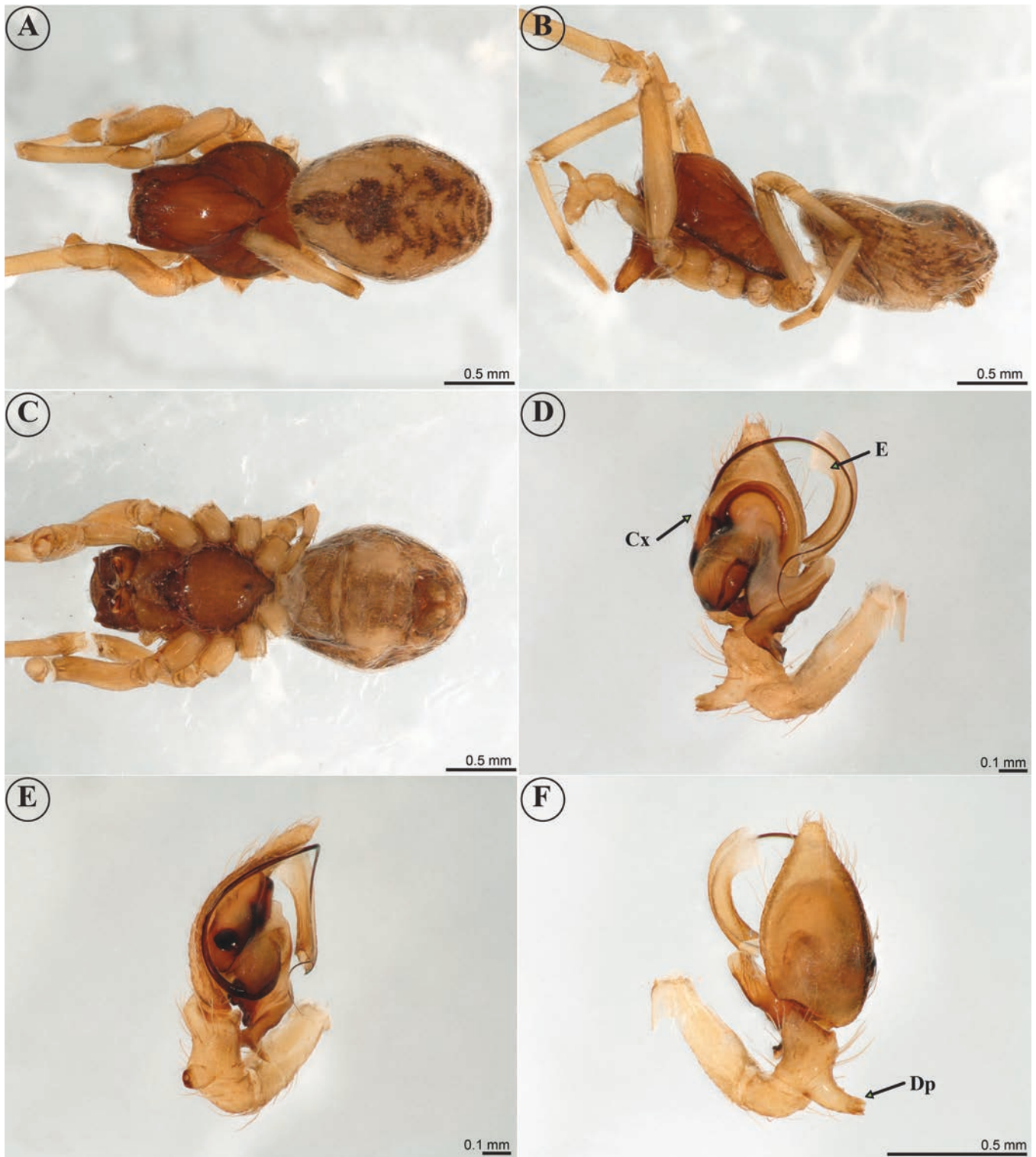


Figure 65. Habitus and palp of male *Arethyna coloradensis* (Chamberlin, 1919) comb. n., (MCZ-IZ15151): A, dorsal view; B, lateral view; C, ventral view; D, palp, ventral view; E, proteral view; F, retrolateral dorsal view. Abbreviations: Cx, conductor; Dp, dictynid process; E, embolus.

elev., 4.iv.2014, Coll. Keke Liu, Zhiwu Chen, Zeyuan Meng, Yifan Zhao, Guangfeng Li (Holotype, 1 female, ASM-JGSU, examined by photo). *Lathys fibulata*: China, Jiangxi Prov., Ji'an City, Jinggangshan County Level City, Huang'ao Town, Menxiandong Village, broad-leaf forest, 26°28'33.6"N 114°14'38.4"E, 383 m elev., 4.iv.2014, Coll. Keke Liu, Zhiwu Chen, Zeyuan Meng, Yifan Zhao, Guangfeng Li (Holotype, 1 male, ASM-JGSU,

examined by photo; Paratype, 1 female, ASM-JGSU, examined by photo). *Lathys huangyangjieensis*: China, Jiangxi Prov., Ji'an City, Jinggangshan County Level City, Maoping Town, Huangyangjie Scenic Spot, coniferous and broad-leaved mixed forest, 26°27'21.6"N 114°06'21.6"E, 958 m elev., 5.iv.2014, Coll. Keke Liu, Zhiwu Chen, Zeyuan Meng, Xiaoping Huang and Yubao Tang (Holotype, 1 male, ASM-JGSU, examined by photo;

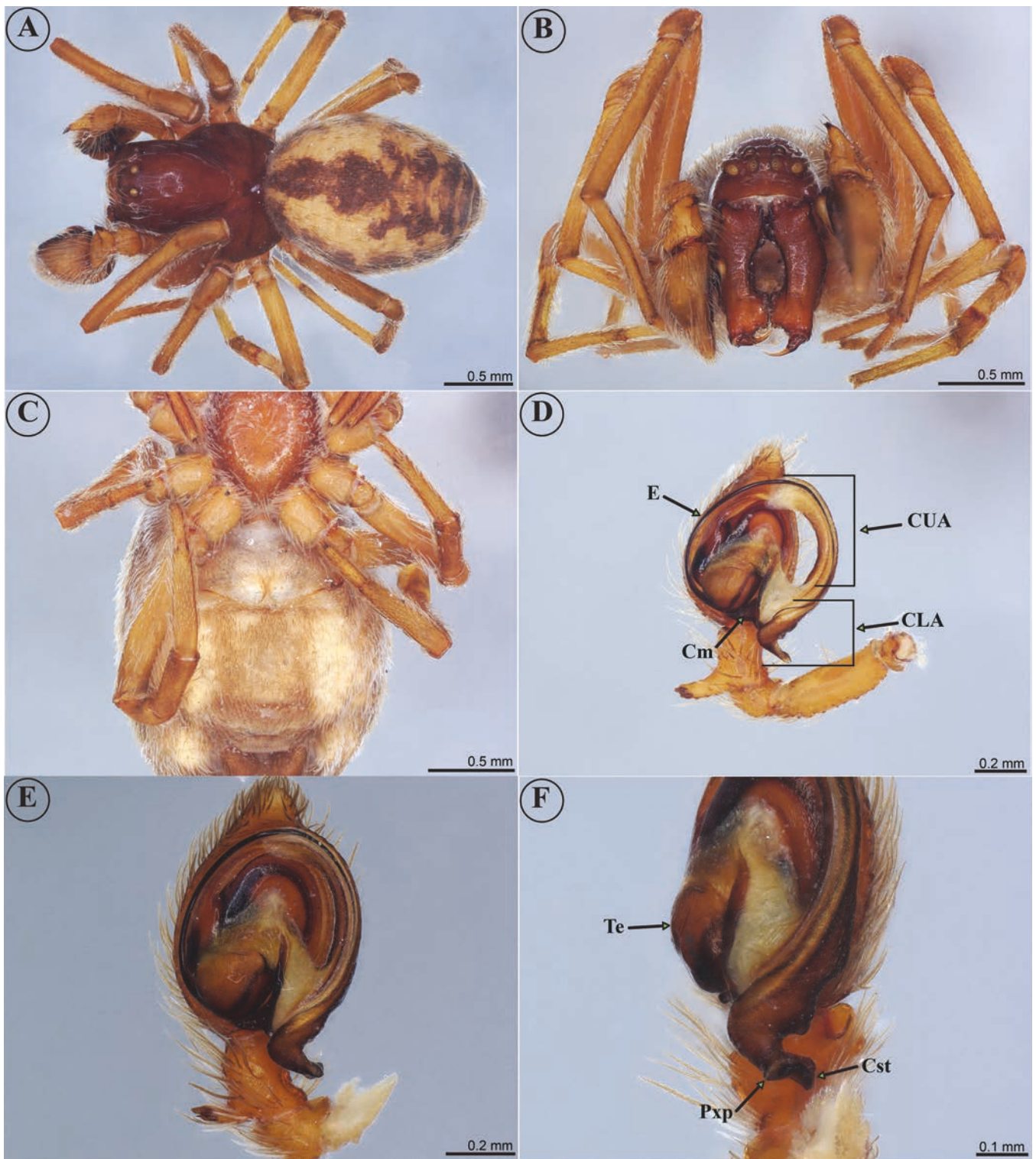


Figure 66. Habitus and palp of male *Arethyna coloradensis* (Chamberlin, 1919) comb. n. (CASENT9129536): A, male habitus, dorsal view; B, frontal view; C, female habitus, ventral view; D, palp, ventral view. Palp of male *Arethyna volucripes* (Keyserling, 1881) comb. n. (CASENT9129394): F, palp, ventral view; E, prolateral view. Abbreviations: CLA, conductor lower arm; Cm, conductor locking mechanism; CSt, conductor scaly tip; CUA, conductor upper arm; E, embolus; Pxp, paraconductor process; Te, tegulum.

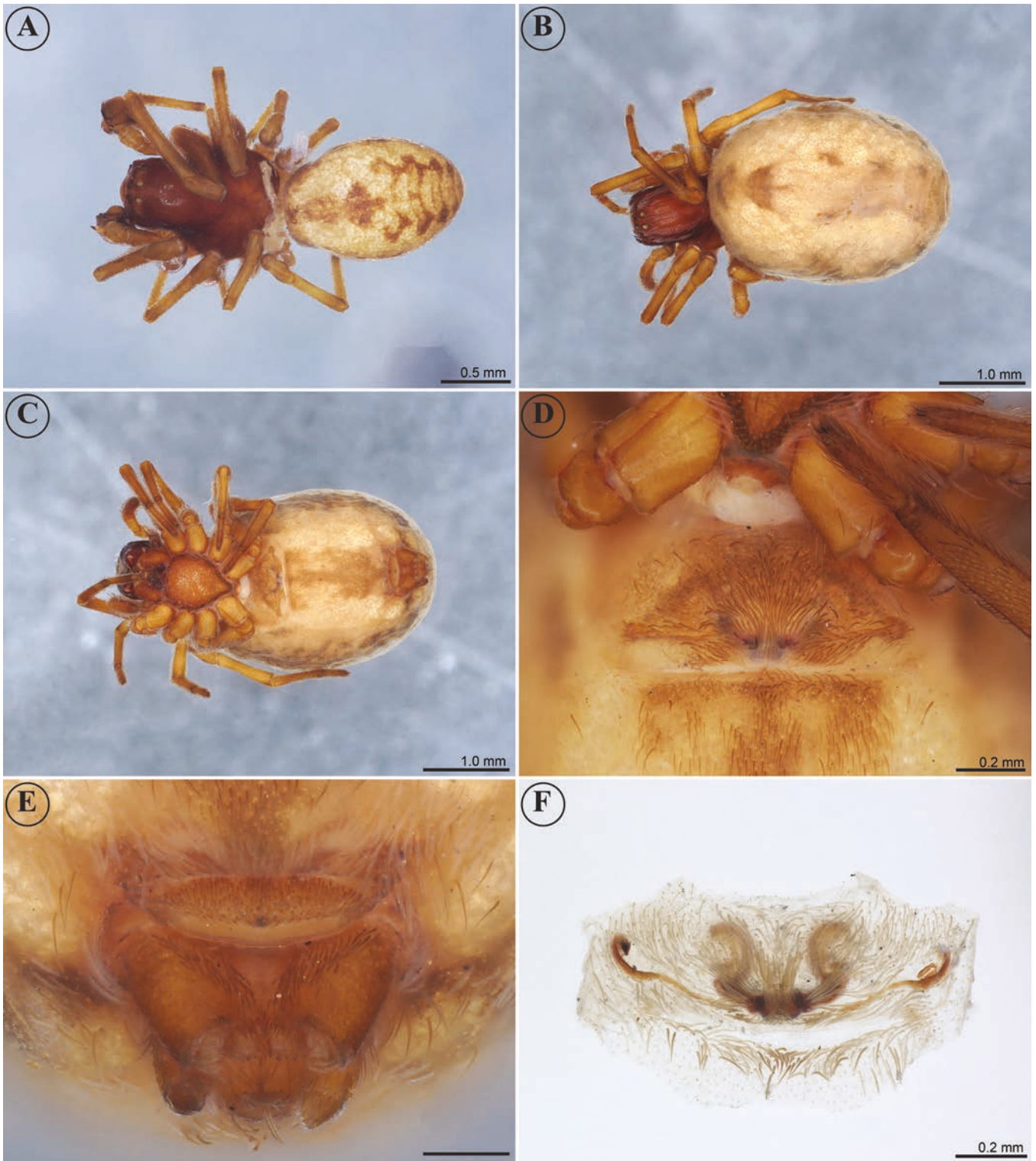


Figure 67. Male and female habitus and epigyne of *Simziella major* (Menge, 1869) comb. n. (CASENT9129252): A, male habitus, dorsal view; B, female habitus, dorsal view; C, ventral view; D, epigyne, ventral view; E, cribellum; F, cleared epigyne, ventral view.

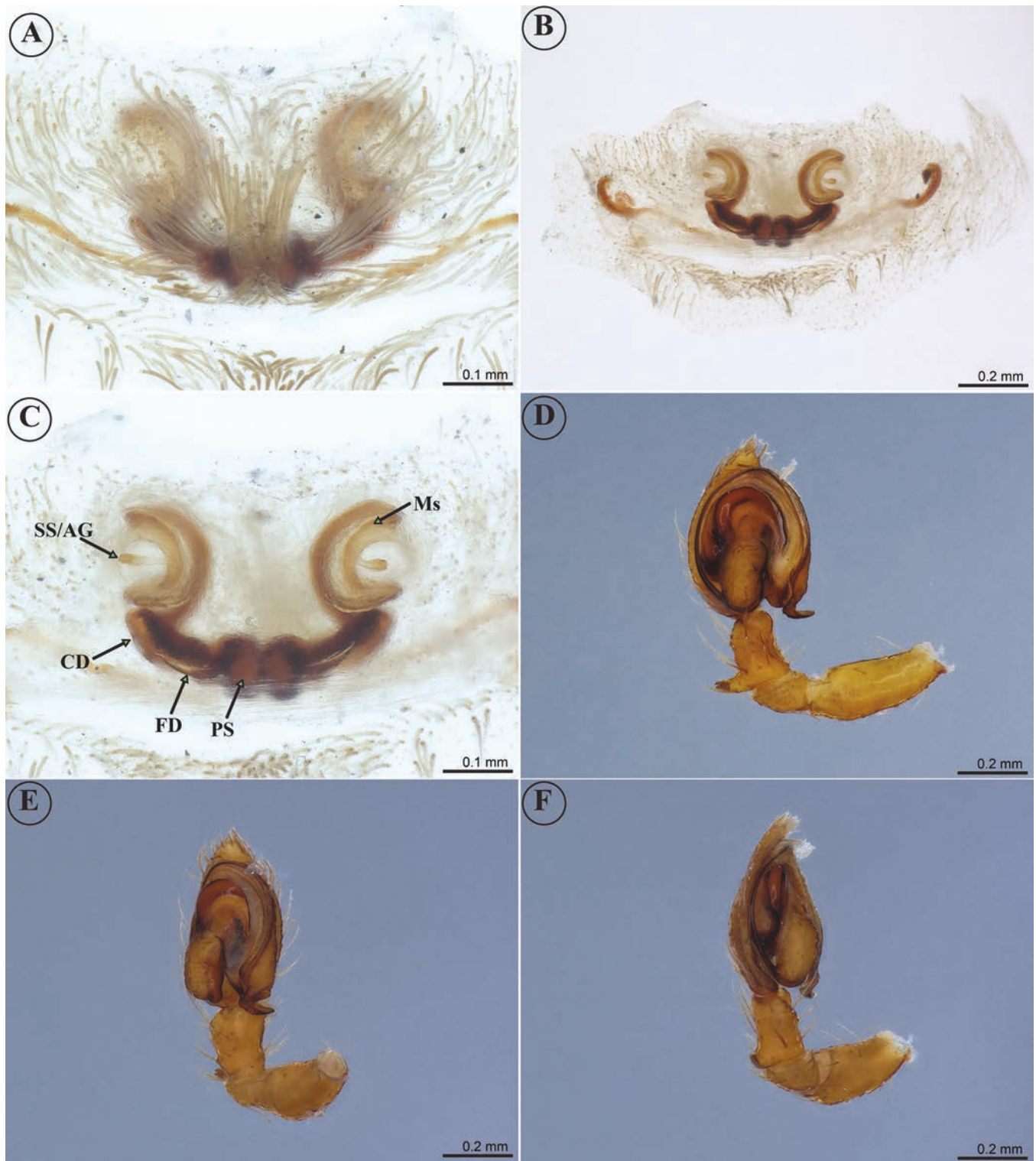


Figure 68. Epigyne and male palp of *Simziella major* (Menge, 1869) comb. n. (CASENT9129252): A, cleared epigyne, ventral view; B, C, dorsal view; D, male palp, ventral view; E, retrolateral ventral view; F, prolateral view; Abbreviations: CD, copulatory duct; FD, fertilization duct; PS, primary spermatheca; Ms, membranous sac; SS/AG, secondary spermathecae accessory gland.

Paratype, 2 males, ASM-JGSU, examined by photo). *Lathys zhanfengi*: China, Jiangxi Prov., Ji'an City, Jinggangshan County Level City, Ciping Town, Xiaojing Village, Longtan Scenic Spot, broad-leaf forest, 26°34'58.8"N 114°08'06.0"E 951 m elev., 1.vi.2014, Coll. Keke Liu, Zhiwu Chen, Zeyuan Meng, Xiaoping Huang, Yubao Tang, Zhanfeng Wang (Holotype, 1 female, ASM-JGSU, examined by photo).

Etymology: The generic epithet is a combination of the word 'Asia', referring to the area where the genus is distributed, and the word *Lathys*, referring to the generic name *Lathys*, another member of the family; gender feminine.

Diagnosis: *Asialathys gen. n.* can be distinguished from other Lathyidae fam. n. genera by having narrower AME than ALE (Liu

et al. 2018: figs 4A, B, 7A, B, 9A, B) (AME absent in *Scotolathys* s.s. and *Bannaella*, ***Afrolathys* gen. n.**); the embolus originates distally on the bulb, usually coiled no more than 1080° (*Liu et al.* 2018: figs 7C, D, 11A–C) $\leq 1080^\circ$ in *Lathys* s.s.); the male palpal patella without an apophysis (*Liu et al.* (2018): figs 7C, D, 11A–C) (palpal patellar apophysis present in *Analtella* stat. reinst., *Lathys* s.s.); and the conductor tip elongated and uncoiled (*Liu et al.* 2018: fig. 11A–C). Females can be distinguished by the reduced SS/AG, copulatory duct elongated and coiled around itself 180°, and 180° or less near the primary spermathecae; the fertilization duct usually located mesal proximal between the copulatory duct and primary spermathecae (*Liu et al.* 2018: figs 6A, B, 9C, D, 11D, E).

List of included species: *Asialathys deltoidea* (Liu, 2018) comb. n., *A. fibulata* (Liu, 2018) comb. n., *A. huangyangjieensis* (Liu, 2018) comb. n., *A. spiralis* (Z.S. Zhang, Hu, Y.G. Zhang, 2012) comb. n., and *A. zhanfengi* (Liu, 2018) comb. n.

Genus *Denticulathys* Cala-Riquelme, Al-Jamal, Crews gen. n.

urn:lsid:zoobank.org:act:306B9795-0481-471B-BBFE-575C1618E5E9.

Type species: *Denticulathys amaataaidoo* sp. n.

Etymology: The generic name is derived from the Latin for ‘tooth’, *dent-*, referring to the denticulation observed on the palpatellar apophysis of the male palp, and the generic name *Lathys*, another member of the family; gender feminine.

Diagnosis: ***Denticulathys* gen. n.** (Figs 21A–F, 36A–F, 37A–D) can be distinguished from other Lathyidae fam. n. by lacking AME (Fig. 36A) (AME present in *Lathys* s.s., *Analtella* stat. reinst., ***Andronova* gen. n.**); and by having a palpal patellar dorsal bump with several ctenidia (Fig. 21E, F). Females can be distinguished by the short, uncoiled copulatory duct, and a receptacle in addition to the primary spermathecae (Fig. 37D).

***Denticulathys amaataaidoo* Cala-Riquelme, Al-Jamal, Crews sp. n.**

urn:lsid:zoobank.org:act:CFCA6957-C5E0-4B10-9C00-F5FC89774A9A.

Type material: Male holotype (CASENT9118716) from Central African Republic: Prefecture Sangha-Mbaéré, Dzanga-Ndoki National Park, 37.9 km 169°S Lidjombo, Elev. 360 m, 2°22'14"N 16°10'21"E, rainforest, beating low vegetation, 20–28.v.2001, Coll. B.L. Fisher. Female paratype (CASENT9118606) from Gabon: Ogooue-Maritime Prov., Reserve de Faune de la Moukalaba-Dougoua, 12.2 km 305°NW Doussala, Elev. 110 m, 2°17'0"S 10°29'49"E, rainforest, beating vegetation, 24.ii.2000, Coll. B.L. Fisher.

