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Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae)

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This paper offers the first cladistic analysis of a wide selection of theridiid genera based on morphological data. The analysis treats 53 theridiid taxa representing 32 genera (*Achaearanea*, *Anelosimus*, *Ameridion*, *Argyrodes*, *Ariamnes*, *Carniella*, *Cerocida*, *Chrysso*, *Coleosoma*, *Dipoena*, *Emertonella*, *Enoplognatha*, *Episinus*, *Euryopis*, *Faiditus*, *Kochiura*, *Latrodectus*, *Neospintharus*, *Nesticodes*, *Pholcomma*, *Phoroncidia, Rhomphaea*, *Robertus*, *Selkirkiella*, *Spintharus*, *Steatoda*, *Stemmops*, *Theridion*, *Theridula*, *Thymoites, Thwaitesia, Tidarren*) and eight outgroup taxa representing the families Nesticidae (*Eidmanella* and *Nesticus*), Synotaxidae (*Synotaxus*, two species), Pimoidae (*Pimoa*), Linyphiidae (*Linyphia*), Tetragnathidae (*Tetragnatha*) and Araneidae (*Argiope*). The parsimony analysis of 242 morphological and behavioural characters found a single, most parsimonious tree. The monophyly of theridiids and their sister relationship with nesticids is strongly supported. The recent resurrection of *Ariamnes* and *Rhomphaea* from *Argyrodes* made the latter paraphyletic. However, *Ariamnes* and *Rhomphaea* are characterized by an array of characters, and *Argyrodes* still contains dramatically distinct clades for which names are available: *Faiditus* (removed from synonymy – RS) and *Neospintharus* (RS). These revalidations provide a classification with greater information content and utility. These three genera, along with *Ariamnes*, *Rhomphaea* and *Spheropistha*, comprise the subfamily Argyrodinae. The monophyly and composition of the subfamilies Hadrotarsinae, Spintharinae, Pholcommatinae, Latrodectinae and Theridiinae are discussed. *Theridion* is paraphyletic and in need of revision. *Anelosimus* as currently circumscribed is paraphyletic, a problem resolved by revalidating *Selkirkiella* (RS) and *Kochiura* (RS). Numerous new combinations are established. The results suggest the monophyletic origin of both kleptoparasitism and araneophagy in the lineage leading to Argyrodinae, negating hypotheses that either arose from the other. Sociality evolved multiple times within the family, accounting for as much as one fourth of the origins of social behaviour among all spiders. No losses of sociality are implied. The hypothesis of maternal care as the pathway to sociality receives support. Evolution of theridiid webs is complex, with multiple modifications and loss of the basic theridiid cobweb. *Zoological Journal of the Linnean Society*, 2004, **141**, 447–626.

ADDITIONAL KEYWORDS: *Anelosimus* – araneophagy – *Argyrodes* – Argyrodinae – cladistics – comb footed spiders – Hadrotarsinae – kleptoparasitism – Latrodectinae – maternal care – Pholcommatinae – Spintharinae – sociality – Theridiinae – web evolution.

INTRODUCTION

The cobweb spiders, family Theridiidae, constitute one of the largest spider families, with over 2300 species in 79 genera (Platnick, 1997, 2003; Agnarsson, 2000, 2003a; Yoshida, 2001a, b) distributed worldwide. The awesome reputation of the widow spiders (*Latrodectus* Walckenaer, 1805), earned by their post-mating cannibalism and potent venom, epitomizes arachnophobia, while the comparatively timid and less feared common house spider [*Achaearanea tepidariorum* (Koch, 1841)] and the red house spider [*Nesticodes rufipes* (Lucas, 1846)], share quarters with people worldwide. Theridiids exhibit extreme diversity in morphology, ecology and behaviour, ranging from solitary web-less hunters that specialize in myrmecophagy, e.g. the hadrotarsines, to species in which

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thousands of individuals cooperate to build webs several cubic meters in size, e.g. *Anelosimus eximius* (Keyserling, 1884).

Sociality is extremely rare among spiders, yet most social species are theridiids (Avilés, 1997). *Anelosimus* Simon, 1891 is a model organism in the study of social behaviour and its evolution (see e.g. Simon, 1895; Kullmann, 1972; Brach, 1977; Buskirk, 1981; Avilés, 1986, 1997; Nentwig & Christenson, 1986; Vollrath, 1986; Elgar & Godfray, 1987; Avilés & Maddison, 1991; Rypstra, 1993; Smith & Hagen, 1996; Pasquet *et al.*, 1997; Avilés & Gelsey, 1998; Avilés & Tufino, 1998; Furey, 1998; Avilés *et al.*, 2000; Saffre, Mailleux & Deneubourg, 2000; Vakanas & Krafft, 2001; Bukowski & Avilés, 2002; Jones & Parker, 2002).

Also, no other family includes as many kleptoparasites. Kleptoparasitic spiders occupy heterospecific webs to steal prey or silk. *Argyrodes* Simon, 1864 includes the most famous and conspicuous kleptoparasites, found worldwide in the webs of the largest known orb-weavers, *Nephila* Leach, 1815 (Tetragnathidae), and numerous other spiders (Exline & Levi, 1962). The biology of the members of *Argyrodes* (e.g. Vollrath, 1987; Cangialosi, 1990; Eberhard *et al.* 1993; Elgar, 1993; Whitehouse & Jackson, 1993; Grostal & Walter, 1997; Higgins & Buskirk, 1998; Tso & Severinghaus, 1998; Henaut, 2000; Agnarsson, 2002; Whitehouse *et al.*, 2002) and their distribution among their host webs (e.g. Elgar, 1989; Grostal & Walter, 1999; Miyashita, 2001, 2002; Agnarsson, 2003b) are areas of active research. Both sociality and most instances of kleptoparasitism typically entail 'web sharing', and the two types of behaviour may be phylogenetically related (Agnarsson, 2002).

Theridiids show a particularly diverse array of web types, offering fertile ground for the study of web evolution. The webs of most species remain little known and the relationship of web types is extremely perplexing in the absence of a phylogenetic hypothesis. The study of web-building behaviour, which in orb-web weavers has proven extremely fruitful both in terms of understanding behaviour and as a source of phylogenetic characters (Robinson & Robinson, 1973, 1975; Eberhard, 1982, 1990; Coddington, 1986b; Coddington & Sobrevila, 1987; Hormiga *et al.* 1995) has only just begun with theridiids and related families (Benjamin, Düggelin & Zschokke, 2002; Benjamin & Zschokke, 2002, 2003). The lack of a phylogenetic hypothesis hinders interpretation of the patterns found by the latter studies: 'In the absence of a phylogeny, the interpretation of the evolution of the diverse range of [theridiid] webs and their corresponding behaviours is somewhat arbitrary' (Benjamin & Zschokke, 2003: 301).

Sexual behaviour in combination with genital morphology has been studied in detail in several theridiids, revealing interesting patterns, often shared by several genera (Knoflach, 1994, 1995, 1996, 1997, 1998, 1999; Knoflach & van-Harten, 2000, 2001). Among the most fascinating discoveries made in these studies is voluntary loss of the male palp (the intromittent organ), single palp copulation, and obligatory mate consumption in *Tidarren* Chamberlin & Ivie, 1934 and *Echinotheridion* Levi, 1963 (Branch, 1942; Knoflach & van-Harten, 2000, 2001; Knoflach, 2002). The evolution of sexual behaviour in theridiids is another field that urgently needs phylogenetic context to progress. Finally, few spiders have received more public or commercial interest than the widow spiders (*Latrodectus* spp.). The phylogenetic distribution and evolution of their venom is of medical importance.

Although extensively studied taxonomically [most extensive are the numerous works of Herbert W. Levi (1953a, b, 1954a, b, c, d, 1955a, b, c, 1956, 1957a, b, c, 1958, 1959a, b, c, 1960, 1961, 1962a, b, 1963a, b, c, d, e, f, 1964a, b, c, d, e, f, 1966, 1967a, b, c, 1968, 1969, 1972) and Levi & Levi, 1962], an explicit phylogenetic hypothesis based on morphological data has never been offered (but see Arnedo *et al.*, 2004 for a molecular phylogeny). The main aims of this paper are as follows:

1. To provide an introduction to the comparative morphology of theridiids.
2. To estimate their phylogeny via a modern cladistic analysis of morphological data.
3. To provide a platform for a subsequent revision of the social *Anelosimus*, a large, behaviourally diverse and most likely paraphyletic genus.
4. To use the phylogeny to evaluate the more prominent hypotheses for the evolution of spider sociality, kleptoparasitism and web construction, as well as the evolution of morphological features within the family.

Over 700 illustrations are included, grouped at the end of the paper.

TAXONOMIC OVERVIEW

The first valid descriptions of cobweb spiders were made by Clerck (1757) in his *Aranei sueciici*, where he described four theridiid species: *Enoplognatha ovata* (Clerck, 1757), *Steatoda castanea* (Clerck, 1757), *Theridion sisyphium* (Clerck, 1757) and *Achaearanea lunata* (Clerck, 1757). The family Theridiidae was established by Sundevall (1833) (the invalid original spelling of 'Theridiides' was corrected by later authors and Theridiidae is now an official name (see Levi & Levi, 1962) based on *Theridion* Walckenaer, 1805, type species *Aranea picta* Walckenaer, 1802 (= *Theridion pictum*). Sundevall (1833) also established the subfamily Theridiinae, pertaining to *Theridion* and related genera.

Simon (1894) separated the 72 genera known to him into 18 tribal level groups (see Appendix 2). His genera represented about 36 of those currently recognized, due to subsequent synonymies and transfers. Simon emphasized eye arrangement, a rather unfortunate character choice for theridiid spiders (Levi & Levi, 1962). Thus of Simon's tribal level groups containing more than one taxon, only Argyrodeae (*Argyrodes*, *Ariamnes* Thorell, 1869, *Rhomphaea* Koch, 1872) and perhaps Pholcommateae (*Pholcomma* Thorell, 1869, *Styposis* Simon, 1894) are likely to be monophyletic (Arnedo *et al.*, 2004; pers. observ.).

Petrunkevitch (1928) offered a formal classification of Theridiidae using subfamily ranks. He recognized 11 theridiid subfamilies, briefly discussing their composition. Most of them mirrored Simon's tribes and inherited their problematic composition. Petrunkevitch's system differed from Simon's in that Spintharеae and Synotaxeae were synonymized with Argyrodinae (including also *Argyrodes*, *Ariamnes* and *Argyrodes*). His Theridiinae included Simon's Theridieae, *Hetschkia*, *Propostira*, *Episinoides* and Euryopeae, and the name Latrodectinae was used for Simon's Dipoeneae. Furthermore, numerous genera now placed in other families were scattered amongst the theridiid subfamilies. Archer's (1950) classification had only three subfamilies containing true theridiids: Episininae, Theridiinae and Conopisthinae. The bizarre combinations of these subfamilies resulted in his classification generally being ignored or dismissed by subsequent workers (e.g. Levi & Levi, 1962), leaving theridiids in a state of taxonomic anarchy.

The most recent comprehensive treatment of the family is Levi & Levi's (1962) monumental effort. They reduced the number of theridiid genera from 140 to less than 50, produced a much more natural classification than previous efforts, removed numerous misplaced taxa and cleaned up a vast number of taxonomical problems, thus laying a firm foundation for all subsequent workers. However, they did prefer very large genera, and some, including *Theridion*, *Achaearanea* Strand, 1929 and *Anelosimus* ended up as 'waste baskets', containing many species with little in common (Forster, Platnick & Coddington, 1990). In recent years several authors, most notably Wunderlich (1986, 1988, 1992, 1995a, b, c) and Yoshida (2001a, b, 2002) have split some of Levi & Levi's generic concepts, especially *Theridion* and *Argyrodes*. Platnick (2003) recognizes 79 theridiid genera; an interactive key to these is now available (Agnarsson, 2003a).

Levi & Levi (1962) explicitly avoided ranks higher than genus. They addressed generic interrelationships only superficially in a simple sketch conveying the distribution of presumptively important morphological characters (Levi & Levi, 1962: 67). They especially emphasized the importance of the colulus and colular setae in separating basal and distal theridiids. Given just seven characters and 43 taxa, a cladistic treatment of their data provides almost no resolution (pers. observ.). More recently, Wunderlich (1978), Heimer (1982), Heimer & Nentwig (1982), Coddington (1983, 1986a, c, 1989), Forster *et al.* (1990), Griswold *et al.* (1998), and Yoshida (2001a, b, 2002) have included brief discussions on theridiid phylogeny, and all consider nesticids to be the sister group of theridiids. Forster *et al.* (1990) transferred *Synotaxus* Simon, 1895 to its own family Synotaxidae, and recognized the Cyatholipidae (revised by Griswold, 2001) as its sister group. The transfer of *Synotaxus* was corroborated by Agnarsson (2003c).

Following Wunderlich (1978), both Forster *et al.* (1990) and Griswold *et al.* (1998) recognized Hatrotarsinae (*Dipoena* Thorell, 1869, *Audifia* Keyserling, 1884, *Anatea* Berland, 1927, *Dipoenata* Wunderlich, 1988; *Euryopis* Menge, 1868, *Gmogala* Keyserling, 1890, *Guaraniella* Baert, 1984, *Hadrotarsus* Thorell, 1881, *Lasaeola* Simon, 1881 and *Yoroa* Baert, 1984) as a theridiid subfamily [Berland (1932) and Gertsch (1949: 169–170) earlier suggested the association of Theridiidae and Hadrotarsidae] and established Nesticidae as the sister group of theridiids (see also Heimer & Nentwig, 1982). All these studies concluded that a fleshy colulus was primitive for theridiids, and that its reduction or absence might define distal theridiid lineages.

Griswold *et al.* (1998), based on a taxonomic sample of four theridiids and one nesticid, suggested several synapomorphies for theridioids (Theridiidae plus Nesticidae), including the appearance of a male palpal sclerite called the 'theridiid tegular apophysis', a comb of curved serrated macrosetae lying ventrally on tarsus IV, the presence of huge aggregate gland spigots on the posterior lateral spinnerets, and the construction of gumfoot webs. They characterized Theridiidae by the loss of the paracymbium and the appearance of a distal hook near or on the ectal margin of the cymbium that locks the unexpanded bulb to the cymbium. Theridioids, Synotaxidae and Cyatholipidae composed the 'spineless femur clade', characterized by the absence of macrosetae from leg femora and the use of sticky silk during attack behaviour, although data on the latter are lacking for many taxa.

The reader should note that the current limits of Araneoidea have recently been questioned, and several araneoid-like palpimanoid families (e.g. malkarids, micropholcommatids, mimetids and textricellids) may belong in Araneoidea (Schütt, 2000, 2002). A phylogenetic analysis of Araneoidea considering these families challenges most previous phylogenetic work on the group, with potentially important implications for the placement of theridiids (Schütt, 2002).

Forster *et al.* (1990) discussed possible phylogenetic relationships within the family Theridiidae. They provided evidence for the monophyly of Hadrotarsinae and agreed with Wunderlich (1978) that several characters unite them with theridiids. However, they pointed out that hadrotarsines might just as well be sister to theridiids as nest within them. Yoshida (2002) revised the Japanese hadrotarsines, adding *Yaginumena* Yoshida, 2002, and resurrecting *Emertonella* Bryant, 1945, and *Trigonobothrys*, Simon, 1889. Forster *et al.* (1990) also revalidated Spintharinae (based on Simon's Spinthareae) containing those genera that, like *Spintharus* Hentz, 1850, have a paracymbial hood; they explicitly included *Anelosimus*, *Chrosiothes* Simon, 1894, *Chrysso* O. P.-Cambridge, 1882, *Coleosoma* O. P.-Cambridge, 1882, *Helvibis* Keyserling, 1884, *Nesticodes* Archer, 1950, *Rugathodes* Archer, 1950, *Spintharus*, *Tekellina* Levi, 1957, *Theridula* Emerton, 1882, *Thwaitesia* O. P.-Cambridge, 1881 and *Thymoites* Keyserling, 1884.

Yoshida (2001a) discussed the Spintharinae of Forster *et al.* (1990) and pointed out that species of *Theridion*, *Paidiscura* Archer, 1950, *Moneta* O. P.-Cambridge, 1870, and *Achaearanea* also have hooded paracymbia. He then placed Spintharinae and Simon's (1884) Moneteae within Theridiinae (Sundevall, 1833) and defined the latter by two putative synapomorphies: hooded paracymbium and absence of colulus. Yoshida (2001b) discussed the composition of the subfamily Argyrodinae and synonymized Conopisthinae (Archer, 1950) with it. He resurrected the genera *Rhomphaea* and *Ariamnes* (*contra* Exline & Levi, 1962), and *Spheropistha* Yaginuma, 1957 (*contra* Tanikawa, 1998), from *Argyrodes* (Fig. 94B) arguing that: 'Compared with other genera of Theridiidae, the distinction among *Argyrodes*-related groups seems to be rather clear' (Yoshida, 2001b: 183).

A molecular phylogeny of theridiid genera has recently been made available (Arnedo *et al.*, 2004). It deals with 32 theridiid genera, represented by 40 taxa, using about 2500 base pairs from nuclear (histone 3, 18S rDNA, 28S rDNA) and mitochondrial (16S rDNA, CoI) DNA. The results marginally support the monophyly of theridiids and for the following subfamilies (genera included in the molecular study are shown in parentheses): Latrodectinae (*Crustulina* Menge, 1868, *Latrodectus*, *Steatoda* Sundevall, 1833), Argyrodinae (*Argyrodes*, *Ariamnes*, *Rhomphaea*), Hadrotarsinae (*Dipoena*, *Emertonella*, *Euryopis*), Spintharinae (*Chrosiothes*, *Episinus* Walckenaer, 1809, *Spintharus*, *Stemmops* O. P.-Cambridge, 1894, *Thwaitesia*), and Theridiinae (*Achaearanea*, *Ameridion* Wunderlich, 1995, *Chrysso*, *Helvibis*, *Keijia* Yoshida, 2001, *Neottiura* Menge, 1868, *Nesticodes*, *Rugathodes*, *Theridion*, *Theridula*, *Thymoites*, *Tidarren*).

The present study is the first phylogenetic analysis of theridiid spiders based on morphology and behaviour. It includes 32 theridiid genera, selected to represent as much as possible of the known diversity of morphology and behaviours in the family. Particular attention is paid to the composition and position of the large and behaviourally diverse genus *Anelosimus* (ten species). Argyrodinae is represented by six species, including members of five of the major species groups of Exline & Levi (1962).

MATERIAL AND METHODS

TAXON CHOICE

Ideally, when studying the interrelationships of genera, one would like to know the primitive (or groundplan) condition for each character pertaining to the genus. However, the reconstruction of a generic groundplan requires a phylogeny at the species level; without that, character polarization within genera cannot be logically addressed. In some studies genera are instead represented by an artificial, or best guess groundplan, which is synthesized from generic descriptions or common characteristics of the genera. This approach can easily mistake common for primitive and character codings are rather ad hoc (Yeates, 1995). In any case, character definitions and coding inevitably change with the definition of genera (Prendini, 2001). Here, actual species are used to exemplify genera. This method is explicit, repeatable and verifiable. Character coding is not arbitrary and does not change with definitions of genera. However, the combination of sparse taxon sampling with the use of particular species can make fairly trivial convergences behave like synapomorphies. While nomenclatural considerations recommend the use of the type species (followed here as far as possible), the type species of a genus may not be a good model for a higher taxon groundplan (e.g. *Theridion pictum* (Walckenaer, 1802) as groundplan for Theridiidae). With material of the type species sometimes unavailable, and a need to maximize overlap with molecular phylogenetic work (Arnedo *et al.*, 2004), several genera are represented by whichever species (described or not) from which sufficiently fresh material could be obtained.

OUTGROUPS

I relied on the work of Griswold *et al.* (1998: fig. 7) when choosing outgroups for Theridiidae. The putative sister group is Nesticidae (together forming theridioids) and the family is here exemplified by *Eidmanella pallida* (Emerton, 1875) and *Nesticus silvestrii* Fage, 1929. The synotaxids *Synotaxus monoc-*

eros (Caporiacco, 1947) and *Synotaxus waiwai* Agnarsson, 2003 represent the cyatholipoids (cyatholipids plus synotaxids), which are sister to theridioids. Pimoids [*Pimoa rupicola* (Simon, 1884)] and linyphiids [*Linyphia triangularis* (Clerck, 1757)] comprise linyphioids and are thought to be sister to the spineless femur clade (cyatholipids plus theridioids). Tetragnathidae [*Tetragnatha extensa* (Linnaeus, 1758)] and Araneidae [*Argiope argentata* (Fabricius, 1775)] were chosen to represent taxa that all previous analyses have placed well outside the problem at hand. The resulting cladograms are therefore rooted at *Argiope argentata*.

Although most major araneoid lineages are included here, numerous taxa of potential importance are not, e.g. cyatholipids, symphytognathoids (see Griswold *et al.*, 1998), malkarids, micropholcommatids, mimetids and nicodamids (see Schütt, 2000, 2002). Practical limitations ultimately constrain the number of taxa and characters included in any study. Theridiid intergeneric relationships are entirely unknown (but see Arnedo *et al.*, 2004), while the outgroup structure has been rigorously studied (Griswold *et al.*, 1998; Agnarsson, 2003c; Schütt, 2002). The sister relationship of theridiids with nesticids has been particularly well corroborated morphologically (Wunderlich, 1978; Heimer & Nentwig, 1982; Heimer, 1982; Coddington, 1983, 1986a, c, 1989; Forster *et al.*, 1990; Griswold *et al.*, 1998; Agnarsson, 2003c) although it should be noted that molecular data recently made available disagree (Arnedo *et al.*, 2004).

With this in mind, I biased taxon choice towards the ingroup (the unknown), rather than excessively test the structure of Araneoidea inferred in previous phylogenies. The potential pitfalls of this are that excluded taxa may have pivotal effects on the analysis, and sparse taxon sampling increases the chances that convergences behave as synapomorphies. However, resolving the controversy in araneoid phylogeny (see Griswold *et al.*, 1998; Schütt, 2002) is beyond the realm of this study. Rather, I rely on the assumption that nesticids are the likely sister group of theridiids, and that the eight outgroup taxa included here are adequate for a test of theridiid, and theridioid, monophyly. No studies to date suggest that the lack of the aforementioned groups is likely to seriously undermine this approach. It should furthermore be noted that fusing the matrices of Griswold *et al.* (1998) and the matrix included below provides identical results with regard to theridiid monophyly and intergeneric relationships (Agnarsson, 2003c).

In order to make optimum use of the available data, maximize the comparability of the results and facilitate future construction of 'supertree cladograms', the same exemplar species have been used as in Griswold *et al.* (1998) whenever possible.

Ingroup taxa

Taxa were chosen in order to represent as much as possible of the theridiid morphological and behavioural variation (see Appendix 3). I aimed to include as many relatively common or speciose genera as possible, at the expense of monotypic and rare genera (some of which have not been seen since their description). Monotypic genera are problematic theoretically, taxonomically and practically. They are suspect because they provide no grouping information (e.g. Platnick, 1976; Zujko-Miller, 1999); occasionally, cladistic results mandate monotypic higher taxa (see, e.g. Hormiga, 1994a), but 19th century monotypic genera known from a single specimen, or a handful of specimens, scarcely fulfil that criterion. Additionally, thorough, competent comparative morphology is nearly impossible if only a few specimens are available. The present analysis has been written with the aim of providing information to assist with future evaluation of the 20 or so monotypic theridiid genera.

Several species were included from large genera suspected of being paraphyletic (for number of species per genus see Platnick, 2003). Most of the morphological and behavioural variation of *Anelosimus* (45 described species) is represented using 14 species, including the classical *Anelosimus* as well as the type species of *Kochiura* and *Selkirkiella* (the latter currently in synonymy). This focus on *Anelosimus* allows testing of the monophyly of the genus (or rather the demonstration of its likely polyphyly, see Forster *et al.*, 1990), and serves as a platform for revision of the genus (I. Agnarsson, unpubl. data).

Argyrodes (over 220 described species) *sensu* Exline & Levi (1962) is represented by six species, including members of five major subgroups. In addition to *Argyrodes*, these represent *Rhomphaea* and *Ariamnes*, resurrected by Yoshida (2001b), and *Faiditus* Keyserling, 1884, and *Neospintharus* Exline, 1950, currently in synonymy. Other genera represented by more than one species are: *Theridion* (over 620 described species) with four, *Achaearanea* (over 140 described species) with three, and *Ameridion* (about 30 described species), *Enoplognatha* Pavesi, 1880 (about 70 described species), and *Latrodectus* Walckenaer, 1805 (about 30 described species) all with two.

To test the monophyly and examine the placement of hadrotarsines, three genera are included: *Dipoena*, *Emertonella* and *Euryopis*. The remaining genera are represented by a single species (*Cerocida* Simon, 1894, *Carniella* Thaler & Steinberger, 1988, *Chrysso, Episinus*, *Nesticodes*, *Pholcomma* Thorell, 1869, *Robertus* O. P.-Cambridge, 1879, *Spintharus*, *Steatoda*, *Theridula, Thymoites, Thwaitesia, Tidarren*).

Even when only a single species of a genus is represented in the matrix, more than one species was examined, given sufficient material (see Appendix 3).

This was done in an attempt to maximize character information content – characters that appear as autapomorphies of taxa in this analysis have in most cases been seen in (at least some) other species of that genus (pers. observ.). In addition to taxa included in the 'material examined' sections, numerous additional specimens were examined less rigorously and often haphazardly as material became available during sorting of collections in the five year course of this study. Although not fit for publication, data from these surveys served the purpose of verifying character information, ascertaining that an exemplar species is not an atypical member of a genus, and aided taxonomic decisions. For example, sorting through hundreds of argyrodines from all over the world confirmed the cohesiveness of groups based on a single exemplar species that are discussed here.

Character choice

Characters from Griswold *et al.* (1998) relevant to the relationships among theridiids and the outgroups (34 characters, see Appendix 1) in this study were used, with some adjustments. The interpretation of palpal sclerite homologies in this paper sometimes differs from that of Griswold *et al.* (1998), e.g. in regards to the conductor, theridiid tegular apophysis, and the median apophysis (see discussion on these characters). All characters suggested by Forster *et al.* (1990) and Levi & Levi (1962) as being phylogenetically important are used in some form. Furthermore, about 200 new characters have been added, with some characters and character systems either not used previously or under-explored in spider phylogenetics (e.g. details of the palpal sperm duct trajectory, character nos. 51–61; details of the abdomen-prosoma stridulatory apparatus, nos. 149–162; abdominal proprioreceptors, nos. 163–164; details of the epiandrous gland spigots, nos. 168–170; egg-sac ultrastructure, nos. 230–233; and mating behaviour, nos. 236–242).

The data comprise 242 characters, including: female genital morphology (13), male genital morphology (88), somatic morphology (99), spinneret morphology (23), and behaviour and web building (19). Thirteen characters (nos. 21, 42, 46, 81, 94, 149, 166, 176, 210, 229, 233, 236, 242) are parsimony uninformative in the present context, but are included because of their likely relevance to future studies on theridiids and their relatives. Character descriptions and definitions are given in Appendix 1.

Specimen preparation

Specimens were examined under a Wild M-5 A dissecting microscope. Male palps were immersed in concentrated KOH (~1 g/mL) for 1 min and then transferred to distilled water where rapid expansion took place in less than 1 min (see, e.g. Coddington, 1990a, modified from Shear, 1967). Full expansion often required unhooking the MA from the bulb-to-cymbium lock mechanism, and occasionally re-immersion in KOH. Expanding palps is essential to the understanding of theridiid palpal morphology (Levi & Levi, 1962), and in some cases, dissection of several palps of each species was necessary to unravel the intricacies of this structure. After examining the expanded palp, the embolus (and sometimes other sclerites) was usually removed to facilitate examination of the tegulum and tegular sclerites that may reside behind the embolus. Sketches were made of expanded palps using a camera lucida.

Other genitalia were drawn using a compound microscope with a camera lucida. For the latter, specimens were temporarily mounted as described in Coddington (1983). The trajectory of the sperm duct in the male palpal tegulum was examined in expanded palps in ethanol, and in unexpanded palps made transparent by immersion in methyl salicylate (Holm, 1979). The trajectory was duplicated in a wire model (Coddington, 1990a). Detailed and accurate modelling requires excellent preparations and exhaustive examination from every angle of the tegulum. Such models were made for several species allowing the exploration of this character system, and the delimitation of characters and their states. The remainder of the species trajectories were modelled more rapidly with emphasis on understanding these character states.

For SEM, examination specimens were cleaned ultrasonically for 1 min and then transferred to 100% ethanol overnight. The specimens were then dissected; most were submitted to critical point drying, though a few were air-dried (mostly male palps). Usually, five preparations were made for each species: abdomen of both sexes, prosoma of both sexes with all legs but the fourth removed, and male palp. Successful SEM of spinnerets requires good specimen preparations where spinnerets are well separated (Figs 25A, 33A, 43F, 82C). In most cases, careful choice of specimens which happen to have the spinnerets spread out is sufficient. In a few cases, the spinnerets were spread forcibly, as described in Coddington (1989). Specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin, and then sputter coated.

All drawings were rendered in Adobe Photoshop, and plates assembled and labelled in Adobe Illustrator. The illustrations, grouped at the end of the paper, are arranged in the following order: scanning electron micrographs, drawings, photographs and cladograms. The micrographs are arranged with outgroups first, then Hadrotarsinae, followed by other theridiids in alphabetical order, with the exceptions of Figure 30 (comparison of carapace modifications of different

argyrodines) and Figure 88 (comparison of egg-sac ultrastructure of several species).

CHARACTER CODING

Many coding methods have been suggested for dealing with complex characters (see Strong & Lipscomb, 1999, for review). Strong & Lipscomb (1999) argue convincingly for the superiority of two coding methods, based on information content, which avoid redundancy and character dependence (see also Jenner, 2002): (1) reductive (binary) coding with inapplicables treated as '?', and (2) ordered multistate character coding where absences are treated in a separate binary character. The order of states in a transformation series is seen as a nested set of synapomorphies where their degree of similarity implies state adjacency (the order) but outgroup comparison establishes polarity (Lipscomb, 1992). However, multistate characters should be left unordered when adjacency cannot be established using similarity criteria (Slowinski, 1993). In this paper I use a mixture of both methods: variation is represented using binary characters as far as logical dependence will allow, with the remainder treated as multistate. None of the latter contains states that in my opinion can be justifiably ordered based on similarity criteria and all are thus left unordered.

The vast majority of morphological characters were coded following direct observation on museum specimens. Very occasionally, where I could not code characters unambiguously from the available material, species descriptions deemed reliable and/or previous phylogenetic work were used. On the other hand, a large proportion of the behavioural and web building data is taken from the literature. The most important references are as follows: (1) web building and prey capture data (Wiehle, 1931, 1937; Nielsen, 1932; Holm, 1939; Nørgaard, 1956; Bristowe, 1958; Kullmann, 1959a, b, 1960, 1971; Szlep, 1965, 1966; Lamoral, 1968; Cutler, 1972; Eberhard, 1977, 1979, 1981, 1982, 1991, 1995; Vollrath, 1977, 1979a; Carico, 1978; Kaston, 1981; Lubin, 1986; Nentwig & Christenson, 1986; Whitehouse, 1986, 1987b; Jones, 1992; Hormiga, 1994b; Hormiga *et al.*, 1995; Roberts, 1995; Griswold *et al.*, 1998; Benjamin & Zschokke, 2002, 2003; Benjamin *et al.*, 2002); (2) sexual behaviour data (Gerhardt, 1921, 1923, 1924a, b, 1925, 1926, 1928, 1933 – summarized in Huber, 1998; Locket, 1926, 1927; Braun, 1963; Knoflach, 1994, 1995, 1996, 1997, 1998, 1999, 2002; Knoflach & van-Harten, 2000, 2001).

The remainder are coded following personal observations (my own and J. A. Coddington pers. comm.). Missing information (about 5.5%) is represented by '?' in the matrix, inapplicable entries by '–', although current software makes no distinction between the two. Character coding problems and sources of information are discussed, where appropriate, under each character description.

Due to problems related to availability of material, in some cases species used for illustrations are other than those coded in the matrix. The reader should always assume, however, that the data presented here are based on observations of specimens of the species listed in the matrix, unless otherwise indicated.

Character data were compiled and managed in NEXUS Data Editor 0.5.0. (Page, 2001). Polymorphism was scored as two or more states present.

The data matrix is available at: http://www.gwu.edu/~spiders/cladograms.htm.

CHARACTER DESCRIPTION

Character definitions and descriptions are perhaps the most vital components of any phylogenetic analysis. This component is often trivialized, resulting in unclear primary homology statements, apparent subjectivity, and loss of repeatability (Jenner, 2001, 2002; Rieppel & Kearny, 2002).

In character descriptions, illustrations are of primary importance for several reasons. First, they are original primary data that, like sequences in GenBank, allow reuse, reinterpretation and reassessment of morphological homologies by any researcher (see e.g. Hormiga, 2002). They may also lead to the discovery of new characters, overlooked by the original researcher. Many character systems explored here are complex; character identity and delimitation and coding of states are in many cases difficult, speculative and of necessity assumption-laden. At a time when morphology is often criticized due to its supposed subjectivity, it is vital that authors reusing morphological datasets have, as far as possible, access to the same visual data as the original researcher.

The common uncritical recycling of original morphological datasets (e.g. in Metazoa, see Jenner, 2001) no doubt in part reflects the lack of access of subsequent authors to original illustrations to evaluate original character identities and homology assessments. Since similarity is the only available 'test' of character identity (e.g. Jenner, 2002; Rieppel & Kearny, 2002; but see Kluge, 2003) and is crucial to primary homology assessment of character states, verbal descriptions alone are insufficient if morphology is going to continue to contribute effectively to phylogenetic reconstruction (see also Jenner, 2002). I believe these reasons justify, and indeed demand, the numerous illustrations included here.

I have tried to clearly define each character verbally in order to accompany, and sometimes supplement, the illustrations. In some cases the interpretation of

primary data requires explicit argumentation and discussion with reference to the literature. In others, an illustration can make lengthy verbal description redundant, and I have tried to avoid paraphrasing what appears in the illustration. Some characters are evident from a single illustration, while others benefit from multiple illustrations. For this reason, character descriptions differ in length and detail. The primary objective is that the reader can critically evaluate and revise the characters with minimal effort.

Analyses

The character data were analysed using parsimony, seeking hypotheses that maximally explain observed similarity as due to common ancestry (synapomorphy) – in other words, that minimize ad hoc hypotheses of homoplasy (Farris, 1983). 'Descent with modification' is taken as background knowledge, and viewed as essential justification for seeking hierarchical patterns based on similarity (Kluge, 2001). It is assumed that while each character constitutes independent evidence of phylogeny, not all characters are necessarily of equal importance. Their phylogenetic strength cannot be determined a priori; arguments for a priori unequal weights are weak, make interpretation difficult, and necessarily reduce the explanatory power of the resulting hypotheses (Kluge, 1997; Grant & Kluge, 2003).

Although similarity provides the only available evidence on cladogenesis, it is not assumed that homoplasy is rare (see Farris, 1983), rather that the simplest available explanation of similarity is common ancestry. Thus, the method may fail if, in general, homoplasy provides a 'better' explanation of similarity than homology does. Highly saturated regions of a DNA sequence and morphological reduction characters are examples where homology may not be an appropriate explanation of observed similarity (Felsenstein, 1978; Siddall, 1998). Finally, homology need not be common; observed similarity that emerges as synapomorphy on a cladogram is viewed as not *necessarily* constituting homology (thus synapomorphy does not equal homology, *contra* Patterson, 1982; see Farris, 1983), merely as evidence that does not require ad hoc dismissal as homoplasy. Synapomorphies are corroborated hypotheses of homology, but like any scientific hypotheses, they are subject to testing by addition of data.

The data set (Table 1) comprises 62 taxa and 242 characters, of which 229 are phylogenetically informative in this study. Cladistic analysis was performed as follows: (1) NONA (Goloboff, 1993b) using the mult*1000 command and the ratchet 'island hopper' (Nixon, 1999) with 1000 replications, holding ten trees and selecting 25 characters for each; (2) PAUP* (Swofford, 2002) with 1000 random stepwise additions, and subtree-pruning and regrafting branch swapping algorithm (all searches done with both amb – and amb =) searching for minimal length trees under the criterion of parsimony. These search algorithms are heuristic because exact algorithms (e.g. branch and bound) are not computationally feasible for matrices of this size.

Sensitivity analyses

Successive weighting (Farris, 1969) was performed in NONA using the swt.run file (a small routine file not in earlier versions, but now distributed with the program) and the command line 'run swt.run hold10000 hold/1000 mult*1000 jump50 (the jump command is used to find multiple islands of trees by branch swapping on optimal and suboptimal trees) and in PAUP* with equivalent settings. NONA reweights characters based on CI. In PAUP* I re-weighted characters using the rescaled CI, in both cases using default settings (weights are recalculated on a scale of 0 to 100). Successive weighting can be used either to discover new trees based on 'cladistically reliable characters' (Farris, 1969), to select among multiple most parsimonious trees (Carpenter, 1988), or, as in this study, to assess the sensitivity of the results to weighting against homoplasies (Wheeler, 1995; Prendini, 2001).

Parsimony analyses under implied weights were performed using Pee-Wee (Goloboff, 1993c) (command line: hold10000; hold/1000; mult*1000; jump50). This method resolves character conflict in favour of the characters that have less homoplasy on the trees (see Goloboff, 1993a for justification). It does so by seeking trees with maximum total fit, F ($F = \Sigma f_i$, and $f_i = k/(k + ES_i)$, where f_i is fit of character $_i$, k is a constant of concavity, and ES_i is the number of extra steps for character $_i$). The influence of homoplastic characters can be controlled by varying k (from 1 to 6).

Sensitivity was further analysed with bootstrapping and parsimony jackknifing. Bootstrapping (Felsenstein, 1985) randomly re-samples characters with replacement, and thus, in effect, reweights characters (each character can randomly receive a weight of 0% up to 100% in each replicate). The result of a bootstrap analysis may thus be taken to indicate the sensitivity of the data to random perturbations of character weight (but see Grant & Kluge, 2003). Parsimony jackknifing similarly randomly reweights characters but is computationally much more efficient (Farris *et al.*, 1996). As the resampling is done without replacement, character weight will be randomly either 0 (character not chosen) or approximately 1.6 (character chosen, given about 40% character removal), in each replicate.

Table 1. Character state matrix. Rows represent characters and columns taxa. The first state is '0', second '1' etc. '?' represent missing data, '–' inapplicable states. Character descriptions are abbreviated, refer to Appendix 1 for full character names and descriptions. Taxon abbreviations (species only if more than one per genus in matrix): Ag, *Argiope*; Te, *Tetragnatha*; Pi, *Pimoa*; Li, *Linyphia*; Ss and Sc, *Synotaxus waiwa*; and *monoceros*; Ei, *Eidmanella*; Ne, *Nesticus*; Di, *Dipoena*; Ea, *Emertonella*; Eu, *Euryopis*; Ta, *Thwaitesia*; Ep, *Episinus*; Sp, *Spintharus*; Lg, *Latrodectus geometricus*; Ls, *L. mactans*; Cr, *Crustulina*; St, *Steatoda*; Ca, *Carniella*; Ro, *Robertus*; Ph, *Pholcomma*; El, *Enoplognatha latimana*; Eo, *E. ovata*; Sg, *Selkirkiella magallanes*; Sa, *S. alboguttata*; Pa, *Phoroncidia*; Ce, *Cerocida*; Se, *Stemmops*; Aa, *Argyrodes argyrodes*; Ae, *A. elevatus*; Ne, *Neospintharus*; Rh, *Rhomphaea*; Ar, *Ariamnes*; Fa, *Faiditus*; Ka, *Kochiura aulica*; Kr, *K. rosea*; Al, *Anelosimus lorenzo*; Au, *A. rupununi*; Ap, *A. pulchellus*; Av, *A. vittatus*; A1, *A.* sp. 1; A2, *A.* sp. 2; Ay, *A. analyticus*; Ax, *A. eximius*; Aj, *A.* cf. *jucundus*; As, *A. studiosus*; Ch, *Chrysso*; Nr, *Nesticodes*; Tf, *Theridion frondeum*; Tl, *T. longipedatum*; Tv, *T. varians*; Tp, *T. pictum*; Co, *Coleosoma*; Td, *Tidarren*; He, *Helvibis*; Th, *Theridula*; Ad, *Ameridion* sp.; Ai, *A.* cf. *petrum*; Ty, *Thymoites*; Ao, *Achaearanea tepidariorum*; Az, *A. vervoorti*; Aq, *A. wau*. The last columns give length (L), consistency index (CI) and retention index (RI) of characters

	A T P L S S E N D E E T E S L L C S C R P E E S S P C S A A N R A F K K A A A A A A A A A A A C N T T T T C T H T A A T A A A		
	g e i i s c i e i a u a p p g s r t a o h l o g a a e e a e e h r a a r l u p v 1 2 y x j s h r f l v p o d e h d i y o z q L	CI	RI
FEMALE GENITALIA			
001. Epigynal ventral margin: entire; with scape;	0 0 0 1 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 1 1 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 1 0 0 0 0 | 0 0 3	0.33	0.33
002. Epigynal dorsal plate: absent; present;	**0 0 1 1 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 1**	1	1
003. Epigynal plate surface: smooth; ridged;	0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 1 1 1 1 | 0 0 1 1 1 1 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 2	0.5	0.85
004. Copulatory pore position: caudal; ventral;	**0 - 0 0 0 0 1 1 0 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 0 0 1** | **1 1 3**	0.33	0.71
005. Copulatory pore shape: wide; narrow slits;	0 0 0 0 0 0 0 0 0 1 | 1 0 1 0 0 0 0 1 0 1 | 1 0 0 1 1 1 1 1 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 5	0.2	0.6
006. Copul. bursa ant. margin: entire; medially acute;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 1 1 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 1 0 0 1 1 0 0** | **0 0 0 0 0 0 1 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 4**	0.25	0.4
007. Cop. duct to spermath: posterior; lat./anterior;	? 0 0 0 0 0 0 0 1 1 | 1 0 1 0 1 1 1 1 0 1 | 1 0 0 0 0 0 ? 0 0 0 | 0 0 1 1 0 0 1 1 0 0 | 0 0 0 0 0 0 0 1 0 0 | 0 0 0 0 1 0 0 0 0 0 | 0 0 9	0.11	0.46
008. Copulatory duct: simple loop; 2 or more loops;	**0 0 0 1 1 1 0 0 0 0** | **0 0 1 1 1 1 1 0 0 1 0** | **1 0 0 1 1 1 1 1 1 0 0** | **0 0 0 0 0 1 1 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 1 0 0 0 0 0** | **0 0 9**	0.11	0.5
009. Copul. duct rel. to spermath.: apart; encircling;	- - - 0 0 0 - - - - | - - 0 0 1 1 - - 0 - | 0 - - 0 0 1 1 1 - - | - - - - - 1 1 - - - - | - - - - - - - - - - - | - - - - 0 - - - - - - | - - 3	0.33	0.66
010. Spermathecal number: two; four;	**0 1 0 0 0 0 0 0 1 1** | **1 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 2**	0.5	0.66
011. Spermathecal shape: ovoid; elongate; dumbbell;	0 0 0 1 0 0 0 0 0 0 | 0 0 0 0 2 2 0 0 0 2 | 0 0 0 0 0 0 0 2 0 0 0 | 0 0 1 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 5	0.4	0.25
012. Spermathecal accessory lobes: absent; present;	**0 0 0 0 0 0 1 1 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 1**	1	1
013. Fertilization duct sclerot.: light; heavy;	0 0 0 0 1 1 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 1	1	1
MALE GENITALIA			
014. Tibial distal end: subequal to base; broadened;	0 1 0 0 0 0 0 0 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 2	0.5	0.83
015. Tibial rim: slightly asymmetric; scoop-shaped;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 1 1 1 1 1 1** | **1 0 0 0 0 0 0 0 1 1** | **1 0 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 4**	0.25	0.85
016. Tibial rim setae: irregular; regular, strong setae;	0 0 0 0 0 0 0 0 0 0 | 0 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 0 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 2	0.5	0.9
017. Tibial rim protrution: dorsal to cymb.; faces bulb;	**0 0 0 0 0 0 0 0 0 0** | **0 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 0 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 2**	0.5	0.9
018. Tibial retrol. trichob.: =>three; two; one or none;	0 0 0 0 1 1 1 1 1 2 | 2 1 1 1 1 1 2 1 2 2 | 2 1 1 1 2 2 2 2 2 1 | 1 2 2 1 1 1 1 1 1 1 | 1 1 1 1 1 1 2 1 1 1 | 2 2 2 2 2 2 2 2 2 1 | 1 1 8	0.25	0.76
019. Tibial prol.trichob.: =>two; one; none;	**0 0 0 1 1 1 1 1 1 1** | **2 1 1 1 1 1 2 1 2 2** | **2 1 1 1 1 2 2 1 1 1** | **1 2 2 1 1 1 1 1 1 1** | **1 1 1 1 1 1 2 2 2 2** | **2 2 2 2 2 2 2 2 2 2** | **2 2 8**	0.25	0.76
020. Patellal spur: absent; present	0 0 0 0 1 1 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 1	1	1
021. Cymbium: entire; expanded retrolaterally;	**0 0 1 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 1**	unin.	unin.
022. Cymbial retromargin: entire; w/apoph.; groove	0 0 0 0 2 2 0 10 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 1 1 0 | 0 0 0 2	1	1
023. Cymb. dorsob. margin: entire; incised; ridged	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **1 1 2**	1	1
024. Cymbial dist. prom.: entire; w/apoph.; Latrod.;	0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 2 2 1 0 0 0 | 0 0 0 0 0 0 0 0 1 1 | 0 0 1 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 4	0.4	0.5
025. Cymbial mesal margin: entire; incised;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 1 0** | **0 0 0 0 0 0 1 1 0 0** | **1 1 1 1 1 1 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 2**	0.5	0.87
026. Cymbial tip sclerotization: normal; light;	0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 1 1 1 1 1 1 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 1	1	1
027. Cymbial tip setae: normal; thick and curved;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 1 1 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 1**	1	1
028. Cymbial sheath: absent; present;	0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 1 1 0 0 0 0 | 0 0 0 0 0 1 0 0 0 0 | 0 0 0 0 1 1 1 1 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 4	0.25	0.5
029. Paracymbium (PC): present; absent;	**0 0 0 0 0 0 0 0 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1**	1	1
030. PC: Argio.; Tetrag.; Pimoa; Liny.; cup; Nestic.;	0 1 2 3 4 4 5 5 - - | - - - - - - - - - - | - - - - - - - - - - | - - - - - - - - - - | - - - - - - - - - - | - - - - - - - - - - | - - 5	1	1
031. Bulb-cymbium lock mechan.: absent; present;	**0 0 0 0 0 0 0 0 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1**	1	1
032. Lock placement: basal; distal; central;	- - - - - - - - 1 1 | 1 1 1 1 1 1 1 1 0 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 2 2 | 1 1 1 1 1 1 1 1 1 1 | 1 1 1 1 1 1 1 1 1 1 | 1 1 2	1	1
033. Lock mechanism: hook; hood; Theridula;	**- - - - - - - - 0 0** | **0 0 0 1 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 1 1 1** | **1 1 1 1 1 1 1 1 1 1** | **1 1 1 0 1 1 1 1 2 1** | **1 1 4**	0.5	0.91
034. Cymbial hook orient.: downwards; upwards;	- - - - - - - - 0 0 | 0 0 0 - 0 0 0 0 1 1 | 1 1 1 1 1 1 1 1 0 0 | 0 0 0 0 1 1 - - - - | - - - - - - - - - - | - - - 0 - - - - - - | - - 2	0.5	0.9
035. Cymbial hook: inside cymbium; ectal margin;	**- - - - - - - - 0 0** | **0 0 0 - 0 0 0 0 1 1** | **1 1 1 1 1 1 1 1 0 0** | **0 0 0 0 0 0 - - - -** | **- - - - - - - - - - -** | **- - - 1 - - - - - - -** | **- - 3**	0.33	0.77
036. Cymbial hook inferior groove: absent; present;	- - - - - - - - 1 1 | 1 1 1 1 1 1 1 1 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 1 1 - - - | - - - - - - - - - - | - - - 0 - - - - - - | - - 2	0.5	0.9
037. Cymbial hook tip: blunt; strongly tapering;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 - 0 0 0 0 1 1** | **1 0 0 1 1 0 0 0 0 0** | **0 0 0 0 0 0 - - - -** | **- - - - - - - - - - -** | **- - - 0 - - - - - - -** | **- - 2**	0.5	0.75
038. Cymbial hood size: narrow; broad; Spintharus;	- - - - - - - - - - | - - - 2 - - - - - - | - - - - - - - - - - | - - - - - - 1 1 0 0 | 0 0 0 0 0 0 1 0 1 1 | 0 0 0 - 0 0 0 0 - 0 | 0 0 4	0.5	0.5
039. Cymbial hood region: translucent; opaque;	**- - - - - - - - - -** | **- - - 1 - - - - - -** | **- - - - - - - - - -** | **- - - - - - 1 1 1 1** | **0 0 0 0 0 0 1 1 1 1** | **1 1 1 - 1 1 1 1 - 1** | **1 1 1**	1	1
040. Bulbal sclerite of lock mechanism: MA; E base;	- - - - - - - - 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 - 1 | 1 1 1	1	1
041. Alveolus placement: ectal; central; mesal;	**0 1 2 1 1 1 1 1 2 2** | **2 2 2 2 2 2 2 2 2 2** | **2 2 2 2 2 2 2 2 2 2** | **2 2 2 2 2 2 2 2 2 2** | **2 2 2 2 2 2 2 2 2 2** | **2 2 1 2 1 2 2 2 2 1** | **1 1 6**	0.33	0.6
042. Alveolar cavity: simple; with alveolar sclerite;	0 0 0 0 0 0 0 0 0 0 | 0 1 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 1	unin.	unin.
043. Alveolus shape: suboval; mesal extension;	**0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 1 1 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 0 0 0 0 0 0 0 0** | **0 0 1**	1	1

Table 1. *Continued*

Character	A g	T e	P i	L i	S s	S c	E i	N e	D i	E a	E u	T a	E p	S p	L g	L s	C r	S t	C a	R o	P h	E l	E o	S g	S a	P a	C e	S e	A a	A e	N e	R h	A r	F a	K a	K r	A l	A u	A p	A v	A 1	A 2	A y	A x	A j	A s	C h	N r	T f	T l	T v	T p	C o	T d	H e	T h	A d	A i	T y	A o	A z	A q			
044. Subtegular retrolateral margin: entire; lobed;	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
045. Tegulum size: normal; huge;	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0.33	0.33
046. Tegulum ectal margin: entire; protruded;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	unin.	unin
047. Tegular groove: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
048. Tegular arch: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1
049. Tegular pit: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	3	0.33	0.75
050. Tegular pit, E interaction: E base; E apophysis;	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	1	1	1	1	1	0	0	0	-	-	-	-	-	-	1	1	1
051. SDT Switchbacks I & II: present; absent;	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	6	0.16	0.37
052. SDT SB I: separate; touching;	0	0	0	0	-	-	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	-	-	0	0	0	0	1	1	1
053. SDT SB II: entirely in tegulum; terminates in E;	0	0	0	0	-	-	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	-	-	0	1	1	1	1	1	1
054. SDT post-SB II turn: absent; present;	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	-	0	0	-	-	0	0	0	0	1	1	1
055. SDT SB I & II segm. alignment: diverg.; parallel;	0	0	0	0	-	-	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	-	1	0	-	-	0	0	0	0	4	0.25	0.7
056. SDT SB I & II orient.: in plane; out of plane;	0	0	0	0	-	-	0	0	0	0	0	-	0	0	0	0	0	0	0	0	1	-	-	0	0	0	-	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	1	1	-	-	0	1	1	1	3	0.33	0.9
057. SDT RSB I & II: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.83
058. SDT SB III: absent; present;	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	7	0.14	0.76
059. SDT SB IV: absent; present;	-	-	-	-	-	-	1	1	0	0	0	0	1	0	-	-	-	-	0	0	-	0	0	0	0	0	-	-	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	-	1	-	-	-	-	-	-	-	4	0.25	0.75
060. SDT entering E: clockwise; counter-clockwise;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
061. SDT constriction: gradual; abrupt before SB I;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
062. Conductor: present; absent ;	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	7	0.14	0.25
063. C tip width: subequal to base; enlarged;	0	0	0	-	-	-	-	0	0	-	-	1	1	1	0	0	0	0	?	0	0	0	0	1	1	-	-	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	4	0.25	0.57
064. C with a groove for embolus; entire;	0	0	1	-	-	-	-	1	1	-	-	0	0	0	1	1	1	1	?	1	1	0	0	0	0	-	-	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	-	0	0	0	8	0.12	0.68
065. C surface: smooth; heavily ridged;	0	0	0	-	-	-	-	0	0	-	-	0	1	1	0	0	0	0	?	0	0	1	1	1	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-	1	1	1	5	0.2	0.55
066. C folding: entire; complex; Helvibis;	0	0	0	-	-	-	-	0	0	-	-	1	1	1	0	0	0	0	?	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	-	0	0	0	2	1	1
067. C tip sclerotization: like base; more than base;	0	0	0	-	-	-	-	0	0	-	-	1	1	1	0	0	0	0	?	0	0	1	1	1	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	-	1	1	1	6	0.16	0.64
068. C base: entire; grooved;	0	0	0	-	-	-	-	0	0	-	-	0	0	0	1	1	1	1	?	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	1	1	1
069. C origin: tegular margin; apical to teg. margin;	0	0	0	-	-	-	-	0	0	-	-	0	0	0	0	0	0	0	?	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	-	0	0	0	2	0.5	0.85
070. Subconductor: absent; present;	0	0	0	-	-	-	-	0	0	-	-	0	0	0	0	0	0	0	?	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	3	0.33	0.66
071. Median apophysis: present; absent;	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	4	0.25	0.4
072. MA and sperm duct: not in MA; inside MA;	0	-	0	-	-	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	4	0.25	0.85
073. MA-tegulum attachment: membraneous; fused;	0	-	1	-	-	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	-	-	-	2	0.5	0.66
074. MA-tegular connection: broad; narrow;	0	-	-	-	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	-	-	-	2	0.5	0.95
075. MA form: unbranched; two branches;	0	-	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	1	1	1
076. MA central region: entire; w/apophysis;	0	-	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	1	0	-	-	-	4	0.25	0.57
077. MA apophysis II: absent; present;	0	-	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	-	-	-	1	1	1
078. MA distal tip: entire; hooded;	0	-	0	-	-	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	-	-	-	5	0.2	0.84
079. MA hood form: narrow, pit-like; scoop-shaped;	-	-	-	-	-	-	-	-	0	0	0	0	0	-	0	0	0	0	1	1	1	0	0	1	1	-	1	1	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	2	0.5	0.88
080. Theridioid tegular apophysis: absent; present;	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	4	0.25	0.62
081. TTA branches: unbranched; two branches;	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	1	unin.	unin
082. TTA apex: entire; with a small apophysis;	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	1	1	1
083. TTA form: entire; grooved; excavate;	-	-	-	-	2	2	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	5	0.4	0.66
084. TTA basal portion: bulky; huge, membranous;	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	3	0.33	0.33
085. TTA distal tip: entire; hooked;	-	-	-	-	0	0	0	0	0	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	-	-	-	-	6	0.16	0.66
086. TTA surface: smooth; ridged;	-	-	-	-	0	0	0	0	0	1	1	0	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	-	-	-	-	7	0.14	0.64
087. E and TTA: loosely assoc.; E enclosed in TTA;	-	-	-	-	1	1	1	1	0	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	4	0.25	0.66