Etymology: The species epithet is a noun in apposition in honour of Ama Ata Aidoo, Ghanaian author, poet, playwright, politician, and academic; gender feminine.

Diagnosis: See diagnosis for genus.

Description: *Male* (CASENT9118716, Central African Republic): Carapace (Fig. 36A–C) pale honey yellow, darker

anteriorly. Eyes on short, hyacinth red tubercles. Chelicerae, labium, endites, sternum, and legs pale honey yellow. Abdomen (Fig. 36B–D) dorsum cream-yellow with pale broccoli brown chevrons, venter cream-yellow. Sternum squared-off anteriorly. Total length 1.85. Carapace length 0.88, width 0.70, height 0.33. Clypeus height 0.03, PME 0.10, ALE 0.09, PLE 0.08, PME–PME 0.05. Sternum length 0.48, width 0.45. Palp: femur length 0.28, tibia length 0.20. Leg I: femur 0.83, patella 0.28, tibia 0.80, metatarsus 0.58, tarsus 0.43. II: 0.76, 0.25, 0.64, 0.46, 0.36. III: 0.65, 0.18, 0.49, 0.43, 0.36. IV: 0.71, 0.23, 0.59, 0.49, 0.36. Abdomen length 0.98, width 0.75. Male palp (Figs 21A–F, 36E, F, 37A–C) with femur straight, as long as patella + tibia; patella slightly curved, with a retrolateral proximal process with twelve ctenidia grouped in two fields of five and seven; tibia slightly longer than patella, the tibial lock mechanism with a deep longitudinal furrow, an RTA two times longer than wide, and a hook-shaped tibial process (Fig. 21C, D); conductor upper arm shorter than conductor lower arm length (Fig. 21B); embolus connected prolateral distal to the tegulum, and coiled no more than 250° (Fig. 21B).

Female (CASENT9118606, Gabon): Carapace pale cream-yellow. Chelicerae pale cream-yellow, darker distally. Labium, endites, sternum, legs, and abdomen pale cream-yellow. Sternum squared-off anteriorly. Total length 1.85. Carapace length 0.75, width 0.63, height 0.25. Clypeus height 0.02, PME 0.08, ALE 0.09, PLE 0.06, PME–PME 0.05. Sternum length 0.43, width 0.48. Palp: femur length 0.23, tibia length 0.14. Leg I: femur 0.68, patella 0.23, tibia 0.68, metatarsus 0.55, tarsus 0.44. II: 0.74, 0.28, 0.56, 0.39, 0.26. III: 0.64, 0.14, 0.50, 0.45, 0.36. IV: 0.71, 0.21, 0.59, 0.51, 0.34. Calamistrum 1.00. Abdomen: length 1.18, width 0.83. Cribellum length 0.15, entire, as long as the width between the ALS, straight, with the spigots strobilate, grouping uniformly, arranged in a continuous field. Epigyne (Fig. 37D): copulatory openings mesal, close to each other, anterior to the primary spermathecae; membranous sac shorter than primary spermathecae diameter; copulatory duct shorter, connected mesal distal to the primary spermathecae; SS/AG reduced; primary spermathecae connected ectal proximal with a receptacle (Fig. 37D).

List of included species: *Denticulathys amaataaidoo* sp. n.

Remarks: In Figure 1, *Denticulathys amaataaidoo* sp. n. is not recovered as monophyletic. This is probably because the two terminals representing this species have two and eight loci present in the 50% occupancy matrix (Supporting Information, Table S1), respectively. When incorporating the legacy Sanger data (six more loci; Fig. 2), this is resolved, and we recover the species as monophyletic, consistent with our morphological hypothesis.

Genus *Lathys* Simon, 1885 s.s.

Type species: *Lethia varia* Menge, 1869, currently *Lathys humilis* (Blackwall, 1855).

Type material: *Lathys humilis*: England, Cambridge, 1.i-31.xii.1854, Coll. Koch (holotype, 1 male, 1 female, NHMUK1635149-5310-14).

Material examined: *Lathys humilis*: Germany, Grütz, Coll. Koch (Syntype, 1 female, NHMUK1635149-5289-5308). England (Syntype, 1 male, NHMUK1635149-185-34). France, Provence-Alpes-Côte d'Azur, Saint-Laurent-du-Var (1 female, MNHN-AR-ARS264). *Lathys sexpustulata*: Morocco, Atlas Mountains, Jbel Ayachi, 3250 m, Coll. Meinsohn (1 female, MNHN-AR-AR440). *Lathys sexoculata* Seo and Sohn 1984: Japan, Shikoku, Tokushima-ken, Anan City, Arita Asebicho, along road 28, 33°52'42.0"N 134°33'08.4"E, 15.v.2019, Coll. F. Ballarin, in the litter in a forest of sugi trees (*Cryptomeria japonica*) (4 males, 1 female, FBPC). *Lathys insulana* Ono, 2003: Japan, Okinawa Pref., Iriomote-jima Is., Shirahama, 26.xii.1991, Coll. A. Tanikawa (Holotype, 1 male, NMST5295). Japan, Okinawa Pref., Iriomote-jima Is., Uranai, 25.xii.1990, Coll. A. Tanikawa (1 male, NMST9993). Japan, Kagoshima Pref., Amami Ōshima Is., Sumiyo, 16.iii.2008, Coll. M. Yoshida (2 females, NMST-8398). Japan, Okinawa Pref., Izena Is., Shimajiri Distr., 26°54'56.4"N 127°56'34.2"E, 24.ii.2021, Coll. F. Ballarin, dry forest, litter along the road (5 males, 14 females, FBPC).

Diagnosis: *Lathys s.s.* (Figs 5A–C, 8A, 10A, B, 11A–D, 13A–F, 20A–F, 39A–G) can be distinguished from other Lathyidae fam. n. genera by having the AME smaller than the ALE (Figs 5A–C, 39A, B; Marusik et al. 2009: figs 5, 6, 13, Özkütük et al. 2016: fig. 6) (AME absent in *Scotolathys*, *Bannaella*, *Afrolathys* gen. n., and *Denticulathys* gen. n.; present but similar in size to ALE, PLE, and PME in *Andronova* gen. n.); male palp with a patellar dorsal distal apophysis (Figs 20B, 39F, G; Marusik et al. 2009: figs 23, 43, 45, 46) (absent in *Scotolathys*, *Bannaella*, *Afrolathys* gen. n., *Andronova* gen. n., and *Analtella* stat. reinst.; patellar dorsal proximal bump with ctenidia in *Denticulathys* gen. n.); palpal tibia with a retrolateral ventral apophysis in addition to the RTA, and hook-shaped tibial process (Fig. 20C, E, F; Marusik et al. 2009: figs 43, 45, 46); embolus usually coiled 1080° or less, and usually with a distal prolateral origin (Fig. 20A, D; Marusik et al. 2009: fig. 43). Females (Fig. 13A, B; Marusik et al. 2009: figs 23, 43, 45, 46, Özkütük et al. 2016: fig. 41) can be distinguished by the reduced SS/AG so that it is inconspicuous, copulatory duct short, usually curved but not coiled around itself and primary spermathecae; fertilization duct located mesal distally on the primary spermathecae.

List of included species: *Lathys bin* Marusik and Logunov, 1991, *L. borealis* Z.S. Zhang, Hu, Y.G. Zhang, 2012, *L. brevitibialis* Denis, 1956, *L. coralynae* Gertsch and Davis, 1942, *L. dixiana* Ivie and Barrows, 1935, *L. foxi* (Marx, 1891), *L. heterophthalma* Kulczyński, 1891, *L. humilis* (Blackwall, 1855), *L. humilis meridionalis* (Simon, 1874), *L. lepida* O. Pickard-Cambridge, 1909, *L. mantarota* Wunderlich, 2022, *L. sexpustulata* (Simon, 1878), and *L. subhumilis* Z.S. Zhang, Hu, Y.G. Zhang, 2012.

Genus *Scotolathys* Simon, 1885 s.s.

Type species: *Scotolathys simplex* Simon, 1885.

Material examined: *Lathys delicatula*: USA, New Mexico, Bernalillo Co., Tijeras, Tunnel Canyon Trail, 7.iii.2021, Coll. M. Pleisher (1 male, CASENT9087234). USA, New Mexico, Otero Co., Tularosa, 3 Rivers, 9.x.2020, Coll. M. Pleisher (1 female, CASENT9087235). *Lathys maculina*: USA, Alabama,

Mobile, c. 1902, Coll. Hugo Soltau, Nathan Banks, (Holotype, 1 female, MCZ-IZ21934). USA, Florida, Gainesville, Newman Lake, 16.vi.1935, Coll. W.J. Gertsch (1 male, 2 females, MNHN-AR-AR426). USA, New Hampshire, Lake Winnepesaukee, Coll. N. Banks (1 male, 1 female, MNHN-AR-AR445). *Lathys pallida* (Marx, 1891): Canada, Ontario, Point W. Bay, Lake Temagami, 15.vii.1964, Coll. W.J. Gertsch, W. Ivie, T.B. Kurata (1 male, 2 females, MNHN-AR-AR426). *Scotolathys simplex*: Algeria, Oran [note: there is no further information given with this specimen] (1 female, MNHN-AR-AR426).

Diagnosis: *Scotolathys s.s.* can be distinguished from other Lathyidae fam. n. by lacking AME (Fig. 5D–F; Marusik et al. 2009: figs 1–3, 9, 28) (AME present in *Lathys s.s.*, *Analtella* stat. reinst., and *Andronova* gen. n.); male palp without patellar apophysis (Marusik et al. 2009: figs 33–37) (present in *Lathys*, *Bannaella*, and *Denticulathys* gen. n.); cymbium with a prolateral proximal process (Marusik et al. 2009: figs 41, 42, 48) (absent in *Afrolathys* gen. n., *Andronova* gen. n., *Bannaella*, *Denticulathys* gen. n., *Analtella* stat. reinst., and *Lathys s.s.*); embolus usually coiled 1080° or less, usually with a distal retrolateral origin (Marusik et al. 2009: Figs 39, 40, 42, 49); the conductor tip is thin, elongated, usually coiled 360°, and with a paraterminal process (Marusik et al. 2009: figs 39, 48, 50). Females (Marusik et al. 2009: figs 58–61) can be distinguished by the reduced SS/AG so that it is inconspicuous; copulatory duct elongated and coiled 720° or more around itself and bent 360° around the primary spermatheca; fertilization duct located mesal distally.

List of included species: *Scotolathys delicatula* Gertsch and Mulaik, 1936 stat. reinst., *S. immaculata* Chamberlin and Ivie, 1944 stat. reinst., *S. maculina* (Gertsch, 1946) stat. reinst., *S. pallida* (Marx, 1891) stat. reinst., and *S. simplex* (Simon, 1885).

Genus *Tolokonniella* Cala-Riquelme, Crews, Esposito gen. n.
urn:lsid:zoobank.org:act:CB5C2ACD-C071-4D40-B977-C8F68D8EAE7D.

Type species: *Lethia stigmatisata* Menge, 1869, currently *Lathys stigmatisata* (Menge, 1869).

Material examined: *Lathys stigmatisata* (Menge, 1869): France, Paris, 18.vi.1913, Coll. J.E. Simon (1 male, 1 female, NHMUK1635150).

Etymology: The generic epithet is in honour of the Russian musician, conceptual artist, and feminist Nadezhda Andreyevna Tolokonnikova; gender feminine.

Diagnosis: The male of *Tolokonniella* gen. n. resembles *Lathys s.s.* by having the AME narrower than the ALE (Özkütük et al. 2016: figs 2, 4); the male palp with a patellar dorsal distal apophysis (Marusik et al. 2009: figs 29, 44, 52, Marusik et al. 2015: fig. 50, Özkütük et al. 2016: figs 8–15); palpal tibia with a ventral lateral apophysis in addition to the RTA and a hook-shaped tibial process; however, this genus can be distinguished from *Lathys s.s.* by having the embolus coiled more than 1080°, and usually with a proximal prolateral origin (Marusik et al. 2015: fig. 51); the conductor tip elongated and coiled three or

more times (Marusik *et al.* 2006b: fig. 9). Females (Marusik *et al.* 2009: figs 31, 32, Marusik *et al.* 2015: figs 48, 49, Özkütük *et al.* 2016: figs 17–21; 37–40) can be distinguished by the reduced SS/AG, the copulatory duct elongated and coiled 720° around itself, and 180° around the primary spermatheca; the fertilization duct located mesal distally.

List of included species: *Tolokonniella ankaraensis* (Özkütük *et al.*, 2016) comb. n., *T. mallorcensis* (Lissner, 2018) comb. n., *T. maura* (Simon, 1911) comb. n., *T. stigmatisata* (Menge, 1869) comb. n., and *T. truncata* (Danilov, 1994) comb. n.

Family Dictynidae O.Pickard-Cambridge, 1871 s.s.

Type genus: *Dictyna* Sundevall, 1833 (type species *Aranea benigna* Walckenaer, 1802).

Material examined: *Aebutina binotata*: Brazil, Amazonas, São Paulo de Olivença, Fonte Boa, Coll. Mathan, M. de (Syntypes, 3 females, MNHN-AR-AR159). *Adenodictyna kudoae*: Japan, Kagoshima Pref., Amami-Ōshima Is., Naze city, Kinsakubaru, 20.IV.2008, Coll. Y. Kudo (Holotype, 1 male, NMST7953). *Ajmonia gratiosa*: Algeria, Constantine (7 males, 34 females, MNHN-AR-AR606). *Ajmonia marakata*: India, Ootacamund, Nilgiris, 19–20.vii.1960, Coll. Pres. Dr. W. Rae-Sherriffs (Holotype, 1 male, 1 female, NHMUK1635133). *Ajmonia numidica*: Algeria, Mila Prov. (prev. Dept. Constantine), Zouagha Forest, 15.v.1935 (2 males, 3 females, MNHN-AR-AR657). *Ajmonia smaragdula*: Sri Lanka, Central Province, Nuwara Eliya to Kandy, 1.i–31.xii.1892, Coll. E. Simon (Syntypes, 1 male, 1 female, MNHN-AR-AR714). *Ajmonia velifera*: India, Sikkim (Syntypes, 1 male, 1 female, MNHN-AR-AR713). *Anaxibia difficilis*: São Tomé-et-Príncipe, São Tomé, Bombaim, Traz-os-Montes, 7.vi.1956, Coll. P. Viette (Holotype, 1 male, MNHN-AR-AR477). São Tomé and Príncipe, São Tomé, Lobata, Muquiqui Peak, near Guadalupe, 0°22'49.2"N 6°38'47.1"E, Elev. 190 m, beating foliage, 22.xi.2016, Coll. L.A. Esposito (8 males, 6 females, 3 imm., CASENT9118598; 1 female, 1 male, 1 imm., CASENT9118599). São Tomé and Príncipe, São Tomé, Mé-Zóchi, São Nicolau Waterfall, 0°17'08.8"N 6°37'31.9"E, Elev. 927 m, 15.xi.2016, Coll. L.A. Esposito (1 male, CASENT9118601). *Archaeodictyna anguiniceps*: Egypt, Siwa, Bahrein, east lake shore, 26.iv.1939, Coll. M. Cameron, Dr. G. Denis (Holotype, 1 male, 1 female, NHMUK1635121). *Archaeodictyna consecuta*: Morocco/Algeria, Saida (7 males, 4 females, MNHN-AR-AR604). *Archaeodictyna ammophila*: France, Île-de-France, Seine-et-Marne Prov., Fontainebleau, Coll. E. Simon (1 male, 1 female, MNHN-AR-ARS30). *Ar. ulova* South Africa, Natal Spioenkop Dam, south shore, 30 km SW Ladysmith, el. 900m, 28°40'60"S, 25°27'59.00"E, mixed grasslands and dry bushveld, 1.vii.1986, Coll. T. Meikle-Griswold, C.E. Griswold (Holotype, 1 male, 1 female, NHMUK 1635102). *Brigittea innocens* (O. Pickard-Cambridge, 1872): Myanmar, Magway Division, Shwesettaw Wildlife Reservation, guest house, 20°3'37.3"N 94°35'39.8"E, at night, deciduous forest, 28.ix.2003, Coll. D. Ubick, (1 female, CASENT9017108). Israel, Har Horshan, North of Ma'agan Mikh'el, 32°32'60"N 34°54'59.99"E, at night, deciduous forest, 26.iv.1987, Coll. V.D. Roth (1 male, CASENT9118698).

Tanzania, Tanganyika, 6 mi W of Ngare Nanyuki, Elev. 1500 m, 19.xi.1957, Coll. E.S. Ross, R.E. Leech (1 female, CASENT9118704). *Callevophthalmus albus*: Australia, Western Australia, 1.5 km E Cranbrook, low bushes in bottom sandy land, open scrub, 11.ix.2003, Coll. E.I. Schlinger, M.E. Irwin (1 female, CASENT9118676). Australia, Sydney, 1854–58 (Holotype, 1 female, NHMUK 1635107). *Callevophthalmus maculatus*: Australia, Sydney, 1.i–31.xii.1887 (Holotype, 1 female, NHMUK 1635108). *Mallos dugesi* (Becker, 1886): USA, Arizona, Pima Co., Tucson, vii.1930, Coll. Gertsch (1 female, MNHN-AR-AR493). *Mallos dugesi*: USA, Arizona, Huachuca Mountains, Miller Canyon, 17.xi.1910, Coll. William Morton Wheeler (Holotype, 2 females, MCZ-IZ29976). *Mallos hesperius* (Chamberlin, 1916): Peru, San Miguel, vii.1911, Coll. H.W. Foote, Yale Peruvian Expedition (Holotype, 1 male, MCZ-IZ15690). *Mallos mians* (Chamberlin, 1919): USA, California (no specific locality data), 1909 and 1913 (from publication), Coll. R.V. Chamberlin (Holotype, 1 female, MCZ-IZ15096). *Mallos niveus* O. Pickard-Cambridge, 1902: Mexico, San Luis Potosi, Rio Frio, 29.xi.1940, Coll. Gertsch (1 male, 1 female, MNHN-AR-AR481). USA, Arizona, Cochise Co., Chiricahua Mtns., SWRS, 5 mi W Portal, 14.viii.1972, Coll. P.R. Craig (1 male, CASENT9118619). USA, Arizona, Mohave Co., 2 mi S Davis Dam, Elev. 500 ft, salt brush, 14.vi.1968, Coll. L.D. Nelson (1 female, CASENT9118639). USA, New Mexico, Otero Co., Oliver Lee State Park, Dog Canyon, 32°44'57.6"N 105°54'46.6"W, 7.x.2021, Coll. M. Pleisher (1 male, 1 female, 2 imm., CASENT9087236). *Mallos pallidus* (Banks, 1904): USA, California, Mt. Shasta, pre-1904 publication date, Coll. Nathan Banks, (Syntype, 1 male, 2 females, MCZ-IZ22473). USA, California, Santa Barbara Co., Santa Cruz Island, Stanton Beach, 17.iv.1973, Coll. D. Haralson (1 female, CASENT9118623). USA, California, Mendocino Co., Angelo Reserve, S Fork Eel R. near Wilderness Lodge, 9.7 km N Branscomb, 39°44.450'N 123°37.944'W, Elev. 420 m, redwood/Douglas fir forest, extraction from concentrated forest, 28.ix.2013, Coll. B. Mathat (1 female, CASENT9056350). USA, California, Kern Co., Indian Wells Canyon, 35°41'9"N 117°55'38.99"W, Elev. 1125 m, malaise, damp creek bed, 8–14.v.2014, Coll. M.E. Irwin (1 male, CASENT9118662). *Mexitilia trivittata*: USA, New Mexico, Albuquerque, pre-1901 publication date, Coll. Hugo Soltau, Nathan Banks (Syntype, 1 male, 1 female, MCZ-IZ23355). USA, New Mexico, Sandoval Co., Jemez Mountains, E fork Jemez River, near Battleship Rock, 27.iv.2021, Coll. M. Pleisher (2 females, CASENT9087231). USA, Arizona, 17 miles NE, 8.vii.1940, Coll. Gertsch (1 male, 1 female, MNHN-AR-AR482). *Nigma flavescens* (Walckenaer, 1830): Israel, Jerusalem, The Hebrew University Fac. Agric., Dept. Ent., 2.vi.2000, Coll. Mendel (1 male, 2 females, 1 imm., CASENT9118690). *Nigma gertschi* (Berland and Millot 1940): Kenya, Rift Valley Province, West Pokot District, Marich Pass Field Studies Centre, 1°32.2'S 35°27.4'E, Elev. 3000 ft, 26–29.vii.1999, Coll. W.J. Pulawski, J.S. Schweikert (1 male, CASENT9118714). *Nigma longipes*: Kenya, Mau Forest du Kenya, 22.i.1912, Coll. C. Alluaud, R. Jeannel (Type, 1 male, MNHN-AR-ARS302). Kenya, Nakuru Co., Naivasha, 1–31.xii.1911, Coll. C. Alluaud, R. Jeannel (Syntypes, 1 female, MNHN-AR-ARS291). *Paradictyna rufoflava* (Chamberlain, 1946): New Zealand, North Island, L. Tikitapu