	A	T	P	L	S	S	E	N	D	E	E	T	E	S	L	L	C	S	C	R	P	E	E	S	S	P	C	S	A	A	N	R	A	F	K	K	A	A	A	A	A	A	A	A	A	A	C	N	T	T	T	T	C	T	H	T	A	A	T	A	A	A			
	g	e	i	i	s	c	i	e	i	a	u	a	p	p	g	s	r	t	a	o	h	l	o	g	a	a	e	e	a	e	e	h	r	a	a	r	l	u	p	v	1	2	y	x	j	s	h	r	f	l	v	p	o	d	e	h	d	i	y	o	z	q			
088. E tip: entire; bifid;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
089. E origin: retroventral on tegulum; retrolateral;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.25	0.5
090. E surface: smooth; ridged;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	?	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.2	0.42
091. E shape: short to moderate; extremely long;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0.25	0.4
092. E spiral: normal; thick, much broader than tip;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
093. E spiral: suboval or round; distinctly flattened;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
094. E form: entire; with transverse suture;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	unin.	unin.
095. E distal rim: entire; deeply grooved;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
096. E terminus: abrupt; with a distal apophysis;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.33	0.5
097. E-tegulum junction: fixed; membraneous;	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	4	0.25	0.4
098. E base: entire; lobed;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	6	0.16	0.8
099. Embolic division b: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.33	0.33
100. E spiral insertive piece: entire; break-off point;	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
101. Extra tegular sclerite: absent; present ;	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.25	0.57
SOMATIC MORPHOLOGY																																																																		
102. Lateral eyes (male): juxtaposed; separate;	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.5
103. ME (M): normal; on tubercle; eye region raised	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
104. AME size vs. ALE (M): subequal; smaller;	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0.16	0.64
105. AME-ALE separ. (F): >1 diam.; =.0141diam.;	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	1	1
106. Chel. promargin: toothed; smooth;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.5	0.75
107. Chel. anterior tooth shape: blunt; pointed;	0	0	0	0	0	0	0	0	-	-	-	1	1	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
108. Chel. ant. tooth no.: four+ three; two; one;	0	0	1	0	1	1	1	1	-	-	-	1	2	3	-	-	3	3	1	1	1	1	1	1	1	3	0	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	?	?	2	2	2	2	2	2	?	?	2	2	2	1	1	0.33	0.64
109. Chel. prox. tooth size: =.014adjacent; >adjacent;	0	0	0	0	0	0	0	0	-	-	-	0	0	-	-	-	-	-	1	0	0	1	1	0	0	-	1	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	1	1	0	1	0	0	1	1	1	1	1	1	9	0.2	0.76
110. Chel. posterior margin: toothed; smooth;	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	5	0.2	0.84
111. Chel. post. tooth no.: four+ three; two; one;	1	0	2	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	2	2	0	3	3	1	1	-	0	-	3	3	3	3	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	5	0.3	0.58
112. Chel. furrow: smooth; denticulate;	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0.33	0.71
113. Chel. sexual dimorph.: subequal; male larger;	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.33	0.33
114. Chel. ectal surface (M): smooth; stridulatory;	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1
115. Chel. ant.base: rounded; with a distinct knob;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0.5	0.75
116. Chel. apophysis (M): absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
117. Chel. paturon length: normal; short;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.5	0.75
118. Chel. paturon width: normal; thin;	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.33	0.71
119. Chel. fang length (M): normal; huge;	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.33	0.33
120. Chel. fang shape: cylindrical; sickle-shaped;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1
121. Chel. hairs: weakly serrate; strongly serrate;	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33	0.71
122. Chel. boss: present; absent;	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	0.5	0.5
123. Carap.: smooth; rugose; scaly; rippled; bumpy;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	2	1	1
124. Carap. height (M): normal; raised (hadrotarsid);	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	1
125. Carap. color.: uniform; longitudinal dark band;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0.33	0.33
126. Carapace shape: longer than wide; subequal;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	3	1	1
127. Carapace hairiness: sparse or patchy; uniform;	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.5	0.83
128. Carap. pars stridens: irregular; regular ridges;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.16	0.83
129. Regular pars stridens: separate; continuous;	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	1	0	0	1	1	-	-	-	0	0	0	0	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6	0.5	0.8
130. Interocular area: flush with clypeus; projecting;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.8

Table 1. *Continued*

	Ag	Te	Pi	Li	Ss	Sc	Ei	Ne	Di	Ea	Eu	Ta	Ep	Sp	Lg	Ls	Cr	St	Ca	Ro	Ph	El	Eo	Sg	Sa	Pa	Ce	Se	Aa	Ae	Ne	Rh	Ar	Fa	Ka	Kr	Al	Au	Ap	Av	A1	A2	Ay	Ax	Aj	As	Ch	Nr	Tf	Tl	Tv	Tp	Co	Td	He	Th	Ad	Ai	Ty	Ao	Az	Aq			
131. Clypeus: concave or flat; projected;	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.25	0.4
132. Ocular area setae (M): sparse; in a dense field;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.83
133. Clypeal setae (M): normal; modified;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
134. Labium distal margin: rebordered; not rebord.;	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.5	0.8
135. Labium-sternum connection: seam; fused;	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	14	0.07	0.5
136. Labium shape: subrectangular; triangular;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
137. Sternum: elongate; subequal or wider than long;	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	5	0.2	0.63
138. Sternocoxal tubercles: present; absent;	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.6
139. Sternum setal bases: unmodified; raised;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
140. Pedicel location: anterior; medial;	0	0	?	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	?	0	1	0	1	1	1	1	1	1	1	8	0.12	0.72
141. Pedicel lyriform organs: narrow; broad;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
142. Abdomen: w/paired humps; ellipisoid, smooth;	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	5	0.2	0.33
143. Abd. color pattern: folium; uniform or unpigm.;	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0.2	0.5
144. Abd. folium: spots or blotches; central band;	0	1	0	1	0	0	-	-	0	0	0	0	0	0	0	0	0	0	-	-	-	1	1	1	-	0	-	-	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	-	1	1	0	0	0	0	8	0.12	0.69
145. Dorsal band: edge light; edge dark; Ameridion;	-	1	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	-	1	1	1	-	-	-	2	2	-	-	-	-	4	0.5	0.75
146. Abd. dot pigment: silver; non-reflective, dull;	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	3	0.33	0.75
147. Abd. pedicel area (M): smooth; sclerotized;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	1	0	1	1	0	0	0	1	1	1	7	0.14	0.75
148. Abd. pedicel area sclerot.: continuous; separ.;	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	-	-	-	0	-	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	?	0	-	0	0	-	-	-	1	1	1	4	0.25	0.57
149. Abd. supra-pedicellate nubbins: abs.; present;	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	unin.	unin.
150. Stridulatory pick row (SPR): absent; present;	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.83
151. SPR form: weakly keeled; strongly keeled;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	1	1	1	1	1	1	0	0	-	-	0	1	1	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	8	0.12	0.46
152. SPR pick number: three or less; four or more;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	1	0	1	0	1	1	0	0	-	-	0	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	?	1	1	1	1		0	0	0	1	1	1	0	1	1	1	8	0.12	0.46
153. SPR ectally-oriented picks: present; absent;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
154. SPR insertion: flush with abd. surface; on ridge;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	-	-	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	6	0.16	0.68
155. SPR region: smooth; grooved;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
156. SPR mesal pointing picks: absent; present;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	1	1	0	1	1	1	1	1	-	-	1	1	1	0	0	0	1	1	1	1	1	?	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	5	0.2	0.55
157. SPR mp-picks angle: dorsal; perp. or ventral;	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	-	-	-	0	0	0	-	-	-	0	0	0	0	0	?	-	0	0	1	1	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
158. SPR setal bases: low, gently ridged; acute;	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	0	0	-	-	0	0	0	-	-	-	0	0	0	-	-	?	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	1	1	0	0	0	1	1	1
159. SPR: straight; distinctly curved; argyrodine;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	-	0	0	-	-	-	-	-	2	2	2	2	2	0	0	0	0	0	?	0	1	1	1	1	1	1	0	0	0	0	0	?	0	-	0	0	0	0	0	0	0	0	2	1	1
160. SPR dorsal pick spacing:normal; compressed;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	1	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
161. SPR relative to pedicel: lateral; dorsal;	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	0	1	1	1	1	0	0	1	1	-	-	1	0	0	0	0	0	0	1	1	0	0	?	1	1	1	1	1	1	1	1	0	1	1	0	?	1	1	1	1	1	1	1	1	1	1	6	0.16	0.58
162. Additional stridulatory picks: absent; present;	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	1	1	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	0	0	0	0	0	1	1	1	3	0.33	0.71
163. Suprapedicillate dorsal proprio.: abs.; present;	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	0.25	0.66
164. Suprapedicillate ventrolat. proprio.: abs.; pres.;	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	0.33	0.84
165. Abd. suprapedicellate apod.: rugose; smooth;	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
166. Abd. surface: smooth; with scuta;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	unin.	unin.
167. Sigilla: conspicuous; inconspicuous, unicolor.;	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	5	0.2	0.63
168. Epiandrous fusules: present; absent;	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.2	0.2
169. Epiandrous fusule: in pair of sockets; in a row;	0	0	1	1	1	1	1	?	0	-	-	?	0	-	1	1	1	0	-	0	0	0	0	0	0	0	-	0	0	0	0	-	1	0	0	0	0	0	?	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	0.16	0.79
170. Epiandrous fusule pair number: >ten; <=eight;	1	0	0	0	0	0	1	1	1	-	-	1	1	-	1	1	1	1	-	1	1	0	0	1	1	1	-	1	1	1	1	-	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	5	0.2	0.55
171. Male seminal vesicula: small; large and dark;	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	0	1	1	1
172. Colulus: present; absent; invaginated;	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	0.66	0.96
173. Colulus size: large; small;	0	0	0	0	0	0	0	0	0	-	-	1	1	1	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0.33	0.6
174. Colular setae: present; absent;	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.5	0.93

	A g	T e	P i	L i	S s	S c	E i	N e	D i	E a	E u	T a	E p	S p	L g	L s	C r	S t	C a	R o	P h	E l	E o	S g	S a	P a	C e	S e	A a	A e	N e	R h	A r	F a	K a	K r	A l	A u	A p	A v	A 1	A 2	A y	A x	A j	A s	C h	N r	T f	T l	T v	T p	C o	T d	H e	T h	A d	A i	T y	A o	A z	A q			
175. Colular setae number (F): three or more; two;	0	0	0	0	0	0	1	1	1	1	-	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	2	0.5	0.88
176. Palpal claw (female): present; absent;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0		unin.	unin.
177. Palpal claw: attenuate; palmate; semi-palmate;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	2	2	3	0.66	0.8
178. Palpal claw dentition (female): dense; sparse;	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	-	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	?	1	0	0	1	0	0	0	8	0.12	0.63
179. Palpal tibial trichob. (F): >six; 3–5; 1–2;	0	0	0	1	1	1	1	1	1	2	2	1	1	2	1	1	2	1	2	2	2	1	1	2	2	2	2	2	1	1	1	2	2	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	1	2	2	2	2	2	1	1	1	9	0.22	0.74
180. Palpal tarsal setae (F): smooth; serrated;	?	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	2	0.5	0.75
181. Palpal tarsus dorsal setae (F): present; absent;	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
182. Femur I relative to II: subequal; robust, larger;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	3	0.33	0.5
183. Femoral macrosetae: present; absent;	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
184. Leg IV rel. length (M): third; second; longest;	0	0	1	1	0	0	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	7	0.28	0.75
185. Leg IV rel. length (F): third; second; longest;	0	?	1	1	0	0	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	1	2	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	7	0.28	0.44
186. Femur vs. metat.: metat. longer; metat. shorter;	0	0	?	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	7	0.14	0.7
187. Metat. vs. tibia: metat. longer; metat. shorter;	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	8	0.12	0.73
188. Metatarsal ventral macrosetae: normal; thick;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.5
189. Metat. I trichob. pos.: proxim.; distal; submed.;	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	0	0	0	2	2	0	0	0	0	8	0.25	0.6
190. Metatarsus III trichobothrium: present; absent;	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0.33	0
191. Metatarsus IV trichobothrium: absent; present;	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.5
192. Patella-tibia autospasy: absent; present ;	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
193. Tarsus IV setae: smooth; serrate (tarsal comb);	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
194. Tarsus IV comb: smooth; theridiid grooves;	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
195. Tarsus IV comb: simple, straight; curved hooks;	-	-	-	-	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	1	0	0	0	0	0	1	1	1	6	0.16	0.7
196. Tarsus IV comb dors. margin: straight; notched;	-	-	-	-	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
197. Tarsus I ventral setae: ungrouped; grouped;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
198. Tarsal organ size: small (normal); enlarged;	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
199. Tarsus IV central claw vs. lat. (M): short; longer;	0	?	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1	1	1	1	1	1	3	0.33	0.92
200. Tarsus IV central claw (F): normal; long; minute;	0	0	2	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	0	2	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.4	0.72
SPINNERETS																																																																	
201. Spinneret insert.: normal; abd. extend. beyond;	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	5	0.2	0.6
202. Spinneret sclerotized ring: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
203. ALS median surface: normal; w/parallel ridges;	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
204. ALS PI spigot bases: normal; reduced;	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
205. ALS piriform field size: large; small;	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	4	0.25	0.72
206. PLS FL spigot: = PLS CY; longer than PLS CY;	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	?	0	0	0	0	1	1	0	0	0	-	-	-	0	0	-	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	?	1	1	?	0	0	1	1	1	1	4	0.25	0.85
207. PLS post CY base: normal; enlarged;	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1
208. CY spigot bases: =.014ampullates; huge;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
209. CY shaft surface: smooth; grooved;	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.5	0.83
210. PLS CY spigot number: two; one;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0	1	unin.	unin.
211. PLS AC spigot number: 5+; four or less;	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.25	0.7
212. PLS FL spigot: present; absent;	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	4	0.25	0.57
213. PLS AG spigot number (F): two; one;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
214. PLS AG spigot size: <=CY; larger than CY;	0	0	1	0	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.5	0.5
215. PLS anterior AG spigot shape: normal; flat;	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.5	0.87
216. PLS posterior AG spigot shape: normal; flat;	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	0	1	1	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	0.25	0.78
217. PLS aggregate gland form: entire; lobed;	?	0	?	0	?	?	?	1	?	?	1	?	1	?	1	1	1	1	?	?	?	1	1	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	1	1	1

Table 1. *Continued*

Character	Ag	Te	Pi	Li	Ss	Sc	Ei	Ne	Di	Ea	Eu	Ta	Ep	Sp	Lg	Ls	Cr	St	Ca	Ro	Ph	El	Eo	Sg	Sa	Pa	Ce	Se	Aa	Ae	Ne	Rh	Ar	Fa	Ka	Kr	Al	Au	Ap	Av	A1	A2	Ay	Ax	Aj	As	Ch	Nr	Tf	Tl	Tv	Tp	Co	Td	He	Th	Ad	Ai	Ty	Ao	Az	Aq			
218. PLS theridiid AG position: parallel; end to end;	-	-	-	-	-	-	-	-	-	1	1	1	1	1	0	0	0	0	-	-	-	0	0	-	-	0	-	0	1	1	0	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	0	1	1	1	4	0.25	0.66
219. PLS AG and FL (M): absent; present;	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	?	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.2	0.6
220. PMS mAP nubbins: present; absent;	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0.5	0.8
221. PMS CY spigot base: distinct; indistinct, abs.;	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1
222. PMS AC spigot no.: 5+; 4; 3; 2; 1; 0;	0	2	5	2	2	2	2	2	3	3	3	3	3	3	1	1	1	1	5	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	6	0.83	0.88
223. PMS mAP spigot shaft: short; >CY shafts;	0	0	-	1	0	0	?	?	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	5	0.2	0.85
BEHAVIOR AND WEB BUILDING																																																																	
224. Prey-catching web: present; absent;	0	0	0	0	0	0	0	0	?	1	1	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	?	0	?	?	0	0	0	0	?	0	0	0	0	0	0	0	?	0	?	?	?	0	0	0	1	1	1
225. Web: orb; sheet; rect.; cob; H; mesh; line; Ph.;	0	0	1	1	2	2	3	3	?	-	-	6	4	4	3	3	3	3	?	?	?	3	3	3	3	6	?	?	6	6	6	6	6	6	3	3	5	5	?	3	?	?	1	1	1	1	?	3	3	3	3	3	3	3	?	3	?	?	?	5	5	3	10	0.6	0.77
226. Sticky silk in web: present; absent;	0	1	?	0	0	0	0	0	?	-	-	1	0	0	0	0	?	0	?	?	?	?	?	1	1	0	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	1	1	1	1	?	0	?	?	0	?	0	1	?	?	?	?	?	?	?	0	6	0.16	0.5
227. Sticky silk placement: sheet; on gumfoot lines;	0	-	?	0	0	0	1	1	?	-	-	-	1	1	1	1	?	1	?	?	?	?	?	-	-	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	-	-	-	-	?	1	?	?	0	0	?	-	?	?	?	?	?	?	?	1	2	0.5	0.8
228. Wrap-bite attack: present; absent;	0	1	1	1	0	0	0	0	?	0	?	?	0	?	0	0	?	0	?	?	?	?	0	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	0	0	0	0	?	0	?	?	?	0	?	0	?	?	?	?	?	?	?	0	2	0.5	0.5
229. Sticky silk wrap attack: absent; present;	0	-	-	-	1	1	1	1	?	1	?	?	1	?	1	1	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	1	1	1	1	?	1	?	?	?	1	?	1	?	?	?	?	?	?	?	1	1	unin.	unin.
230. Egg sac: spherical to lenticular; stalked;	0	0	?	0	0	0	0	0	?	?	?	?	?	?	0	0	?	?	?	0	0	?	0	0	0	?	?	?	1	1	1	1	1	1	?	?	0	0	?	0	?	?	0	0	0	0	?	0	0	?	0	0	0	0	?	0	?	?	?	?	0	0	1	1	1
231. Egg case: round; knob.; rhomb.; elong.; spiky;	0	0	?	0	0	0	0	0	?	?	?	?	?	?	4	0	?	?	?	?	0	?	0	0	0	?	?	?	1	1	1	2	3	1	?	?	0	0	?	0	?	?	0	0	0	0	?	0	0	?	0	0	0	0	?	0	?	?	?	?	0	0	4	1	1
232. Egg sac outermost fibers: fine; thick, loose;	0	0	?	0	?	?	?	?	?	?	?	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
233. Egg sac fiber ultrastructure: smooth; spiny;	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	1	unin.	unin.
234. Web construction: solitary; communal;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	-	-	-	0	0	0	0	0	1	1	?	0	?	?	1	1	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0	1	1	0	2	0.5	0.85
235. Sex ratio: subequal; >three x female-biased;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	?	0	0	0	?	1	1	1	0	0	0	0	0	?	0	0	0	0	0	0	0	1	1	0	3	0.33	0.66
236. Male palp amputation: absent; present;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	unin.	unin.
237. First palpal insert.: transfer sperm; pseudocop.;	?	0	?	1	?	?	?	0	0	?	?	?	?	?	?	0	0	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	?	?	?	?	?	?	0	0	2	0.5	0.66
238. Palpal insertions: ipsilateral; contralateral;	?	1	?	0	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	0	2	0.5	0.66
239. Sperm induction: indep.; during copulation;	?	0	?	1	?	?	?	0	0	0	0	?	?	?	?	0	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	?	?	?	?	?	?	?	0	2	0.5	0.66
240. Mating thread: present; absent;	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	?	?	?	?	?	?	?	1	4	0.25	0.25
241. Bulbal movements: no; rythmic haematodocha;	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	2	0.5	0.5
242. Male during sperm depos.: below; above;	?	0	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	unin.	unin.

Sensitivity of the data to taxon removal was assessed to a degree. Clades or taxa were arbitrarily excluded, one at a time, as follows: *Argiope*, *Tetragnatha*, linyphioids, Synotaxidae, Nesticidae, Hadrotarsinae, Latrodectinae, Spintharinae, *Episinus*, Pholcommatinae, *Enoplognatha*, Argyrodinae, *Faiditus*, *Kochiura*, *Anelosimus*, *A. vittatus* plus *A. pulchellus*, Theridiinae, *Chrysso*, and the data rerun each time without the taxon in question.

Ideally, sensitivity to any combination of taxon removal would be tested, but such an approach is computationally unattainable for all except very small datasets. Thus, taxa were removed based on a posteriori identification of 'major clades' (families and subfamilies) or other taxa deemed to be in a key placement in the phylogeny (e.g. *Chrysso*, sister to the remaining Theridiinae). I also tried the effect of including only a single member (the basal one, when relevant) of each major clade (*Argiope*, *Tetragnatha*, *Pimoa*, *Synotaxus monoceros*, *Nesticus*, *Spintharus*, *Steatoda*, *Enoplognatha ovata*, *Faiditus*, *Kochiura aulica*, *Anelosimus vittatus*, *Chrysso*). I focus discussion on the strict consensus of the pruned matrices analyses as it maximizes disagreement (and thus highlights sensitivity) when comparing results.

To further assess the robustness of individual clades, Bremer support (BS) values (Bremer, 1988, 1994) were calculated. A rapid estimation of low BS values was calculated in NONA (command line: H100000 bsupport6). This was then compared with a more specific search of increasing length differences that is designed to ignore very suboptimal trees (command line: out 'filename'; < enter > hold 1000; sub 1; find*; < enter > hold 2000; sub 3; find*; < enter > hold 4000; sub 5; find*; < enter > bsupport; bsupport*; < enter > 0. The results can be viewed in a text editor.

High BS values are computationally taxing with these methods. Values above six were calculated in PAUP* by constraining nodes in question (using the 'constrain' command), one by one, and then searching for minimal length trees that break up that node (command lines: constraints * 'name' [of your choice] = (('clade')) [taxa spelled out exactly as in matrix, replacing spaces with '_', separating taxa with commas]; hsearch addseq = random nreps = 1000 enforce conv constraints = 'name'). Finally, character support for each node is indicated by mapping characters onto the preferred tree.

Results that are stable under a wide variety of parameters can be viewed as more internally congruent, or robust, than those that quickly alter as parameters change (but see Grant & Kluge, 2003). Thus, successive weighting, implied weighting, bootstrapping/jackknifing, and taxon removal in this way assess

robustness. Perhaps most importantly, these methods are useful in highlighting weakly supported groups. Such ambiguous hypotheses demand further scientific inquiry, and adding data to further test them is particularly likely to be fruitful.

Continuous jackknife function analysis (CJFA) (Miller, 2003) was performed on the data. CJFA is designed to visualize progress in systematics, specifically whether the data are converging on a phylogeny, and to measure the sensitivity of tree structure to character removal. The results can be summarized numerically by reporting the minimum amount of data removal at which congruence is N. Miller compared his sample datasets using 50% and 90% congruence (expressed as S_{50} and S_{90}, respectively) as landmarks, and this is followed here.

Character optimization

I used MacClade 4.01 (Maddison & Maddison, 2002) and Winclada 1.00.08 (Nixon, 2002) to optimize and trace characters on the preferred tree. Data were transferred from the NEXUS Data Editor to Winclada via Mesquite (Maddison & Maddison, 2001), allowing the transfer of character information with the data matrix and thus facilitating data exploration.

In the absence of compelling evidence to the contrary, ambiguous optimization was resolved in favour of secondary losses over parallel gains of complex structures. In accelerated transformation (ACCTRAN) changes are assigned along branches as quickly as possible (passing up), in delayed transformation (DELTRAN) as late as possible. These terms are sometimes used to describe preference for secondary losses or secondary gains, respectively. However, this is misleading as ACCTRAN does not always result in preference for secondary losses and DELTRAN does not always prefer parallel gains. In some instances ACCTRAN results in illogical optimization for taxa coded as inapplicable for that character. For example, in a phylogeny (*a* (*b* (*c* (*d* (*e, f*))))), if *e* and *f* share the derived state, *d* is inapplicable for the character, and all other taxa have the primitive state, DELTRAN is necessary to avoid illogical optimization, although only a single gain is inferred. DELTRAN may also favour secondary losses when the derived state is the absence of something. In (*a* (*b*(*c* (*d, e*)))), if *c* and *e* lack a complex structure present in all others, ACCTRAN would result in parallel gains of this structure, while DELTRAN would preserve homology of it and suggest parallel loss. Therefore, the optimization of each character was examined in Winclada and ACCTRAN or DELTRAN commands used as necessary, favouring the preservation of homology of complex structures and avoiding illogical optimizations.

Anatomical abbreviations

AC	aciniform gland spigot(s)
Acl	accessory claw(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinneret
ASP	abdominal stridulatory picks
AT	anal tubercle
BCH	basal cymbial hood
BL	booklung covers
C	conductor
CA	cymbial apophysis
Cb	conductor base
Chd	cymbial hood
Chk	cymbial hook
CI	consistency index
Cy	cymbium
CY	cylindrical gland spigot(s)
E	embolus
EA	embolic apophysis
Eb	embolic division b
Ebp	embolic basal process
El	embolus lobe
EL	embolus loop
Ep	epigynum
ETA	extra tegular apophysis
ETL	embolus-tegulum lock mechanism
etm	embolus-tegulum membrane
FL	flagelliform gland spigot(s)
Fu	fundus
G98	in character descriptions, refers to characters taken from Griswold *et al.* (1998)
H	hypothesis
K	constant of concavity
La	labium
MA	median apophysis
mAP	minor ampullate gland spigot(s)
MAP	major ampullate gland spigot(s)
m	membrane
mpt	most parsimonious tree
PC	paracymbium
PE	pedicel
PI	piriform gland spigot(s)
PLS	posterior lateral spinneret
PMS	posterior median spinneret
PR	setal proprioreceptor
PSR	prosomal stridulatory ridges
PST	postswitchback turn
RCI	rescaled consistency index
RI	retention index
RSB	reverse switchback
SB	switchback
SC	subconductor
SDT	sperm duct trajectory
SN	stridulatory nubbins
SP	stridulatory pick(s)
SPR	stridulatory pick row

Ss	slit sensilla
SS	sticky silk
ST	subtegulum
T	tegulum
Tb	trichobothria
Tc	tarsal comb
THD	Theridiidae
Ti	tibia
TO	tarsal organ
Tp	tegular pit
TS	tegular spines
TTA	theridiid tegular apophysis

Institutional abbreviations

AMNH	American Museum of Natural History, New York, USA
CAS	California Academy of Sciences, San Francisco, USA
IB	Instituto Butantan, São Paulo, Brazil
ICN	Instituto de Ciencias Naturales, University of Colombia, Colombia
INBio	Instituto Nacional de Biodiversidad, Costa Rica
IZUI	Institut für Zoologie der Universität, Insbruck, Austria
MNHG	Museum of Natural History, Geneva, Switzerland
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
WAM	Western Australian Museum, Perth, Australia
ZMUC	Zoological Museum, University of Copenhagen, Denmark

NOTE

While this paper was being reviewed a molecular phylogeny of theridiid spiders was published [Arnedo *et al.*, 2004 (published online in 2003)]. The decision not to include the molecular data here does not imply preference for separate analyses (taxonomic congruence) as a means of reconstructing phylogenies, or comparing different datasets. Simultaneous analysis of all available data in a single matrix (total evidence *sensu* Kluge, 1989) arguably produces the least assumption-burdened estimate of genealogy, and it maximally explains and describes all the available character evidence (Kluge, 1989, 1997; Nixon & Carpenter, 1996; Grant & Kluge, 2003). However, for practical reasons, a combined analysis has been deferred here.

RESULTS

The cladistic analysis favoured a single most parsimonious cladogram (L = 759, CI = 0.37, RI = 0.73); this is therefore the current preferred phylogenetic hypothesis of theridiid relationships (Figs 102, 105).

Successive weighting found a single tree, regardless of whether CI or RCI was used to reweigh characters. This differs from the preferred tree only in one minor detail; clade 35 (*Carniella* (*Pholcomma, Robertus*)) becomes (*Pholcomma* (*Carniella*, *Robertus*)). Results from parsimony analyses under implied weights are summarized in Table 3. The weakest concavity function (k = 6), found two optimal trees (length 760 and 761), which differ from the preferred tree only in that *Tidarren* moves within Theridiinae, either sister to *Chrysso*, or sister to clade 14. Other low concavity functions (k = 5–4) resulted in nearly identical topologies to the k = 6 analysis with tree length varying between 760 and 762. The default concavity function (k = 3) gave a single tree, 11 steps longer than the mpt under equal weighting. This tree differs within Pholcommatinae in that *Carniella* and *Pholcomma* trade places, as do clades 37 and 39, and within Theridiinae where a new clade (*Tidarren* (*Chrysso*, *Helvibis*)) is sister to the remaining Theridiinae.

The k = 2 results are identical to k = 3 with regards to Pholcommatinae, but further changes take place within Theridiinae. Under the strongest concavity function (k = 1) Pholcommatinae moves sister to *Kochiura* and several taxa move around within Pholcommatinae and Theridiinae. The optimal tree under k = 1 was much longer (length = 787) than the mpt found in the equally weighted analysis. The use of strong concavity functions has been criticized (Goloboff, 1993a, 1995), and when k = 1, very little heed is given to characters showing any homoplasy

Results from bootstrapping and parsimony Jackknifing were nearly identical, and thus only the bootstrapping scores are shown (Fig. 102). The majority of nodes are relatively insensitive to random perturbations of character weight, with some important exceptions. Major clades that are sensitive to this type of character reweighting include the relative placement of Spintharinae, Latrodectinae, and the monophyly of Pholcommatinae, the 'lost colulus clade' (Theridiinae plus *Anelosimus*), the 'elongated central claw clade' (clade 33), and *Anelosimus*.

Taxon removal had no effect on the tree structure (as if a clade had simply been pruned off the tree) with the following exceptions:

1. Removal of either *Argiope* or *Synotaxus* rendered linyphioids paraphyletic.
2. When hadrotarsines were removed, *Synotaxus* and Nesticidae became sister taxa.
3. When argyrodines were removed, latrodectines became sister to the lost colulus clade and spintharines sister to pholcommatines; in one of the resultant four trees Theridiinae was paraphyletic,

with *Tidarren* placed sister to the lost colulus clade. Any single argyrodine taxon was sufficient to recover the (pruned) mpt with all data.
4. When *Kochiura* was removed, spintharines were again sister to pholcommatines and latrodectines sister to clade 33.
5. When Theridiinae was removed, latrodectines became sister to clade 33; including only a single member per clade recovered the pruned mpt, except that latrodectines (*Steatoda*) were sister to clade 33.

Most clades have Bremer support values of 2 or more; thus alternative hypotheses challenging their monophyly would require postulating two or more additional instances of homoplasy not required by the mpt (Fig. 102). Important exceptions are again support for the relative placement of latrodectines, spintharines and pholcommatines, and the monophyly of *Anelosimus*, with a support value of only 1.

Results of the CJFA (Fig. 111) compare well with other datasets explored by Miller (2003), indicating that the current analysis is indeed converging on the preferred hypothesis. The stability of the data is greater than in any of the morphological (and most of the molecular or total evidence) datasets explored by Miller. In other words a *comparatively* small amount of data is necessary to recover, e.g. 50% and 90%, of the nodes, supported by the entire matrix ($S_{50} = 77$, $S_{90} = 18$). Interestingly, at 50% probability of character removal, 73% of the nodes are retained.

Character support for all nodes (synapomorphies) is mapped in Figures 103 and 104; autapomorphies of species are listed in Table 2.

In summary, the preferred phylogeny is optimal under equal weights, and results from successive weighting, while implied weighting generally differs only in minor details. Sensitivity analyses show a fairly low level of sensitivity to data perturbations; the results are not strongly dependent on character weight and withstand moderate character removal. The stability of most clades to taxon removal tests indicates that taxon selection is adequate – in other words, that 'missing taxa' problems are not severe. However, the CJFA shows that complete stability is certainly not achieved, and certain nodes are sensitive to perturbations of character weight and character and taxon removal. The relative positions of Latrodectinae, Spintharinae and Pholcommatinae, and the monophyly of *Anelosimus sensu stricto* (minus *Kochiura* and *Selkirkiella*), are weakly supported groups that can be considered particularly likely to change with the addition of data. Therefore, future work might fruitfully emphasize testing these ambiguous hypotheses (see Grant & Kluge, 2003).

DISCUSSION

The discussion of synapomorphies of major clades focuses on characters that are deemed more reliable in the recognition and diagnosis of those clades – in general those showing relatively little homoplasy. The optimization of all characters is shown in Figures 103, 104 and Table 2. Character numbers in both the text and figure captions (where states are also listed) are typeset in bold. Informal clade names are indicated by insertion within quotation marks the first time they are mentioned in the text.

Araneoid sheet web weavers: clade 59

Synapomorphies of the 'araneoid sheet web weavers' include the following: ALE juxtaposed to AME (**105**, Fig. 46G), and ALS piriform spigot base reduced (**204**, Figs 25B, 65B). One putative synapomorphy of *Synotaxus* plus theridioids from Griswold *et al.* (1998: character 78) – PLS aggregate spigot ('huge') – is here (**214**), ambiguously optimized to araneoid sheet web weavers (ACCTRAN), as the AG of *Pimoa* are no less 'huge' (see Hormiga, 1994a: fig. 41), than those of, for example, *Synotaxus* (Fig. 1F). Another notable ambiguous synapomorphy is a reduction in female palpal tibial trichobothria (**179**, Fig. 74D; ACCTRAN).

Placement of Theridiidae and its relatives

This analysis tested the placement of *Synotaxus* (formerly an argyrodine theridiid) in a matrix containing argyrodine theridiid genera. In concordance with Forster *et al.* (1990), Griswold *et al.* (1998) and Agnarsson (2003c), *Synotaxus* is not a theridiid. The web, egg-sac guarding web and general somatic morphology make *Synotaxus* unlike any theridiid (Fig. 95A–D). Instead, it is sister to the theridioids (clade 55), as also suggested by Griswold *et al.* (1998), who informally named the clade containing cyatholipoids (cyatholipids plus synotaxids) and theridioids as the spineless femur clade (clade 57).

Forster *et al.* (1990) expressed doubts concerning the position of *Carniella* within Theridiidae, based on the basal position of the 'paracymbium' (Fig. 36C) and the lack of flattened AG spigots (Fig. 36I) so typical of theridiids. However, the results of this study strongly support such a placement (see Thaler & Steinberger, 1988) as sister to the clade (*Pholcomma*, *Robertus*) (Fig. 102). Knoflach (1996) suggested affinities between *Carniella* and *Theonoe*, based on the absence of the male palpal tibial trichobothrium and modification of the cymbial tip (Fig. 36A–C). *Theonoe* shares several additional features with the clade containing *Carniella*, *Pholcomma* and *Robertus* and thus Knoflach's argument seems well founded.

Table 2. Species autapomorphies, numbers refer to characters; synapomorphic characters are mapped in Figures 103 and 104

Species	Autapomorphic characters
Argiope argentata	111, 112, 170
Tetragnatha extensa	10, 14, 30, 71, 102, 113, 119, 144, 145, 209, 226, 228, 238, 241
Pimoa rupicola	21, 30, 41, 108, 111, 122, 178, 191, 200, 211, 222
Linyphia triangularis	1, 8, 11, 19, 30, 62, 71, 97, 104, 113, 119, 135, 144, 186, 189, 214, 223, 237, 239, 242
Synotaxus monoceros	131
Synotaxus waiwai	71
Eidmanella pallida	62, 163
Dipoena nigra	4, 45, 201
Euryopis gertschi	19, 174
Thwaitesia margaritifera	8, 42, 51, 65, 146, 212, 225, 226, 233
Episinus amoenus	5, 7, 59, 108
Spintharus flavidus	33, 38, 78, 104, 108, 168, 179
Latrodectus geometricus	231
Crustulina sticta	18, 19, 24, 90, 135, 140, 161, 178, 179, 187
Steatoda grossa	5, 169, 189, 223, 240
Carniella siam	5, 32, 80, 89, 111, 131, 132, 168, 185, 190, 215, 222
Robertus frontatus	8, 11, 83, 89, 98, 111, 152, 156, 219
Pholcomma hirsutum	56, 58, 72, 123, 166, 222
Enoplognatha ovata	135
Selkirkiella magallanes	143
Phoroncidia sp.	16, 17, 28, 57, 58, 78, 130, 135, 137, 142, 143, 149, 150, 167, 172, 176, 182, 225
Cerocida strigosa	11, 51, 108, 112, 121, 123, 150, 163, 168, 173, 190, 210
Stemmops nr. *servus*	19, 25, 35, 62, 83, 84, 87, 89, 91, 184, 200
Neospintharus trigonus	64, 90, 135, 142
Rhomphaea metaltissima	15, 125, 168, 195, 231
Ariamnes attenuatus	7, 11, 24, 96, 128, 138, 231
Faiditus cf. *chickeringi*	6, 7, 85, 142, 185
Kochiura aulica	85
Kochiura rosea	81, 111
Anelosimus analyticus	188
Anelosimus cf. *jucundus*	46, 170
Anelosimus eximius	99
Anelosimus vittatus	156
Chrysso cf. *nigriceps*	6, 38, 70, 76, 128, 148, 151, 178, 201, 205
Nesticodes rufipes	7, 161, 177, 189
Theridion longipedatum	110, 111, 140
Theridion varians	146, 160
Coleosoma floridanum	41, 76, 135, 152
Tidarren sisyphoides	23, 33, 35, 45, 51, 78, 86, 129, 147, 151, 152, 226, 236
Helvibis cf. *longicaudatus*	7, 8, 41, 55, 63, 66, 69, 91, 123, 152, 199, 201
Thymoites unimaculatum	1, 137, 143, 178, 190
Ameridion sp.	115
Theridula emertoni	33, 56, 62, 80, 97, 125, 152, 178, 218, 223
Achaearanea tepidariorum	94, 108, 240

As suggested by Berland (1932), Gertsch (1949), Wunderlich (1978) and Forster *et al.* (1990) hadrotarsines are related to theridiids, and here form the sister clade to the remaining theridiids. Hadrotarsine monophyly is supported by an array of morphological peculiarities, making them unlike any other theridiid. They also lack several characteristics typical of other theridiids (see below). For these reasons, revalidating Hadrotarsidae seems logical. However, such an act has major nomenclatural consequences and is currently contradicted by molecular evidence (see Arnedo *et al.*, 2004). Therefore, the elevation of Hadrotarsinae

Table 3. Summary of results of the PeeWee analyses

Concavity	Fit	No. trees	Tree length(s)	Differences between PeeWee trees and the equally weighted mpt
6	1809.2	2	760, 761	*Tidarren* sister to *Chrysso* or sister to clade 14
5	1752.9	2	761, 762	*Tidarren* sister to *Chrysso; Pholcomma* and *Carniella* trade places in one of the two trees
4	1683.6	1	761	*Tidarren* sister to *Chrysso*
3	1588	1	770	Clade 37 trades places with clade 39*; Pholcomma* and *Carniella* trade places*;* (*Tidarren* (*Chrysso*, *Helvibis*)) form a clade sister to the remaining Theridiinae
2	1448.9	3	767-769	Clade 37 trades places with clade 39; *Pholcomma* and *Carniella* trade places; *Chrysso* and *Helvibis* sister, or as a grade, sister to clade 9, in one of the trees *Thymoites* move sister to clade 8
1	1234.2	1	787	Clade 42 (Pholcommatinae) moves sister to clade 26 (*Kochiura*), and within Pholcommatinae, *Pholcomma* and *Carniella* trade places, and clade 36 moves sister to clade 40; *Chrysso* and *Helvibis* form a clade sister to clade 9, with further changes inside clades 13 and 9.

to family rank will be reconsidered following combined analysis (see 'Note' above).

Spineless femur clade: clade 57

Several synapomorphies for the spineless femur clade of Griswold *et al.* (1998) can be inferred from this study, but the reader should bear in mind that cyatholipoids are represented here only by *Synotaxus*. Synapomorphies include: presence of exactly two (vs. three in outgroups) retrolateral trichobothria on the male palpal tibia (**18**, Figs 31G, 44E, 56D, 92D–F), but note that further reduction in trichobothria numbers takes place within the theridiids (Figs 42E, 73D), the TTA (**80**, Figs 15A, B, 71A–C, 89C, D, 90A, C, F, G), female palpal tarsus dorsal macrosetae lacking (**181**, Fig. 43E), serrated setae on female palpal tarsi (**180**, Fig. 9E), femoral macrosetae lacking (**183**, Fig. 63F), tarsi IV comb (**193**, Fig. 11E, F), and reduced PLS piriform spigot field (**205**, Figs 23C, 25B). The absence of cheliceral boss (**122**, Figs 41C, 66D, 79F, 80B) is an ambiguous synapomorphy (DELTRAN, also absent in *Pimoa*).

Given that *Synotaxus* is a fairly atypical member of the cyatholipoids (*sensu* Griswold *et al.*, 1998), the synapomorphies listed above need to be tested with a much denser sampling of cyatholipoids. For instance, to my knowledge, tarsal combs have not been reported in other cyatholipids. The presence of sticky silk wrap attack (**229**) is another putative synapomorphy of the spineless femur clade (Griswold *et al.*, 1998). The behaviour has, however, only been observed in very few taxa; its presence in *Synotaxus* requires verification, being based on a single observation (Coddington, 1986a: 335). Based on this cladogram the optimization of SS wrap attack is ambiguous.

Theridioids (Nesticidae, Theridiidae): clade 55

Theridioids are supported by several unambiguous synapomorphies, including: reduced number of epiandrous gland spigots (**170**, Figs 14F, G, 22F), exactly two colular setae (**175**, Fig. 9D, reversed to three or more in latrodectines, Fig. 55H), lobed PLS AG glands (**217**), cobweb (**225**, Figs 96D–F, 99A, B, 100A–F, 101A–F), and sticky silk on gumfoot lines (**227**, Figs 96F, 97B–D, 101B, D).

Nesticidae Simon, 1894: clade 54

Unambiguous synapomorphies of Nesticidae here include: spermathecal accessory lobes (**12**), nesticids paracymbium (**30**, Figs 2A–C, 89D), retrolateral subtegular lobe (**44**, Fig. 2A, B), SDT SB IV (**59**), small AMEs (**104**), metatarsus IV trichobothrium (**191**), and few (four or less) PLS AC spigots (**211**).

Theridiidae Sundevall, 1833: clade 53

The monophyly of Theridiidae receives strong support in this study. Unambiguous synapomorphies on this cladogram include: male palpal tibia distally broadened (**14**, Fig. 4E), paracymbium lost (**29**, Fig. 92A–M), bulb-cymbium lock mechanism (**31**, Fig. 31F), alveolus flush on mesial cymbial margin (**41**, Fig. 92D–I, M), MA containing loop of sperm duct (**72**, Figs 90F, 91A), MA, tegulum membrane (**73**), a distal hood on MA (**78**, Fig. 31F), retromarginal cheliceral teeth lost (**110**, Fig. 5F, several reversals), abdominal suprapedicellate apodemes weakly sclerotized and fairly smooth (**165**, Figs 4F, 63H, 82E, F), highly flattened anterior PLS AG spigots (**215**, Figs 11B, 78B), PMS mAP nubbins lost (**220**, Figs 18F, G, 25C, D),

exactly two PMS AC spigots (**222**, Fig. 18G). Notable ambiguous synapomorphies are a nonrebordered labium (**134**, Fig. 5A, DELTRAN, also in *Synotaxus*), and highly flattened posterior PLS AG spigots (**216**, ACCTRAN, not in *Dipoena*).

Theridiid relationships

The preferred cladogram offers the first phylogenetic hypothesis of a wide selection of theridiid genera based on morphological data. It broadly agrees with recent studies that have included theridiid genera in higher level morphological phylogenies (Coddington, 1990a; Forster *et al.*, 1990; Hormiga, 1994a, b; Griswold *et al.*, 1998), and with ongoing molecular work (Arnedo *et al.*, 2004). Colulus with a pair of setae and complex male palps are plesiomorphic for theridiids, present in basal genera but sometimes lost, reduced, or modified in more distal theridiid clades (e.g. Forster *et al.*, 1990). Hadrotarsines are sister to the remaining theridiids and latrodectines sister to the large tarsal organ (TO) clade containing all other theridiids.

A basal position of Latrodectinae was already suspected, based on their rather generalized plesiomorphic features, such as the large and setose colulus (Fig. 55H). In fact, the colulus in related families is not particularly large and typically has only a pair of setae; the latrodectine condition is thus derived. In this study, the best evidence for the relatively basal position of latrodectines is the size of the TO. A uniquely enlarged TO (Fig. 33F) is present in all theridiids minus Latrodectinae and Hadrotarsinae (clade 46); this character perfectly fits the cladogram (**198**, Fig. 103). However, this placement of Latrodectinae is weakly supported, as shown by both support metrics and sensitivity analyses. In many of the sensitivity analyses latrodectines are sister to clade 33 and moving them there involves only a single step.

The circumscription and likely composition of theridiid subfamilies are here discussed for clarification. Recent and early usage of subfamily (or tribe) names has been confusing and mostly conflicting (e.g. Simon, 1894; Petrunkevitch, 1928; Archer, 1950; Forster *et al.*, 1990; Yoshida, 2001a, b, 2002). I do, however, discuss subfamily names informally. Less than half of the theridiid genera are included here, and the placement of several taxa is in conflict with the study of Arnedo *et al.* (2004); a formal classification thus seems premature.

Hadrotarsinae: clade 52

Hadrotarsine monophyly is strongly supported, although one of the putative synapomorphies, ALS stridulatory ridges, suggested by Forster *et al.* (1990) and Griswold *et al.* (1998: character 67) is doubtful. *Hadrotarsus* has stridulatory ridges on the ALS and Griswold *et al.* observed these in both *Emertonella*, and *Dipoena*. However, I have examined three *Dipoena* species, including their exemplar (*D. nigra* Emerton; Fig. 6D) as well as *D. torva* Thorell, and *D.* cf. *hortoni* (pers. observ.), and none have stridulatory ridges. *Gmogala* also lacks such stridulatory ridges (pers. observ.). Either *Dipoena* has secondarily lost this supposed hadrotarsine synapomorphy, or the character is synapomorphic for a subsidiary hadrotarsine clade [so far known only from *Hadrotarsus*, *Emertonella*, and *Euryopis* (**203**, Fig. 9B)].

An identical stridulatory mechanism also occurs in *Chilenodes* (Malkaridae: Palpimanoidea) (Platnick & Forster, 1987). The placement of *Chilenodes* and many other palpimanoids is dubious at best (Schütt, 2002). Classical palpimanoids are two-clawed with claw tufts, have plumose body setae, lack paracymbia and have a palpal conformation entirely different from araneoids. *Chilenodes* (Malkaridae), however, along with (at least) the families Mimetidae, Holarchaeidae, Pararcheidae and Micropholcommidae (all currently Palpimanoidea, but see Schütt, 2000, 2002 for alternative placement) are three-clawed, have serrate body setae (otherwise a highly conserved araneoid synapomorphy), have a typical araneoid palpal conformation (e.g. with an embolic tegular membrane) and a paracymbium; an araneoid synapomorphy. Lehtinen (1996) came to similar conclusions based on leg cuticle ultrastructure. If the placement of *Chilenodes* in Araneoidea is confirmed, this character may indicate relatedness with hadrotarsines. Interestingly, another malkarid, *Sternodes foraminatus* Butler, shares some unique features with *Phoroncidia* (see Fig. 62A–D, and legend).

Nonetheless, several characters unite hadrotarsines including *Dipoena*, such as: the presence of two pairs of spermathecae (**10**, Fig. 93I), sperm duct entering the embolus (left palp, ventral view) counter-clockwise (**60**), cheliceral promargin without teeth (**106**, Fig. 5F), shortened paturon (**117**, Fig. 5C), thin cheliceral bases (**118**, Fig. 5D), long and slender cheliceral fangs (**120**, Fig. 9F), high carapace (**124**, Fig. 5D), carapace nearly as wide as long (**126**), triangular labium (**136**, Fig. 5A), palmate female palpal claws (**177**, Fig. 9E), grouped flat-tipped sensory setae on tarsus I (**197**, Fig. 8C, D), FL absent (**212**, Fig. 8A), a functional male AG (**219**, Fig. 6F, males, as females, lack FL). The loss of prey-catching webs (**224**) is an ambiguous synapomorphy, but there have been no observations of prey-catching on *D. nigra*.

Wunderlich's (1978) synonymy of Hadrotarsidae with Theridiidae produced a monophyletic group, but resulted in a family name with much broader circumscription and less utility. The distinctness of hadrotarsines and the absence of some classical theridiid

synapomorphies – male palpal tibial rim setae (**16**, Fig. 13C), rim orientation (**17**, Fig. 10A), abdominal stridulatory picks (**150**, Fig. 18B–D), dorsal suprapedicellate proprioreceptors (**163**, Fig. 43A, B), and theridiid type tarsal comb (**194**, Fig. 11E, F; **195**, Fig. 59A, B) – speak of the revalidation of Hadrotarsidae (see also Baert, 1984a, b), *contra* Wunderlich (1978) and Griswold *et al.* (1998). However, the phylogenetic position of this clade is contradicted in current molecular research, where Hadrotarsinae is embedded within Theridiidae (Arnedo *et al.*, 2004). If correct, elevating Hadrotarsinae to family level would render Theridiidae as here circumbscribed paraphyletic; such a decision therefore awaits a combined analysis.

Griswold *et al.* (1998) found hadrotarsines to nest within Theridiidae, but that result is not strongly supported by their data. A single character (Griswold *et al.*, 1998; character 65) unifies *Anelosimus* and the hadrotarsines in their cladogram; colulus reduced to less than half the length of its setae. However, as discussed in this study (**172–175**), *Anelosimus* lacks a colulus, in *Dipoena* the colulus is clearly larger than half the length of its setae, and the condition in *Emertonella* (colular area strongly invaginated) is unique. If only these entries in the matrix of Griswold *et al.* (1998) are changed accordingly, a sister relationship between Hadrotarsinae and the remaining theridiids becomes an equally good explanation of their data.

Hadrotarsinae includes the following 14 genera: *Anatea*, *Audifia*, *Dipoena*, *Dipoenata*, *Emertonella*, *Euryopis*, *Eurypoena* Wunderlich 1992, *Gmogala*, *Guaraniella*, *Hadrotarsus*, *Lasaeola*, *Trigonobothrys*, *Yaginumena* and *Yoroa*.