(Blue Lake), Elev. 350 m, malaise, dry hillside, 29.x.–4.xi.1977, Coll. E.I. Schlinger (1 male, CASENT9118610). New Zealand, South Island, S. Auckland, Waitomo Co., Pio Pio Dist., 2 km NW Mangakowhai Rd., sweeping, native bush, 29.x.–8.ii.1996, Coll. B. Zuparko (1 female, CASENT9118688). *Phantyna bicornis* Emerton, 1915: USA, Massachusetts, Ipswich, sand near seashore, 24.vi.1905, Coll. James H. Emerton (Syntype, 1 female, MCZ-IZ43954). USA, Massachusetts, Ipswich, sand near seashore, 24.vi.1905, Coll. James H. Emerton (Syntype, 1 male, MCZ-IZ20499). *Phantyna remota* (Banks, 1924): Ecuador, Galapagos, Daphne, 23.iv.1923, Coll. William Beebe, Williams Galapagos Expedition 1923 (Syntype, 1 male, 2 females, MCZ-IZ22879). *Phantyna terranea* (Ivie, 1947): USA, Washington, Vantage, 6.v.1936, Coll. M.H. Hatch (Syntype, 1 female, MCZ-IZ22451). USA, Washington, Vantage, 1.v.1936, Coll. M.H. Hatch (Syntype, 1 female, MCZ-IZ24763). *Rhion pallidum*: Sri Lanka, Kandy, Coll. E. Simon (MNHN-AR-AR378). *Tahuantina zapfeae*: Chile, Curicó Province, Loma Hueca-Huecan, 15 km E Curicó, 35°03'59.4"S 71°07'21.4"W, Elev. 400 m, malaise, dry hillside, 29.x.–10.ix.1997, Coll. J.E. Barriga, M.E. Irwin (1 male, CASENT9062312). Chile, Prov. Coquimbo, Hacienda Illapel, 31°36'S 71°07'W, Elev. 900 m, malaise, dry hillside, 19.x.1966, Coll. E.I. Schlinger, M.E. Irwin, Peña (3 males, 6 females, 3 imm., CASENT9118813). *Thallumetus acanthochirus* Simon, 1904: Chile, Valparaiso Prov., Marga Marga, Quilpué, Coll. C.E. Porter (MNHN-AR-AR383). Chile, Diguillín Prov., Ñuble Region, Sierra de Chillán, Coll. E. Simon (1 male, MNHN-AR-AR377). Venezuela, Carabobo, Parque Nacional San Esteban, Coll. E. Simon (1 male, MNHN-AR-AR384). *Thallumetus parvulus* Bryant, 1942: US Virgin Islands, St. Croix, pre-1942, Coll. Harry A. Beatty (Holotype, 1 male, MCZ-IZ22541). *Thallumetus pullus* Chickering, 1952: Panama, Canal Zone, Biol. Area, viii.1950, Coll. Arthur M. Chickering (Allotype, 1 female, MCZ-IZ44022). Panama, Canal Zone, Biol. Area, 1–31.vii.1950, Coll. Arthur M. Chickering (Holotype, 1 male, MCZ-IZ22788). *Thallumetus pusillus* Chickering, 1948: Panama, Canal Zone, Biol. Area, 1–30.viii.1939, Coll. Arthur M. Chickering (Allotype, 1 female, MCZ-IZ44021). Panama, Canal Zone, Biol. Area, 1–30.viii.1939, Coll. Arthur M. Chickering (Holotype, 1 male, MCZ-IZ22815). *Tivyna moaba*: USA, California, Imperial Co., East Mesa Geothermal Site, 8.0 mi ESE Holtville, 32°42'N 115°15'W, Elev. 17 m, pitfalls, 23.iii.1978, Coll. R. Aalbu (1 female, CASENT9062468). *Tivyna spatula*: Cuba, Cienfuegos, Soledad, 22.viii.1933, Coll. Weber (1 male, MCZ-IZ20964). Peru, Cajamarca Prov., Sector La Pampa, Fundo La Paloma, 3 km W Chilite, 07°13.42'S 78°51.84'W, Elev. 865 m, malaise, dry gulch, 31.iii–7.iv.2008, Coll. M.E. Irwin, G. Antón Amaya (1 female, CASENT9061652). Peru, Cajamarca Prov., Sector La Pampa, Fundo La Paloma, 3 km W Chilite, 07°13.42'S 78°51.84'W, Elev. 865 m, malaise, 17–24.i.2008, Coll. M.E. Irwin, G. Antón Amaya (1 female, CASENT9061673). Mexico, Colima, Revillagigedo Archipelago, Isla Socorro, ~2 km NW Bahía Braithwaite, in orchard, 31.i.1966, Coll. L. Baptista (1 female, CASENT9118791).

Diagnosis: Small cribellate spiders (Figs 9A–F, 10E, F, 12A–F, 43E–F, 47A–B, 52A–C, E–F, 53A–C, 54A, 63D, 66B) with the

carapace longer than broad, quite high and convex (Figs 6E, F, 7B, D–F) (two times higher in *Archaedictyna*, in part: Fig. 45A–B, E) (Chamberlin and Gertsch 1958); clypeus typically high (Figs 6E, F, 7D, F, 47A, 50A, 51F, 53A) (clypeus low in Lathyidae fam. n. and Argyronetidae stat. reinst.); chelicerae concave medially, gradually narrowed apically, subparallel, with a conspicuous lateral condyle sometimes developed into a horn (Figs 6E, F, 7A–F, 43A–B, 45B); tarsi lacking trichobothria, present at the apical end of the metatarsi; male palpal tibia usually with a dictynid process with typically two ctenidia (Figs 30E, F, 31F, 44E, 51D, E, 53E–F, 55C, D, 56B, D–F, 57A, C, 59E, F, 62A–D); embolus of variable thickness, acuminate to apex or variously modified apically (Figs 28A, B, D–F, 29A–E, 31E, 50E, 52D, 53D, 56D–F, 57A–D, 58A–F, 59E, F); conductor upper arm variable in size but never coiled more than 225° (conductor upper arm shorter than lower arm in Argyronetidae); conductor lower arm widens to a conductor-tegulum lock mechanism (Fig. 27C), coiled to produce a spiral of variable form (Figs 25B, D, F, 26C, 27C, 29F, 30B, C, 31C, 53D–F) (Chamberlin and Gertsch 1958) that usually ends in a scaly tip (Figs 27C, D, 30B, 31C).

Remarks: Dictynidae *s.l.* has long been a receptacle for a mixture of cribellate and ecribellate RTA clade spiders. Wheeler et al. (2017) argued that the cribellate genera could be a natural group considering that they all have a characteristic male palp, and many males have medially concave chelicerae. With our restructuring of the family and the transfer of species into Lathyidae fam. n. and Argyronetidae stat. reinst., Dictynidae *s.l.* becomes morphologically structured with clear synapomorphies. The results of Spagna and Gillespie (2008), Miller et al. (2010), Spagna et al. (2010), and Wheeler et al. (2017) have explored the molecular phylogenetics of the RTA clade using Sanger loci but with few terminals, and all of their results initially suggested Dictynidae *s.l.* to be monophyletic; however, the relationship between the genera has changed in each of these studies, suggesting a paraphyletic or polyphyletic composition. Most recently, Crews et al. (2020), also using Sanger data, and Kulkarni et al. (2023), using UCE + Sanger loci, recovered Dictynidae *s.s.* as paraphyletic, and Gorneau et al. (2023a) using UCEs + Sanger loci recovered Dictynidae *s.l.* as monophyletic. Our results corroborate the results obtained by Gorneau et al. (2023a). We find support for including cribellate genera that present: (i) a dictynid process (with the exception of *Tivyna*, *Mallos*, *Ajmonia*, *Dictynomorpha* Spassky, 1939, *Nigma*, and *Califorenigma* gen. n.) and (ii) males and females with the chelicerae medially concave.

The monotypic genus *Clitistes* Simon, 1902 described from only a female specimen was declared a *nomen dubium* by Miller (2007: 259). Dupérré and Harms (2018: 8) revised the type of the species and transferred it from the Linyphiidae to Dictynidae. After examining several specimens of males and females of *Cybaeolus pusillus* Simon, 1884 at CAS [CASENT9118799 (1 male), 9118750 (2 males, 1 female), 9118752 (2 males), 9118758 (1 male), 9118764 (1 male, 1 female), 9118783 (1 male, 1 juv.), 9118833 (1 female), 9118839 (1 male), 9118843 (1 male), 9118845 (1 female)], based on the morphology of *Clitistes velutinus* Simon, 1902 (see: Dupérré and Harms 2018: 8), we consider *Clitistes velutinus* Simon, 1902 a junior synonym

of *Cybaeolus pusillus* Simon, 1884 (*Clitistes velutinus* Simon, 1902 syn. n.).

The genus *Aebutina* Simon, 1892, by having reduced AME, the retromargin of the cheliceral fang furrow with one to several differential denticles (Griswold *et al.* 2005: fig. 130E), and a tegular median apophysis (Fig. 19D; Griswold *et al.* 2005: fig. 169C, D) is transferred to Macrobonidae. *Hoplolathys* Caporiacco, 1947 was originally described from a currently lost juvenile, and here we consider the genus a *nomen dubium*. *Lathys changtunesis* Hu, 2001 was previously considered a member of the genus *Ajmonia* by Zhang *et al.* (2012: 1); however, this transfer was not accepted due to lack of evidence. We conclude that *L. changtunesis* is not a representative of the Lathyidae fam. n. (see diagnosis of Lathyidae fam. n.). The presence of a conductor with the upper arm shorter than the lower arm, the tegular path of the spermaphor without a loop, the cymbial dorsal process developed, and the patellar dorsal apophysis present indicate that this species should be placed in *Ajmonia*. Here, we transfer *L. changtunesis* to *Ajmonia* [*Ajmonia changtunesis* (Hu, 2001) comb. n.].

The morphology of the palp of *Dictyna aguasverdes* Wunderlich, 2022, *D. bispinosa* Simon, 1906, *D. fuerteventurensis* Schmidt, 1976, and *D. lanzarotensis* Wunderlich, 2022 places these species outside the delimitation of *Dictyna* (see diagnosis of *Dictyna* below) but within *Archaeodictyna* (Figs 45A–F, 46A–D) by having the embolus thick, coiled approximately 250°, originating prolaterally from the bulb (Fig. 46B); the conductor lower arm coiled no more than 45°, with the tip directed distally in most species, and with the conductor locking mechanism longer than the conductor tip; dictynid process without an evident tubercle (Fig. 46C, D).

Nigma albida (O. Pickard-Cambridge, 1885) is represented by a single illustration of the epigyne (Dyal 1935: pl. 14, fig. 79) that does not resemble the epigyne of *N. flavescens*, the type of the genus. It likely does not belong in *Nigma*, but only examination of the type of *N. albida* will allow that determination. *Nigma gertschi* is also not similar to the type of *N. flavescens*. There is only a single illustration of the palp and the epigyne (Berland and Millot 1940), and the authors indicate that it is similar to *Dictyna viridissima* Roewer, 1951, which has been synonymized with *N. walckenaeri*; however, we do not agree that they are similar to *N. walckenaeri* or *Nigma s.s.* Lehtinen (1967) indicated that the types are located in Paris; however, we were unable to locate this specimen and did not find evidence that it was deposited there previously. The scarce morphological evidence for the monotypic genera *Qiyunia* Song and Xu 1989 and *Tandil* Mello-Leitão, 1940 suggest placing these species outside Argyronetidae stat. reinst., Lathyidae fam. n., and Dictynidae s.s.; however, despite our efforts we were unable to view the material. Based on this argument, we consider the taxa mentioned in this paragraph as *incertae sedis*.

Transferred to other families: *Aebutina* Simon, 1892 (Macrobonidae).

In synonymy: *Clitistes velutinus* Simon, 1902 = *Cybaeolus pusillus* Simon, 1884.

Nomina dubium. *Hoplolathys* Caporiacco, 1947.

List of included genera: *Adenodictyna* Ono, 2008, *Ajmonia* Caporiacco, 1934 [*Aj. aurita* Song and Lu, 1985, *Aj. bedeshai* (Tikader, 1966), *Aj. capucina* (Schenkel, 1936), *Aj. changtunesis* (Hu, 2001) comb. n., *Aj. gratiosa* (Simon, 1881), *Aj. lehtineni* Marusik and Koponen 1998, *Aj. marakata* (Sherriffs, 1927), *Aj. numidica* (Denis, 1937), *Aj. patellaris* (Simon, 1911), *Aj. procera* (Kulczyński, 1901), *Aj. psittacea* (Schenkel, 1936), *Aj. rajaei* Zamani and Marusik 2017, *Aj. smaragdula* (Simon, 1905), and *Aj. velifera* (Simon, 1906)], *Anaxibia* Thorell, 1898, *Arangina* Lehtinen, 1967, *Archaeodictyna* Caporiacco, 1928 [*Archaeodictyna aguasverdes* (Wunderlich, 2022) comb. n., *Archaeodictyna ammophila* (Menge, 1871), *Archaeodictyna anguinceps* (Simon, 1899), *Archaeodictyna bispinosa* (Simon, 1906) comb. n., *Archaeodictyna conducta* (O. Pickard-Cambridge, 1876), *Archaeodictyna consecuta* (O. Pickard-Cambridge, 1872), *Archaeodictyna fuerteventurensis* (Schmidt, 1976) comb. n., *Archaeodictyna lanzarotensis* (Wunderlich, 2022) comb. n., *Archaeodictyna minutissima* (Miller, 1958), *Archaeodictyna sexnotata* (Simon, 1890), *Archaeodictyna suedicola* (Simon, 1890), *Archaeodictyna tazzeiti* (Denis, 1954), and *Archaeodictyna ulova* Griswold and Meikle-Griswold, 1987], ***Arethyna* gen. n.** [*Arethyna coloradensis* (Chamberlin, 1919) comb. n., *Arethyna idahoana* (Chamberlin and Ivie, 1933) comb. n., *Arethyna osceola* (Chamberlin and Gertsch, 1958) comb. n., *Arethyna peon* (Chamberlin and Gertsch, 1958) comb. n., *Arethyna personata* (Gertsch and Mulaik, 1936) comb. n., *Arethyna saltona* (Chamberlin and Gertsch, 1958) comb. n., *Arethyna secuta* (Chamberlin, 1924) comb. n., *Arethyna sierra* (Chamberlin, 1948) comb. n., *Arethyna ubsumurica* (Marusik and Koponen, 1998) comb. n., *Arethyna volucripes* (Keyserling, 1881) comb. n., and *Arethyna volucripoides* (Ivie, 1947) comb. n.], *Argennina* Gertsch and Mulaik, 1936, *Atelolathys* Simon, 1892, *Banaidja* Lehtinen, 1967, *Brigittea* Lehtinen, 1967 [*B. avicenna* Zamani and Marusik, 2021, *B. civica* (Lucas, 1848), *B. colona* (Simon, 1906) comb. n., *B. innocens* (O. Pickard-Cambridge, 1872), *B. latens* (Fabricius, 1775), *B. vicina* (Simon, 1873)], ***Califorenigma* gen. n.** [*C. linsdalei* (Chamberlin and Gertsch, 1958) comb. n.], *Callevophthalmus* Simon, 1906, *Dictyna* Sundevall, 1833 [*Dictyna abundans* Chamberlin and Ivie, 1941, *D. alaskae* Chamberlin and Ivie, 1947, *D. albicoma* Simon, 1893, *D. albovittata* Keyserling, 1881, *D. alyceae* Chickering, 1950, *D. apachea* Chamberlin and Ivie, 1935, *D. arundinacea*, *D. brevitarus* Emerton, 1915, *D. cafayate* Mello-Leitão, 1941, *D. chandrai* Tikader, 1966, *D. cofete* Wunderlich, 2022, *D. columbiana* Becker, 1886, *D. cronebergi* Simon, 1889, *D. crosbyi* Gertsch and Mulaik, 1940, *D. dauna* Chamberlin and Gertsch, 1958, *D. ectrapela* (Keyserling, 1886), *D. fluminensis* Mello-Leitão, 1924, *D. guineensis* Denis, 1955, *D. hamifera* Thorell, 1872, *D. kosiorowiczi* Simon, 1873, *D. laeviceps* Simon, 1911, *D. linzhiensis* Hu, 2001, *D. livida* (Mello-Leitão, 1941), *D. marilina* Chamberlin, 1948, *D. moctezuma* Gertsch and Davis, 1942, *D. namulinensis* Hu, 2001, *D. navajoa* Gertsch and Davis, 1942, *D. pictella* Chamberlin and Gertsch, 1958, *D. pusilla* Thorell, 1856, *D. quadrispinosa* Emerton, 1919, *D. ranchograndei* Caporiacco, 1955, *D. saepei* Chamberlin and Ivie, 1941, *D. similis* Keyserling, 1878, *D. simoni* Petrunkevitch, 1911, *D. sinaloa* Gertsch and Davis, 1942, *D. siniloanensis* Barrion and

- Litsinger, 1995, *D. tarda* Schmidt, 1971, *D. togata* Simon, 1904, *D. tristis* Spassky, 1952, *D. trivirgata* Mello-Leitão, 1943, *D. tullgreni* Caporiacco, 1949, *D. turbida* Simon, 1905, *D. uncinata* Thorell, 1856, *D. uvs* Marusik and Koponen, 1998, *D. vittata* Keyserling, 1883, *D. vultuosa* Keyserling, 1881, and *D. yongshun* Yin, Bao and Kim, 2001], *Dictynomorpha* Spassky, 1939, *Emblyna* Chamberlin, 1948 [*Emblyna acreensis* Wunderlich, 1992, *E. aiko* (Chamberlin and Gertsch, 1958), *E. altamira* (Gertsch and Davis, 1942), *E. ampla* Chamberlin, 1948, *E. angulata* (Emerton, 1915), *E. annulipes* (Blackwall, 1846), *E. ardea* (Chamberlin and Gertsch, 1958), *E. artemisia* (Ivie, 1947), *E. borealis* (O.Pickard-Cambridge, 1877), *E. borealis cavernosa* (Jones, 1947), *E. branchi* (Chamberlin and Gertsch, 1958), *E. brevidens* (Kulczyński, 1897), *E. budarini* Marusik, 1988, *E. burjatika* (Danilov, 1994), *E. callida* (Gertsch and Ivie, 1936), *E. capens* Chamberlin, 1948, *E. cavata* (Jones, 1947) comb. n., *E. chitina* (Chamberlin and Gertsch, 1958), *E. completa* (Chamberlin and Gertsch, 1929), *E. completoides* (Ivie, 1947), *E. consulta* (Gertsch and Ivie, 1936), *E. cornupeta* (Bishop and Ruderman, 1946), *E. coweta* (Chamberlin and Gertsch, 1958), *E. crocana* Chamberlin, 1948, *E. decaprini* (Kaston, 1945), *E. evicta* (Gertsch and Mulaik, 1940), *E. florens* (Ivie and Barrows, 1935), *E. formicaria* Baert, 1987, *E. hentzi* (Kaston, 1945), *E. horta* (Gertsch and Ivie, 1936), *E. hoyia* (Chamberlin and Ivie, 1941), *E. joaquina* (Chamberlin and Gertsch, 1958), *E. lina* (Gertsch, 1946), *E. linda* (Chamberlin and Gertsch, 1958), *E. manitoba* (Ivie, 1947), *E. marissa* (Chamberlin and Gertsch, 1958), *E. melva* (Chamberlin and Gertsch, 1958), *E. nanda* (Chamberlin and Gertsch, 1958), *E. oasa* (Ivie, 1947), *E. palomara* Chamberlin, 1948, *E. pinalia* (Chamberlin and Gertsch, 1958), *E. piratica* (Ivie, 1947), *E. peragrata* (Bishop and Ruderman, 1946), *E. reticulata* (Gertsch and Ivie, 1936), *E. roscida* (Hentz, 1850), *E. saylori* (Chamberlin and Ivie, 1941), *E. scotta* Chamberlin, 1948, *E. seminola* (Chamberlin and Gertsch, 1958), *E. shasta* (Chamberlin and Gertsch, 1958), *E. shoshonea* (Chamberlin and Gertsch, 1958), *E. stulta* (Gertsch and Mulaik, 1936), *E. sublatoides* (Ivie and Barrows, 1935), *E. suwaneana* (Gertsch, 1946), and *E. zaba* (Barrows and Ivie, 1942)], *Eriena* gen. n. [*Er. minuta* (Emerton, 1888) comb. n., *Er. mora* (Chamberlin and Gertsch, 1958) comb. n.], *Helenactyna* Benoit, 1977, ***Khalotyna* gen. n.** [*K. calcarata* (Banks, 1904) comb. n.], *Kharitonovia* Esyunin, et al., 2017, *Mallos* O. Pickard-Cambridge, 1902, *Marilynia* Lehtinen, 1967, *Mashimo* Lehtinen, 1967, *Mexitlia* Lehtinen, 1967, *Myanmaridictyna* Wunderlich, 2017, *Nigma* Lehtinen, 1967, ***Nopalityna* gen. n.** [*N. francisca* (Bishop and Ruderman, 1946) comb. n., *N. jonesae* (Roewer, 1955) comb. n., *N. orbiculata* (Jones, 1947) comb. n., *N. sublata* (Hentz, 1850) comb. n., *N. suprenans* (Chamberlin and Ivie, 1935) comb. n., and *N. uintana* (Chamberlin, 1919) comb. n.], *Paradictyna* Forster, 1970, ***Pangunus* gen. n.** [*Pangunus kaszabi* (Marusik and Koponen, 1998) comb. n., *Pangunus umai* (Tikader, 1966) comb. n., and *Pangunus xizangensis* (Hu and Li, 1987) comb. n.], *Penangodyna* Wunderlich, 1995, *Phantyna* Chamberlin, 1948 [*Ph. agressa* (Ivie, 1947) comb. n., *Ph. bicornis* (Emerton, 1915), *Ph. estebanensis* (Simon, 1906), *Ph. formidolosa* (Gertsch and Ivie, 1936) comb. n., *Ph. mandibularis* (Taczanowski, 1874), *Ph. meridensis* (Caporiacco, 1955), *Ph. micro* (Chamberlin and Ivie, 1944), *Ph. mulegensis* (Chamberlin, 1924), *Ph. pixi* (Chamberlin and Gertsch, 1958), *Ph. provida* (Gertsch and Mulaik, 1936), *Ph. remota* (Banks, 1924), *Ph. rita* (Gertsch, 1946), *Ph. segregata* (Gertsch and Mulaik, 1936), *Ph. terranea* (Ivie, 1947), *Ph. varyna miranda* (Chamberlin and Gertsch, 1958), and *Ph. varyna* (Chamberlin and Gertsch, 1958)], ***Purplecornia* gen. n.** [*Pu. gloria* (Chamberlin and Ivie, 1944) comb. n., *Pu. guerrerensis* (Gertsch and Davis, 1937) comb. n., *Pu. incredula* (Gertsch and Davis, 1937) comb. n., *Pu. lecta* (Chickering, 1952) comb. n., *Pu. meditata* (Gertsch, 1936) comb. n., *Pu. miniata* (Banks, 1898) comb. n., and *Pu. terrestris* (Emerton, 1911) comb. n.], *Rhion* O.Pickard-Cambridge, 1871, *Shango* Lehtinen, 1967, ***Shikibutyna* gen. n.** [*Sh. felis* (Bösenberg and Strand, 1906) comb. n., *Sh. foliicola* (Bösenberg and Strand, 1906) comb. n., *Sh. guanachae* (Schmidt, 1968) comb. n., *Sh. mongolica* (Marusik and Koponen, 1998), comb. n., *Sh. procerula* (Bösenberg and Strand, 1906) comb. n., *Sh. schmidti* (Kulczyński, 1926) comb. n., *Sh. szaboii* (Chyzer, 1891) comb. n., *Sh. wangi* (Song and Zhou, 1986) comb. n., and *Sh. zherikhini* (Marusik 1988) comb. n.], ***Simziella* gen. n.** [*Si. annexa* (Gertsch and Mulaik, 1936) comb. n., *Si. canadas* (Wunderlich, 2022) comb. n., *Si. cebolla* (Ivie, 1947) comb. n., *Si. dunini* (Danilov, 2000) comb. n., *Si. major* (Menge, 1869) comb. n., *Si. palmgreni* (Marusik and Fritzen, 2011) comb. n., *Si. paramajor* (Danilov, 2000) comb. n., *Si. sancta* (Gertsch, 1946) comb. n., *Si. sotnik* (Danilov, 1994) comb. n., *Si. sylvania* (Chamberlin and Ivie, 1944) comb. n., *Si. tridentata* (Bishop and Ruderman, 1946) comb. n., *Si. tucsona* (Chamberlin, 1948) comb. n., *Si. tyshchenkoi* (Marusik, 1988) comb. n., *Si. tyshchenkoi wrangeliana* (Marusik, 1988) comb. n., and *Si. teideensis* (Wunderlich, 1992) comb. n.], ***Spagnius* gen. n.** [*Sp. albopilosa* (Franganillo, 1936) comb. n., *Sp. foliaceus* (Hentz, 1850) comb. n., *Sp. jacalana* (Gertsch and Davis, 1937) comb. n., and *Sp. nebraska* (Gertsch, 1946) comb. n.], *Sudesna* Lehtinen, 1967, *Tahuantina* Lehtinen, 1967, *Thallumetus* Simon, 1893, *Tivyna* Chamberlin, 1948 [*Ti. moaba* (Ivie, 1947), *Ti. pallida* (Keyserling, 1887), *Ti. petrunkevitchi* (Gertsch and Mulaik, 1940), *Ti. sonora* (Gertsch and Davis, 1942) comb. n., and *Ti. spatula* (Gertsch and Davis, 1937)], ***Tolkienus* gen. n.** [*To. armatus* (Thorell, 1875) comb. n., *To. bellans* (Chamberlin, 1919) comb. n., *To. bellans hatchi* (Jones, 1948) comb. n., *To. estoc* sp. n., *To. longispina* (Emerton, 1888) comb. n., and *To. ottoii* (Marusik and Koponen, 2017) comb. n.], and *Viridictyna* Forster, 1970.