Stridulatory pick row clade: clade 50

The traditional reference to theridiids as either 'cobweb' or 'comb-footed' spiders (implying presence of three-dimensional cobwebs and a theridiid-type tarsal comb) applies only to nonhadrotarsine theridiids (see also discussion above). The typical and elaborate theridiid abdomen-prosoma stridulatory mechanism also is confined to this clade. Synapomorphies of the 'typical' theridiids, here termed the 'SPR clade' include: the presence of a regular row of long serrated setae on the male palpal tibial rim (**16**, Fig. 13C), male palpal tibial rim facing palpal bulb (**17**, Fig. 10A), presence of abdominal stridulatory picks (**150**, Fig. 18B–D), presence of dorsal suprapedicellate proprioreceptors (**163**, Fig. 43A, B) and the theridiid type of tarsus IV comb (**194**, Fig. 11E, F). The hook-like tarsal comb bristle serrations (**195**, Fig. 59A, B), is an important, yet ambiguous, additional synapomorphy.

The 'classical' theridiid comb has strong hook-like serrations on the tarsal bristles (Fig. 11F). This condition occurs in the some basal theridiid lineages including Latrodectinae (but not *Crustulina*, Fig. 42D) and Spintharinae, and sporadically throughout the theridiids. Such hooks are absent in Synotaxidae, Nesticidae and Hadrotarsinae, whose bristles have simple notches (Fig. 6A). Given the current phylogeny, the typical hooked condition is not homologous across theridiids, and surprisingly no less than four origins of typical theridiid comb bristles are required (six steps in the character). Given that theridiid hooks are practically identical, the alternative makes this state primitive for theridiids, but that requires no less than 11 steps (1 gain, 10 losses).

Kovoor (1977) suggested a novel synapomorphy for Theridiidae – crescent-shaped major ampullate glands – but these remain to be examined in hadrotarsines and nesticids.

Latrodectinae: clade 49

The medically important widow spiders (*Latrodectus* spp., Fig. 96A–F) in this phylogeny group with the genera *Steatoda* and *Crustulina*. The subfamily name Latrodectinae is used for this group of genera. Latrodectinae was used by Petrunkevitch (1928) for *Latrodectus* and 'related' genera, but the current circumscription shares only *Latrodectus*. This clade is supported by several unambiguous synapomorphies, including: sperm duct sharply constricted during first loop (**61**), conductor base grooved (**68**, Fig. 54E), lobed embolic base (**98**, Fig. 54E), carapace densely hirsute (**127**, Fig. 71D, E), reversal to additional (three or more) colular setae (**175**, Fig. 55H), PLS AG parallel (**218**, Fig. 43G), exactly four PMS AC spigots present (**222**, Figs 43F, 72G). A peripheral retreat (Fig. 96C), is another putative synapomorphy (see also Benjamin & Zschokke, 2002, 2003).

It is of interest that the only theridiids outside *Latrodectus* known to be potently venomous to vertebrates are *Steatoda paykulliana* (Walckenaer) (Maretiæ *et al.* 1964) and *S. nobilis* (Thorell) (Warrell *et al.*, 1991). Given the clade (*Latrodectus* (*Steatoda*, *Crustulina*)) and the known distribution of potent venom, the results here imply that such toxins may be primitively present in the subfamily and that other *Steatoda* and *Crustulina* species may be similarly venomous.

Spintharinae: clade 45

Forster *et al.* (1990) discussed the possible composition of Spintharinae. They pointed out that a hooded 'paracymbium' (Figs 75B, 92F–I, M) was present in *Spintharus* and many other genera (explicitly including *Anelosimus*, *Chrosiothes*, *Chrysso*, *Coleosoma*, *Helvibis*, *Nesticodes*, *Rugathodes*, *Spintharus*, *Tekellina*, *Theridula*, *Thwaitesia* and *Thymoites*). Yoshida (2001a) synonymized Spintharinae with Theridiinae,

based on the same character, which he realized is also present in *Theridion*. The character of choice was unfortunate, as is evident from the present analysis.

First, *Chrosiothes* and *Thwaitesia* both, in fact, have a *hook-lock* system (Fig. 92K, presumably overlooked by these authors), albeit with a groove present underneath the hook, whereas the remainder only have a hood. Second, both the current study and that of Arnedo *et al.* (2004) indicate that the hood found in *Spintharus* is not homologous to that found in the lost colulus clade (see Fig. 105); rather, it may be homologous to the groove lying underneath the hook of *Thwaitesia* and several related taxa. Here the subfamily Spintharinae is again used (following, e.g. Arnedo *et al.*, 2004; *contra* Yoshida, 2001b).

The following genera included in this study belong in Spintharinae: *Episinus*, *Spintharus* and *Thwaitesia*. Based on similarity in morphology (e.g. abdominal shape and humps) and web type (H-shaped spintharine) it is likely that *Chrosiothes* and *Moneta* belong in this group. The remaining genera in Spintharinae *sensu* Forster *et al.* all belong to the lost colulus clade and have all been transferred to Theridiinae (Yoshida, 2001b). Molecular evidence suggests that *Stemmops* may belong to Spintharinae (Arnedo *et al.*, 2004); morphologically this arrangement may be supported by a spintharine cymbial hood that is found in some *Stemmops* (pers. observ.).

Unambiguous synapomorphies of Spintharinae include: conductor huge (**63**, Figs 46A–D, 83A–D, 90F, G), conductor folded (**66**, Fig. 90F, G), cheliceral base thin (**118**, Fig. 84C), abdomen with humps (**142**), colulus small (**173**, Fig. 70A), tarsal comb bristle dorsal margin notched (**196**, Fig. 84E), and web modified (**225**, Fig. 97A). Egg sac outermost fibre loosely spun (**232**, Fig. 88C) is an ambiguous synapomorphy (ACCTRAN); there are no observations recorded for *Spintharus*.

PHOLCOMMATINAE: CLADE 42

Pholcommatinae (see Kaston, 1981: 94) is based on Simon's (1894) tribal group Pholcommateae, and here includes *Enoplognatha*, *Selkirkiella*, *Cerocida*, *Phoroncidia*, *Stemmops*, *Pholcomma*, *Carniella* and *Robertus*.

Unambiguous synapomorphies of the Pholcommatinae include: cymbial hook pointing upwards (**34**, Figs 66B, 67D, E), cymbial hook on ectal margin (**35**, Figs 66B, C, 67E, 92L), TTA grooved (**83**, Figs 44C, 60B, C), portions of E spiral entirely enclosed in TTA (**87**, Fig. 44C), E base shifted ectally and partially hidden by cymbium (**89**, Fig. 60A–C), AME small (**104**), PLS AG parallel (**218**, Figs 45B, 63C, D).

The composition of this subfamily is uncertain: *Phoroncidia*, *Stemmops* and *Cerocida* all lack some of the unambiguous synapomorphies of the clade, and may be misplaced here (see also Arnedo *et al.*, 2004). *Phoroncidia*, indeed, lacks many of the theridiid synapomorphies, while some characteristics associate it with the Hadrotarsinae (if all other pholcommatines are removed from the analysis *Phoroncidia* moves sister to Hadrotarsinae).

Implied weighing, bootstrapping and taxon removal experiments showed that the Pholcommatinae is the one major clade most sensitive to data perturbations. Thus the current phylogenetic position of at least *Phoroncidia*, *Stemmops* and *Cerocida* should be considered likely to change. *Phoroncidia* has an unusual combination of characters and sits on a long branch (18 steps, Fig. 103). This may in part explain its instability, but the placement of *Phoroncidia* does not alter when its sister taxon (*Stemmops*) and other closely related taxa (one or more at the time) are removed (but see above). Pholcommatinae may be limited to those taxa with the ectal cymbial hook moderately (*Enoplognatha*) or strongly tapered (Figs 66B, 67D, E; in this matrix present in *Carniella*, *Pholcomma*, *Selkirkiella* and *Robertus*). Note, however, that *Phoroncidia* and *Stemmops* are extremely morphologically diverse and quite possibly nonmonophyletic genera. Given that the exemplar species used in this study are not types, these conclusions may only apply to the species included here.

Based on the synapomorphies of the group it is likely that *Craspedisia* Simon, 1894, *Helvidia*, *Proboscidula*, *Styposis*, *Theonoe* and *Wirada* belong to this subfamily. All have cymbial hook on ectal margin, pointing upward, and distinctly tapered, and an ectally shifted embolus. Many members of this group have cephalic modifications (proboscis) and prosomal warts.

ARGYRODINAE: CLADE 32

The six species of argyrodines included in this study represent the five of the six species groups of Exline & Levi (1962), including the newly resurrected genera *Rhomphaea* and *Ariamnes* (see Yoshida, 2001b). Although all groups differ considerably in morphology and behaviour, they also share numerous peculiarities and argyrodine monophyly is strongly supported (Fig. 103), as Exline & Levi (1962) hypothesized (see also Arnedo *et al.*, 2004).

However, simply synonymizing all available names in this group with *Argyrodes* has turned out to be too broad a formulation, in part because species range from free living araneophages to obligatory kleptoparasites (see 'Kleptoparasitism and araneophagy' below). Typical biological summaries are thus misleading and confusing: 'Tropical spiders of the theridiid genus *Argyrodes* Simon inhabit the webs of other

spiders' (Vollrath, 1979b: 1149); 'Spiders of the genus *Argyrodes* (Theridiidae) are generally known as kleptoparasitic' (Tanaka, 1984: 363); 'Some species of *Argyrodes* (Theridiidae) can regularly be found in the webs of other spiders… Other *Argyrodes* are free-living, some feed on spiders' (Vollrath, 1984: 70). It has even been suggested that the expression of behaviour (either kleptoparasitism or free living araneophagy) is environmentally controlled, rather than showing a phylogenetic pattern (see Whitehouse *et al.*, 2002).

However, morphology and behaviour are coherent within species groups. All studied *Ariamnes* species have a characteristically elongated abdomen (Fig. 94A), construct simple nonsticky line webs, and specialize on nematocerous flies and wandering male spiders that use the lines to travel (e.g. *Ariamnes attenuatus* (O. P.-Cambridge) (see Eberhard, 1979), *A. colubrinus* (Keyserling) (see Clyne, 1979), and *A. flagellum* (Doleschall) (see Roberts, 1952). All studied '*Argyrodes argyrodes* group' (*sensu* Exline & Levi, 1962) species seem to be obligate kleptoparasites, e.g. *A. antipodianus* O. P.-Cambridge (see Whitehouse, 1986; Whitehouse & Jackson, 1993; Grostal & Walter, 1997), *A. argentatus* O. P.-Cambridge (see Robinson & Robinson, 1973), *A. argyrodes* (Walckenaer) (see Wiehle, 1928; Kullmann, 1959a, b) *A. elevatus* Taczanowski (see Vollrath, 1977, 1979a, 1984, 1987), and *A. nephilae* Taczanowski (see Vollrath, 1987).

Most authors do not keep track of informal species group names as they would generic names, and thus these patterns have been obscured. The Linnaean rank system has been criticized on many grounds (e.g. de Queiroz & Cantino, 2001), but prevails, in part due to the information ranks (in particular family and genus) *can* convey. In order to maximize this information content, the genus rank should, when possible, identify a coherent group, whose morphology and biology can be summarized efficiently based on any of its members. Some authors (e.g. Whitehouse, 1987b; Forster & Forster, 1999) never accepted all of Exline and Levi's synonymies, and continued treating *Ariamnes* and *Rhomphaea* (the most distinct nonkleptoparasitic Argyrodinae) as valid genera. Tanikawa (1998) added *Spherophista* to the growing *Argyrodes*, before Yoshida (2001b) explicitly rejected the synonymies of *Argyrodes*, *Ariamnes*, *Rhomphaea* and *Spheropistha*, and resurrected the latter three (note that Platnick, 2003, did not follow Yoshida, 2001b). Following Arnedo *et al.* (2004), I agree with Yoshida's revalidation of *Ariamnes* and *Rhomphaea*, although it is insufficient, as it renders the remaining '*Argyrodes*' paraphyletic (Fig. 102), and ignores other distinct argyrodine clades. Therefore, *Faiditus* and *Neosphintharus* also should be recognized as genera (see Taxonomy).

Argyrodinae is supported by an array of synapomorphies, including: sperm duct reverse switchbacks (**57**, Fig. 93D, E), cheliceral furrow denticulated (**112**, Figs 33H, 37D), clypeal projection (**131**, Figs 30A–D, 94B–E), dense field of setae in ocular area (**132**, Figs 30A–D, 34F), silvery dots on abdomen (**146**), abdominal stridulatory picks on ridge, parallel with pedicel (**154**, **161**, Figs 32C, D, 56G, 64D), ventrolateral suprapedicellate setal proprioreceptors absent (**164**, Figs 32C, 64D), female fourth tarsal central claw much longer than laterals (**200**, Figs 32H, 57F), abdomen extending beyond the spinnerets (**201**, Figs 94A–E, 98F), huge and elongated, strongly grooved, CY spigots (**208**, 209, Figs 33B, 57C, 65C, D), PLS FL absent (**212**, Fig. 33B, possibly reversed in *Ariamnes* (Fig. 35A), *Rhomphaea* (Fig. 65C), see character description), simple nonsnare webs (**225**), and egg case stalked and modified (**230**, 231, Figs 88E, F, 98C–E). Unusually, the AGs are functional in all argyrodine males examined here (19 species) (**219**, Fig. 48F) except *Argyrodes* (Fig. 33D); this condition is an ambiguous synapomorphy of Argyrodinae (ACCTRAN). Kovoor & Lopez (1983: 35) claim that argyrodines have larger ampullate silk glands than do other theridiids, and some lack flagelliform glands.

Lost colulus clade: clade 25

The lost colulus clade consists of *Anelosimus* plus Theridiinae. It is especially important because all known instances of theridiid sociality and most known instances of maternal care occur here (see 'maternal care' under 'Sociality', below). The monophyly of the lost colulus clade is supported by synapomorphies including: cymbial hood present (hooded lock system, **33**, Figs 18A, 28E, F, 75B), MA entire (**78**, Fig. 28F), MA broadly and medially attached to tegulum (**74**, Fig. 75B), and colulus absent (**172**, Figs 25E, 78A).

Anelosimus: clade 24

As predicted by Forster *et al.* (1990), the results strongly refute the monophyly of *Anelosimus sensu lato* (which included *Kochiura* and *Selkirkiella*) (Fig. 102). None of the 17 Chilean species currently placed in *Anelosimus* seem to belong there; they differ in many key characteristics from the type species *A. eximius*, such as plesiomorphic retention of the hooked cymbial notch (Fig. 67B, D, E), hooded MA (Fig. 67D), and colulus (Fig. 68F). Some Chilean '*Anelosimus*' are clearly pholcommatines (*A. alboguttatus* and *A. magallanes* are here transferred to the resurrected pholcommatine *Selkirkiella,* clade 39), based for example, on cymbial hook position and its structural details (**34**, **35**, 37, Fig. 67D), embolus position (**89**, Fig. 67B), and spinneret spigot morphology (**216**, Fig. 68D, E) (see Taxonomy section). Others belong to a clade containing the European

A. aulicus, whose placement in *Anelosimus* is also refuted (*A. aulicus* and *A. roseus* are sister to the lost colulus clade and are here transferred to the resurrected *Kochiura*, clade 26; see Taxonomy section).

As circumscribed here, the monophyly of *Anelosimus* rests on only one unambiguous synapomorphy: ridges on the surface of the epigynal plate (**3**, Figs 19B, 21G, 93F). Bremer support for the clade is low (1), the clade is sensitive to data perturbation, and making clade 23 sister to Theridiinae involves only one step. On the other hand, clade 18, which contains the 'classical' new world *Anelosimus*, is well supported (Fig. 104). Many new species have come to light (for example, from Madagascar; pers. observ.), and the taxonomy will probably change as new data are added.

Theridiinae is well defined (see below) and easily diagnosed, including all nonhadrotarsine theridiids without any trace of colulus. The inclusion of *Anelosimus* in Theridiinae would muddle the diagnosis of the subfamily and add to what is already the largest theridiid subfamily. As the position of *Anelosimus* outside the lost colular setae clade is corroborated by molecular evidence (Arnedo *et al.*, 2004), I do not include it in Theridiinae. The placement of *Kochiura* is uncertain; here it is outside the lost colulus clade, while in Arnedo *et al.* (2004) it is sister to *Anelosimus*. The subfamily placement of *Kochiura* and *Anelosimus* thus awaits future combined analysis. The results suggest dual origin of quasisociality within *Anelosimus* (see 'Sociality', below).

THERIDIINAE (LOST COLULAR SETAE CLADE): CLADE 15

Yoshida (2001a: 158) defined Theridiinae based on two synapomorphies: 'paracymbium of male palpus hooded' and 'colulus usually absent' and synonymized Spintharinae with it. Yoshida's Theridiinae is apparently not monophyletic and is redefined here, while Spintharinae is again recognized (see above).

Theridiinae (including at least *Achaearanea, Ameridion, Chrysso, Helvibis, Nesticodes, Theridion, Theridula, Thymoite and Tidarren*) is well supported in this study. It is unambiguously defined by: a reduction in both retrolateral (**18**, with some reversals within the subfamily) and prolateral trichobothria (**19**) on the male palpal tibia (Figs 85B, 86B), epiandrous gland spigots spread over genital plate (**169**, Figs 58E, 76F, 77G), and absence of colular setae (no trace of colulus, **174**, Fig. 78A). In addition, most species in this clade have notably long and thin legs.

Other nonhadrotarsine theridiid genera lacking the colulus probably belong here, including *Achaearyopa* Barrion & Litsinger, 1995, *Cabello* Levi, 1964, *Cephalobares* O. P.-Cambridge, 1870, *Cyllognatha* L. Koch, 1872, *Echinotheridion* Levi, 1963, *Exalbidion* Wunderlich, 1995, *Histagonia* Simon, 1895, *Jamatidion* Wunderlich, 1995, *Keijia*, *Macaridion* Wunderlich, 1992, *Molione* Thorell, 1892, *Neottiura*, *Nipponidion* Yoshida, 2001, *Paratheridula* Levi, 1957, *Propostira* Simon, 1894, *Rugathodes* Archer, 1950, *Sardinidion* Wunderlich, 1995, *Simitidion* Wunderlich, 1992, *Takayus* Yoshida, 2001, *Tekellina* Levi, 1957, *Wamba* O. P.-Cambridge, 1896, and perhaps others.

This group is similar to the colulus-less group discussed by Levi & Levi (1962). About half of theridiid species belong to Theridiinae; the group is therefore relatively poorly understood. Most genera still have no identified synapomorphies and relatively few appear to be monophyletic. The name Theridiinae refers to Simon's tribal group Theridieae, which was based on *Theridion* and related genera.

REMAINING THERIDIIDS

Several theridiid genera are here not explicitly placed in a subfamily, including *Kochiura* and *Anelosimus* although present in this study (see above). Other genera are not placed if they are not well known to the author or have a peculiar combination of key characteristics: *Chorizopella* Lawrence, 1947, *Coscinida* Simon, 1895; *Hetschkia* Keyserling, 1886, *Icona* Forster, 1955, *Landoppo* Barrion & Litsinger, 1995, *Marianana* Georgescu, 1989, *Paidiscura* Archer, 1950, *Tomoxena* Simon, 1895 (may be a hadrotarsine, see Levi & Levi, 1962: 50), and *Zercidium* Benoit, 1977.

SOCIALITY

Four categories of spider sociality are typically recognized, depending on duration (periodic or permanent) and degree of tolerance (territorial or nonterritorial) (see Avilés, 1997 for review). However, if sociality presupposes cooperation, only nonterritorial spiders exhibiting 'web-sharing sociality' are truly social (Agnarsson, 2002). Social theridiids share webs, either for their entire lives (permanent or quasisociality), or more briefly (periodic or subsociality). This phylogenetic study includes three subsocial (*Anelosimus analyticus*, *A.* cf. *jucundus* and *A. studiosus*) and five quasisocial species (*A. eximius*, *A. lorenzo*, *A. rupununi*, *Achaearanea vervoorti* and *A. wau*), which is about half of the known theridiid social species. Subsociality evolved once, but quasisociality at least three times, twice within *Anelosimus* and once in *Achaearanea* (Fig. 104). A fourth origin is likely in *Theridion nigroannulatum*, a quasisocial species not yet studied cladistically but probably related to *T. pictum* (pers. observ.). All cases of sociality occur within the lost colulus clade (Fig. 105). Considering how rare sociality is in spiders, its repeated evolution in this particular clade is puzzling (see below). No losses of quasisociality are inferred.

KLEPTOPARASITISM AND ARANEOPHAGY

Argyrodines generally exploit other spiders (reviews include Exline & Levi, 1962; Elgar, 1993; Whitehouse *et al.*, 2002). Most species either use webs of other spiders to obtain resources (kleptoparasitism), or prey on the host directly (araneophagy). The concentration of kleptoparasitic or araneophagic (or both) species in Argyrodinae has prompted extensive discussion about the possible evolution of these traits.

Current ideas span nearly all possible outcomes. Smith-Trail (1980) suggested the evolution of araneophagy from kleptoparasitism (hypothesis 1), arguing that the stealth necessary for kleptoparasitism may be a preadaptation for safely stalking and capturing the host itself. Vollrath (1984) advocated the opposite: originally the spiders invaded other spiders' webs and chased out the owners. With increasing stealth, they evolved araneophagy and only then became kleptoparasites (H2).

Whitehouse (1987b) observed that predominantly araneophagic groups (*Rhomphaea* and *Ariamnes*) use a wrap-bite attack, but predominantly kleptoparasitic groups (e.g. *Argyrodes*) only bite. Also *Ariamnes* and *Rhomphaea* attack by using both legs IV in unison to throw a few sticky threads towards the prey, whereas most other theridiids fling copious sticky silk using alternating movements of legs IV. Given these differences, she suggested that kleptoparasitism and araneophagy were strategies that evolved independently and via separate pathways (H3). Finally, Whitehouse *et al.* (2002) recently suggested that environmental control, not phylogeny, might explain the observed pattern (H4).

None of these hypotheses have been tested against a phylogenetic framework. Whitehouse *et al.* (2002) summarized three conflicting preliminary phylogenetic hypotheses, each including a few species of argyrodines, but no clear picture could be drawn. Each phylogeny supported a different scenario. However, two general conclusions emerged: (1) kleptoparasitism and araneophagy seem to be primitively present within the lineage; (2) araneophagic techniques in *Rhomphaea* and *Ariamnes* evolved independently.

This analysis discriminates among the hypotheses. First, as mentioned above, argyrodine biology is obviously structured phylogenetically. Second, both araneophagy and kleptoparasitism seem to be primitively present in the lineage leading to argyrodines (Fig. 107, see also Whitehouse *et al.*, 2002). Thus, neither is derived directly from the other; specialists in either technique probably evolved from generalists using both. Third, the specialized araneophagic *Ariamnes* and *Rhomphaea* are sisters (clade 28), nested deep within the argyrodines. Their unique silk-casting behaviour is probably homologous (Whitehouse, 1987b; *contra* Whitehouse *et al.*, 2002). Rather surprisingly, their reliance on their own webs is secondary, which may explain the peculiarity of their webs.

Araneophagy and kleptoparasitism are more subtly related than previously envisioned. Hypotheses about either trait being directly derived from each other (H1, H2) can be rejected, as can the idea that the expression of behaviour is entirely environmentally controlled (H4). Furthermore, although current results support Whitehouse's (1987b) distinction between the free-living *Ariamnes–Rhomphaea* araneophagy, and kleptoparasitic facultative araneophagy, the two are probably not entirely independent as the unique araneophagic technique of *Ariamnes* and *Rhomphaea* is derived from a condition found in more basal, facultatively araneophagic argyrodines (rejecting H3).

The problem of explaining kleptoparasitism and araneophagy may lie in the terms themselves. Kleptoparasitism entails many components, one of which can be the consumption of spiders. Invasion of a foreign web is one feature that unites argyrodines (although secondarily lost). Spiders generally take any prey they can handle, and prey choice in those invaded webs was no doubt originally as general, including both items stuck in the web and the web's host. Many extant species show such generalized behaviour (such as the basal *Faiditus chickeringi*) whereas others specialize either in eating the host or its prey. Thus, obligatory kleptoparasitism may represent the suppression of araneophagy in order not to kill a host that continues to provide food. Conversely, obligatory araneophagy in *Ariamnes* and *Rhomphaea* may represent the suppression of ancestral kleptoparasitism.

MATERNAL CARE, THE COMMON DENOMINATOR OF SOCIALITY AND KLEPTOPARASITISM?

Maternal care entails many behavioural components and is vaguely defined (see Agnarsson, 2002). Many, perhaps most, theridiids and relatives guard the egg sac (Figs 95B, C, E, 101F, G), but for present purposes I define maternal care as the cohabitation of young with their mother for some time (typically at least one moult outside the egg sac). Many authors have argued that features required for maternal care can result in postjuvenile tolerance and sociality if siblings continue to cohabit after leaving the egg sac (e.g. Shear, 1970; Kullmann, 1972; Burgess, 1978; Krafft, 1979; Cangialosi & Uetz, 1987; Avilés, 1997; Agnarsson, 2002; Jones & Parker, 2002; Schneider, 2002).

Subsociality is maternal care that spans several, rather than few, juvenile instars. Quasisociality is another point on the continuum in which maternal care never ceases. Quasisociality resulting from the gradual prolongation of maternal care has been termed the 'maternal care pathway', or the 'subsocial route' to sociality (Avilés, 1997). It predicts that mater-

nal care should precede subsociality phylogenetically, which in turn should precede quasisociality. Although widely accepted (see authors cited above) this hypothesis is here evaluated cladistically for the first time in spiders. My results support the hypothesis (Fig. 106).

Female-biased sex ratio is characteristic for social theridiids, and the bias is generally greater in quasisocial than in subsocial species (Avilés, 1986; Avilés & Maddison, 1991; Avilés *et al.*, 2000). Interestingly, Stiles & Coyle (2001) reported slightly biased sex ratios (about two females per male) in *Theridion frondeum* and *Rugathodes aurantius*, which both show some maternal care, beyond care of egg sac. The degree of maternal care (e.g. the length of time juveniles spend at their mother's nest) and degree of sex ratio bias thus may be correlated; understanding the interaction of the two may help understand the mechanisms of the maternal pathway to sociality.

This result corroborates Agnarsson's (2002) argument that sociality, as exemplified by web sharing, contrasts sharply with territorial 'sociality' (aggregations of individual webs), which never involves sharing a web and appears to have no special connection with maternal care. 'maternal care', 'subsociality' and 'quasisociality' do not represent clearly divided, distinct concepts. A more useful categorization of conspecific web sharing requires focusing on its specific components (cooperation in web building and attacking prey, feeding by regurgitation, intra- and interspecific tolerance mechanisms, sex ratio, communication, etc.).

Whitehouse (1986), and Whitehouse & Jackson (1993), suggested that kleptoparasitism might also be an expression of maternal care, having arisen through neoteny as an extension of a fundamental 'feeding with host' response of juveniles. Agnarsson (2002) observed that origins of sociality and kleptoparasitism are phylogenetically juxtaposed in theridiid spiders. Given that both entail web sharing and mutual tolerance, this phenomenon prompted him to suggest that 'If sociality is the prolongation of the tolerance required for maternal care, kleptoparasitism can be viewed as co-opting or the exaptive application of juvenile tolerance in a novel context in which the much larger host is no longer a conspecific relative but an entirely different species' (Agnarsson, 2002: 184). In other words, both behaviours could be modifications of homologous ancestral maternal care, via the retention of juvenile web sharing and peer tolerance to adulthood.

In the phylogeny presented here, Argyrodinae are sister to clade 27, which contains all social theridiids (note that the molecular evidence presented by Arnedo *et al.*, 2004, where Argyrodinae is sister to *Enoplognatha*, conflicts with this placement). The optimization of maternal care is problematic due to missing information for most taxa (Fig. 106). However, maternal care is unambiguously positioned on the node leading to all occurrences of sociality (clade 25). If viewed as putatively homologous to kleptoparasitism, 'juvenile web sharing' is positioned at clade 33, which contains nearly all instances of kleptoparasitism, maternal care and sociality in theridiids. The current phylogeny therefore corroborates this hypothesis.

These results also imply that maternal care should be very widespread within the lost colulus clade; in other words, they predict that hundreds of species not known to show maternal care, do so. This conclusion seems provocative, but its unexpectedness may stem rather from the absence of evidence (lack of field studies on basic biology and behaviour of these spiders) than evidence of absence. Maternal care is probably not universal in the clade, but many instances of it almost certainly remain to be discovered (pers. observ.).

Evolution of the theridiid web

'The web of the Linyphiidae was improved by the Theridiidae, who merely omitted the sheet; the Epeiridae have made the next step by rearranging the tangle that was left' (Savory, 1928: 141).

The evolutionary 'invention' of the two-dimensional sticky orb web has been thought of as a key innovation resulting in the diversification of the Orbiculariae (Bond & Opell, 1998). Classically (e.g. the above quote from Savory) it was seen as an endpoint in the evolutionary perfection of the web. Modern cladistic analyses have shown otherwise (e.g. Coddington, 1986c, 1989, 1990b; Griswold *et al.*, 1998). The most species-rich and abundant group within Orbiculariae is the 'araneoid sheet web weavers' whose members have transformed the orb web beyond recognition (Coddington & Levi, 1991; Griswold *et al.*, 1998).

This change towards three-dimensional webs is associated with 43% increase in species diversity and up to 400% increase in abundance in most ecosystems (Blackledge, Coddington & Gillespie, 2003; Platnick, 2003). Blackledge *et al.* (2003) point out that the success of araneoid sheet web weavers is correlated with an 'escape' from predation by sphecid wasps. Sphecid wasps are among the dominant predators of many spiders (Laing, 1979; Blackledge & Wenzel, 2001) and among orbicularians show a strong preference for species with planar webs. Among the araneoid sheet web weavers, theridiids appear to be the most species-rich and abundant in many areas where sphecid wasps are common and the evolution of the theridiid cobweb is thus of great interest.

A cobweb is here considered to be a three-dimensional mesh whose catching area is not limited to a plane (**225**, Figs 97G, 99A, B, 100A–F, 101A–E). Terminal sticky globules on lines attached to a substrate (gumfoot lines, **227**, Figs 96E, F, 101B, D) are present in some, but not all, cobwebs, and in some non-

cob theridiid webs (Fig. 97B–D). Simple cobwebs with gumfoot lines are present in Nesticidae and on the current cladogram; the origin of both can be optimized at the node leading to the theridioids (clade 55, Figs 103, 105). The evolution of the theridiid web appears complex, and interpretation is hindered by lack of field observations on the specific taxa of this phylogeny (Fig. 108).

Benjamin & Zschokke (2003: 302) suggested that modification of web construction behaviour may have occurred many times independently. 'The evolutionary trend seems to be from extensive to reduced amounts of viscid silk in webs, and finally to total absence.' The current cladogram, generally supports this view. The simplest evolutionary inference is that the basic theridiid gumfoot cobweb has been reduced, lost, or modified numerous times. A few hadrotarsines, e.g. *Dipoena tristis* (Hahn, 1833) (see Wiehle, 1937) and *D. torva* (Thorell, 1875) (see Roberts, 1995), are known to build reduced gumfoot webs, similar to those of nesticids. Most others, seem to have lost a snare web altogether (e.g. Carico, 1978; Kaston, 1978).

Most spintharines make simple line webs, either a H-shaped web with two gumfoot lines, which the spider holds with its front legs (*Episinus* and *Spintharus*, Fig. 97A, see also Holm, 1939; Ikeda *et al.*, 1983; Roberts, 1995: 261), or a few, presumably nonsticky lines (*Thwaitesia* spp., pers. observ.). Interestingly, *Chrosiothes* species vary; some make typical spintharine H-shape webs (J. A. Coddington, pers. comm.), others make simple nonsticky line webs after the prey has been encountered (Eberhard, 1991) or make sheet webs with knock-down threads (Eberhard, 1991). *Enoplognatha* builds a sticky cobweb, probably without gumfoot lines (e.g. Nielsen, 1932; Kullmann, 1971; Preston-Mafham & Preston-Mafham, 1984). *Selkirkiella* is similar (Fig. 99B, albeit sticky silk may be absent, pers. observ.). *Phoroncidia* retains a highly specialized gumfoot web with one (or sometimes a few) gumfoot lines typically fastened to the substrate at both ends, with the spider holding it together in the middle with opposite legs I, IV (Fig. 97B–D, see also Eberhard, 1981).

Other pholcommatine webs are poorly known. They may have been reduced or lost in some litter-dwelling taxa, or simply have been overlooked. Interestingly, *Pholcomma gibbum* (Westring, 1851) has a fairly typical cobweb with gumfoot lines (Holm, 1939; Jones, 1992). Argyrodines have lost or modified the basic cobweb snare; kleptoparasites often make nonprey-catching retreat webs in the host barrier area (Robinson & Robinson, 1973; Whitehouse, 1986; Agnarsson, 2003b), while the ambushing araneophages use simple webs to attract and detect, but not entangle, the prey (Eberhard, 1979; Whitehouse, 1987b). Still, exceptions exist, and may be common. *Argyrodes antipodianus*, for example, can make simple sticky snare-webs in addition to pilfering prey from host webs (Whitehouse, 1986), and *Neospintharus trigonum* is famously versatile (e.g. Cangialosi, 1997).

Social species have two main web types. *Anelosimus rupununi* and *A. lorenzo*, and *Achaearanea wau* and *A. vervoorti* build networks in the canopy and forage beneath the 'platform' (e.g. Levi, 1972: fig. 10), whereas other social *Anelosimus* (Fig. 99C) make nests with aerial trap lines that knock down insects in flight, similar to the webs of some linyphioids (Levi *et al.* 1982; Lubin, 1982; 1995; Avilés & Salazar, 1999; Vakanas & Krafft, 2001).

Within Theridiinae, the 'star web' (a compact, globular central retreat with support and gumfoot lines radiating from it, Figs 100, 101) is one of the most obvious and abundant theridiid web types in many tropical forests (pers. observ.), yet its phylogenetic distribution is unclear. Star webs are made by species of *Achaearanea*, *Chrysso* and *Theridion*, but are certainly not universal in any of these (see Benjamin & Zschokke, 2003). The web architecture may be a particularly effective defence against sphecid wasps. These three genera together account for nearly half of all theridiids, and the correlation of this particular web form with species richness is provocative. Rigorous testing of such speculations will require work on the phylogenetic structure of Theridiinae, circumscription of the likely paraphyletic *Achaearanea*, *Chrysso* and *Theridion*, and documentation of the behaviour of numerous species.

Theridiid web construction behaviour is poorly known, but appears to be less stereotypical than that of orb-weavers (Benjamin & Zschokke, 2002, 2003). Thus delimiting web-building characters, so useful in phylogenetic studies of orb-weavers (Robinson & Robinson, 1973, 1975; Eberhard, 1982, 1990; Coddington, 1986b; Coddington & Sobrevila, 1987; Hormiga *et al.*, 1995), has not been attempted here. Possible, and unique, theridioid web-building features include: absence of 'cut and reel' behaviour, structure web dragline reinforcing by doubling, unique stereotyped gumfoot line building behaviour, and gradual (over several days) web construction (Benjamin & Zschokke, 2003). Among the few behaviours clearly shared with orb-weavers are the terminal construction of sticky silk lines in a single bout (e.g. Benjamin & Zschokke, 2003), and araneoid-like attachment of sticky silk lines to dry silk lines, observed in *Achaearanea tepidariorum* (Eberhard, 1982).

While obscuring behavioural homologies, reduced stereotypy no doubt played a primary role in the generation of web architecture diversity of theridiids. 'Breaking away from the mould' may have allowed theridiids to explore a range of web types unavailable to most orbweb spiders (Eberhard, 2000). Perhaps the

great fortune of cobweb spiders is that they forgot how to make an orbweb.

Mating behaviour

The mating behaviour of about 30 theridiid species has been studied in considerable detail, unravelling several intriguing behaviours (e.g. Gerhardt, 1921, 1923, 1924a, b, 1925, 1926, 1928, 1933, summarized in Huber, 1998; Locket, 1926, 1927; Braun, 1963; Forster, 1992; Knoflach, 1994, 1995, 1996, 1997, 1998, 1999, 2002; Knoflach & van-Harten, 2000, 2001; Andrade, 1996; Andrade & Banta, 2002). Generally rare in spiders, sexual cannibalism occurs in *Latrodectus* (e.g. Forster, 1992; Andrade & Banta, 2002) and is obligatory in at least some *Tidarren* and *Echinotheridion* (Knoflach & van-Harten, 2000, 2001; Knoflach, 2002). Given this distribution, at least two origins of sexual cannibalism can be inferred.

Male 'sacrifice' is believed to be a sexually selected trait, which may increase copulation time, and the likelihood of other males being subsequently rejected by the female (Andrade, 1996). Details of the behaviour differ between and within the genera, but interestingly all are sexually size dimorphic. In *Tidarren* and *Echinotheridion* the male furthermore voluntarily amputates one palp prior to its final moult (**236**), a unique behaviour amongst spiders (e.g. Knoflach & van-Harten, 2000, 2001; Knoflach, 2002). Although only *Tidarren* is included here, *Echinotheridion* is certainly a theridiine and preliminary evidence suggests a monophyletic origin of this striking behaviour (pers. observ.).

Ipsilateral palpal insertions (right palp inserted on right side of epigynum) appear to be the norm in araneoids (Gerhardt, 1921–33; Helversen, 1976) and have been shown for several theridiids: *Achaearanea tepidariorum*, *Argyrodes argyrodes*, *Enoplognatha ovata*, *Latrodectus mactans*, *Neottiura bimaculata* and *Steatoda castanea* (Gerhardt, 1921, 1923, 1924b, 1926, 1928). However, contralateral insertions occur, e.g. in some tetragnathids (Huber & Senglet, 1997), and Knoflach (1998, 1999) discovered contralateral insertions (**238**) in several *Theridion*, including *T. varians*, *T. pictum* and *Coleosoma floridanum*.

Given the current phylogeny, the switch from ipsilateral to contralateral palpal insertions is synapomorphic for a group of distal theridiines (Fig. 104), and can be predicted in, e.g. *T. longipedatum* and *T. frondeum*. Interestingly, *Tidarren cuneolatum* (Tullgren, 1910), which has only one palp, uses ipsilateral insertions only when mating with a previously mated female plugged on the contralateral side (Knoflach & van-Harten, 2000). Possibly, such flexibility precedes the switch to contralateral insertions in distal theridiines; however, given the phylogenetic position of *Tidarren*, optimization is unclear and testing such speculations requires data on further species. Pseudocopulation (**237**) and sperm induction as a part of copulation sequence (**239**) are behaviours that, in the current phylogeny, optimize to the same theridiine clade (clade 4, Figs 104, 105). This pattern is intriguing and demonstrates the need for further studies on mating behaviour.

Prosoma-abdomen stridulatory mechanism

Various araneoids have some kind of stridulation mechanism (for reviews see Legendre, 1963; Barth, 1982; Uetz & Stratton, 1982). Legendre (1963) classified the various types of spider stridulatory systems and termed the prosoma-abdomen stridulatory mechanism present in theridiids as 'type a'. This system, first described by Westring (1843), involves pairs of elevated setal bases (here called stridulatory picks (SP); the terms 'scraper' and 'plectrum' refer to such stridulatory parts in general) around the pedicel on the abdomen (**150**, Figs 11A, 16B, C, 32C, D) that interact with ridges ('pars stridens' or 'file') on the posterior end of the carapace (**128**, Figs 10D, E, 42G, 66G; see also Juberthie & Lopez, 1994).

Although commonly present in both sexes, both the picks (compare B and C in Fig. 18, G and H in Fig. 42) and the ridges (compare A and B in Fig. 32), are usually much reduced in the female, and the stridulatory role in male courtship shown for a number of species (e.g. Lee *et al.*, 1986) can thus be presumed to be universal. Legendre (1963) provided a list of the 35 theridiid species known to him to have such a system. The list included members of *Argyrodes*, *Crustulina*, *Steatoda*, *Theonoe*, *Anelosimus*, *Neottiura*, *Theridion* and *Enoplognatha*, representing many of the more obvious cases. According to recent species descriptions, the 'type a' mechanism appears to occur only sporadically within the family, or its presence is not mentioned. However, this study indicates that a 'type a' mechanism is characteristic of theridiid spiders, and the presence of SPR is a synapomorphy of theridiids minus hadrotarsines (clade 50). Although quite variable, SPRs are present in nearly all members of the SPR clade.

Regular files on the carapace are less widespread than stridulatory picks on the abdomen and are quite homoplasious (six steps). Under DELTRAN (preferred here) two origins are implied, one in *Steatoda* plus *Crustulina*, the other in clade 43. A monophyletic origin of prosomal ridges, at the same node at which SPR evolved, requires a single extra step (one gain, six losses). ACCTRAN in this case leads to preference for parallel gains, and three origins are implied, with a loss defining the lost colulus clade and a regain supporting clade 14.

Even in taxa lacking regular prosomal ridges, it must be considered likely that the rubbing of an abdominal SPR against any uneven surface on the carapace produces some vibrations. As mentioned above, in many araneoids that have been studied to date, the male vibrates his abdomen as a part of courtship. It has been assumed that vibrations are thus produced either by 'drumming' the abdomen directly on the web, or that they are simply the results of the body being shaken and transmitted via the legs to the web.

The discovery during the course of this study of abdominal suprapedicellate nubbins (**149**, Figs 11A, 34H, 36H, 57B) may throw new light on that question. These nubbins are sclerotized and placed around the pedicel on the abdomen. They occur in all taxa examined in this study (except *Phoroncidia*), and probably constitute an araneoid synapomorphy. In theridiids, these nubbins are between and around the stridulatory picks (Figs 4F, 10F, 14A, 24D, E, 26D, E, 47A). I thus presume that violent shaking of the abdomen in courting araneoid males produces vibrations via true stridulation; the theridiid SPs are merely a modification of this system.

It is interesting to note that similar picks are present in at least some cyatholipids, e.g. *Toddiana daviesae* Forster (Griswold, 2001: fig. 9D), where they are also presumed to be involved in stridulation. Griswold (2001) furthermore suggests that sclerotization around male abdomens, commonly found in cyatholipids, may take part in abdomen-prosoma stridulation.

Evolution of the colulus

The presumed phylogenetic importance of colular characters (e.g. Levi & Levi, 1962; Forster *et al.*, 1990; Griswold *et al.*, 1998) is supported. Although the system shows considerable homoplasy, loss of additional colular setae (**175**, clade 55), reduction in colulus size (**173**, clades 27 and 45), loss of the colulus (**172**, clade 25), and the paired central colular setae (**174**, clade 15), are nested synapomorphies (Fig. 109).

Independently, in the hadrotarsines *Emertonella* plus *Euryopis* (clade 51) the colulus is absent; they share with *Phoroncidia* the condition 'colular area invaginated' (**172**).

It has been argued that evolutionary speculations about characters dependent on topologies themselves totally dependent on the same speculations is a very weak form of evolutionary inference (e.g. Coddington, 1988). Others have argued convincingly that such an approach is defensible within the 'total evidence' framework: including all available evidence in a cladistic analysis results in the most severely tested hypothesis with the greatest explanatory power (Kluge, 1997). Regardless, speculations are at least less circular if the corroborating topology does not require the evidence supplied by the character being tested. Accordingly, I deactivated the four colular characters and obtained the same single most parsimonious tree supported by all characters. The value of the colulus character system as an independent indicator of the phylogeny is in this sense supported.

Are eye arrangements unreliable characters in theridiids?

Eye arrangements are difficult to code objectively. In theridiids, eye spacing and relationships vary greatly between sexes and species. When investigating Levi & Levi's (1962) assertion that eye arrangements are unreliable characters, I arbitrarily coded AME, PME spacing as follows: (0) less than one diameter apart; (1) one diameter apart; (2) more than one diameter apart. I then reran the analysis. On the cladogram, PME separation, for example, required no less than 20 steps (CI = 10, RI = 40), and 22 steps on the strict consensus of the two resulting mpts (Fig. 110). Coded as a binary character – e.g. (0) less than or equal to one diameter apart; (1) more than one diameter apart – the character needed 13 steps on the cladogram (CI = 8, RI = 55). Eye separation is influenced by at least three nonhomologous characters – eye position, eye size and carapace shape – so the lack of phylogenetic structure is not surprising. In addition, truly continuous character state values cannot be logically distinguished.

Future studies

Even though it has summarized information on 242 morphological and behavioural characters, this study has far from exhausted the goldmine of morphology and behaviour as a source of information for phylogenetic inference for cobweb spiders. Rather, it has likely been biased towards the more obvious, and more comprehensible, variation. Without doubt the characters included here will change as further data are added, character delimitation and coding further scrutinized and improved, and errors uncovered.

Additionally, many potential character systems were not explored here. For example, the types and distribution of setae, both on appendages, and on the body, remain mostly unknown (for examples of different types of setae see Figs 1E, 5B, G, 6C, 8F, 18D, 26F, G, 30A–D, 35D, 53C, E, 59A, B). Setal bases are also variable (e.g. Figs 50D, 65F), as is abdomen ultrastructure. The distribution of sensory organs, such as trichobothria and slit sensilla, has not yet received sufficient attention. Tarsus IV claws provided several characters here, but other variations, such as the asymmetric dentation of outer vs. inner paired claws (Fig. 66E) and features of the typically shorter and

stouter claws of tarsi I–III (Fig. 87F), were not studied systematically.

Internal anatomy is practically unknown. There have been a few promising studies on silk-gland structure (Apstein, 1889; Kovoor, 1977). The study of web-building behaviour is still in its infancy in theridiids (Benjamin & Zschokke, 2002, 2003) but promises to provide numerous new characters. Egg-sac ultrastructure is a promising source of new characters (Fig. 88A–H). Mating behaviour contributed many characters, but was mostly allocated '?' due to lack of observations. The seemingly widespread production of mating plugs (Figs 33E, 45F, 82B), was not included; the plugs result from different, and mostly unknown, mechanisms in different species (see Knoflach, 1998; Knoflach & van-Harten, 2001).

This study constitutes a first attempt to synthesize a portion of the available information. It highlights the limits of our knowledge and will hopefully stimulate further studies of theridiid morphology and behaviour.

TAXONOMY

KOCHIURA ARCHER, 1950

Kochiura Archer, 1950, type species by original designation and monotypy, *Theridium aulicum* C. L. Koch, 1838, not examined.

Removed from synonymy of *Anelosimus*, *contra* Levi (1956: 412). In addition to *K. aulica* (C. L. Koch, 1838), several former *Anelosimus* species are transferred and the following new combinations established: *K. attrita* (Nicolet, 1849), *K. casablanca* (Levi, 1963), *K. episinoides* (Levi, 1963), *K. ocellata* (Nicolet, 1849), *K. rosea* (Nicolet 1849), *K. temuco* (Levi, 1963), and *K. decolorata* (Keyserling, 1886).

Synapomorphies of *Kochiura* in this study (*K. aulica* and *K. rosea*) include: copulatory ducts convolute and encircling spermathecae (**8**, **9**, Fig. 93J), cymbial ridge setae curved towards bulb (**21**, Figs 51B–D, 52B, C; **27**, Fig. 52C), cymbial sheath (**28**, Fig. 52C), enlarged conductor (**63**, Fig. 52B), elongate embolus (**91**, Figs 51B, 52B, C). Based on descriptions and illustrations in Levi (1963, 1967, treating seven species), these seem to be general in *Kochiura*.

Diagnosis

Kochiura differs from the similar *Anelosimus* by the long filiform embolus, large conductor, absence of epigynal plate ridges (Fig. 53E, F), presence of a small colulus, and hooked bulb-cymbium lock. The last two features also separate it from all theridiines.

SELKIRKIELLA BERLAND, 1924

Selkirkiella Berland, 1924, type species by monotypy *Selkirkiella alboguttata* Berland, 1924, not examined.

Removed from synonymy of *Anelosimus contra* Levi (1972: 536). In addition to *S. alboguttata* (Berland, 1924), several former *Anelosimus* species are transferred and the following new combinations established: *S. carelmapuensis* (Levi, 1963), *S. luisi* (Levi, 1967), *S. magallanes* (Levi, 1963), *S. michaelseni* (Simon, 1902), *S. purpurea* (Nicolet, 1849), *S. ventrosa* (Nicolet, 1849), and *S. wellingtoni* (Levi, 1967).

Synapomorphies of *Selkirkiella* in this study (*S. alboguttata* and S. *magallanes*) include: conductor enlarged and fan shaped (**63**, Fig. 67A, C), conductor heavily ridged (**65**, Fig. 67C), TTA apex with small apophysis (**82**, Fig. 67A, B), SPR ectally orientated picks absent (**153**, Fig. 67F), grooved SPR region (**155**, Fig. 67F), and elongate FL spigot (**206**, Fig. 68E). Also, characteristically in *Selkirkiella* the conductor and TTA are strongly compressed together, separated by a narrow seam (Fig. 67B). Based on Levi's (1963, 1967) drawings and descriptions, at least the enlarged and fan shaped conductor, TTA apex apophysis, and TTA and C compressed are universal in *Selkirkiella*.

Diagnosis

Selkirkiella differs from related pholcommatines by the shape and texture of the conductor, TTA apophysis, TTA and C compressed, lack of ectally orientated SPR, and possibly by mode of egg-sac protection, where a small sheet is woven to cover the egg sac (Fig. 95E).

ARGYRODINAE

I support Yoshida's (2001b) elevation of '*Argyrodes*' *sensu* Exline & Levi (1962) and Levi & Levi (1962) to subfamily level, Argyrodinae, based on Simon's (1894) tribe name Argyrodeae (see also Arnedo *et al.*, 2004). *Ariamnes*, *Rhomphaea* and *Spheropistha* are very likely monophyletic, but render the remaining '*Argyrodes*' paraphyletic (Fig. 102). The informal 'generic groups' *Faiditus* (*A. cancellatus* and *A. cordillera* groups) and *Neospintharus* (*A. trigonum* group) are therefore again recognized as genera. Although monophyletic, Exline & Levi's '*Argyrodes*' includes so much diversity and so many distinct groups, that clarity, increased information content, ease of information retrieval and communication, demand its division. Few theridiid genera are as readily diagnosable and recognizable as these five argyrodines, even after a superficial examination of somatic characteristics. Exline & Levi (1962) explicitly rejected the monophyly of these *Argyrodes* components, but this study has uncovered numerous synapomorphies that define each group (see below) and appear uniformly distributed amongst their members (pers. observ.).

The phylogeny presented here only explicitly tests one of the new circumscriptions, *Argyrodes s.s.* To test the monophyly of the other argyrodine genera I ran a

preliminary analysis adding *Ariamnes* sp., *Faiditus ululans*, *Neospintharus concisus* and *Rhomphaea projiciens* to the data matrix (see Table 4). The results (single most parsimonious tree: L = 759, CI = 0.37, RI = 0.75, not shown) support the monophyly of all argyrodine genera included here and are otherwise identical to the mpt of the core matrix. A more detailed analysis, adding other putative generic synapomorphies, as well as further character information, e.g. details of the palpal organs so characteristic of each group, is likely to further support this result. The modified data matrix is available at http://www.gwu.edu/~spiders/cladograms.htm.

Morphological observations (sorting through hundreds of argyrodines of all five genera, from all over the world), as well as behavioural data (I. Agnarsson, unpubl. data), further support the validity of all these groups. Furthermore, 2–7 species of each genus (see specimens examined, Appendix 3) were examined using light microscopy to verify the presence of putative generic synapomorphies. The diagnosis offered here for each genus is preliminary and speculative with regard to the features that require SEM to verify their presence (or absence). These features have been examined only in the species in the core matrix, and examining in such detail all the >230 argyrodine species is clearly outside the scope of this study. However, I also explicitly propose putative synapomorphies of all genera that have been verified in other species examined in detail (see Appendix 3), and synapomorphies based on conspicuous somatic characters, evident in even superficial examination of specimens, and from species descriptions and drawings. These putative generic synapomorphies appear highly consistent.

Full transfer of all valid species currently in *Argyrodes* is a task that cannot be attempted here. However, based on Exline & Levi (1962) and González & Carmen (1996), species groups (and descriptions) of the vast majority of New World *Argyrodes* can be correctly placed. Zhu's (1998) work, likewise, allows the placement of Chinese species. Furthermore, species are transferred to *Rhomphaea* and *Ariamnes* if originally described in those genera, and later work has not contradicted this placement. The remaining species must remain in *Argyrodes* for the time being.

ARGYRODES SIMON, 1864

Argyrodes Simon, 1864, type species by tautonomy, *Linyphia argyrodes* Walckenaer, 1842 (see Levi & Levi, 1962), not examined.

Synonyms

Conopistha Karsch, 1881 – type *C. Bona Dea* Karsch, 1881 [= *A. bonadea*] (Levi & Levi, 1962: 19), not examined.

Argyrodina Strand, 1928, new name for *Argyrodes*, preoccupied – objective synonymy of *Argyrodes* (Levi & Levi, 1962: 16)

Microcephalus Restrepo, 1944 – type *M. fur* Restrepo [= *A. elevatus*] (Levi, 1972: 534), not examined.