Genus *Arethyna* Cala-Riquelme gen. n.

urn:lsid:zoobank.org:act:28788E69-D7C0-4F87-8527-0129BC37E9DA.

Type species: Dictyna volucripes Keyserling, 1881.

Material examined: Dictyna coloradensis: USA, Colorado, El Paso Co., Colorado Springs, pre-1919 publication date, Coll: R.V. Chamberlin (Holotype, 1 male, MCZ-IZ15151). USA, Colorado, Electra Lake, 1.vii.1919, Coll. F.E. Lutz (1 female, AMNH). *Dictyna secuta*: Mexico, Baja California, Gulf of California, San Estaban Island, 19.iv.1921, Coll. Joseph C. Chamberlin, California Academy of Sciences Expedition (Holotype, MCZ-IZ15594). *Dictyna volucripes*: USA, Massachusetts, [no specific locality data], pre-1881 publication date, [(type status

needs research), 1 male, MCZ-IZ23523]. USA, Massachusetts (no specific locality data), pre-1881 publication date, [(type status needs research), 1 female, MCZ-IZ43955].

Etymology: The generic epithet is derived from 'Areth-', in honour of Magdalena Aretha Louise Franklin (Aretha Franklin), an American singer, songwriter and pianist with over 75 million records sold worldwide and 112 singles on the US Billboard charts, and *-yna*, a rhyming morph of the last two syllables of *Dictyna*, another genus in the family; gender feminine.

Diagnosis: Males of *Arethyna* gen. n. (Figs 65A-F 66A-C) resemble *Dictyna* s.s. by the thin embolus without distal modifications that converge inside the conductor (Figs 65D-F, 66D-E; Chamberlin and Gertsch 1958: pl. 26, figs 7, 10), and *Simziella* gen. n. by the embolus coiled 275°, originating proximo-prolateral from the bulb (Fig. 65D-F, 66D-E; Chamberlin and Gertsch 1958: pl. 26, figs 1, 5, 8, 10, 12); however, it can be distinguished from *Dictyna* s.s., *Simziella* gen. n., and other Dictynidae s.s. by the conductor upper arm longer than the conductor lower arm, thin, coiled no more than 90°, and separated from the tegulum by its width (Fig. 65D-F; Chamberlin and Gertsch 1958: pl. 26, figs 1, 5, 8, 10, 12); the conductor lower arm coiled no more than 45°, with the tip directed retrolateral-proximal, the paraconductor process conspicuous (Fig. 66F), and with the conductor locking mechanism as long as conductor tip; dictynid process conspicuous, shorter than the tibia length (Fig. 65D-F; Chamberlin and Gertsch 1958: pl. 26, figs 3, 6, 9, 13). Females can be distinguished by having a conspicuous membranous sac; the copulatory duct forming loops close to the copulatory opening, and the SS/AG.

List of included species: *Arethyna coloradensis* (Chamberlin, 1919) comb. n., *Ar. idahoana* (Chamberlin and Ivie, 1933) comb. n., *Ar. osceola* (Chamberlin and Gertsch, 1958) comb. n., *Ar. peon* (Chamberlin and Gertsch, 1958) comb. n., *Ar. personata* (Gertsch and Mulaik, 1936) comb. n., *Ar. saltona* (Chamberlin and Gertsch, 1958) comb. n., *Ar. secuta* (Chamberlin, 1924) comb. n., *Ar. sierra* (Chamberlin, 1948) comb. n., *Ar. ubsunurica* (Marusik and Koponen, 1998) comb. n., *Ar. volucripes* (Keyserling, 1881) comb. n., and *Ar. volucripes volucripoides* (Ivie, 1947) comb. n.

**Genus *Califorenigma* Cala-Riquelme, Gorneau,
Esposito gen. n.**

urn:lsid:zoobank.org:act:88E0C01A-AE03-4F70-A1E3-5896FAE6A299.

Type species: *Heterodictyna linsdalei* Chamberlin and Gertsch, 1958, currently *Nigma linsdalei* (Chamberlin and Gertsch, 1958).

Type material: *Nigma linsdalei*: USA, California, Monterey Co., Hastings Natural History Reserve, 16.vii.1940, Coll. J.M. Linsdale (Holotype, 1 male, AMNH). USA, California, Monterey Co., Hastings Natural History Reserve, 16.vii.1940, Coll. J.M. Linsdale (Allotype, 1 female, AMNH).

Material examined: USA, California, Monterey Co., Hastings Natural History Reserve, 36°22'N 121°33'W, date unknown, Coll. J.M. Linsdale (1 male, 1 female, 1 imm., CASENT9122646). USA, California, Alameda Co., Berkeley, Lawrence Radiation Laboratory, 4.v.1964, Coll. P.R. Craig (1 male, CASENT9122758). USA, California, Alameda Co., Berkeley, Lawrence Radiation Laboratory, 3.vi.1964, Coll. P.R. Craig (1 male, CASENT9122590). USA, California, Santa Barbara Co., Channel Islands Research Station, 14.vi.1964, Coll. D. Rentz, D. Weissman (1 male, CASENT9122674). USA, California, Santa Barbara Co., Channel Islands Research Station, 21.v.1964, Coll. D. Rentz, D. Weissman (1 male, CASENT9122730). USA, California, San Mateo Co., Edgewood Park (NE), 26.iv.1992, Coll. D. Ubick, mixed woodland, shaking oak foliage (1 male, CASENT9122730). USA, California, San Francisco Co., San Francisco, Golden Gate Park 37°46'14"N 122°27'47"W, 19.v.2023. Coll. A.M. Al-Jamal, J.A. Gorneau, K.O. Montana (1 male, CASENT9112276).

Etymology: The genus epithet is a combination of California, where the genus is endemic, and 'enigma', a play on words referencing the enigmatic features of this species as well as *Nigma*, the name of the genus in which the type species was formerly placed; gender feminine.

Diagnosis: The male of *Califorenigma* gen. n. (Figs 27A-F, 48A-D, 49A-D, 50A-F, 51A, B) resembles *Nigma* by lacking the dictynid process (Figs 28F, 51A, B); however, it can be distinguished from *Nigma* and other Dictynidae s.s. by having a spermaphor loop (Chamberlin and Gertsch 1958: pl. 10, fig. 12) (spermaphor loop absent in *Ajmonia* and *Nigma*); end of the conductor coiled in the same plane, perpendicular to the longitudinal axis of the bulb, with the conductor scaly tip three times longer than wide (Figs 28A-D, 50E; Chamberlin and Gertsch 1958: pl. 10, fig. 12); cymbium with a dorso-posterior extension, conformed by the cavity of a dorsal extension of the cymbium (Figs 27E, 49B-D, 51A, B; Chamberlin and Gertsch 1958: pl. 10, fig. 9) (present in *Dictynomorpha*, see: Esysunin et al. 2017); patella convex with a conspicuous, long lobe on the retrolateral side (Figs 27E, 49A, C, D, 50E, 51B; Chamberlin and Gertsch 1958: pl. 10, figs 9, 12, Griswold et al. 2005: fig. 176A). Females can be distinguished by having a slightly elevated area on the epigyne with a pair of round, very shallow and indistinct atria separated by a broad septum (Chamberlin and Gertsch 1958: pl. 10, fig. 11, Esysunin et al. 2017).

Remarks: The genus *Nigma* is a substitute name for *Heterodictyna* Dahl, 1924. Esysunin et al. (2017), based on Wunderlich (2011), argued that *N. conducens* (O. Pickard-Cambridge, 1876), *N. laeta* (Spassky, 1952), *N. longipes* (Berland, 1914), and *N. linsdalei* have been incorrectly placed within the genus *Nigma*. We found sufficient evidence to conclude that *N. linsdalei* is a new genus here proposed by us as *Califorenigma* gen. n. *Heterodictyna linsdalei* was initially considered *Ajmonia* or *Dictynomorpha* by Lehtinen (1967: 210). Some morphological traits of the male palp of *C. linsdalei* (Chamberlin and Gertsch, 1958) comb. n. are similar to those of *Ajmonia capucina* (Schenkel, 1936), *A. lehtineni* Marusik and Koponen, 1998, and *A. psittacea* (Schenkel, 1936); however, these can be differentiated by the shape and configuration of the

patellar process (see: Chamberlin and Gertsch 1958: 48, figs 9, 12, Griswold et al. 2005: fig. 176A, Esyunin et al. 2017), the modification of the palpal tibial apophysis (Esyunin et al. 2017), and the presence of a developed tegular spermaphor loop. Brignoli (1983: 515) did not accept Lehtinen's proposal and transferred the species to *Nigma*. Although the WSC (2024) formally accepts *N. linsdalei* as a valid name, Esyunin et al. (2017) indicated certain morphological characteristics that differentiate the species from other congeners of *Nigma s.s.* As mentioned in the etymology section, this monotypic genus is endemic to California, generally found within 75 km of the coast. The majority of endemic arachnids in California are either Opiliones Sundevall, 1833 (especially the Phalangodidae Simon, 1879) or spiders in Mygalomorphae Pocock, 1892 (Harrison 2013). This work adds *Califorenigma* to the endemic Araneomorphae genera in California, which also includes the endemic genera *Lutica* Marx, 1891 (Zodariidae Thorell, 1881) and *Titiotus* Simon, 1897 (Zoropsidae Bertkau, 1882) (Harrison 2013).

List of included species: *Califorenigma linsdalei* (Chamberlin and Gertsch, 1958) comb. n.

Genus *Dictyna* Sundevall, 1833 s.s.

Type species: *Aranea benigna* Walckenaer, 1802, currently *Dictyna arundinacea* (Linnaeus, 1758).

Material examined: *Dictyna abundans*: USA, California, Lassen Co., 2 mi N Doyle, 12.vii., Coll. C. Griswold (1 female, CASENT9118636). Mexico, Baja California, 20 km E Parador Punta Prieta, 29°03.86'N 114°02.61'W, Elev. 470 m, malaise, 26–29.iii.2014, Coll. M.E. Irwin, M.J. Sharkey (1 male, CASENT9058905). *Dictyna agressa*: USA, California, Los Angeles Co., 15 mi west of Santa Monica, 20.iii.1941, Coll. W. Ivie (Paratype, 1 male, 1 female, MNHN-AR-AR688). Mexico, Baja California, 1 km S Cataviña, Rio La Bocana, 29°43.57'N 114°42.82'W, Elev. 500 m, sandy wash near water, 26–30.iii.2014, Coll. M.E. Irwin, M.J. Sharkey (1 female, CASENT9118646). USA, California, Marin Co., San Rafael, 8 mi Park Ridge Road, 38°1.1'N 122°33.2'W, border of suburb and open space, grasses/oaks, 9.v.2015, Coll. J. Schweikert (1 female, CASENT9068332). *Dictyna alyceae*: Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Allotype, 1 male, 1 female, 1 imm., MCZ-IZ43946). Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Holotype, 1 male, MCZ-IZ20244). *Dictyna apachea*: (Paratype, 1 male, 1 female, MNHN-AR-AR671) [note: there is no collecting information given with this specimen. In Chamberlin and Ivie (1935), a holotype and allotype are mentioned, but they did not name a paratype]. *Dictyna arundinacea*: USA, Colorado, Electra Lake, 1.vii.1919, Coll. F.E. Lutz (1 male, AMNH). *Dictyna bostoniensis*: USA, Washington, Wawawai, pre-1919 publication date (Holotype, 1 female, MCZ-IZ15971). USA, Massachusetts, Boston, fence of Public Garden, 23.v.1873, Coll. James H. Emerton (Syntype, 3 male 3 female, MCZ-IZ20564). *Dictyna brevatarsus*: USA, Massachusetts, Danvers (no verbatim date data), Coll. James H. Emerton, Henry W. Winkley (Syntype, 1 male, 1 female, MCZ-IZ20588). *Dictyna cavata*: Bermuda, Grasmere, 11.vii.–4.viii.1921, Coll. E.B. Bryant (Allotype, 1 female, MCZ-IZ24758). Bermuda, Grasmere, 11.vii.–4.viii.1921,

Coll. E.B. Bryant (Holotype, 1 male, MCZ-IZ20740). Bermuda, Grasmere, 11.vii.–4.viii.1921, Coll. E.B. Bryant (Paratype, 1 female, MCZ-IZ24759). Bermuda, Grasmere, 11.vii.–4.viii.1921, Coll. E.B. Bryant (Paratype, 1 male, MCZ-IZ24760). *Dictyna cholla*: Mexico, Baja California Sur, 1 mi N Ejido Guillermo Prieto, 27°48'32"N 113°18'31"W, Elev. 150 m, ethylene glycol pitfall traps, 14.iii–19.vii.1999, Coll. R. Aalbu et al. (1 male, 1 female, CASENT9062560). USA, New Mexico, Socorro Co., Sevilleta Wildlife Refuge, 34°28'27.48"N 113°27'33.66"W, Elev. 1450 m, malaise, sandy basin of Rio Grande River, 19–24. vi.2013, Coll. M.E. Irwin (1 female, CASENT9118657). Mexico, Baja California, Cañon de Guadalupe, 32°9.77'0"N 115°46.91'0"W, Elev. 300 m, malaise, damp wash near palms, 23–31.iii.2014, Coll. M.E. Irwin, M.J. Sharkey (1 female, CASENT9118658). *Dictyna denisi*: Nigeria, Massif de l'Air, Monts Bageuzan, 1–4. ix.1947, Coll. L. Chopard & A. Villiers (Syntypes, 1 male, 1 female, MNHN-AR-AR683). *Dictyna donaldi*: Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Allotype, 1 female, MCZ-IZ44000). Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Holotype, 1 male, MCZ-IZ21112). Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Paratype, 1 male, MCZ-IZ24320). Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Paratype, 1 male, MCZ-IZ24318). Panama, Chiriqui Province, Boquete, vii.1939, Coll. Arthur M. Chickering (Paratype, 1 female, MCZ-IZ24319). *Dictyna formidolosa*: USA, North Carolina, Black Mt., N. fork Swannanoa River. 18–30.v.1903–1910 (based on information in introduction of publication), Coll. Nathan Banks (Syntype, 1 male MCZ-IZ20351). *Dictyna jacalana*: Mexico, Morelos, Cuernavaca, Salto San Anton, 18–19.ix.1976, Coll. C. Griswold, R. Jackson (1 male, CASENT9118784). Mexico, Nayarit, Nayarit, 18–19.ix.1976, Coll. S.C. Williams, K. Blair, C. Mullinex (1 male, CASENT9118822). *Dictyna kosiorowiczi*: France, Provence-Alpes-Côte d'Azur, Bouches-du-Rhône, Saintes-Maries-de-la-Mer, 1–30.vi.1913, Coll. J. and L. Berland (1 male, 1 female MNHN-AR-AR536). *Dictyna segregata*: USA, Texas, Clear Creek Woods, 9.iv.1942, Coll. Sarah E. Jones (Holotype, 1 male, MCZ-IZ22549).

Diagnosis: The males of *Dictyna s.s.* (Figs 30A–F, 31A–F, 63A–F) can be distinguished from other Dictynidae s.s. genera by the palp with a simple, thin embolus without distal modifications, coiled no more than 225°, originating prolateral distal from the bulb (Figs 31E, 57B, 63E; Chamberlin and Gertsch 1958: pl. 22, figs 5, 10, Marusik et al. 2015: fig. 26) (embolus thick and distally modified in *Emblina s.s.*, *Nopalityna* gen. n.); the dictynid process usually shorter to slightly developed, but never as long or longer than the tibia length (Fig. 30E, F; Chamberlin and Gertsch 1958: pl. 22, fig. 7, Marusik et al. 2015: fig. 26) (dictynid process absent (Figs. 25C, 26F, 27E, 47C–F) in *Ajmonia*, *Califorenigma* gen. n., *Dictynomorpha*, *Mallos*, *Mexitlia*, *Nigma*, *Thallumetus* and *Tivyna*); the conductor upper arm longer than the conductor lower arm, coiled no more than 110° (Fig. 31E; 57B; 63E; Chamberlin and Gertsch 1958: pl. 22, figs. 5, 10, Marusik et al. 2015: fig. 26); the conductor lower arm coiled more than 360°, with the tip directed prolateral proximal, the paraconductor process inconspicuous or absent, and with the conductor locking mechanism shorter

than conductor tip. Additionally, it can be distinguished by lacking a patellar apophysis and/or other modifications (present in *Californigenia* gen. n.), and a cymbial process (Figs 30A–D, 31A, B, D, F, 63E, F) (present in *Ajmonia*, *Dictynomorpha*, and *Californigenia* gen. n.). Females can be distinguished by having the first section of the copulatory duct modified and connected to a typically enlarged membranous sac; copulatory duct longer than primary spermathecae width, forming loops near the primary spermathecae; primary spermathecae reduced, as wide as or slightly wider than the widest section of the copulatory duct.

Remarks: Westring (1861) considered *Dictyna* s.l. a senior synonym of *Ergatis* Blackwall, 1841 and *Operaria* Blackwall, 1841. Chamberlin (1948) described the genus *Tosyna* Chamberlin 1948 (= *Dictyna* see: Chamberlin and Gertsch 1958) based on the morphological characteristics of *Dictyna apachea*. Several species have been described as *Dictyna* s.l., and several have been transferred to *Emblyna* s.l. *Dictyna* s.s., together with *Emblyna* s.s., continue to be tailor's drawer genera, and greater attention to morphology and molecular phylogenetics should be given in future studies. Previous phylogenetic studies have shown *Dictyna* s.l. and *Emblyna* s.l. to be polyphyletic (see: Wheeler et al. 2017, Crews et al. 2020, Gorneau et al. 2023a, Kulkarni et al. 2023). Traits such as the morphology of the embolus, conductor, cymbium, tibial apophysis, patellar apophysis, membranous sac, copulatory duct, and primary spermathecae appear to be putative synapomorphies that support the delimitation of genera.

List of included species: *Dictyna abundans* Chamberlin and Ivie, 1941, *D. alaskae* Chamberlin and Ivie, 1947, *D. albicoma* Simon, 1893, *D. albobittata* Keyserling, 1881, *D. alyceae* Chickering, 1950, *D. apachea* Chamberlin and Ivie, 1935, *D. arundinacea* (Linnaeus, 1758), *D. bostoniensis* Emerton, 1888, *D. brevitaris* Emerton, 1915, *D. cafayate* Mello-Leitão, 1941, *D. chandrai* Tikader, 1966, *D. cofete* Wunderlich, 2022, *D. columbiana* Becker, 1886, *D. cronebergi* Simon, 1889, *D. crosbyi* Gertsch and Mulaik, 1940, *D. dauna* Chamberlin and Gertsch, 1958, *D. ectrapela* (Keyserling, 1886), *D. fluminensis* Mello-Leitão, 1924, *D. guineensis* Denis, 1955, *D. hamifera* Thorell, 1872, *D. kosiorowiczi* Simon, 1873, *D. laeviceps* Simon, 1911, *D. linzhiensis* Hu, 2001, *D. livida* (Mello-Leitão, 1941), *D. marilina* Chamberlin, 1948, *D. moctezuma* Gertsch and Davis, 1942, *D. namulinensis* Hu, 2001, *D. navajoa* Gertsch and Davis, 1942, *D. pictella* Chamberlin and Gertsch, 1958, *D. pusilla* Thorell, 1856, *D. quadrispinosa* Emerton, 1919, *D. ranchograndei* Caporiacco, 1955, *D. saepei* Chamberlin and Ivie, 1941, *D. similis* Keyserling, 1878, *D. simoni* Petrunkevitch, 1911, *D. sinaloa* Gertsch and Davis, 1942, *D. siniloanensis* Barrion and Litsinger, 1995, *D. tarda* Schmidt, 1971, *D. togata* Simon, 1904, *D. tristis* Spassky, 1952, *D. trivirgata* Mello-Leitão, 1943, *D. tullgreni* Caporiacco, 1949, *D. turbida* Simon, 1905, *D. uncinata* Thorell, 1856, *D. uvs* Marusik and Koponen, 1998, *D. vittata* Keyserling, 1883, *D. vultuosa* Keyserling, 1881, and *D. yongshun* Yin, Bao and Kim, 2001.

Genus *Emblyna* Chamberlin, 1948 s.s.

Type species: *Dictyna completa* Chamberlin and Gertsch, 1929, currently *Emblyna completa* (Chamberlin and Gertsch, 1929).

Type material: USA, Utah, Moab, 15.iv.1928, Coll. A.M. Woodbury (Holotype, 1 female, AMNH).

Material examined: *Emblyna altamira*: USA, Massachusetts, Duxbury, 4.vi.21, Coll. E.B. Bryant (1 male, MCZ-IZ20606). *Emblyna andesiana*: Ecuador, Piñán, 1.i–32.xii.1903, Coll. P. Rivet (Lectotype, 1 male, MNHN-AR-AR5292). Ecuador, Tungurahua Prov., Ambato, 9–14.vi.1943, Coll. H. Exline-Frizzell, D.L. Frizzell (3 males, 19 females, CASENT9118818). *Emblyna angulata*: USA, Massachusetts, Hyde Park (no verbatim date data), probably 1900–15, Coll. James H. Emerton (Syntype, 1 male, MCZ-IZ20279). *Emblyna annulipes*: USA, Washington, Olympia (no verbatim date data) (1 male, MCZ-IZ29974). *Emblyna borealis cavernosa*: USA, Washington, Spokane, vi.45, Coll. E.D. Parmer (Holotype, 1 male, MCZ-IZ20743). *Emblyna completa*: USA, California, Plumas Co., Sierra Valley Marsh, Elev. 4900 ft., pitfall traps, 12.viii.1976, Coll. K. Richardson (1 male, CASENT9118615). USA, Nevada, Reno, vi.1940, Coll. R.V. Chamberlin (1 male, AMNH). USA, Nevada, Reno, vi.1940, Coll. R.V. Chamberlin = (1 female, AMNH). *Emblyna cruciata*: USA, Connecticut, New Haven, pre-1888 publication date, Coll. James H. Emerton (Syntype, 1 male, MCZ-IZ151460). *Emblyna hentzi*: USA, Michigan, St. Clair, 3.viii.36, Coll. M.H. Hatch (Exline Coll.) (1 male, MCZ-IZ20983). USA, Michigan, St. Clair, 3.viii.36, Coll. M.H. Hatch (Exline Coll.) (1 female, MCZ-IZ24761). *Emblyna maxima*: USA, New York, Ithaca, 1888–90 (from publication), Coll. Nathan Banks (Holotype, 1 female, MCZ-IZ22012). *Emblyna olympiana*: USA, Washington, Edmunds Lake, 2.vi.35, Coll. M.H. Hatch (Exline Coll.) (1 female, MCZ-IZ24762). USA, Washington, Edmunds Lake, 2.vi.35, Coll. M.H. Hatch (Exline Coll.) (1 male, MCZ-IZ21254). USA, Washington, Olympia, [no verbatim date data] (Holotype, 1 male, MCZ-IZ29975). *Emblyna roscida*: USA, Connecticut, New Haven. 15.v.pre-1888 publication date, Coll. James H. Emerton (1 male, MCZ-IZ22935).

Diagnosis: Males of *Emblyna* s.s. (Figs 58D, 59A–F) can be distinguished from other Dictynidae s.s. by having a thick palpal embolus that is distally modified (Figs 58D, 59E, F; Chamberlin and Gertsch 1958: pl. 22, figs 2, 3, 8, 12) (embolus thin and unmodified in *Dictyna* s.s.); the dictynid process conspicuous (Fig. 59E, F; Chamberlin and Gertsch 1958: pl. 42, fig. 4) (dictynid process absent in *Tivyina* and *Mallos*); conductor lower arm with a paraconductor process in addition to the conductor scaly tip, coiled no more than 360° (Figs 58D, 59E). Females can be distinguished by the wide copulatory duct, usually up to four times longer than the primary spermatheca, connected to an enlarged membranous sac; the primary spermathecae are reduced, as wide as or slightly wider than the widest section of the copulatory duct.

List of included species: *Emblyna acoreensis* Wunderlich, 1992, *E. aiko* (Chamberlin and Gertsch, 1958), *E. altamira* (Gertsch and Davis, 1942), *E. ampla* Chamberlin, 1948, *E. angulata* (Emerton, 1915), *E. annulipes* (Blackwall, 1846), *E. ardea* (Chamberlin and Gertsch, 1958), *E. artemisia* (Ivie, 1947), *E. borealis* (O.Pickard-Cambridge, 1877), *E. borealis cavernosa* (Jones, 1947), *E. branchi* (Chamberlin and Gertsch, 1958), *E. brevidens* (Kulczyński, 1897), *E. budarini* Marusik, 1988, *E.*

burjatica (Danilov, 1994), *E. callida* (Gertsch and Ivie, 1936), *E. capens* Chamberlin, 1948, *E. cavata* (Jones, 1947) comb. n., *E. chitina* (Chamberlin and Gertsch, 1958), *E. completa* (Chamberlin and Gertsch, 1929), *E. completeoides* (Ivie, 1947), *E. consulta* (Gertsch and Ivie, 1936), *E. cornupeta* (Bishop and Ruderman, 1946), *E. coweta* (Chamberlin and Gertsch, 1958), *E. crocana* Chamberlin, 1948, *E. decapri* (Kaston, 1945), *E. evicta* (Gertsch and Mulaik, 1940), *E. florens* (Ivie and Barrows, 1935), *E. formicaria* Baert, 1987, *E. hentzi* (Kaston, 1945), *E. horta* (Gertsch and Ivie, 1936), *E. hoya* (Chamberlin and Ivie, 1941), *E. joaquina* (Chamberlin and Gertsch, 1958), *E. lina* (Gertsch, 1946), *E. linda* (Chamberlin and Gertsch, 1958), *E. manitoba* (Ivie, 1947), *E. marissa* (Chamberlin and Gertsch, 1958), *E. melva* (Chamberlin and Gertsch, 1958), *E. nanda* (Chamberlin and Gertsch, 1958), *E. oasa* (Ivie, 1947), *E. palomara* Chamberlin, 1948, *E. peragrata* (Bishop and Ruderman, 1946), *E. pinalia* (Chamberlin and Gertsch, 1958), *E. piratica* (Ivie, 1947), *E. reticulata* (Gertsch and Ivie, 1936), *E. roscida* (Hentz, 1850), *E. saylori* (Chamberlin and Ivie, 1941), *E. scotta* Chamberlin, 1948, *E. seminola* (Chamberlin and Gertsch, 1958), *E. shasta* (Chamberlin and Gertsch, 1958), *E. shoshonea* (Chamberlin and Gertsch, 1958), *E. stulta* (Gertsch and Mulaik, 1936), *E. sublatoides* (Ivie and Barrows, 1935), *E. suwaneia* (Gertsch, 1946), and *E. zaba* (Barrows and Ivie, 1942).

Genus *Eriena* Cala-Riquelme, Crews, Esposito gen. n.

urn:lsid:zoobank.org:act:A178E265-F734-4CA1-rnA42E-1A3215EA6CE6.

Type species: Dictyna minuta Emerton, 1888.

Type material: USA, Rhode Island, Providence, 21.viii.1871, Coll. James H. Emerton (Holotype, 1 male, MCZ-IZ22095).

Etymology: The generic epithet refers to the Indigenous Erie people, also known as the Eriechronon, Yenresh, Erielhonan, Eriez, Nation du Chat, and Riquéronon, historically living on the south shore of Lake Erie in the Northeastern USA; gender feminine.

Diagnosis: The males of *Eriena* gen. n. can be distinguished from other Dictynidae s.s. by having a short, unmodified embolus that originates prolaterally distal on the bulb (Chamberlin and Gertsch 1958: pl. 19, fig. 7) (embolus thick and distally modified in *Emblyna* s.s.); the dictynid process with tubercle inconspicuous or absent (Chamberlin and Gertsch 1958: pl. 19, figs 5, 6) (dictynid process absent in *Tivyna*, *Mallos*, *Ajmonia*, *Dictynomorpha*, *Nigma*, and *Califorenigma* gen. n.); conductor lower arm three or more times longer than the conductor upper arm, coiled no more than 180°, and with a long and thin conductor scaly tip, (Chamberlin and Gertsch 1958: pl. 19, fig. 4). Females can be distinguished by having the primary spermathecae slightly wider to two times wider than the copulatory duct length, connected to a membranous sac two times as wide as the primary spermathecae.

List of included species: Eriena minuta (Emerton, 1888) comb. n. and *E. mora* (Chamberlin and Gertsch, 1958) comb. n.

Genus *Khalotyna* Cala-Riquelme, Alequín, Esposito gen. n.

urn:lsid:zoobank.org:act:43122FE3-C797-48C6-8291-DC4C1EDB6CD6.

Type species: Dictyna calcarata Banks, 1904.

Type material: USA, California, Los Angeles Co., San Pedro, pre-1904 publication date, Coll. T.D.A. Cockerell, Nathan Banks (Holotype, 1 male, MCZ-IZ20638).

Material examined: Dictyna calcarata: USA, Texas, Brewster Co., Big Bend, Boquillas Canyon, 9.vii.2021, Coll. M. Pleisher (6 females, CASENT9087232). USA, Arizona, Pinal Co., Gila R. Management Area 'The Shores', 2 km N Winkelman, 33°10.26'N 110°44.32'W, Elev. 600 m, dry outwash, malaise, 17.iv.2015, Coll. M.E. Irwin (1 male, CASENT9087249). USA, California, Los Angeles Co., 1–31.x.1965, Coll. F. Delsue (1 male, CASENT9118632). USA, California, Los Angeles Co., Long Beach, 25.vii.1963, Coll. W.D. Stockton (1 female, CASENT9118640). Mexico, Baja California, Cañon de Guadalupe, 32°09.28'N 115°47.42'W, Elev. 370 m, upper canyon near pool with reeds, palms, 23–31.iii.2014, Coll. M.E. Irwin, M.J. Sharkey (1 male, 4 females, 1 imm., CASENT9118644). Same as previous, Elev. 380 m, malaise, upper canyon, damp sandy wash (3 males, 3 females, 5 imm., CASENT9118654). USA, California, Kern Co., Delano, 35°46'12.0"N 119°12'36.0"W, 18.iv.2010, Coll. D.P. Carroll (1 male, CASENT9056276). USA, Arizona, Cochise Co., 1429 Franklin Street, 31°24'23"N 109°55'57"W, Elev. 1585 m, malaise, 7–18.v.2014, Coll. A.S. Menke (1 male, CASENT9058902). USA, Arizona, Pima Co., Vail, Mountain Creek Ranch, 32°04.99'N 110°39.56'W, Elev. 1100 m, malaise, small dry wash, 18–30.iv.2014, Coll. M.E. Irwin (1 male, CASENT9118569). Mexico, Yucatan, Izamal, 1–31.vii.1981, Coll. C. Gold (1 female, CASENT9118814).

Etymology: The genus epithet is named in honour of Magdalena Carmen Frida Khalo y Calderon (Frida Khalo), a Mexican painter known for employing a naïve folk art style to explore questions of identity in Mexican society. It is combined with *-yna*, a rhyming morph of the last two syllables of *Dictyna* where the type species was originally placed; gender feminine.

Diagnosis: Males of *Khalotyna* gen. n. (Fig. 64A–F) can be distinguished from other Dictynidae s.s. by having the conductor upper arm three or more times longer than the retrolateral arm, following the path of the tegulum prolaterally, extending well beyond it apically (Fig. 64D, F; Chamberlin and Gertsch 1958: pl. 17, fig. 1) (present in *Purplecornia* gen. n.; absent in *Dictyna* s.s.; *Emblyna* s.s.); embolus thin, originating from the proximal to slightly prolateral part of the bulb, coiled 360° (Fig. 64D; Chamberlin and Gertsch 1958: pl. 17, fig. 1, 3); conductor scaly tip directed retrolaterally (Fig. 64D; Chamberlin and Gertsch 1958: pl. 17, fig. 1); the dictynid process with tubercle two or more times longer than the tibia (Fig. 64D, E; Chamberlin and Gertsch 1958: pl. 17, figs 1, 4). Females can be distinguished from other congeners by having a looped copulatory duct that is ten or more times longer than the primary spermathecae width; SS/AG conspicuous.

Table 2. The genera of Argyronetidae stat. reinst., Lathyidae fam. n., and Dictynidae s.s. and their distribution. Formerly Dictynidae s.l. genera that are transferred to other families are also included. Zoogeographic distributions assigned by [Gorneau et al. \(2023b\)](#), loosely following [Morrone \(2014, 2015\)](#), distinguishes the Andean region from the Neotropical region. To avoid confusion of zoogeographic regions that would be nested within a historical biogeographic region (e.g. Andean, Caribbean), these regions are listed in parentheses.

Family	Genera	Distribution
Argyronetidae stat. reinst.	<i>Altella</i> Simon, 1884	Palearctic, Oriental
Argyronetidae stat. reinst.	<i>Arctella</i> Holm, 1945	Palearctic, Oriental, Nearctic
Argyronetidae stat. reinst.	<i>Argenna</i> Thorell, 1870	Palearctic, Oriental, Nearctic, Neotropical
Argyronetidae stat. reinst.	<i>Argyroneta</i> Latreille, 1804	Palearctic, Oriental
Argyronetidae stat. reinst.	<i>Chaerea</i> Simon, 1884	Palearctic
Argyronetidae stat. reinst.	<i>Devade</i> Simon, 1884	Palearctic
Argyronetidae stat. reinst.	<i>Hackmania</i> Lehtinen, 1967	Palearctic, Nearctic
Argyronetidae stat. reinst.	<i>Iviella</i> Lehtinen, 1967	Nearctic
Argyronetidae stat. reinst.	<i>Mizaga</i> Simon, 1898	Palearctic, Ethiopian
Argyronetidae stat. reinst.	<i>Paratheuma</i> Bryant, 1940	Palearctic, Nearctic, Neotropical
Argyronetidae stat. reinst.	<i>Saltonia</i> Chamberlin and Ivie, 1942	Nearctic
Argyronetidae stat. reinst.	<i>Tricholathys</i> Chamberlin and Ivie, 1935	Palearctic, Nearctic
Lathyidae fam. n.	<i>Afrolathys</i> gen. n.	Ethiopian
Lathyidae fam. n.	<i>Analtella</i> stat. reinst.	Nearctic
Lathyidae fam. n.	<i>Andronova</i> gen. n.	Nearctic, Palearctic, Oriental, Ethiopian
Lathyidae fam. n.	<i>Asialathys</i> gen. n.	Oriental
Lathyidae fam. n.	<i>Bannaella</i> Zhang and Li, 2011	Palearctic, Oriental
Lathyidae fam. n.	<i>Denticulathys</i> gen. n.	Ethiopian
Lathyidae fam. n.	<i>Langlibaitiao</i> Lin and Li, 2024	Oriental
Lathyidae fam. n.	<i>Lathys</i> Simon, 1885 s.s.	Palearctic, Oriental, Nearctic, Neotropical
Lathyidae fam. n.	<i>Scotolathys</i> Simon, 1885 s.s.	Palearctic, Nearctic, Oriental
Lathyidae fam. n.	<i>Tolokonniella</i> gen. n.	Palearctic
Dictynidae s.s.	<i>Adenodictyna</i> Ono, 2008	Palearctic, Oriental
Dictynidae s.s.	<i>Ajmonia</i> Caporiacco, 1934	Palearctic, Oriental
Dictynidae s.s.	<i>Anaxibia</i> Thorell, 1898	Oriental, Ethiopian
Dictynidae s.s.	<i>Arangina</i> Lehtinen, 1967	Novozelandic, Australian
Dictynidae s.s.	<i>Archaeodictyna</i> Caporiacco, 1928	Palearctic, Ethiopian, Oriental
Dictynidae s.s.	<i>Arethyna</i> gen. n.	Nearctic
Dictynidae s.s.	<i>Argennina</i> Gertsch and Mulaik, 1936	Nearctic
Dictynidae s.s.	<i>Atelolathys</i> Simon, 1892	Oriental
Dictynidae s.s.	<i>Banaidja</i> Lehtinen, 1967	Polynesian
Dictynidae s.s.	<i>Brigittea</i> Lehtinen, 1967	Palearctic, Oriental, Ethiopian
Dictynidae s.s.	<i>Califorenigma</i> gen. n.	Nearctic
Dictynidae s.s.	<i>Callevophthalmus</i> Simon, 1906	Australian
Dictynidae s.s.	<i>Dictyna</i> Sundevall, 1833 s.s.	Neotropical (incl. Andean), Nearctic, Palearctic, Oriental, Palearctic, Ethiopian
Dictynidae s.s.	<i>Dictynomorpha</i> Spassky, 1939	Palearctic
Dictynidae s.s.	<i>Emblyna</i> Chamberlin, 1948 s.s.	Nearctic, Palearctic, Neotropical
Dictynidae s.s.	<i>Eriena</i> gen. n.	Nearctic
Dictynidae s.s.	<i>Helenactyna</i> Benoit, 1977	Ethiopian
Dictynidae s.s.	<i>Khalotyna</i> gen. n.	Nearctic
Dictynidae s.s.	<i>Kharitonovia</i> Esyunin et al., 2017	Palearctic
Dictynidae s.s.	<i>Mallos</i> O.Pickard—Cambridge, 1902	Nearctic, Neotropical
Dictynidae s.s.	<i>Marilynia</i> Lehtinen, 1967	Palearctic
Dictynidae s.s.	<i>Mashimo</i> Lehtinen, 1967	Ethiopian
Dictynidae s.s.	<i>Mexitlia</i> Lehtinen, 1967	Nearctic, Neotropical
Dictynidae s.s.	<i>Myanmardictyna</i> Wunderlich, 2017	Oriental
Dictynidae s.s.	<i>Nigma</i> Lehtinen, 1967	Oriental, Ethiopian, Palearctic
Dictynidae s.s.	<i>Nopalityna</i> gen. n.	Nearctic, Neotropical

Table 2. Continued

Family	Genera	Distribution
Dictynidae s.s.	<i>Pangunus</i> gen. n.	
Dictynidae s.s.	<i>Paradictyna</i> Forster, 1970	Novozelandic
Dictynidae s.s.	<i>Penangodyna</i> Wunderlich, 1995	Oriental
Dictynidae s.s.	<i>Phantyna</i> Chamberlin, 1948	Neotropical, Nearctic
Dictynidae s.s.	<i>Purplecornia</i> gen. n.	Nearctic, Neotropical
Dictynidae s.s.	<i>Rhion</i> O.Pickard—Cambridge, 1871	Oriental
Dictynidae s.s.	<i>Shango</i> Lehtinen, 1967	Ethiopian
Dictynidae s.s.	<i>Shikibutyna</i> gen. n.	Palearctic, Oriental
Dictynidae s.s.	<i>Simziella</i> gen. n.	Nearctic, Palearctic, Oriental
Dictynidae s.s.	<i>Spagnius</i> gen. n.	Nearctic
Dictynidae s.s.	<i>Sudesna</i> Lehtinen, 1967	Palearctic, Oriental
Dictynidae s.s.	<i>Tahuantina</i> Lehtinen, 1967	Neotropical (Andean only)
Dictynidae s.s.	<i>Thallumetus</i> Simon, 1893	Nearctic, Neotropical (incl. Andean)
Dictynidae s.s.	<i>Tivyna</i> Chamberlin, 1948	Nearctic, Neotropical (incl. Caribbean)
Dictynidae s.s.	<i>Tolkienus</i> gen. n.	Nearctic, Palearctic
Dictynidae s.s.	<i>Viridictyna</i> Forster, 1970	Novozelandic
Hahniidae	<i>Clitistes</i> Simon, 1902 = <i>Cybaeolus</i> Simon, 1884	Neotropical (Andean only)
Macrobnidae	<i>Aebutina</i> Simon, 1892	Neotropical
<i>Incertae sedis</i>	<i>Tandil</i> Mello-Leitão, 1940	Neotropical
<i>Incertae sedis</i>	<i>Qiyunia</i> Song and Xu, 1989	Oriental, Palearctic
<i>Nomen dubium</i>	<i>Hoplolathys</i> Caporiacco, 1947	Ethiopian

List of included species: *Khalotyna calcarata* (Banks, 1904) comb. n.