Species attributed to the '*A. argyrodes*' group of Exline & Levi (1962) and Zhu (1998) belong to this genus: *A. argentatus* O. P.-Cambridge, 1880, *A. argyrodes* (Walckenaer, 1842), *A. bonadea* (Karsch, 1881), *A. elevatus* Taczanowski, 1873, *A. nephilae* Taczanowski, 1873, *A. fissifrons* O. P.-Cambridge, 1869, *A. flavescens* (O. P.-Cambridge, 1880), *A. miltosus* Zhu & Song, 1991, *A. pluto* Banks, 1906, *A. rostratus* Blackwall, 1873, *A. weyrauchi* Exline & Levi, 1962, *A. zhui* Zhu & Song, 1991. The intensely studied *A. antipodiana* O. P.-Cambridge, 1880 (Whitehouse, 1986, 1987a; Whitehouse & Jackson, 1993) also belongs here.

Argyrodes synapomorphies in this study (*A. argyrodes* and *A. elevatus*) include: cymbial distal promargin with apophysis (**24**, Fig. 31B, D),

Table 4. Character coding for *Neospintharus concisus*, *Rhomphaea projiciens*, *Ariamnes* sp., and *Faiditus ululans*

Neospintharus concisus 00010000-0000111111000000000 1-1100000--0200000000-??????????00100000001010001010?00?100000000001?000000100110??000000000100000101111100?00?100-01011?????????????101?01?000100111101111100000011??01111001??0110010111?01??3006?????????00??????

Rhomphaea projiciens 00010000-0000101122000000000 1-1100000--0200000000-??????????000000000010100010 10?00?1000?0000001?000000100110??0000000001001001 010111100?00?100-01111?????????????101????000100121101111100000 11??011110 0 1??0110?0111-?-1??30061????2??000??????

Ariamnes sp. 00010010-0100111122000010000 1-?100000--0200000000-??????????000000000010100010 10?000?000?000 0001?000000100110??0000000001000000-10111100 1001100-01111?????????????101011?000100121101111100000111001 111001??0110? 0111-?-1??30061???????000??????

Faiditus ululans 00010110-0000111111000000000 1-1100000--0200000000-??????????000000000010100010 10100010000?0 000001?000000100110 1?000000001000001001 10 11000000000-1011?????????????101????000100111101001100000 11???1 111001??01 10??0111?11??3006????????000????

embolic terminal apophysis (**96**, Fig. 31E), male median eyes on tubercle (**103**, Figs 32E, F, 94B), and male triplet absent (**219**, Fig. 33D). At least cymbial distal promarginal apophysis and male median eyes on tubercle seem universal in the genus (see e.g. Exline & Levi, 1962; Zhu, 1998). Embolic terminal apophysis and absence of male triplet were furthermore confirmed in all *Argyrodes* examined in detail, namely *A. bonadea*, *A. fur*, *A. nephilae* and *A. pluto* (absence of male triplet should be verified through SEM, as spigots may be overlooked in light microscopy).

The synonymy of *Conopistha* and *Microcephalus* with *Argyrodes* is corroborated after examination of nontype specimens of their respective generotypes, *A. bonadea* and *A. fur*.

Diagnosis

Argyrodes differs from other argyrodines by: lack of a functional triplet in the male, tight folding of the embolus and conductor (Fig. 31D), details of male carapace modifications, including median eyes on tubercles, details of life history (obligate kleptoparasitism), and highly characteristic palpal organs, the TTA snug with a distinct cymbial apophysis, and E and C intertwined (Fig. 31B). The shape and coloration of the abdomen is highly variable (e.g. Chikuni, 1989: 34). Interestingly, in many *Argyrodes* the males are larger than the females (Exline & Levi, 1962).

ARIAMNES THORELL, 1869

Ariamnes Thorell, 1869, type species by monotypy *Ariadne flagellum* Doleschall, 1857 [= *Ariamnes flagellum*] (see Levi & Levi, 1962: 17), not examined.

Synonymy: Ariadne Doleschall, 1857 – type species by monotypy *A. flagellum* Doleschall, 1857, preoccupied by *Ariadne* Latreille, 1829 (junior synonym of *Ariadna* Audouin, 1826 (Segestriidae). *Ariamnes* is a replacement name for *Ariadne*.

Removed from the synonymy of *Argyrodes* by Yoshida (2001a: 183–184), *contra* Levi & Levi (1962: 17). See also Arnedo *et al.* (2004). All species attributed to the '*Ariamnes*' group of Exline & Levi (1962) and Zhu (1998), or originally described as *Ariamnes* are explicitly transferred to *Ariamnes*: *A. attenuata* O. P.-Cambridge, 1881, *A. birgitae* Strand, 1917, *A. campestratus* Simon, 1903, *A. colubrinus* Keyserling, 1890, *A. corniger* Simon, 1900, *A. cylindrogaster* Simon, 1889, *A. flagellum* (Doleschall, 1857), *A. flagellum nigritus* Simon, 1901, *A. haitensis* (Exline & Levi, 1962) **comb. nov.**, *A. helminthoides* Simon, 1907, *A. jeanneli* Berland, 1920, *A. longicaudata* O. P.-Cambridge, 1872, *A. longissimus* Keyserling, 1891, *A. mexicanus* (Exline & Levi, 1962) **comb. nov.**, *A. patersoniensis* Hickman, 1927, *A. pavesii* Leardi, 1902, *A. rufopictus* Thorell, 1895, *A. russulus* Simon, 1903, *A. schlingeri* (Exline & Levi, 1962) **comb. nov.**, *A. setipes* Hasselt, 1882, *A. simulans* O. P.-Cambridge, 1892, *A. triangulatus* Urquhart, 1887, *A. triangulus* Thorell, 1887.

Diagnosis: Ariamnes differs from other argyrodines by the following putative synapomorphies (based on *A. attenuata*) elongate spermathecae (**11**), embolus terminal apophysis (**96**, Fig. 34D, E), carapace pars stridens irregular (**138**), epiandrous gland spigots not in sockets (**169**, Fig. 34G), elongated egg sac (**231**, Fig. 98E), abdomen extremely elongated (Fig. 95A), unusual arrangement of proprioreceptors (Fig. 35C), sturdy setae on male metatarsus and tarsus I (Fig. 35D), as well as details of head modification (Fig. 34F), palpus (Fig. 34A–D), and prey-catching strategy (e.g. Eberhard, 1979). At least elongate spermathecae, elongated abdomen, and head modifications appear uniform in the genus (see e.g. Exline & Levi, 1962; Zhu, 1998). Irregular carapace pars stridens, arrangement of proprioreceptors and sturdy setae on male metatarsus and tarsus I were confirmed in the two other *Ariamnes* examined in detail, *Ariamnes* sp. and *A. longissimus*. I have observed the elongated egg sac in several undescribed species, but at least some species presumably build shorter egg sacs similar to other argyrodines (e.g. Chikuni, 1989: 35).

FAIDITUS KEYSERLING, 1884

Type – *F. ecaudatus* Keyserling, 1884, designated by Petrunkevitch (1928), not examined.

Synonyms: Bellinda Keyserling, 1884 – type *Theridion cancellatum* Hentz, 1850 [= *Bellinda cancellata*], not examined, **syn. nov.** *Bellinda* appears in the same publication as *Faiditus*. Usage may suggest priority of *Faiditus*, as *Bellinda* is only mentioned in Keyserling's publication, but Petrunkevitch (1928) includes *Faiditus* in his *Systema Aranearum*.

Faiditus is removed from synonymy of *Argyrodes*, *contra* Levi & Levi (1962: 21). *F. ecaudatus* Keyserling, 1884, and all other species attributed to the '*A. cancellatus*' and '*A. cordillera*' groups of Exline & Levi (1962) and Zhu (1998) are explicitly transferred to *Faiditus* and the following new combinations established:

F. acuminatus (Keyserling, 1891), *F. affinis* (O. P.-Cambridge, 1880), *F. alticeps* (Keyserling, 1891), *F. altus* (Keyserling, 1891), *F. amates* (Exline & Levi, 1962), *F. americanus* (Taczanowski, 1874), *F. amplifrons* (O. P.-Cambridge, 1880), *F. analiae* (González & Carmen, 1996), *F. arthuri* (Exline & Levi,

1962), *F. atopus* (Chamberlin & Ivie, 1936), *F. bryantae* (Exline & Levi, 1962), *F. cancellatus* (Hentz, 1850), *F. caudatus* (Taczanowski, 1874), *F. chickeringi* (Exline & Levi, 1962), *F. caronae* (González & Carmen, 1996), *F. chicaensis* (González & Carmen, 1996), *F. cochleaformus* (Exline, 1945), *F. convolutus* (Exline & Levi, 1962), *F. cordillera* (Exline, 1945), *F. cristinae* (González & Carmen, 1996), *F. cubensis* (Exline & Levi, 1962), *F. darlingtoni* (Exline & Levi, 1962), *F. davisi* (Exline & Levi, 1962), *F. dracus* (Chamberlin & Ivie, 1936), *F. duckensis* (González & Carmen, 1996), *F. exiguus* (Exline & Levi, 1962), *F. fulvus* (Exline & Levi, 1962), *F. gapensis* (Exline & Levi, 1962), *F. gertschi* (Exline & Levi, 1962), *F. globosus* (Keyserling, 1884), *F. godmani* (Exline & Levi, 1962), *F. iguazuensis* (González & Carmen, 1996), *F. jamaicensis* (Exline & Levi, 1962), *F. laraensis* (González & Carmen, 1996), *F. leonensis* (Exline & Levi, 1962), *F. maculosus* (O. P.-Cambridge, 1898), *F. mariae* (González & Carmen, 1996), *F. morretensis* (González & Carmen, 1996), *F. nataliae* (González & Carmen, 1996), *F. peruensis* (Exline & Levi, 1962), *F. plaumanni* (Exline & Levi, 1962), *F. proboscifer* (Exline, 1945), *F. quasiobtusus* (Exline & Levi, 1962), *F. rigidus* (Exline & Levi, 1962), *F. rossi* (Exline & Levi, 1962), *F. sicki* (Exline & Levi, 1962), *F. solidao* (Levi, 1967), *F. spinosus* (Keyserling, 1884), *F. striatus* (Keyserling, 1891), *F. subdolus* (O. P.-Cambridge, 1898), *F. subflavus* (Exline & Levi, 1962), *F. sullana* (Exline, 1945), *F. taeter* (Exline & Levi, 1962), *F. ululans* (O. P.-Cambridge, 1880), *F. vadoensis* (González & Carmen, 1996), *F. woytkowskii* (Exline & Levi, 1962), *F. xiphias* (Thorell, 1887), *F. yacuiensis* (González & Carmen, 1996), *F. yutoensis* (González & Carmen, 1996).

Diagnosis: Faiditus here differs from other argyrodines (based on *F.* cf. *chickeringi*) by the following putative synapomorphies: copulatory bursa anterior margin medially acute (**6**) a strongly hooked TTA distal tip (**85**, Fig. 48A, B), abdomen with paired (or multiple) humps (**142**, Fig. 94C, also in some *Neosphintharus* (Fig. 57F), E hidden by TTA (Fig. 48B), and details of male cephalic modification (a shallow clypeal groove with a dense field of setae, Fig. 48C, D). All known *Faiditus* are kleptoparasitic and, as in *Argyrodes*, males are often larger than females (Exline & Levi, 1962). At least details of cephalic modifications appear universal in *Faiditus* (see e.g. Exline & Levi, 1962; Zhu, 1998). Medially acute anterior copulatory bursa margin, hooked TTA distal tip, and E hidden by TTA were confirmed in other *Faiditus* examined in detail: *F. americanus*, *F. amplifrons*, *F. cancellatus*, *F.* cf. *caudatus*, *F. spinosus* and *F. ululans*. Abdomen humps were lacking only in *F. ululans*.

The synonymy of *Bellinda* with *Faiditus* was corroborated with examination of nontype specimens of the *Bellinda* generotype, *F. cancellatus*.

NEOSPINTHARUS EXLINE, 1950

Neospintharus Exline, 1950, type *Neospintharus parvus* Exline, 1950 by original designation and monotypy (type specimen lost).

Neospintharus is removed from synonymy of *Argyrodes*, *contra* Levi & Levi (1962: 24). *N. parvus* and all species attributed to the '*A. trigonum* group' of Exline & Levi (1962) and Zhu (1998) are explicitly transferred to *Neospintharus* and the following new combinations established: *N. baboquivari* (Exline & Levi, 1962), *N. bicornis* (O. P.-Cambridge, 1880), *N. concisus* (Exline & Levi, 1962), *N. furcatus* (O. P.-Cambridge, 1894), *N. obscurus* (Keyserling, 1884), *N. fur* (Bösenberg & Strand, 1906), *N. nipponicus* (Kumada, 1990), *N. rioensis* (Exline & Levi, 1962), *N. syriacus* (O. P.-Cambridge, 1872), *N. triangularis* (Taczanowski, 1873), *N. trigonum* (Hentz, 1850).

Diagnosis: Neospintharus here differs (based on *N. trigonum*) from other argyrodines by the following putative synapomorphies: conductor entire (**64**, Fig. 56C), embolus not ridged (**90**, Fig. 56A–C), clypeal projection elongate (Fig. 56E), modified setae on clypeal as well as ocular projections (Fig. 30D), details of male cephalic modifications, AME in clypeal groove (Fig. 30D), retention of only a single triplet spigot (an AG, Fig. 57C), and details of male palp, including a 'teapot-shaped' embolus, and a distally broad TTA. At least elongate clypeal projection, modified clypeal and ocular setae, and other details of cephalic modifications appear uniform in *Neosphintharus* (see e.g. Exline & Levi, 1962; Zhu, 1998). Entire conductor, lack of embolic ridges, single triplet spigot, and characteristic palpal organs were confirmed in other *Neosphintharus* examined in detail: *N. concisus* and *N. furcatus*. The presence of a single triplet spigot should be verified with SEM as spigots can be overlooked in light microscopy.

RHOMPHAEA L. KOCH, 1872

Rhomphaea L. Koch, 1872, type *Rhomphaea cometes* L. Koch, 1872 by monotypy, not examined.

Rhomphaea was removed from synonymy of *Argyrodes* by Yoshida (2001b: 185–187) *contra* Levi & Levi (1962: 27), see also Arnedo *et al.* (2004). All species attributed to the '*Rhomphaea*' group of Exline & Levi (1962) and Zhu (1998), or originally described as *Rhomphaea* are explicitly transferred to *Rhomphaea*:

R. aculeata Thorell, 1898, *Rhomphaea affinis* Lessert, 1936, *R. altissima* Mello-Leitão, 1941,

R. angulipalpis Thorell, 1877, *R. brasiliensis* Mello-Leitão, 1920, *R. cometes* L. Koch, 1872, *R. ceraosus* (Zhu & Song, 1991) **comb. nov.**, *R. cona* (González & Carmen, 1996) **comb. nov.**, *R. fictilium* (Hentz, 1850), *R. hyrcana* (Logunov & Marusik, 1990), *R. irrorata* Thorell, 1898, *R. labiata* (Zhu & Song, 1991), *R. lactifera* Simon, 1909, *R. metaltissima* Soares & Camargo, 1948, *R. nasica* (Simon, 1873), *R. oris* (González & Carmen, 1996) **comb. nov.**, *R. ornatissima* Dyal, 1935, *R. palmarensis* (González & Carmen, 1996) **comb. nov.**, *R. paradoxa* (Taczanowski, 1873) **comb. nov.**, *R. pignalitoensis* (González & Carmen, 1996) **comb. nov.**, *R. procera* (O. P.-Cambridge, 1898), *R. projiciens* O. P.-Cambridge, 1896, *R. rostrata* (Simon, 1873), *R. sagana* (Dönitz & Strand, 1906), *R. sinica* (Zhu & Song, 1991) **comb. nov.**, *R. sjostedti* Tullgren, 1910, *R. tanikawai* Yoshida, 2001, *R. urquharti* Bryant, 1933, *R. velhaensis* (González & Carmen, 1996) **comb. nov.**

Diagnosis: Rhomphaea here differs (based on *R. metaltissima*) from other argyrodines by the following putative synapomorphies: tibia elongate, but not scoop-shaped (**15**, Fig. 64A), epiandrous gland spigots absent (**168**, Fig. 64F), egg sac rhomboid-shaped (**231**), embolus tip elongate and strongly ridged basally (Fig. 64B, C), ocular projection elongate (Figs 30C, 94D), abdomen boomerang-shaped (Fig. 94D), posterior tip of abdomen with modified sturdy setae (Fig. 94D), and possibly unique prey-capture strategy (see Whitehouse, 1987b). At least elongate ocular projection (but see below) and boomerang-shaped abdomen appear highly consistent in *Rhomphaea* (see e.g. Exline & Levi, 1962; Zhu, 1998; but see below). Furthermore, to the best of my knowledge, all *Rhomphaea* egg sacs hitherto described are rhomboid (e.g. Exline & Levi, 1962; Chikuni, 1989). The details of the palpal organ are also characteristic. Elongate tibia, elongate embolus tip, and modified sturdy abdominal setae were confirmed in other *Rhomphaea* examined in detail: *R. fictillum* and *R. projiciens*. Embolic ridges and epiandrous gland spigots cannot be accurately assessed without SEM. Uniquely in *R. fictillum*, and an undescribed species from Madagascar (pers. observ.), the ocular projection is lacking. Given that otherwise these are typical *Rhomphaea*, this presumably represents secondary loss, possibly defining a subsidiary clade within *Rhomphaea*.

Argyrodinae furthermore contains *Spheropistha* Yaginuma, 1957, type by original designation *Spheropistha melanosoma* Yaginuma, 1957. Other species: *S. miyashitai* (Tanikawa, 1998), *S. nigroris* (Yoshida, Tso & Severinghaus, 2000), *S. orbita* (Zhu, 1998).

NOMEN DUBIUM

As pointed out by Levi & Levi (1962: 21), no specimens are known to exist of the genus *Gnophomytis* Simon, 1895, and the original description (Simon, 1895: 149) is not recognizable; it should thus be treated as a *nomen dubium*.

NOTES ON TAXONOMY OF *DIPOENA NIGRA*

Simon (1881) created *Lasaeola*, replacing *Pachydactylus* Menge, 1868, a homonym of *Pachydactylus* Wiegmann, 1934. The type species of *Pachydactylus* Menge is *P. pronus* Menge, 1868, by monotypy (see Levi & Levi, 1962: 25). Levi & Levi (1962) considered *Lasaeola* as a junior synonym of *Dipoena*. Wunderlich (1988: 148) resurrected *Lasaeola* and transferred *Dipoena tristis* Hahn, 1833, as the type species of *Lasaeola* (incorrectly, as *Lasaeola* must have the same type as the name it replaced, *Pachydactylus pronus*).

Yoshida (2002) created the genus *Yaginumena* for *Dipoena castrata* Bösenberg & Strand, 1906 and indicated that all species of Levi's (1953b) '*D. nigra* group' belong to it. Levi's *D. nigra* group included *Dipoena tristis* (Levi, 1953b: 7, in fact indicates that these two may be synonyms). Wunderlich (1988) furthermore created *Dipoenata* for *D. stipes* Wunderlich, 1988 (a fossil) and related species. He transferred several *Dipoena* to *Dipoenata*, including *Dipoena balboae* Chickering, 1943. Levi (1963: 148) indicates that *D. balboae* and *D. nigra* may be synonymous; at least, they are extremely similar. Levi's (1953b) *Dipoena*, Wunderlich's (1988) *Dipoenata* and *Lasaeola* and Yoshida's (2002) *Yaginumena*, all thus circumscribe *D. nigra*; accordingly, only one of them can be monophyletic, or at best, two or more may be nested. Until these recent circumscriptions have been made exclusive of one another, and their monophyly demonstrated, *D. nigra* cannot be realistically transferred.

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APPENDIX 1

CHARACTER DESCRIPTIONS AND COMMENTS

Characters taken from Griswold *et al.* (1998), whether modified or not, are marked **G98**, followed by the character number (e.g. **G98-26** is character 26 in Griswold *et al.*, 1998).

1. *Epigynal ventral margin*: (0) entire (Fig. 15G); (1) with scape (Fig. 27D). Epigynal scapes are widespread in araneoid spiders (see e.g. Scharff & Coddington, 1997:

character 28), but to my best knowledge, *Anelosimus pulchellus* and *A. vittatus*, along with *A. ethicus* (pers. observ.), are unique among theridiids in having an araneid-like epigynal scape. *Thymoites unimaculatum* has a similar ventral scape-like projection (Fig. 85F), here considered putatively homologous, although the homology is rejected on the cladogram.

2. *Epigynal dorsal plate*: (0) absent; (1) present. Pimoids and linyphiids typically have a distinct dorsal plate in the epigynum (see e.g. Millidge, 1984: fig. 9; Hormiga, 1994a: fig. 60). Such a plate is absent in theridiids and other taxa in this study (e.g. Figs 2E, 7E, 12E, 33E, 45F, 50C, 55A, 59F, 63A, 64G, 86G, 93F, G).
3. *Epigynal plate surface*: (0) smooth (Fig. 12E); (1) ridged (Fig. 21G). In most theridiids the epigynal plate is smooth (e.g. Figs 12E, 40B). On this cladogram the presence of conspicuous ridges on the epigynal plate is a synapomorphy of *Anelosimus* (e.g. Figs 21G, 24G) secondarily lost in clade 19 (Fig. 29A). Presumably the theridiid epigynal plate is a homologue of the ventral plate of linyphioids.
4. *Copulatory pore position*: (0) caudal, under a dorsal plate; (1) ventral. A conspicuous projection overlies the copulatory openings in many araneoids (see e.g. *Pimoa rupicola* in Hormiga, 1994a: figs 27–29). In theridiids and *Synotaxus*, such a projection is generally absent and the openings are thus clearly visible in ventral view (Figs 12E, 22G, 69G). This character is inapplicable to the haplogyne *Tetragnatha*.
5. *Copulatory pore shape*: (0) wide (Figs 45F, 53F); (1) narrow slits (Figs 38F, 41G, 61G, 68G, 74G, 80F).
6. *Copulatory bursa, anterior margin*: (0) entire, broadly transverse (Fig. 19B); (1) medially acute (Figs 22G, 40B).
7. *Copulatory duct, spermathecal junction*: (0) posterior; (1) lateral or anterior. Most commonly the copulatory ducts enter the spermathecae posteriorly or basally (Fig. 93J), but in a few taxa medially or anteriorly (Fig. 93H).
8. *Copulatory duct trajectory*: (0) straight, or at most a single simple loop (Fig. 93H, I); (1) two or more loops (Fig. 93J).
9. *Copulatory duct loops relative to spermathecae*: (0) apart (Fig. 93H, I); (1) encircling (Fig. 93J). In *Latrodectus* and independently in *Kochiura*, the copulatory ducts wrap around the spermathecae.
10. *Spermathecal number*: (0) two (Fig. 93H, J); (1) four (Fig. 93I). **G98-26**. Many hadrotarsines have two pairs of spermathecae: *Anatea*, *Audifia*, *Dipoena*, *Dipoenata*, *Emertonella*, *Euryopis*, *Guaraniella*, *Lasaeola*, *Trigonobothrys*, *Yaginumena, Yoroa* and some *Hadrotarsus* (Hickman, 1943; Levi & Levi, 1962; Wunderlich, 1978; Baert, 1984a, b; Forster *et al.*, 1990; Griswold *et al.*, 1998; Harvey & Waldock, 2000; Yoshida, 2002). The monotypic *Gmogala scarabaeus* Keyserling, however, has one pair of spermathecae, as do some species of *Hadrotarsus* and *Euryopis*, and a number of new genera from Australia (M. Harvey, pers. comm.). Genera with both conditions may not be monophyletic; this character will be important in future phylogenetic studies of Hadrotarsinae. On this cladogram the possession of four spermathecae is synapomorphic for Hadrotarsinae.
11. *Spermathecal shape*: (0) ovoid; (1) elongate; (2) dumbbell. Spermathecae are most commonly ovoid in shape, and this is certainly true of most theridiids (Fig. 93H, I). In this cladogram highly elongate spermathecae are an autapomorphy of *Ariamnes* cf. *attenuatus*, and appear to be a synapomorphy of that genus. Dumbbell-shaped spermathecae are here a synapomorphy of *Latrodectus* (Levi & Levi, 1962: fig. 253).
12. *Spermathecal accessory lobes*: (0) absent; (1) present. Most nesticids have distinct 'accessory lobes' associated with the spermathecae (e.g. Gertsch, 1984: *Nesticus silvestrii*, fig. 184, *Eidmanella pallida*, figs 260, 262).
13. *Fertilization duct sclerotization (Accessory sac)*: (0) light; (1) thick and heavy (*Synotaxus*). Exline & Levi (1965: 179) noted that the fertilization ducts of *Synotaxus* '. . . are much more sclerotized than in the other theridiid genera.'. I have noted sac-like areas of strong sclerotization in *Synotaxus* epigyna (see Agnarsson, 2003c) using the term 'accessory sac'), however, it is not clear that they are a part of the fertilization ducts.
14. *Male palpal tibial distal end*: (0) subequal or slightly wider than base; (1) distinctly broadened, = >2 × base width. Male palpal tibia shape alone usually suffices to identify a spider as a theridiid, although the complexity and variability of tibial shapes make it difficult to define precisely the components involved. This and the following three characters attempt to define and convey the information clearly and objectively. In araneoid spiders the palpal tibia is usually slightly to

moderately tapered, so that the base is considerably narrower than the tibial tip (Fig. 1A, C), and somewhat narrower than the patella at their articulation. The theridiid tibial tip is twice to several times wider, at its widest point, than the base (Figs 4E, 37A, C, 42B, C), and the base is much narrower than the patella at the joint. On this cladogram the modification is a synapomorphy of Theridiidae.