Genus *Nopalityna* Cala-Riquelme and Esposito gen. n.

urn:lsid:zoobank.org:act:69F50B66-7676-403A-B08D-DED9A01D1869.

Type species: *Theridion sublatum* Hentz, 1850, currently *Emblyna sublata* (Hentz, 1850).

Type material: USA, Virginia, Falls Church (no verbatim date data), Coll. Nathan Banks (Neotype, 1 male, 1 female, MCZ-IZ23186).

Material examined: *Dictyna francisca*: USA, California, Siskiyou Co., Juanita Lake Campground, 23.55 km SW Dorris, 41°49.077'0"N 122°07.440'0"W, Elev. 1500 m, dry second growth coniferous forest, 9.viii.2008, Coll. F. Álvarez Padilla, A. Carmichael, D. Dimitrov., C. Griswold, G. Hormiga and A. Saucedo (1 female, CASENT9031870). *Emblyna sublata*: USA, New York, Ithaca, 1888–1890, April and in summer (from publication), Coll. Nathan Banks (1 male, 3 females, MCZ-IZ21022). USA, New York, Ithaca, 1888–90 (from publication), Coll. Nathan Banks (1 female, MCZ-IZ21132). *Emblyna uintana*: USA, Utah, Uintah Mountains, Chalk Creek, pre-1919 publication date, Coll. R.V. Chamberlin (1 male, 1 female, MCZ-IZ25183). USA, Utah, Uintah Mountains, Chalk Creek, pre-1919 publication date, Coll. Ralph V. Chamberlin (Holotype, 1 female, MCZ-IZ15154).

Etymology: The generic name refers to nopalitos, diced prickly pear cactus, a gastronomic treasure of Mexico, with the addition of the *-yna* suffix, a rhyming morph of the last two syllables of *Emblyna* where the type species was originally placed; gender feminine.

Diagnosis: Males of *Nopalityna* gen. n. (Figs 29A–C, 58F) can be distinguished from other Dictynidae s.s. by the embolus with one or two long branches, usually flattened, that converge inside the conductor, unmodified at the tip (Figs 29A–C, 58F; Chamberlin and Gertsch 1958: pl. 39, figs 3, 4, 7, 8, 11, 12) (embolus, thick and distally modified in *Emblyna* s.s.); a wide conductor, usually inflated at the base (Figs 29A–C, 58F; Chamberlin and Gertsch 1958: pl. 39, figs 1, 5, 6, 9, 10, 13); and the dictynid process with a short to inconspicuous tubercle (Chamberlin and Gertsch 1958: pl. 39, figs 3, 4, 7, 8, 11, 12) (dictynid process absent in *Tivyna*, *Mallos*, *Ajmonia*, and *Shango*). Females can be distinguished by having a developed, globose, membranous extension of the proximal copulatory duct (Figs 16D–F; Chamberlin and Gertsch 1958: pl. 38, figs 7, 8); the copulatory duct uncoiled; and the primary spermathecae elongated.

List of included species: *Nopalityna francisca* (Bishop and Ruderman, 1946) comb. n., *N. jonesae* (Roewer, 1955) comb. n., *N. orbiculata* (Jones, 1947) comb. n., *N. sublata* (Hentz, 1850) comb. n., *N. suprenans* (Chamberlin and Ivie, 1935) comb. n., *N. uintana* (Chamberlin, 1919) comb. n.

Genus *Pangunus* Cala-Riquelme gen. n.

urn:lsid:zoobank.org:act:7E62AF72-3860-48F9-8D50-BB9A06D04A55.

Type species: Emblyna kaszabi Marusik and Koponen, 1998.

Material examined: Emblyna kaszabi: Mongolia, Uldzit Somon, 23.viii.1975, Coll. J. Halgos (Holotype, 1 male, SMF332; Paratype, 3 female, SNM).

Etymology: The generic epithet refers to Pangu (Pan-Koo), a Chinese mythology and Taoism figure; gender masculine.

Diagnosis: Males of **Pangunus gen. n.** can be distinguished from other Dictynidae s.s. by the embolus coiled approximately 720°, originating proximal to proximal-prolateral from the bulb (Marusik and Koponen 1998: 80, figs 10, 11, Marusik et al. 2006: 355, fig. 6).

List of included species: Pangunus kaszabi (Marusik and Koponen 1998) comb. n., *P. umai* (Tikader, 1966) comb. n., *P. xizangensis* (Hu and Li, 1987) comb. n.

Genus *Purplecorna* Cala-Riquelme and Esposito gen. n.

urn:lsid:zoobank.org:act:6B4199FC-50F8-44B5-875F-484F841FF54A.

Type species: Dictyna incredula Gertsch and Davis, 1937.

Material examined: Dictyna incredula: Peru, Paita Prov., Amotape, Chira R. Valley, 21.x.1938, Coll. D.L. Frizzell, H. Exline-Frizzell (2 males, 7 females, 5 imm., CASENT9118816). Peru, Piura Region, Sullana, N Mallares, Chira R., 4.i.1942, Coll. D. Frizzell, H. Frizzell (10 males, 9 females, 8 imm., CASENT9118828). Ecuador, from bananas, 4.i.1942, Coll. unknown (1 male, 1 female, CASENT9118830). Peru, Piura Region, Sullana, Mallares, 31.xi.1941, Coll. D.L. Frizzell, H. Exline-Frizzell (2 males, 6 females, CASENT9118832). Ecuador, Guayas Prov., Guayaquil, 15.iii.1943, Coll. Carvallio (from Mello-Leitao) (1 male, CASENT9118851). *Dictyna lecta:* Panama, El Volcan, viii.1950, Coll. Arthur M. Chickering (Holotype, 1 male, MCZ-IZ21815). *Dictyna meditata:* Cuba, La Habana Province, Havana, 1880-publication data, Coll. Baker, Nathan Banks (1 male, 1 female, MCZ-IZ21321). *Dictyna miniata:* Mexico, Baja California Sur, Gulf of California, Monserrate Island, 25.v.1921, Coll. Joseph C. Chamberlin, California Academy of Science Expedition (1 male, MCZ-IZ15596). *Dictyna terrestris:* USA, New Hampshire, Lake Winnepesaukee, Three Mile Island, 1.vi.1909, Coll. James H. Emerton (Syntype, 1 male, MCZ-IZ23261).

Etymology: The generic name refers to purple corn (in Spanish: maiz colorado or maiz morado), a variety originating in South America; gender feminine.

Diagnosis: Males of **Purplecorna gen. n.** (Figs 54A–C; 55A, B) can be distinguished from other Dictynidae s.s. by the cymbium narrow at the base, long and thin, sometimes strongly curved ventrally, and narrowed apically to a slender finger-like structure (Figs 54D–F, 55C, D; Chamberlin and Gertsch 1958: pl. 18, figs 6, 7); the conductor upper arm longer than the conductor lower arm, following the cymbium prolaterally, extending well beyond it apically (Figs 54D–F, 55C, D; Chamberlin and Gertsch 1958: pl. 18, figs 6, 7); embolus thin with the tip unmodified, coiled 360°, originating proximally to slightly prolaterally from

the bulb (Figs 54D–F, 55C, D). The female can be distinguished from other genera by the copulatory duct usually with many loops or coils, thin, but gradually widening near the primary spermathecae, more than 10 times longer than the primary spermathecae width; with the membranous sac as long as or slightly longer than the complete copulatory duct.

List of included species: Purplecorna gloria (Chamberlin and Ivie, 1944) comb. n., *P. guerrerensis* (Gertsch and Davis, 1937) comb. n., *P. incredula* (Gertsch and Davis, 1937) comb. n., *P. lecta* (Chickering, 1952) comb. n., *P. meditata* (Gertsch, 1936) comb. n., *P. miniata* (Banks, 1898) comb. n., *P. terrestris* (Emerton, 1911) comb. n.

Genus *Shikibutyna* Cala-Riquelme, Gorneau, Esposito gen. n.

urn:lsid:zoobank.org:act:5D966098-FBF3-4A39-ACF2-2E806B896EE1.

Type species: Dictyna felis Bösenberg and Strand, 1906.

Material examined: Dictyna felis: Japan, Yokohama, 15.x.1945, Coll. T. Aarons (1 female, CASENT9118672).

Etymology: The generic epithet is in honour of Murasaki Shikibu, a female Japanese writer and poet known worldwide for being the author of *Genji Monogatari*, the first novel in Japanese history and the first modern novel in the world, written in the early 11th century. The name includes the suffix *-yna* referring to the last two syllables of *Dictyna*, the genus in which the type species was originally placed; gender feminine.

Diagnosis: The male of **Shikibutyna gen. n.** (Figs 56A–F, 57A) resembles *Purplecorna* gen. n. by having a narrow, long, and thin cymbium (Figs 56D–F, 57A); the embolus tip is unmodified, coiled 360°, originating proximally to slightly prolaterally on the bulb (Figs 56D–F, 57A); however, it can be distinguished from *Purplecorna* gen. n. and other congeners by having a dictynid process (Fig. 56D–F) (dictynid process absent in *Tivyna*, *Mallos*, *Ajmonia*, and *Shango*); the embolus thick, following a curved path without loops (Figs 56D–F, 57A) (embolus thin and forming a loop close to the embolus base in *Purplecorna* gen. n., embolus thin in *Dictyna* s.s.); the conductor upper arm two or three times longer than the conductor lower arm (Figs 56D, E, 57A). The female can be distinguished from other congeners by having the copulatory duct between the copulatory opening and SS/AG thin and uncoiled; and the copulatory duct between the SS/AG and primary spermathecae wider than the primary spermathecae.

List of included species: Shikibutyna felis (Bösenberg and Strand, 1906) comb. n., *S. foliicola* (Bösenberg and Strand, 1906) comb. n., *S. guanchae* (Schmidt, 1968) comb. n., *S. mongolica* (Marusik and Koponen, 1998) comb. n., *S. procerula* (Bösenberg and Strand, 1906) comb. n., *S. schmidti* (Kulczyński, 1926) comb. n., *S. szaboi* (Chyzer, 1891) comb. n., *S. wangi* (Song and Zhou, 1986) comb. n., *S. zherikhini* (Marusik, 1988) comb. n.

Genus *Simziella* Cala-Riquelme and Alequín, gen. n.

urn:lsid:zoobank.org:act:8F3C1BE1-313C-4830-BFEC-47DBBB87B2F2.

Type species: Dictyna major Menge, 1869.

Material examined: Dictyna major: USA, Washington, Olympia (no verbatim date data), Coll. Nathan Banks (1 male, MCZ-IZ15970). USA, California, Claremont, ~1920, Coll. Unknown (2 males, 3 females, CASENT9129252). USA, Idaho, NE Fruitland, 30.vi.1943, Coll. Wilton Ivie (12 males, 24 females, CASENT9129369). *Dictyna tridentata:* USA, Colorado, Long's Peak Inn, Canadian Zone, vii.1919, Coll. Theodore D.A. Cockerell, Nathan Banks (1 male, MCZ-IZ20427).

Etymology: The generic epithet refers to the Romanian fairy tale *Ileana Simziana* known in English as *The Princess Who Would Be a Prince* (1872–86) by Petre Ispirescu; gender feminine.

Diagnosis: Males of *Simziella gen. n.* (Figs 29D–F, 67A) resemble *Arethyna gen. n.* and *Kharitonovia* by the embolus coiled 275°, originating proximo prolateral from the bulb (Figs 29E, 68D, F); however, it can be distinguished by the conductor upper arm close to the tegulum (Figs 29D, E; 68D); the conductor lower arm with the tip directed retrolateral or slightly retrolateral-proximal [e.g. *S. sancta* (Gertsch, 1946) comb. n.], without a paraconductor, and by the conductor locking mechanism shorter than conductor tip (Figs 29F, 68D, E). Females (Figs 15A–F, 67B–F, 68A–C) resemble *Arethyna gen. n.*, *Embylina s.s.*, and *Nopalityna gen. n.* by having the membranous sac as long as/or longer than the copulatory duct; however, it can be distinguished from these and other congeners by the C-shape of the copulatory duct close to the copulatory opening, and the digitiform SS/AG.

List of included species: Simziella annexa (Gertsch and Mulaik, 1936) comb. n., *Si. canadas* (Wunderlich, 2022) comb. n., *Si. cebolla* (Ivie, 1947) comb. n., *Si. dunini* (Danilov, 2000) comb. n., *Si. major* (Menge, 1869) comb. n., *Si. palmgreni* (Marusik and Fritzen, 2011) comb. n., *Si. paramajor* (Danilov, 2000) comb. n., *Si. sancta* (Gertsch, 1946) comb. n., *Si. sotnik* (Danilov, 1994) comb. n., *Si. sylvania* (Chamberlin and Ivie, 1944) comb. n., *Si. tridentata* (Bishop and Ruderman, 1946) comb. n., *Si. tucsona* (Chamberlin, 1948) comb. n., *Si. tyshchenkoi* (Marusik, 1988) comb. n., *Si. tyshchenkoi wrangeliana* (Marusik, 1988) comb. n., and *Si. teideensis* (Wunderlich, 1992) comb. n.

Genus *Spagnius* Cala-Riquelme and Crews, gen. n.

urn:lsid:zoobank.org:act:1EACFB82-2BAD-4185-9871-39C23B05FEF7.

Type species: Theridion foliaceum Hentz, 1850, currently *Dictyna foliacea* (Hentz, 1850).

Material examined: Dictyna foliacea: USA, New York, Tompkins Co., Mundy Wildflower Garden, Cornell University, 42°27'00.5"N 76°28'08.1"W, 23.vi.2021, Coll. J. Gorneau (1 female, CASENT9103498). Russia, Primorskiy Krai, Ussuriysk Dist, Gornotayozhnoye, 43°39'36.0"N 132°15'00.0"E, pitfall traps, yellow pan trap, 11–12.vi.2000, Coll. M.V. Michailovskaya (1 male, CASENT9118689). USA, Alabama, pre-1947 publication date, Coll. Banks, wild caught (Neotype, 1 male, 1 female, MCZ-IZ21350). USA, Connecticut, New Haven, 1881, Coll. James H. Emerton (1 male, MCZ-IZ21401).

Etymology: The generic epithet is in honour of our late friend and colleague Dr. Joseph Spagna, without whom this project would not have been possible; gender masculine.

Diagnosis: Males of *Spagnius gen. n.* resemble *Eriena gen. n.* by having a short, unmodified embolus that originates prolateral distal on the bulb (Chamberlin and Gertsch 1958: pl. 19, fig. 10); and the dictynid process with the tubercle inconspicuous (Chamberlin and Gertsch 1958: pl. 19, fig. 13); however, it can be distinguished from *Eriena gen. n.* and other Dictynidae s.s. by the tibia three times longer than patella length (Chamberlin and Gertsch 1958: pl. 19, fig. 13); conductor lower arm as long as the conductor upper arm, coiled no more than 180°, and with a conductor scaly tip, long and thin with a paraconductor process at the base; dictynid process with the ctenidia variable in size, the largest hook-shaped (Chamberlin and Gertsch 1958: pl. 19, fig. 13). Females can be distinguished by having the copulatory duct approximately as wide as the primary spermathecae, folded once, close to the copulatory opening, and three to four times longer than the primary spermatheca width (shorter in *Eriena gen. n.*).

List of included species: Spagnius albopilosa (Franganillo, 1936) comb. n., *Sp. foliacea* (Hentz, 1850) comb. n., *Sp. jacalana* (Gertsch and Davis, 1937) comb. n., *Sp. nebraska* (Gertsch, 1946) comb. n.

Genus *Tolkienus* Cala-Riquelme, Crews, Esposito gen. n.

urn:lsid:zoobank.org:act:5C0D5A64-21F0-4C93-862F-B04400A9F196.

Type species: Dictyna longispina Emerton, 1888.

Type material: USA, Connecticut, Meriden, pre-1888 publ. date, Coll. James H. Emerton (Syntype, 1 male, 1 female, MCZ-IZ151459).

Material examined: Dictyna bellans: USA, Alabama, Auburn, pre-1947 publication date, Coll. Baker, Nathan Banks (1 female, MCZ-IZ24751). USA, Alabama, Auburn, pre-1947 publication date, Coll. Baker, Nathan Banks (1 male, MCZ-IZ21258). USA, Alabama, Auburn, pre-1947 publication date, Coll. Baker, Nathan Banks (2 males, 2 females, MCZ-IZ24752). USA, Mississippi, Canton, pre-1919 publication date, Coll. R.V. Chamberlin (Holotype, 1 male, MCZ-IZ15152). *Dictyna bellans hatchi:* USA, Oregon, Roseburg, 14.vi.1938, Coll. M.H. Hatch (Exline Coll.) (Syntype, 1 male, MCZ-IZ24764). USA, Oregon, Roseburg, vii.1939, Coll. M.H. Hatch (Exline Coll.) (Syntype, 1 female, MCZ-IZ21526). *Dictyna longispina:* USA, Arkansas, Washington Co., University farm, low vegetation, open, 11.vii.1955, Coll. W. Peck (1 male, 2 females, 1 imm., CASENT9118614). USA, Arkansas, Washington Co., University farm, low vegetation open field, 12–13.vi.1965, Coll. W. Peck (1 female, CASENT9118618).

Etymology: The generic epithet is in honour of John Ronald Reuel Tolkien, an English writer known worldwide for *The Hobbit* (1937) and *The Lord of the Rings* (1954–55); gender masculine.

Diagnosis: Males of *Tolkienus gen. n.* (Figs 57C, 60A–F, 62A–D; Marusik and Koponen 2017: fig. 1C, D) resemble *Khalotynga gen. n.* and *Phantyna* by having the dictynid process with a tubercle as long as or longer than the tibia length (Figs 57C, 60D, 62A–D; Chamberlin and Gertsch 1958: pl. 16, figs 1, 3, Marusik and Koponen 2017: fig. 2B, C); however, it can be distinguished from other Dictynidae s.s. by the thin embolus originating distally to slightly prolaterally on the bulb, coiled no more than 180° (Fig. 57C; 62A; Chamberlin and Gertsch 1958: pl. 16, fig. 1); conductor lower arm longer than upper arm, coiled twice, with a conspicuous conductor paraterminal process in addition to the conductor scaly tip (Figs 57C, 60B). The females (Fig. 61A–F; Marusik and Koponen 2017: fig. 1A, B) can be distinguished by the AG/SS wider than the copulatory duct, copulatory duct folded once close to the copulatory opening (Fig. 61E, F; Marusik and Koponen 2017: fig. 1F, G), up to three times longer than the primary spermathecae width; and the membranous sac as long as or slightly longer than the complete copulatory duct.

List of included species: *Tolkienus armatus* (Thorell, 1875) comb. n., *T. bellans* (Chamberlin, 1919) comb. n., *T. bellans hatchi* (Jones, 1948) comb. n., *T. estoc* sp. n., *T. longispinus* (Emerton, 1888) comb. n., *T. otto* (Marusik and Koponen 2017) comb. n.

Tolkienus estoc Cala-Riquelme and Al-Jamal sp. n.

urn:lsid:zoobank.org:act:ECA1AA36-C947-426E-BA32-90269208EFE2.

Type material: Male holotype (CASENT9118701) from Equatorial Guinea, Bioko Prov., Moka Wildlife Sanctuary, 3°21'46"N 8°39'52"E, Elev. 1400 m, 2–10.x.1998, Coll. D.K. Dabney, D. Ubick, beating/sweeping foliage; 4 males and 1 female paratypes (CASENT9118701), same data as holotype. Male paratype (CASENT9118720), same data as holotype.

Material examined: Bioko prov., Moka Wildlife Sanctuary, 3°22'0"N 8°39'57"E, 1500 m, beating/sweeping foliage, 6–10.x.1998, Coll. D.K. Dabney, D. Ubick (3 males, 1 female, CASENT9118702). Bioko prov., Moka Wildlife Sanctuary, 3°22'0"N 8°39'57"E, 1500 m, beating/sweeping foliage, 6–10.x.1998, Coll. D.K. Dabney, D. Ubick (3 males, 1 female, CASENT9118702). Bioko prov., Moka Wildlife Sanctuary, Elev. 1403–1419 m, 26.x–1.xi.2007, Coll. R.H. Pine (1 male, FMNH-INS0000085077).

Etymology: The species' epithet is a noun in apposition referring to an estoc sword (tuck in English), a French variation of the longsword used from the 14th to the 17th centuries.

Diagnosis: Males of *Tolkienus estoc* sp. n. (Figs 57C, 60A–F, 62A–D) can be distinguished from other *Tolkienus* gen. n. by having the conductor tip directed proximally and as long as the paraconductor process (Figs 57C, 62B). Females (Fig. 61A–F) can be distinguished from other congeners by having the membranous sac as wide as the primary spermathecae, and the SS/AG in an ectal-medial position (Fig. 61F).

Description: Male (CASENT9118701, Equatorial Guinea): Carapace (Fig. 60A–D) gallstone yellow, anteriorly directed white setae around eyes, darker branching patterns on lateral

surfaces of prosoma. Chelicerae, labium, endites, and sternum honey yellow. Legs pale honey yellow. Abdomen (Fig. 60A) dorsum broccoli brown, with snow white guanidine crystals in fused medial chevron pattern, and a large, square patch of similar crystals at posterior end, venter pale broccoli brown. Sternum slender and squared-off anteriorly, slightly recurved. Total length 2.25. Carapace length 0.88, width 0.80, height 0.50. Clypeus height 0.3. Eye diameters and interdistances: AME 0.03, PME 0.04, ALE 0.05, PLE 0.03, AME–AME 0.08, PME–PME 0.11. Sternum length 0.53, width 0.45. Palp: femur 0.25, tibia 0.14 (dictynid process 0.38). Leg I: femur 0.95, patella 0.25, tibia 0.80, metatarsus 0.59, tarsus 0.40. II: 0.90, 0.25, 0.75, 0.59, 0.40. III: 0.64, 0.25, 0.50, 0.50, 0.31. IV: 0.76, 0.25, 0.56, 0.54, 0.26. Abdomen: length 1.33, width 0.68. Male palp (Figs 57C, 62A–D) with femur straight, shorter than patella + tibia length; patella two times shorter than tibia; tibia shorter than dictynid process, with a small proximal retrolateral dorsal process in addition to the RTA; conductor lower arm two times longer than conductor upper arm length, coiled 360°, with a paraconductor process in addition to the conductor scaly tip; embolus, connected prolaterally distally to the tegulum, and coiled no more than 180°.

Female (CASENT9118701, Equatorial Guinea): Carapace (Fig. 61A–D) pale honey yellow, anteriorly directed white setae around eyes. Chelicerae, labium, endites and sternum pale honey yellow. Legs cream-yellow. Abdomen (Fig. 61B–D) dorsum cream-yellow but slightly darker dorsolaterally, with snow white guanidine crystals distributed broadly and visible laterally, though obscured in dorsal view due to condition of specimen, venter cream-yellow. Sternum squared-off anteriorly, slightly procurved. Total length 1.95. Carapace length 0.78, width 0.58, height 0.33. Clypeus height 0.19. Eye diameters and interdistances: AME 0.04, PME 0.03, ALE 0.05, PLE 0.03, AME–AME 0.02, PME–PME 0.05. Sternum length 0.45, width 0.38. Palp: femur length 0.21, tibia length 0.10. Leg I: femur 0.64, patella 0.21, tibia 0.45, metatarsus 0.39, tarsus 0.31. II: 0.61, 0.25, 0.38, 0.35, 0.28. III: 0.49, 0.21, 0.30, 0.33, 0.26. IV: 0.58, 0.21, 0.40, 0.43, 0.26. Abdomen: length 1.28, width 0.93. Cribellum length 0.2. Epigyne (Fig. 61E, F): copulatory opening ectal, separated by six times the diameter of SS/AG, anterior to the primary spermathecae; membranous sac eight or nine times longer and three times wider than spermathecae diameter; copulatory duct uncoiled, with copulatory duct receptacle as wide as primary spermathecae, and connected ectal proximal with the primary spermathecae; SS/AG reduced but conspicuous, as long as copulatory duct receptacle; fertilization duct located mesal proximally.

DISCUSSION

Utilizing UCEs, our study provides the most robust and representative molecular phylogenetic hypothesis for the evolutionary history of Dictynidae s.l. to date, with 63% of currently recognized genera represented, double the former most-representative phylogeny, with over 200 times more loci (Crews et al. 2020). The backbone of the group is resolved in our UCE-only phylogeny such that there are only a few places where bootstrap support is less than 95%, all in relatively terminal positions and one within a species. Adding Sanger loci both to existing

terminals from the UCE-only tree and to Sanger-only terminals resulted in nearly the same phylogeny with similarly high—or in the case of Lathyidae fam. n.—higher support. Thus, taxa with Sanger-only loci are still informative when incorporated into a UCE phylogeny.

During the course of this study, using mostly museum material, we discovered that relationships among the Dictynoidea were far more complex than imagined, with distributions broadened by thousands of kilometers and the discovery of species from places thought to be devoid of these animals (see below). The results strongly support three families, Lathyidae fam. n., Argyronetidae stat. reinst., and Dictynidae s.s., within the superfamily Dictynoidea. Both the UCE-only phylogeny and the UCE + Sanger loci phylogeny recover the same well-supported relationship of these families: Lathyidae (Argyronetidae + Dictynidae). We have made critical taxonomic changes that bring this new superfamily into better alignment with evolutionary histories, supported by genome-scale molecular evidence and backed by clear morphological synapomorphies for each family and genus. We have also corroborated some recent taxonomic changes. For example, genera formerly considered dictynids that were removed from the family by [Gorneau *et al.* \(2023a\)](#) continued to be recovered outside the group here with greater sampling of the Dictynoidea, i.e. *Brommella* and *Funny*.

Like many marronoid families, Dictynidae *s.l.* has long been a dumping ground for taxa, resulting in several monotypic genera and becoming a revolving door for some taxa like *Argyroneta*. The taxonomic changes herein are largely congruent with [Lehtinen's \(1967\)](#) circumscription of Dictyninae. In this work, [Lehtinen \(1967\)](#) noted: 'It is in this, the largest subfamily of Dictynidae and even the whole of the Amaurobioidea that the limitation of genera has caused the most trouble' (p. 360). Although we have done much tidying of Dictynidae (*s.s.* and *s.l.*), this is a large family, and just as the family was a dumping ground for genera, the genera are a dumping ground for species. The present work samples 33 previously known dictynid *s.l.* genera, including the type species of 15 of those genera, in addition to describing 16 new genera and four new species. However, we recognize that there is still considerable revisionary work remaining at the generic level. The presumably vast number of undescribed taxa, particularly in undersampled biogeographic regions, such as many parts of Africa, South America, Australia, and Asia, will probably provide a better picture of the family and intergeneric relationships. Additionally, many of the genera that we did not sample are monotypic, have inadequate illustrations, or require type examination to determine their taxonomic accuracy. In other cases, genera are very large, with only a minority of species represented in the present study, so the placement of the taxa and their relationships to one another cannot be adequately assessed here. In particular, *Dictyna s.l.* and *Emblyna s.l.* have long been known to be polyphyletic ([Lehtinen 1967](#), [Marusik and Kovblyuk 2011](#), [Esyunin and Sozontov 2016](#), [Crews *et al.* 2020](#)). Here we begin to examine the relationships of *Dictyna* (120 species) and *Emblyna* (78 species) and affirm widespread paraphyly rendering *Dictyna* polyphyletic with respect to *Archaeodictyna*, *Arangina*, *Tivyna*, and *Phantyna*. These relationships are supported, additionally, by the phylogeny that includes only

terminals in the Dictynidae *s.s.* (Supporting Information, [Figs S4, S5](#)). In this work, we have taxonomically organized these two genera in a way that reflects the phylogeny and morphology of the group, including the description of new genera, to accommodate some of the paraphyletic species groups, and we also have provided clear synapomorphies for each genus (*Arethyna* gen. n., *Eriena* gen. n., *Nopalityna* gen. n., *Simziella* gen. n., and *Spagnius* gen. n.). While we recognize that this study does not include all of the described species, it is our hope that this revised framework will allow for new (and existing) species to be placed in these genera or to provide more clarity as to where they belong. Thus, working with these taxa is somewhat less daunting with reduced taxonomic chaos.

It is difficult to pose questions about the evolution of biologically interesting natural histories or ecologies without an evolutionary context for the organisms. Among spiders, observations have been made that some species have an association with water ([Roth 1967](#), [Roth and Brown 1975, 1976](#), [Platnick 1977](#)), though many spiders associated with water were often a part of taxonomic conundrums. In 2010, [Spagna *et al.* \(2010\)](#), while conducting a phylogenetic analysis of marronoid genera, recovered a previously taxonomically unassociated clade of aquatic marronoids. The clade was tentatively dubbed the 'aquatic clade', but more data were needed to determine if the aquatic clade represented evolutionary history or was an artefact of incomplete sampling. [Wheeler *et al.* \(2017\)](#) recovered the same result with more data, but sampling for the group was still sparse. [Crews *et al.* \(2020\)](#), using targeted Sanger genes and greater taxonomic sampling, examined the distribution of aquatic taxa across spider families, illustrating that this lifestyle was widespread throughout the spider tree of life, but with a high number of aquatic taxa represented in the marronoid families Dictynidae and Desidae relative to others. In the present study, we have the largest phylogenetic sampling to date of dictynids (*s.l.*), and the recovered aquatic clade is now the reinstated family Argyronetidae stat. reinst. While not all of the represented species in the clade are known to be associated with water, we see that many (e.g. *Altella*) species have been collected near lakes and seas, some even on salt flats [*A. caspia* (Ponomarev, 2008), *A. opaca* (Simon, 1911), *A. uncata* (Simon, 1885)], suggesting a potential association with water or high humidity environments that may be relevant when considering their evolutionary relationships to their aquatic and semi-aquatic sister-species. Interestingly, we have also recovered evidence for sister-taxa that are thought to be associated with saltwater and freshwater environments, such as intertidal species *Mizaga racovitzai* (Fage, 1909) and *Argyroneta aquatica*, respectively. With denser taxon sampling, the hypothesis that the transition to a marine habitat is more evolutionarily difficult than to a freshwater or salty inland environment, a suggestion postulated by several previous authors, could be examined in the context of these spiders ([Vermeij and Dudley 2000](#), [Leggett *et al.* 2024](#)). Similarly, this resolved phylogenetic framework presents opportunities to evaluate the relationship between cribellar silk evolution and adaptation to aquatic environments.

The genus *Lathys* has been regarded as a diverse group, yet poorly understood in an evolutionary context. The spiders are quite handsome with diverse morphologies, and widespread

species, such as *L. humilis*, are morphologically variable across their range and show deep divergences in genetic data. Unlike most mesh-web weavers that often can be found on the tips of vegetation in conspicuous webs, this genus has a less obvious mesh-web and is found on tree trunks, leaf litter and scree. While it is true that all dictynoids generally have bizarre genitalic conformations, *Lathys* has some of the strangest. The taxonomic placement of the genus in Dictynidae was, prior to this study, considered problematic. That is, despite clearly being viewed as belonging to Dictynidae morphologically, its position in previous molecular phylogenies rendered Dictynidae paraphyletic (Crews *et al.* 2020). *Lathys* as a genus has (until now) never been revised, the difficulty of which was probably best illustrated by Lehtinen (1967: 243): ‘The final revision of this genus is one of the most difficult problems of the taxonomy of the Cribellate spiders, because I have observed a considerable amount of intra-specific variation.’ The genus was also only known to occur in the Holarctic. Here, we have taken the first step in sorting this problematic group, designating a new family (Lathyidae fam. n.) to accommodate the genus, transferring *Bannaella* to the family, re-circumscribing the type genus, and describing eight additional genera that extend the distribution of the family well into tropics.

Long thought to be most diverse in non-tropical regions, our study has illuminated the incredible diversity of Dictynoidea in tropical areas (Table 2). We have expanded the distribution of Dictynoidea by describing two new Lathyidae fam. n. genera from Tanzania, Gabon, the Central African Republic, and Bioko. The only dictynoid previously described from Madagascar is *Copaldictyna madagascariensis*, from ~700-year-old Madagascan copal. Here, we have found evidence for multiple clades of Madagascan dictynoids, which will be the focus of future work. Similarly, the genus *Mashimo* was previously known from a single female specimen from Zambia; however, our work indicates a potentially large radiation in Africa as evidenced by the long branches recovered from the clade of two specimens included in our phylogenetic analysis as well as diverse morphologies and undescribed species at CAS. We also demonstrate several range expansions, including *Brigittea* in Myanmar, India, and South Africa (formerly known only from the Palaearctic and more northern parts of the Oriental biogeographic zone). Several taxa formerly known only from the Northern Hemisphere, such as *Tivyna spatula* (previously only known from North America) and *Phantyna*, have been identified in material from Peru and Ecuador. Only two species of the superfamily were previously known from Australia, *Callevophthalmus albus* (Keyserling, 1890) and *C. maculatus* (Keyserling, 1890). Unsurprisingly, perhaps, given the size of the country, we have uncovered additional genera and species native to Australia in both Argyronetidae and Dictynidae. An undescribed genus is recovered as sister-taxa to the New Zealand endemics *Paradictyna* and *Viridictyna*. Another sister-taxon relationship between New Zealand and Australia recovered here are species of *Arangina*.

One of the most surprising discoveries is the presence of a new genus closely related to *Devade* from salt lakes in Australia. Previously known only from the Mediterranean to Central Asia (Lehtinen 1967, Esyunin 1994, Esyunin and Marusik 2001,

Zamani and Marusik 2017, Crews *et al.* 2020), this discovery extends the range of argyronetids to the Southern Hemisphere and greatly influences how we think about the biogeography of the group. It is possible that other closely related genera will be found in salt flats of South America and Africa.

The present work has focused on building a taxonomic framework for Dictynidae *s.l.* informed by molecular phylogeny. Future work is needed in several key areas. First, given the huge range extensions recognized here across the families and genera, more focused work must be done to support collections and fieldwork to identify further undocumented diversity, particularly in the tropics, Madagascar, and Australia. Second, we now have the opportunity to better understand global biogeographic patterns of Dictynoidea, particularly in groups with major historical biogeographic associations (i.e., Gondwanan), recognized here for the first time. Finally, more applied studies can now be undertaken to better understand the evolution of the diverse ecologies in the group, including aquatic adaptations.

In constructing this molecular phylogenomic hypothesis of Dictynidae, and the new families that have resulted, we have gained valuable experience testing DNA extraction methods, library preparation, and *in silico* isolation of UCEs from low-coverage whole genomes—all techniques that can be useful for arachnologists and other researchers, and we have some recommendations that could be useful to others looking to do similar work. Because our work has been inextricably linked to the relimitation of the marronoid clade overall, we followed very similar protocols to Gorneau *et al.* (2023).

It was challenging to procure enough DNA from the legs of small (2–5 mm), degraded museum specimens, not to mention the more arduous work of pulling legs under the microscope when compared to larger spiders. We also performed whole-body soaks; those did not result in significantly different amounts of DNA, but they did preserve the whole body for morphological analysis and prevented damage done to the cephalothorax or the abdomen by forceps when pulling legs. At the extraction step, the increased proteinase K from the default protocols for the QIAamp DNA Micro kit was helpful in maximizing DNA yield. We sheared extractions to 150 bp for those samples that appeared intact and to have high DNA concentration at fragments longer than 150 bp on the TapeStation. However, we believe that shearing everything would have made for more uniform preparation of the libraries because there was variation in library quality checks (Qubit and TapeStation) between sheared and non-sheared samples, and shearing does not make the shortest (most degraded) fragments shorter. At the computational step, we found that more taxonomically specific UCE probe sets are more appropriate than more general sets. We tested the Kulkarni *et al.* (2020) spider UCE probe set initially, but upon publication of the Zhang *et al.* (2023) RTA-clade UCE probe set (which includes probes from Kulkarni *et al.* 2020), we utilized those probes, which yielded higher numbers of UCEs overall.

We recommend the cost-effective technique of generating low-coverage whole genomes and then isolating the desired loci *in silico*. Low-coverage whole genomes are less expensive and more obtainable with degraded museum samples preserved in ethanol than mechanically isolating UCEs with probes in the lab.

Producing evergreen low-coverage whole genomes also has the advantage of making the dataset flexible to pull multiple types of loci within the same project or in subsequent projects. When the new Zhang *et al.* (2023) UCE probe set became available, rather than re-preparing over 100 libraries to test the set, we only had to switch out a single file in our computational pipeline. We were also able to pull legacy Sanger loci, adding six more loci to our dataset and allowing us to align them with Sanger loci available on GenBank. We see our novel approach of isolating loci, particularly UCEs, from low-coverage whole genome sequences as an innovative, efficient, and cost-effective way to produce data that are phylogenetically informative for spider museum samples.

CONCLUSION

This work is a major step forward in the study of a heretofore-difficult spider group—both taxonomically and phylogenetically. A consistent problem in spider phylogenetics (Wheeler *et al.* 2017, Crews *et al.* 2020) in the Sanger sequencing or ‘legacy loci’ era was the failure to recover basal nodes—generally those dividing families—with high support. Here, that problem is addressed with improved sampling and the addition of UCE data from most taxa. We also provide a useful set of guideposts for future work, particularly pointing out groups that are still unresolved and will benefit from greater sampling. The evolutionary patterns shown here recast a pattern of conserved adaptation to aquatic and semi-aquatic environments, first suggested by Spagna *et al.* (2010) over a decade ago, into a truly global context, namely adding African and South American taxa, many of whose congeners can still be found in museum drawers for those willing to look (or those with access). Our study serves as a call-to-action for researchers of the Global North to make the specimens in those museum drawers more accessible to researchers in the Global South where they originated.

The superfamily Dictynoidea is a remarkably diverse group whose family definitions have now been narrowed. While improvements to generic-level sampling can be made, we have made significant progress in revealing the evolutionary history of this former ‘tailor’s drawer’ group. Our phylogenies utilizing UCEs and Sanger loci of 63% of currently recognized genera, as well as morphological evidence, illustrate that two outstanding clades of former dictynids now belong in separate families, Lathyidae fam. n. and Argyronetidae stat. reinst., and the definition of the family Dictynidae has been made more tractable. Our study offers further support for the approach of combining genomic and legacy (e.g. Sanger) data to produce molecular phylogenies and expand our understanding of the arthropod tree of life, joining the trend of innovations in the utility of museum specimen data practiced by Tin *et al.* (2014), Derkarabetian *et al.* (2019), Gorneau *et al.* (2023), Kulkarni *et al.* (2023), Zhang *et al.* (2019a, b), and others. Our revision is useful for additional phylogenetic studies and provides evolutionary context for future physiological and ecological studies of Dictynoidea.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We would like to thank every person who shared specimens that were the backbone of this study: Adam Baldinger (Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA), Allison Brown and Suresh Naik (Centre for Biodiversity Genomics, University of Guelph), Antonio Brescovit (Instituto Butantan, São Paulo, Brazil), Charles Griswold (California Academy of Sciences, San Francisco, California, USA), Charles Haddad (University of the Free State, South Africa), Christine Rollard (Muséum National d’Histoire Naturelle, Paris, France), Claudia Copley (Royal British Columbia Museum), Cor Vink (Lincoln University, Lincoln, New Zealand), Darko Cotoras, (Pontificia Universidad Católica de Chile, Santiago, Chile), Eduardo Florez (UNAL, Bogota, Colombia), Helen Smith (Australian Museum, Sydney, Australia), Jagoba Malumbres Olarte (University of Helsinki, Helsinki, Finland), Jeremy Miller (Naturalis Biodiversity Center, Leiden, Netherlands), Jonas Wolff (University of Greifswald, Greifswald, Germany), Jørgen Lissner (Aarhus University, Aarhus, Denmark), Julien Pétillion (Université de Rennes, France), Maria Chatzaki (Democritus University of Thrace, Greece), Matthew Leister (University of New Mexico, USA), Nadine Dupérré (University of Hamburg, Hamburg, Germany), Paula Cushing (Denver Museum of Nature and Science, Denver, Colorado, USA), Pedro Cardoso (University of Lisbon, Lisbon, Portugal), Peter Michalik (University of Greifswald, Greifswald, Germany), Phil Sirvid and Shaun Thompson (Museum of New Zealand, Te Papa Tongarewa, New Zealand), Pierre Paquin, Martin Ramírez (MACN, Buenos Aires, Argentina), Shuqiang Li (Institute of Zoology, Chinese Academy of Sciences Beijing), Tamás Szüts (University of Veterinary Medicine Budapest, Hungary), Volker Framenau (Murdoch University, Perth, Western Australia, Australia), and Yejie Lin (Institute of Zoology, Chinese Academy of Sciences Beijing, China). Molecular work was supported by Athena Lam, Lynn Bonomo, and Grace Kim in the Center for Comparative Genomics at the California Academy of Science. Thanks to David Canseco for helping perform DNA extractions during the Summer Systematics Institute at CAS. Thanks to the CAS entomology collections staff for stewarding the in-house collections we used and managing return of specimens to their home institutions. Thanks to Paulo Pantoja for helping to take photographs of specimens at the AMNH and MCZ. Thank you to the feedback received from Eric Stiner, Charles Griswold, Alireza Zamani, the Associate Editor, two anonymous reviewers, and Editor Jeffrey Streicher for their comments on the manuscript.

Funding

This work was supported through a US National Science Foundation award DEB-2026623 to Crews, Esposito, and Spagna.

CREDIT

K.O.M.: Data curation; Formal analysis; Investigation; Methodology; Project administration; Visualization; Writing—original draft; Writing—review & editing. F.C.R.: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Visualization; Writing—original draft; Writing—review and editing. S.C.C.: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing—review and editing. J.A.G.: Data curation; Formal analysis; Investigation; Methodology; Writing—review and editing. A.M.J.: Data curation; Formal analysis; Investigation; Writing—review and editing. L.D.A.: Visualization. J.C.S.: Funding acquisition; Resources; Writing—review and editing. F.B.: Resources; Writing—review and editing. L.A.E.: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing—review and editing.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY

The data underlying this article are available in the article and in its on-line supplementary material.

REFERENCES

- Álvarez-Padilla F, Hormiga G. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. *Journal of Arachnology* 2008;**35**:538–42. <https://doi.org/10.1636/sh06-55.1>
- Azevedo GHF, Bougie T, Carboni M *et al.* Combining genomic, phenotypic and Sanger sequencing data to elucidate the phylogeny of the two-clawed spiders (Dionycha). *Molecular Phylogenetics and Evolution* 2022;**166**:107327. <https://doi.org/10.1016/j.ympev.2021.107327>
- Bankevich A, Nurk S, Antipov D *et al.* SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology: A Journal of Computational Molecular Cell Biology* 2012;**19**:455–77. <https://doi.org/10.1089/cmb.2012.0021>
- Banks N. Some new spiders. *The Canadian Entomologist* 1898;**30**:185–8. <https://doi.org/10.4039/ent30185-7>
- Berland L. *Les Arachnides (Scorpions, Araignées, etc.)*. Paris: Encyclopédie entomologique, 1932, **16**, 1–485.
- Berland L, Millot J. Les araignées de l'Afrique occidentale française, II, Cribellata. *Annales de la Société Entomologique de France* 1940;**108**:149–60.
- Bonnet P. *Bibliographia araneorum, Analyse méthodique de toute la littérature aranéologique jusqu'en 1939, Tome II, Systématique des araignées (Étude par ordre alphabétique) [1re partie: A-B]*. Toulouse: Douladoure, 1955;1–918.
- Bosmans R, Gavalas I. The spiders (Araneae) of the tiny Greek island Iraklia (Kiklades), with the descriptions of 5 new *Harpactea* species (Araneae: Dysderidae), 3 species new to Europe and 8 new to Greece. *Parnassiana Archives* 2023;**11**:1–91.
- Brignoli PM. *A Catalogue of the Araneae Described Between 1940 and 1981*. Manchester, UK: Manchester University Press, 1983.
- Bristowe WS. *The world of spiders*. Collins New Naturalist 1976;**38**:1–304.
- Cala-Riquelme F. Autodesk Sketchbook: an application that minimizes time and maximizes results of taxonomic drawing. *Zootaxa* 2021;**4963**:577e586.
- Cala-Riquelme F, Bustamante AA, Salgado AA. Morphological delimitation of the genus *Cobanus* F.O. Pickard-Cambridge, 1900 (Araneae: Salticidae: Euophryini) with a description of two new species from Colombia. *Zoologischer Anzeiger* 2022;**297**:42–70. <https://doi.org/10.1016/j.jcz.2022.02.002>
- Castresana J. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 2000;**17**:540–52. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Chamberlin RV, Gertsch WJ. The spider family Dictynidae in America north of Mexico. *Bulletin of the American Museum of Natural History* 1958;**116**:article 1.
- Chamberlin RV, Ivie W. Miscellaneous new American spiders. *Bulletin of the University of Utah* 1935;**26**:1–79.
- Chen S, Zhou Y, Chen Y *et al.* fastp: an ultra-fast all-in-one FASTQ preprocessor. *Bioinformatics* 2018;**34**:i884–90. <https://doi.org/10.1093/bioinformatics/bty560>
- Crews SC, Gillespie RG. Desert salt flats as oases for the spider *Saltonia incerta* Banks (Araneae: Dictynidae). *Ecology and Evolution* 2014;**4**:3861–74. <https://doi.org/10.1002/ece3.1242>
- Crews SC, Garcia EL, Spagna JC *et al.* The life aquatic with spiders (Araneae): repeated evolution of aquatic habitat association in Dictynidae and allied taxa. *Zoological Journal of the Linnean Society* 2020;**189**:862–920. <https://doi.org/10.1093/zoolin/zlzl139>
- Dahl M. Spinnentiere oder Arachnoidea, 19 Familie Hahniidae, 20 Familie Argyronetidae. *Die Tierwelt Deutschlands* 1937;**33**:100–18.
- Danecek P, Bonfield JK, Liddle J *et al.* Twelve years of SAMtools and BCftools. *GigaScience* 2021;**10**:p.giab008.
- Denis J. Araignées de France I. Araignées de Vendée avec la description d'une espèce nouvelle des Pyrénées-Orientales. *Revue Française d'Entomologie* 1947;**14**:145–55.
- Derkarabetian S, Benavides LR, Giribet G. Sequence capture phylogenomics of historical ethanol-preserved museum specimens: unlocking the rest of the vault. *Molecular Ecology Resources* 2019;**19**:1531–44. <https://doi.org/10.1111/1755-0998.13072>
- Dunlop JA, Penney D, Jekel D. 2023. A summary list of fossil spiders and their relatives. In: *World Spider Catalog*, v.23.5. Bern, Switzerland: Natural History Museum Bern, online at <http://wsc.nmbe.ch> (date accessed 2024).
- Dupérré N, Harms D. Raising the dead: rediscovery and redescription of some lost spider types (Araneae) described by Eugène Simon. *Evolutionary Systematics* 2018;**2**:1–20. <https://doi.org/10.3897/evolsyst.2.24122>
- Dyal S. Fauna of Lahore, 4–spiders of Lahore. *Bulletin of the Department of Zoology of the Panjab University* 1935;**1**:119–252, pl. 11–17.
- Esyunin SL. Remarks on the spider fauna of the Urals, 3, *Devade* Simon, 1884, a genus new to the Urals, with notes on *Devade indistincta* (O. P.-Cambridge, 1872) (Arachnida Aranei Dictynidae). *Arthropoda Selecta* 1994;**3**:39–47.
- Esyunin SL, Marusik YM. A new species of the genus *Devade* Simon, 1884 from Mongolia, with notes on *D. tenella* (Tyshchenko, 1965) (Aranei: Dictynidae). *Arthropoda Selecta* 2001;**9**:129–31.
- Esyunin SL, Sozontov AN. On a new Eurasian species of *Dictyna* Sundevall, 1833 (Aranei: Dictynidae), with taxonomic notes on poorly known Palaeartic *Dictyna* species. *Arthropoda Selecta* 2016;**25**:199–206.
- Esyunin SL, Zamani A, Tuneva TK. On two poorly known Eurasian dictynid species (Aranei: Dictynidae), with a description of a new genus. *Arthropoda Selecta* 2017;**26**:49062–0. <https://doi.org/10.15298/arthsel.26.1.07>
- Faircloth BC. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 2016;**32**:786–8. <https://doi.org/10.1093/bioinformatics/btv646>
- Faircloth BC, Branstetter MG, White ND *et al.* Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. *Molecular Ecology Resources* 2015;**15**:489–501. <https://doi.org/10.1111/1755-0998.12328>
- Forster R.R. The spiders of New Zealand. Part III. *Otago Museum Bulletin* 1970;**3**:1–184.
- Gertsch WJ. *American Spiders*, D. v. New York: D. van Nostrand, 1949.
- Gorneau JA, Crews SC, Cala-Riquelme F *et al.* Webs of intrigue: museum genomics elucidate relationships of the marronoid spider clade (Araneae). *Insect Systematics and Diversity* 2023a;**7**:1–18.
- Gorneau JA, Kulkarni S, Cala-Riquelme F *et al.* Measuring what we don't know: biodiversity catalogs reveal bias in taxonomic effort. *BioScience* 2023b;**73**:112–23. <https://doi.org/10.1093/biosci/biac116>
- Gregory TR, Shorthouse DP. Genome sizes of spiders. *The Journal of Heredity* 2003;**94**:285–90. <https://doi.org/10.1093/jhered/esh070>
- Griswold CE, Meikle T. *Archaeodictyna ulova*, new species (Araneae, Dictynidae): a remarkable kleptoparasite of group-living eresid spiders (*Stegodyphus* spp., Araneae, Eresidae). *American Museum Novitates* 1987;**2897**:1–11.
- Griswold CE, Coddington JA, Platnick NI *et al.* Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). *The Journal of Arachnology* 1999;**27**:53–63.
- Griswold CE, Ramírez MJ, Coddington JA *et al.* Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 2005;**56**:1–324.
- Grothendieck K, Kraus O. Die wasserspinnne *Argyroneta aquatica*: verwandtschaft und spezialisation (Arachnida, Araneae, Agelenidae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* 1994;**34**:259–73.

- Guindon S, Dufayard JF, Lefort V et al. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 2010;**59**:307–21. <https://doi.org/10.1093/sysbio/syq010>
- Harrison S, *Plant and Animal Endemism in California*. Oakland, California: University of California Press, 2013.
- Hoang DT, Chernomor O, von Haeseler A et al. UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 2018;**35**:518–22. <https://doi.org/10.1093/molbev/msx281>
- International Code of Zoological Nomenclature, 4th edn, London, UK, International Trust for Zoological Nomenclature, 1999.
- Kaston BJ Spiders Of Connecticut. Bulletin of the Connecticut State Geological and Natural History Survey. 1948;**70**:1–874.
- Kishida K. A new scheme of classification of spider families and genera. *Lansania* 1930;**2**:33–43.
- Komatsu T, *Cave Spiders of Japan, Their Taxonomy, Chorology and Ecology*. Osaka, Japan: Arachnological Society of East Asia Osaka, 1961.
- Kubecka P. A possible world record maximum natural ground surface temperature. *Weather* 2001;**56**:218–21. <https://doi.org/10.1002/j.1477-8696.2001.tb06577.x>
- Kulkarni S, Wood HM, Hormiga G. Advances in the reconstruction of the spider tree of life: a roadmap for spider systematics and comparative studies. *Cladistics* 2023;**39**:479–532. <https://doi.org/10.1111/cla.12557>
- Leech RE. The spiders (Araneida) of the Hazen camp area, Ellesmere Island, Northwest Territories, Canada (81 degrees 49' N, 71 degrees 18' W). A taxonomical, biological, and zoogeographical investigation. *Quaestiones entomologicae*. 1966;**2**:153–212.
- Leggett MA, Vink CJ, Nelson XJ. Adaptation and survival of marine-associated spiders (Araneae). *Annual Review of Entomology* 2024;**69**:481–501. <https://doi.org/10.1146/annurev-ento-062923-102457>
- Lehtinen PT. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici* 1967;**4**:199–468.
- Li H, Durbin R. Fast and accurate short read alignment with Burrows–Wheeler Transform. *Bioinformatics* 2009;**25**:1754–60. <https://doi.org/10.1093/bioinformatics/btp324>
- Li X, St Laurent R, Earl C et al. Phylogeny of gracillariid leaf-mining moths: evolution of larval behaviour inferred from phylogenomic and Sanger data. *Cladistics* 2022;**38**:277–300.
- Liu K, Meng ZY, Xiao YH et al. Five new *Lathys* species (Araneae: Dictynidae) from South China and the first description of the male of *Lathys spiralis* Zhang, Hu & Zhang, 2012. *Zootaxa* 2018;**4500**:151–78. <https://doi.org/10.11646/zootaxa.4500.2.1>
- Lockett GH, Millidge AF, *British Spiders*, Vol. II, London: Ray Society, 1953.
- Mammola S, Michalik P, Hebets EA et al. Record breaking achievements by spiders and the scientists who study them. *PeerJ* 2017;**5**:e3972. <https://doi.org/10.7717/peerj.3972>
- Marusik Y, Fritzen N. On a new Dictyna species (Araneae, Dictynidae) from the northern Palaearctic confused with the East Siberian *D. schmidti* Kulczyński, 1926. *ZooKeys* 2011;**138**:93–108. <https://doi.org/10.3897/zookeys.138.1849>
- Marusik YM, Koponen S. New and little known spiders of the subfamily Dictyninae (Araneae: Dictynidae) from south Siberia. *Entomological Problems* 1998;**29**:79–86.
- Marusik YM, Koponen S. On two sibling species of *Dictyna* (Araneae: Dictynidae) from Ukraine and Caucasus. *Entomologica Fennica* 2017;**28**:41–8.
- Marusik YM, Kovblyuk MM, *Spiders (Arachnida, Aranei) of Siberia and Russian Far East*. Moscow: KMK Scientific Press, 2011.
- Marusik YM, Penney D. Conformation of the male palp in some spiders belonging to the RTA-clade and problems in taxonomy. *18th International Congress of Arachnology* 2010, Siedlce, Poland, **506**.
- Marusik YM, Logunov DV, Koponen S, *Spiders of Tuva, South Siberia*. Magadan: Institute for Biological Problems of the North, 2000.
- Marusik YM, Böcher J, Koponen S. The collection of Greenland spiders (Aranei) kept in the Zoological Museum, University of Copenhagen. *Arthropoda Selecta* 2006a;**15**:59–80.
- Marusik YM, Ovchinnikov SV, Koponen S. Uncommon conformation of the male palp in common Holarctic spiders belonging to the *Lathys stigmatisata* group (Araneae, Dictynidae). *Bulletin of the British Arachnological Society* 2006b;**13**:353–60.
- Marusik YM, Koponen S, Potapova NK. Spiders (Aranei) from Oymyakon, the cold pole of the northern hemisphere (Yakutia, Siberia). *Arthropoda Selecta* 2008;**13**:69–75.
- Marusik YM, Kovblyuk MM, Nadolny AA. A survey of *Lathys* Simon, 1884, from Crimea with resurrection of *Scotolathys* Simon, 1884 (Aranei: Dictynidae). *Arthropoda Selecta* 2009;**18**:21–33.
- Marusik YM, Eshyunin SL, Tuneva TK. A survey of Palaearctic Dictynidae (Araneae). Taxonomic notes on Dictynomorpha *Spassky*, 1939, Brigitte Lehtinen, 1967 and *Lathys* Simon, 1884. *Zootaxa* 2015;**3925**:129–44. <https://doi.org/10.11646/zootaxa.3925.1.9>
- Menge A. *Preussische Spinnen*. Gdańsk, Poland: A.W. Kafemann, 1866.
- Menge A. Preussische spinnen, I, Abtheilung, Schriften der Naturforschenden Gesellschaft in Danzig (N.F.). 1871;**2**:265–96.
- Miller JA. Review of Erigonine spider genera in the Neotropics (Araneae: Linyphiidae, Erigoninae). *Zoological Journal of the Linnean Society* 2007;**149**:1–263. <https://doi.org/10.1111/j.1096-3642.2007.00233.x>
- Miller JA, Carmichael A, Ramirez MJ et al. 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* 2010;**55**:786–804. <https://doi.org/10.1016/j.ympev.2010.02.021>
- Millot J, *Ordre des araneides*, In: *Traité de Zoologie, Anatomie, Systematique, Biologie*, Vol. 6. Roret, Paris, 1949.
- Minh BQ, Hahn MW, Lanfear R. New methods to calculate concordance factors for phylogenomic datasets. *Molecular Biology and Evolution* 2020a;**37**:2727–33. <https://doi.org/10.1093/molbev/msaa106>
- Minh BQ, Schmidt HA, Chernomor O et al. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 2020b;**37**:1530–4. <https://doi.org/10.1093/molbev/msaa015>
- Mo YK, Lanfear R, Hahn MW et al. Updated site concordance factors minimize effects of homoplasy and taxon sampling. *Bioinformatics* 2023;**39**:btac741. <https://doi.org/10.1093/bioinformatics/btac741>
- Morrone JJ. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 2014;**3782**:1–110. <https://doi.org/10.11646/zootaxa.3782.1.1>
- Morrone JJ. Biogeographical regionalisation of the world: a re-appraisal. *Australian Systematic Botany* 2015;**28**:81–90. <https://doi.org/10.1071/sb14042>
- Murphy JA, Roberts MJ. Spider families of the world and their spinnerets. *British Arachnological Society, York* 2015;**1 & 2**:i-xii, 1–189, xiii–xvi, 191–553.
- Nguyen LT, Schmidt HA, von Haeseler A et al. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 2015;**32**:268–74. <https://doi.org/10.1093/molbev/msu300>
- Ono H, *The Spiders of Japan with Keys to the Families and Genera and Illustrations of the Species*. Kanagawa: Tokai University Press, 2009.
- Opell BD, Cribellar thread, In: Nentwig W (ed.), *Spider Ecophysiology*. Berlin, Heidelberg: Springer, 2012, 303–15.
- Özkütük RS, Marusik YM, Elverici M et al. A new species of *Lathys* from Turkey (Araneae, Dictynidae). *ZooKeys* 2016;**632**:35–45. <https://doi.org/10.3897/zookeys.632.10130>
- Petrunkovitch A. Catalogue of American spiders. Nwe Haven, CT, USA: *Connecticut Academy of Arts and Sciences* 1939.
- Pickard-Cambridge O. Arachnida. *The Zoological Record* 1871;**7**:207–24.
- Platnick NI. Notes on the spider genus *Paratheuma* Bryant (Arachnida, Araneae). *Journal of Arachnology* 1977;**3**:199–201.

- Ramírez MJ. The morphology and phylogeny of Dionychan spiders (Araneae: Araneomorphae). *Bulletin of the American Museum of Natural History* 2014;**390**:1–374. <https://doi.org/10.1206/821.1>
- Reimoser E. Katalog der echten Spinnen (Araneae) des Paläarktischen Gebietes. *Abhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 1919;**10**:1–280.
- Roewer CF. Katalog der Araneae von 1758 bis 1940, 1, Band (Mesothelae, Orthognatha, Labidognatha: Dysderaeformia, Scytodiformia, Pholciformia, Zodariiformia, Hersiliaformia, Argyopiformia). *Natura, Buchhandlung für Naturkunde und exakte Wissenschaften Paul Budy Bremen* 1942, 1040.
- Roth VD. A redescription of the spider genus *Mizaga* Simon (Agelenidae), with new synonymy. *American Museum Novitates* 1967;**2291**:1–7.
- Roth VD, Brown WL. Comments on the spider *Saltonia incerta* Banks (Agelenidae?). *Journal of Arachnology* 1975;**3**:53–6.
- Roth VD, Brown WL. Other intertidal air-breathing arthropods. In: Cheng L (ed.), *Marine Insects*. La Jolla: Scripps Institute of Oceanography, 1976, 119–50.
- Saito S, *Fauna Nipponica, Vol. 9, fasc. 2 (2) Suborder Arachnomorphae, Tetrasticta*, Tokyo: Trionycha I, Sanseido Co., 1941.
- Santos BF, Brady SG. Leveraging museum specimens, genomics and legacy datasets to unravel the phylogeny and biogeography of cryptin wasps (Hymenoptera, Ichneumonidae, Cryptini). *Zoologica Scripta* 2024;**53**:338–57. <https://doi.org/10.1111/zsc.12639>
- Shear WA. Expanding the palpi of male spiders. *Breviora* 1967;**259**:1–27.
- Simon E. Aranéides nouveaux ou peu connus du midi de l'Europe. *Mémoires de la Société Royale des Sciences de Liège* 1870;**3**:271–358.
- Spagna JC, Gillespie RG. More data, fewer shifts: molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. *Molecular Phylogenetics and Evolution* 2008;**46**:347–68.
- Spagna J, Crews S, Gillespie R. Patterns of habitat affinity and Austral/Holarctic parallelism in dictynoid spiders (Araneae: Entelegynae). *Invertebrate Systematics* 2010;**24**:238–57.
- Syme P. Werner's nomenclature of colours: adapted to zoology, botany, chemistry. *Mineralogy, Anatomy, and the Arts, Smithsonian Institution*. Washington DC, USA, 2018, 80.
- Talavera G, Castresana J. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 2007;**56**:564–77. <https://doi.org/10.1080/10635150701472164>
- Thorell T. On European spiders, Review of the European genera of spiders, preceded by some observations on zoological nomenclature [second part]. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 1869;**3**:1–108.
- Thorell T. On European spiders, Review of the European genera of spiders, preceded by some observations on zoological nomenclature [second part]. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 1870;**3**:109–242.
- Tin MMY, Economo EP, Mikheyev AS. Sequencing degraded DNA from non-destructively sampled museum specimens for RAD-tagging and low-coverage shotgun phylogenetics. *PLoS One* 2014;**9**:e96793. <https://doi.org/10.1371/journal.pone.0096793>
- Van Dam MH, Lam AW, Sagata K *et al.* Ultraconserved elements (UCEs) resolve the phylogeny of Australasian smurf-weevils. *PLoS One* 2017;**12**:e0188044. <https://doi.org/10.1371/journal.pone.0188044>
- Vermeij GJ, Dudley R. Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biological Journal of the Linnean Society* 2000;**70**:541–54. <https://doi.org/10.1111/j.1095-8312.2000.tb00216.x>
- Westring N. Araneae svecicae. *Göteborgs Kungliga Vetenskaps och Vitterhets Samhälles Handlingar* 1861;**7**:1–615. [publ. also as separate in 1862].
- Wheeler WC, Coddington JA, Crowley LM *et al.* The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* 2017;**33**:574–616. <https://doi.org/10.1111/cla.12182>
- Wood HM, González VL, Lloyd M *et al.* Next-generation museumgenomics: phylogenetic relationships among palpimanoid spiders using sequence capture techniques (Araneae: Palpimanoidea). *Molecular Phylogenetics and Evolution* 2018;**127**:907–18. <https://doi.org/10.1016/j.ympev.2018.06.038>
- World Spider Catalog 2024. *World Spider Catalog*. Natural History Museum Bern, online at <http://wsc.nmbe.ch> (8 April 2024, date last accessed).
- Wunderlich J. Extant and fossil spiders (Araneae). *Beiträge zur Araneologie* 2011;**6**:1–640.
- Yaginuma T. The development of araneology in Japan. *Annual Report of the Otemon Gakuin University* 1955;**1**:25–41.
- Zamani A, Marusik YM. Six new species of spiders (Arachnida: Araneae) from Iran. *Oriental Insects* 2017;**51**:313–29. <https://doi.org/10.1080/00305316.2017.1282386>
- Zamani A, Marusik YM, Berry JW. A new species of *Paratheuma* (Araneae: Dictynidae) from Southwestern Asia and transfer of the genus. *Zoology in the Middle East* 2016;**62**:177–83. <https://doi.org/10.1080/09397140.2016.1173927>
- Zhang Z, Hu DS, Zhang GY. Notes on the spider genus *Lathys* Simon, 1884 (Araneae: Dictynidae), with description of four new species from China. *Zootaxa* 2012;**3359**:1–16.
- Zhang C, Rabiee M, Sayyari E *et al.* ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics* 2018;**19**:153.
- Zhang F, Ding Y, Zhu CD *et al.* Phylogenomics from low-coverage whole-genome sequencing. *Methods in Ecology and Evolution* 2019a;**10**:S07–17. <https://doi.org/10.1111/2041-210x.13145>
- Zhang YM, Williams JL, Lucky A. Understanding UCEs: a comprehensive primer on using ultraconserved elements for arthropod phylogenomics. *Insect Systematics and Diversity* 2019b;**3**:3.
- Zhang J, Li Z, Lai J *et al.* A novel probe set for the phylogenomics and evolution of RTA spiders. *Cladistics* 2023;**39**:116–28. <https://doi.org/10.1111/cla.12523>