15. *Male palpal tibial rim*: (0) uniform or only slightly asymmetric (Fig. 1A–C); (1) strongly and asymmetrically protruding, scoop-shaped (Fig. 36D). In most araneoids the male palpal tibial distal rim protrudes only slightly on one side; normally the protruding portion faces the dorsal side of the cymbium. In many theridiids the rim is strongly exaggerated on one side, scoop-shaped, and faces the ventral side of the cymbium or the palpal bulb (Figs 10A, 13A, 22B, 24C, 31A–C, 36B–D, 39A, 42A–C, 48A, 51A, B, 79B, 81A–C, see also character 17).
16. *Male palpal tibial rim setal conformation*: (0) irregular; (1) regular row of long, strong setae. The theridiid tibial rim has a regularly arranged row of long, strong seta (Figs 13C, 15A, C, 42B, 83E), most extreme in *Kochiura aulica* (Fig. 51A–C). The tibial setae of hadrotarsines (Fig. 4A, B), *Synotaxus* (Fig. 1A–C) or *Nesticus* (Fig. 2A–C), as in most other araneoids, are neither so regularly arranged, nor uniformly long and strong. On this cladogram, the feature is a synapomorphy of the SPR clade (clade 50). However, a similar condition occurs in some pimoids and linyphiids (e.g. *Pocobletus coroniger*, G. Hormiga, pers. comm.) and in some hadrotarsines.
17. *Male palpal tibial rim relative to cymbium*: (0) protruding tibial rim faces dorsal cymbial margin; (1) protruding tibial rim faces bulb. In most theridiids the protruding margin of the male tibia faces the palpal bulb (Fig. 51A).
18. *Male palpal tibia*, *retrolateral trichobothria*: (0) three or more; (1) two; (2) one or none. The number and distribution of trichobothria on the male palpi seems quite informative phylogenetically, even though it varies widely among araneoids, even within genera (e.g. Hormiga, 1994a). *Synotaxus* and theridioids primitively have two retrolateral and one prolateral trichobothria (Figs 24C, 31G, 69E, 92D–F, vs. more in other outgroups). Reduction to a single retrolateral trichobothria (Figs 81A, 92G) (or uniquely in *Carniella* in this matrix, to none, Fig. 36B–D) occurred at least five times in theridiids, but although homoplasious (CI = 0.25), in most instances the reduction is informative (RI = 0.76). The same applies to reduction in prolateral trichobothria (19).
19. *Male palpal tibia, prolateral trichobothria*: (0) two or more; (1) one; (2) none.
20. *Male palpal patella spur*: (0) absent (Figs 13F, 46F); (1) present. *Synotaxus* males have a uniquely modified, grossly enlarged, seta on the palpal patella (Fig. 1A, C). This patellar spur is a synapomorphy of *Synotaxus*.
21. *Cymbium*: (0) entire; (1) expanded retrolaterally. **G98-5**. On this cladogram a retrolaterally expanded cymbium is an autapomorphy of *Pimoa*, and therefore uninformative. Because it occurs in Cyatholipidae, it has been scored here in case its distribution becomes relevant to the placement of pimoids, cyatholipoids, or theridioids.
22. *Cymbial retromargin*: (0) entire (Fig. 28E, F); (1) with a small distal apophysis containing the cymbial hood (*Ameridion*, Fig. 13B, E); (2) synotaxid retromargin-groove. **G98-6**.
23. *Cymbium dorsobasal margin*: (0) entire (Figs 28A, C, 31A, C); (1) strongly incised (Figs 10C, 12C); (2) strongly modified, with a ridge of parallel teeth (*Tidarren*, Fig. 86D, F). An incised cymbial dorsobasal margin is a synapomorphy of *Achaearanea* (Fig. 10C). The cymbium of *Tidarren* is extremely modified (Fig. 86D–F), unlike any other taxa in this study, making comparisons difficult. No doubt many features of the *Tidarren* cymbium support the monophyly of the genus, but as only a single species is present here, only one conspicuous feature, a ridge of parallel teeth on (what is presumed to be) the dorsobasal margin, is exemplified (Fig. 86F).
24. *Cymbial distal promargin*: (0) entire; (1) with an apophysis (*Argyrodes*, Figs 31D, 92E; *Crustulina*, Fig. 42A, B); (2) constricted and flattened (*Latrodectus*, Fig. 54B, C).
25. *Cymbial mesial margin*: (0) entire (Figs 31A, 39A, 41A, 44A); (1) incised (*Anelosimus*, Figs 17D, 20A). Many *Anelosimus* have a distinct incision on the cymbial mesial margin (Fig. 17D) and on this cladogram the feature is a synapomorphy of clade 22 [*Anelosimus* exclusive of *A. vittatus* (Fig. 26A, C) and *A. pulchellus*].
26. *Cymbial tip sclerotization*: (0) like rest of cymbium; (1) lightly sclerotized, appears white. The tip of the cymbium appears white,

or lightly sclerotized, in many *Anelosimus* species. As seen in the expanded palp (e.g. *A. eximius*, Fig., 18A) the inner lining of the tip of the cymbium folds down to form a part of the cymbial hood. In air-dried *Anelosimus* specimens the tip of the cymbium typically collapses due to this light sclerotization. On this cladogram the lightly sclerotized cymbial tip is a synapomorphy of clade 20.

27. *Cymbial tip setae*: (0) like other setae (Fig. 1A, B); (1) thick and strongly curved (*Kochiura*, Figs 51B, 52C).
28. *Cymbial sheath*: (0) absent (Fig. 26B, C); (1) present. Several theridiids with extremely long emboli have a sclerotized groove on the ectal cymbial margin that supports the spiralling embolus (Fig. 52C).
29. *Paracymbium*: (0) present (Fig. 92A–C); (1) absent (Fig. 92D–M). **G98-7**. The presence of a proximal, retrolateral process on the cymbium has long been identified cladistically as a synapomorphy of Araneoidea (Coddington, 1986c, 1990a, b; Hormiga *et al.*, 1995). Theridiids lack such a process, but have a distal process on the cymbial ventral margin or inside the cymbium, which forms a hook or a hood that function uniquely to lock the unexpanded bulb in the cymbium (compare the PC in *Nesticus*, Fig. 2B, the cymbial hook in *Argyrodes*, Fig. 31F). Levi (1961), Heimer (1982) and Heimer & Nentwig (1982) pointed out that in what they considered the more basal theridiid genera (e.g. *Robertus*), the hook is structurally similar to the paracymbium of some araneoids and is situated on the ectal margin rather than distally within the cymbium. This led them and other authors (e.g. Shear, 1967; Coddington, 1986c, 1990a; Hormiga *et al.*, 1995; Knoflach, 1996; Levy, 1998) to homologize the theridiid hook with the paracymbium of other araneoids, *contra* Saaristo (1978). However, the structural similarity is superficial, and the condition in the most basal theridiids (which are not those considered basal by previous authors), differs clearly from the paracymbium both in structure, topology and function. Therefore, I conclude that the theridiid process and the araneoid paracymbium are not homologous, in agreement with Griswold *et al.* (1998). On this cladogram the loss of the araneoid PC is a synapomorphy of Theridiidae.
30. *Paracymbial form*: (0) *Argiope*-like (Fig. 92A); (1) *Tetragnatha*-like (Fig. 92B); (2) pimoid-like (Fig. 89A); (3) linyphiid-like (Fig. 89B); (4) cup-shaped (Fig. 89C); (5) *Nesticus*-like (Figs 2B, 89D, 92C). **G98-9**. The paracymbium varies so much that homology statements at the family level are very difficult. Hormiga *et al.* (1995) and Griswold *et al.* (1998) essentially gave up trying to homologize overall form or morphological parts and instead adopted an exemplar approach, naming the various types by the taxa in which they occur. The same approach and coding is followed here. On this cladogram the cup-shaped PC is a synapomorphy of *Synotaxus*. Nesticids are also united by a unique form of PC (Figs 2B, 89D), while those found in other taxa are all autapomorphic for them.
31. *Bulb-cymbium lock mechanism (BC lock)*: (0) absent (Figs 2A, B, 92A–C); (1) present (Figs 28F, 44D). **G98-12**. As mentioned above, theridiids have a unique type of bulb-to-cymbium locking mechanism. The cymbial hook or hood interacts with the bulb (normally the MA) to 'lock' it to the cymbium in the unexpanded palp. The lock may also play an important role in controlling the rotation of the palp during natural expansion (e.g. Knoflach, 1998). On this cladogram the presence of a BC lock mechanism is a synapomorphy of Theridiidae.
32. *Lock placement (Chk and Chd)*: (0) basal (*Carniella*, Fig. 36C); (1) distal (Figs 67B, 92D–I, M); (2) central (Fig. 92H).
33. *Lock mechanism*: (0) hook (Figs 31F, 60D, 91A, 92D, E, J–L); (1) hood only (Figs, 18A, 75B, 92F–I, M); (2) *Theridula* (Fig. 81D). Forster *et al.* (1990), argued convincingly for the homology of the theridiid cymbial hook and the identically situated cymbial hood. Accordingly, these are treated here as alternative states of the same character. On this cladogram the cymbial part of the lock mechanism is primitively hooked. The transition to a hood takes place in the lineage leading to *Anelosimus* plus Theridiinae (the lost colulus clade). The alternative interpretation is less parsimonious, requiring both the loss of a hook and the gain of a hood at the same node on the cladogram. This interpretation would unjustly inflate the number of synapomorphies for the lost colulus clade, beyond the variation observed. The condition in *Theridula* is autapomorphic; a distal sclerite of a membranous texture physically connects the bulb and the cymbium. It seems simplest to assume that this sclerite is a highly modified MA, although, its topology is most unusual.

34. *Cymbial hook orientation*: (0) facing downwards (Figs 91A, 92D, E, J, K); (1) facing upwards (Figs 60C, D, 67B, 92L).
35. *Cymbial hook location*: (0) inside cymbium (Fig. 92D, E, J, K); (1) ectal cymbial margin (Figs 66B, C, 67B).
36. *Cymbial hook inferior groove*: (0) absent (Fig. 66B); (1) present (Fig. 92D, J, K). In some theridiids with the hook-lock system there is a distinct groove beneath the hook. This groove seems not to be homologous to the hood-lock system, based on similarity, as it is absent in the lineages sister to the lost colulus clade (although see below). The 'hood' of *Spintharus* (Fig. 92M), a species nested deep within the hook-lock grade, is quite similar to the hook inferior groove present in other spintharines (*Thwaitesia* and *Episinus*, Fig. 92J), and differs from the typical hood morphology (e.g. *Theridion frondeum* Fig. 75B). The uniqueness of the *Spintharus* condition is strongly supported by character congruence (tree topology is identical regardless of how the *Spintharus* hood is coded), and the homology of the *Spintharus* condition to that of the unrelated lost colulus clade is unambiguously refuted. On this cladogram the secondary hood occurs in the grade Hadrotarsinae-Spintharinae-Latrodectinae, but its absence is a synapomorphy of the remaining theridiids. A complication to this interpretation of cymbium lock system homologies is the presence of a hook inferior groove in *Kochiura*. Although here coded as a groove, the phylogenetic position of *Kochiura* may indicate that its condition is an intermediate between the 'hook' and 'hood' lock systems (33), in which case it should be coded as having both (being polymorphic for 33).
37. *Cymbial hook distal portion*: (0) blunt (Figs 31F, 92D, E); (1) tapering to a sharp tip (Figs 66B, 67D, 92L). A strongly tapered cymbial hook characterizes some pholcommatines. *Enoplognatha* has a moderately tapered hook, which might be represented by a third step.
38. *Cymbial hood size*: (0) narrow (Fig. 92F–H); (1) broad (Fig. 92I); (2) *Spintharus*-like (Fig. 92M). The hood in most theridiids is small relative to the distal width of the cymbium. In *Anelosimus rupununi* and *A. lorenzo*, however, the distinctly widened hood occupies nearly the whole width of the distal cymbium. The hood type found in *Spintharus* is unique and apparently is not homologous to that present in the lost colulus clade.
39. *Cymbial hood region*: (0) translucent, hood visible through cymbium (*Anelosimus*, Figs 90A, 91C); (1) opaque, hood not visible. Usually the cymbial hood is not visible in the unexpanded palp. In some *Anelosimus*, the outline of the hood is clearly visible through the translucent cuticle of the cymbial margin.
40. *Bulbal sclerite of lock mechanism*: (0) MA; (1) embolus base. In most theridiids the BC lock involves the MA (Figs 28F, 31F). Many *Achaearanea* (and some *Theridion* not considered in this study), however, have lost the MA (see below) and in this case the base of the embolus assumes the function (Figs 10B, 12A). On this cladogram the embolus base as part of the BC lock is a synapomorphy of *Achaearanea*.
41. *Alveolus placement*: (0) ectal; (1) central; (2) mesial. In theridiids and *Pimoa* the alveolus usually abuts the mesial margin of the cymbium (Fig. 92D–I, M). In the other outgroup taxa considered here, the alveolus is either central (Fig. 92B, C) or ectal (Fig. 92A) in the cymbium. On this cladogram the shift to a mesial placement of the alveolus is a synapomorphy of theridiids, and the reversal to a central location defines *Achaearanea*.
42. *Alveolar cavity*: (0) simple, unsclerotized; (1) with alveolar sclerite. The alveolar cavity of *Thwaitesia* contains a conspicuous sclerite, which is autapomorphic in this context but possibly a synapomorphy of the genus. The genus *Pimoa*, synapomorphically, has a somewhat similar sclerite present, but that sclerite is clearly distal to the alveolar cavity (Hormiga, 1994a: 6, fig. 303; Hormiga, 2003) and thus not presumed here to be homologous.
43. *Alveolus shape*: (0) circular or oval (Fig. 92A–H); (1) with a mesial extension (Fig. 92I).
44. *Subtegular retrolateral margin*: (0) entire (e.g. Figs 4A, B, 10A); (1) with a prominent rounded lobe (Fig. 2A, B).
45. *Tegulum size*: (0) < half cymbial cavity (normal, e.g. Figs 41A, B, 79C); (1) huge, > half cymbial cavity (*Dipoena*, Fig. 4B, C). On this cladogram the presence of a huge tegulum, occupying more than half of the cymbial cavity, is an autapomorphy of *Dipoena nigra* (Fig. 4B, C), *Tidarren* (Fig. 86E), and a synapomorphy of two *Anelosimus* species from Tanzania (Fig. 28C). However, the condition is found in several *Dipoena* and some other hadrotarsines, e.g. *Eurypoena* (Wunderlich,

1992), *Gmogala* (Wunderlich, 1978), *Guaraniella* (Baert, 1984b), *Emertonella*, *Trigonobothrys*, *Yaginumena* (Yoshida, 2002) *Yoroa* (Baert, 1984a; Harvey & Waldock, 2000), and other undescribed genera (M. Harvey pers. comm.). The conspicuous ridges on the tegulum of *D. nigra* (Fig. 4C, D) have not been seen in other *Dipoena* examined, but may be relevant in a species-level phylogenetic study.

46. *Tegulum ectal margin*: (0) entire (Fig. 1B); (1) protruded (Fig. 20D). *Anelosimus* cf. *jucundus* has a tegular outgrowth on the ectal margin, extending beyond the embolus base. *A.* cf. *jucundus* may be a species complex and the character is included here in anticipation of its use in *Anelosimus* phylogeny.
47. *Tegular groove*: (0) absent (Fig. 10A); (1) present (Fig. 28B). Tanzanian *Anelosimus* sp. 1 and 2 have a unique groove in the tegulum where a part of the E spiral rests.
48. *Tegular arch*: (0) absent (Fig. 10A); (1) present. *Achaearanea wau* and *A. vervoorti* both have an unusual elevated ridge centrally on the tegulum (Fig. 12A, arrow).
49. *Tegular pit*: (0) absent (Fig. 10A, B); (1) present. The inside of the ectal rim of the tegulum bears a conspicuous pit in many members of the Theridiinae (Fig. 75A, B), which seems to function in yet another palpal locking mechanism. The pit interacts with the base of the embolus directly or an embolic apophysis (see next character). The optimization is ambiguous, but under ACCTRAN a tegular pit is synapomorphic for Theridiinae, with secondary loss defining clades 8 and 12.
50. *Tegular pit embolic interaction*: (0) via embolic base (Fig. 39E); (1) via embolic apophysis (Fig. 75A, B).

51–61. Sperm duct trajectory. The palpal sperm duct is often considered as having three distinct parts: the fundus is the proximal end and is enlarged to form a pouch; the reservoir is a long tube spiralling throughout the tegulum and sometimes inside tegular sclerites; the ejaculatory duct is terminal and inside the embolus (Comstock, 1910). Primitively, the sperm duct appears to form approximately one simple spiral in the tegulum (see Coddington, 1990a for discussion and examples). In many araneoids, however, the sperm duct trajectory is moderately to very complex with numerous spirals and switchbacks (Figs 90B, D, 93A–E). Coddington (1986a), homologized individual loops and switchbacks of the theridiosomatid reservoir, and showed that the system can be of great utility in spider systematics. In theridiids the sperm duct trajectory (SDT) varies greatly and understanding the variation requires the laborious construction of wire models (see Methods) whose accuracy may be hard to verify. The following is a preliminary and speculative attempt to reduce this complexity to homology statements (note that tree topology is not dependent on these characters; removing all SDT characters yields the same single mpt). Some switchbacks and loops seem consistent enough to allow specific homology conjectures across theridiids and outgroups. These more consistent and recognizable switchbacks identify regions of the sperm duct, which enable the comparison of less consistent loops and switchbacks. The characters that follow are based on left palps.

51. *SDT Switchbacks (SB) I & II*: (0) present; (1) absent. The sperm duct pathway typically travels clockwise in the left palp and completes about one spiral in the tegulum before forming a double switchback (SB I, II, Figs 90B, D, 93A–E). SB I reverses the trajectory to counter-clockwise, but SB II immediately restores it to clockwise. Both are either absent or present simultaneously in all taxa considered in this study and are thus treated as a single character.
52. *SDT SB I*: (0) separate; (1) touching. The two arms of the switchback may be separated, or so close that they nearly touch.
53. *SDT SB II*: (0) entirely in tegulum; (1) terminates in embolus. In *Achaearanea* the duct enters the embolus during SB II, whereas in other taxa it continues its trajectory within the tegulum after SB II.
54. *SDT post-SB II turn*: (0) absent; (1) present (*Anelosimus*, Fig. 93B). In some *Anelosimus* (clade, 18) the sperm duct makes an abrupt 90-degree dive into the tegulum immediately after the first double switchback. This turn, if present, is more gradual in other taxa.
55. *SDT SB I & II reservoir segment alignment*: (0) divergent; (1) parallel. Three reservoir segments make up SB I & II. They may be nearly perfectly parallel to one another in the tegulum (Fig. 93A), or more commonly the angles between them are somewhat divergent (Fig. 93E, SB I angle much more obtuse than SB II).
56. *SDT SB I & II orientation*: (0) in plane of first loop from fundus; (1) out of plane of first loop, against tegular wall.

57. *SDT RSB I & II*: (0) absent; (1) present. In the argyrodines the trajectory of the sperm duct is unusual in that the duct makes two complete switchbacks before SB I & II. These are in reverse orientation to SB I & II (switching towards the fundus rather than towards the embolus) and are thus termed reverse switchbacks I & II (RSB I & II, Fig. 93D, E).
58. *SDT SB III*: (0) absent; (1) present. Having completed SB I & II the duct may simply loop until entering the embolus (Figs 90D, 93B) or, in some cases, switchbacks even more (Fig. 93D, E). When a SB occurs inside the MA, it is the SB III. In some taxa (e.g. *Crustulina*, *Latrodectus*, *Steatoda*) the duct enters the MA, but does not reverse its trajectory inside it (no SB III). SB III may also be present in taxa where the duct does not enter MA (e.g. *Coleosoma*).
59. *SDT SB IV*: (0) absent; (1) present (Fig. 93E). Given the presence of SB III, in some cases an additional switchback occurs between SB III, the embolus (SB IV, Fig. 93E).
60. *SDT entering embolus*: (0) clockwise (left palp, ventral view); (1) counter-clockwise.
61. *SDT constriction*: (0) relatively gradual; (1) duct narrows abruptly before SB I. Usually the sperm duct diameter is relatively constant or changes gradually, and constricts somewhat prior to entering the embolus. In contrast, in the latrodectines, the duct is unusually broad after leaving the fundus, but constricts markedly and abruptly in the tegulum.
62. *Conductor*: (0) present; (1) absent. **G98-14**. Homology of palpal sclerites of male spiders at higher taxonomic levels is problematic (Coddington, 1990a). The few ontogenetic studies to date suggest that the conductor and the MA are intimately associated in male palp ontogeny, arising from the dorsal lobe of the pedipalpal claw fundament, while all other parts of the palp arise from the ventral lobe (Bhatnagar & Rempel, 1962). Griswold *et al.* (1998) followed the rule of thumb that if only one tegular sclerite is present, by default it is considered to be the conductor. If an additional tegular sclerite is present it is the MA. However, at least within Theridiidae, it seems to be possible to construct sensible primary homology hypotheses based on similarity criteria, in particular topological similarity and relation of sclerites with the tegulum (Griswold *et al.*, 1998 also found such criteria useful when two or more sclerites were present). Here the conductor is considered to be a sclerite that is an outgrowth of the tegulum, lying always on, or lateral to, a distinct sclerotized tegular knob above the embolus in the bulb. In most theridiids the conductor is the only palpal sclerite completely fused to the tegulum, whereas the MA, in the theridiids considered here, is flexibly attached. Superficial examination may mistake the TTA for the C, as the former often functions as a conductor. Dissection of the palp, however, readily allows correct identification. On this cladogram the conductor has been independently lost several times. Its loss is autapomorphic in *Linyphia triangularis* (Fig. 89B), and *Eidmanella pallida* (while present in *Nesticus*, Fig. 2C) and a synapomorphy of *Emertonella* plus *Euryopis*, and of *Synotaxus*. It is further absent in *Cerocida* and *Phoroncidia*. This and the following characters are coded as unknown in *Carniella siam* because the presence of a conductor in *Carniella* is uncertain (Fig. 36A, arrow pointing to an unusual outgrowth of the tegulum, possibly a conductor).
63. *Conductor distal portion*: (0) width subequal to base (Figs 10A, 13D, 91A–I); (1) grossly enlarged (Figs 46A–E, 67B, 69B, 83A, B, 90F, G). Spintharines are characterized by the presence of an enormous conductor (Fig. 46A–E). A huge fan shaped conductor is also a synapomorphy of *Selkirkiella* (Fig. 67B). *Kochiura* has a long, distally widened conductor (Fig. 52B). *Helvibis* cf. *longicaudatus* (Fig. 49A–C) appears autapomorphic in this dataset, but an elongated conductor is probably a generic synapomorphy.
64. *Conductor*: (0) with a groove for the embolus (Figs 10A, 28D, 69B); (1) entire (Figs 13D, 17F, 52C, D).
65. *Conductor surface*: (0) smooth (Figs 75B, 77B, C); (1) heavily ridged (Figs 10B, C, 12B, 44D, 67C, 69D). *Nesticodes* has strong ridges on an outgrowth of the conductor (Fig. 58B), treated here as potentially homologous.
66. *Conductor folding*: (0) entire; (1) complex (spintharines, Figs 46B, 69B, 83B, 90F, G); (2) *Helvibis* (Fig. 49A–C). The spintharine conductor is large and complexly folded, unlike the conductor of any other theridiids. The *Helvibis* conductor is also unique, being thin, extremely elongated and membranous. However, it follows the E tip closely and does not fold upon itself.

67. *Conductor tip sclerotization*: (0) similar to base; (1) more than base.
68. *Conductor base*: (0) entire; (1) grooved. The latrodectine conductor base is hollow and forms a groove into which a hook on the embolus base loosely fits (Fig. 54E). This is possibly homologous with the subconductor (70), or the tegular pit (49), but topology, and structural details seem to negate it, as does the cladogram.
69. *Conductor origin*: (0) sclerotized tegular margin (Figs 10A, 34C, 64C); (1) lightly sclerotized region apical to tegular margin (Figs 75A–C, 77A–C). Most commonly in theridiids, the base of the conductor is merely an extension of the sclerotized tegular margin. In some members of the lost colular setae clade (Theridiinae), however, the conductor originates in a lightly sclerotized apical area of the tegulum.
70. *Subconductor*: (0) absent; (1) present. The presence of a tegular outgrowth at the base of the conductor that overlays part of the embolus (Figs 17B, 20C, 24A) is synapomorphic for a group of New World *Anelosimus* (clade 18). This structure, here termed the subconductor, has sometimes been called the conductor (see e.g. Levi, 1956: plates II, 17, and Coddington, 1990a: fig. 94). The 'true' C, however, ultimately arises from the back of it (Figs 17F, G, 91C, D). It could also be a strongly modified conductor base, thus homologous to 68. *Chrysso* (Fig. 39D, E) has a similar structure, while at the same time having a tegular pit into which the embolus fits. This offers further evidence that the SC, Tp and the latrodectine hollow conductor base are not homologous. Yet homology is possible, and future studies should explore these systems in greater detail.
71. *MA*: (0) present (Fig. 75B); (1) absent (Figs 10A, B, 12A). **G98-16**. In the absence of a detailed comparative survey of palpal homologies at the family level, Coddington (1990a) and Griswold *et al.* (1998) began by considering the second tegular process as the median apophysis, once the conductor has been accounted for. Although explicit, the authors noted that the criterion is inferior to primary homology conjectures based on similarity criteria. I have found similarity criteria useful in Theridiidae, thus superseding more arbitrary criteria. The theridiid MA is a flexibly attached sclerite originating mesially on the tegulum (Figs 91A, B, D–G, H). In some cases the membrane is so narrow that the MA may appear fused to the tegulum (e.g. *Dipoena*, Fig. 4A, B), whereas in pimoids, synotaxids and nesticids the fusion is complete (in other words the MA is an outgrowth of the tegulum, Fig. 89A, D, E). The MA contains a loop of the sperm duct in most basal theridiids (Figs 90F, 91B). The theridiid MA is topologically consistent across genera and, when present, interacts with the cymbium to make the BC-lock. The loss of the MA is a synapomorphy of *Achaearanea*.
72. *MA, sperm duct*: (0) loop not inside MA (Fig. 89E); (1) loop inside MA (Figs 90F, 91B). The MA when present in theridiids may contain a loop or SB (SB III) of the sperm duct, here synapomorphic for Theridiidae. Although absent in *Eidmanella pallida* and *Nesticus sylvestrii*, some nesticid MAs do contain a loop of the sperm duct (e.g. *N. cellulanus*, Fig. 89D), and the feature may ultimately optimize at the base of the theridioids. In most basal theridiids the MA contains a loop, but the condition is repeatedly lost, e.g. in clades 27 and 37. In *Latrodectus* the duct is narrow distally and hard to follow, but probably enters the MA (see e.g. Knoflach & van-Harten, 2002: fig. 22).
73. *MA, tegulum attachment*: (0) membranous (Fig. 75B); (1) fused (Fig. 89A, C–E). See characters 71 and 74.
74. *MA, tegular membrane connection*: (0) broad; (1) narrow. In basal theridiids the MA base tightly attaches to the tegulum via a narrow membrane. Viewed in an SEM image the MA gives the impression of being a direct outgrowth of the tegulum, with a slightly membranous base (Figs 4B, 31B, 44B). In the Theridiinae, however, the membrane is broader, and the attachment looser, to the centre of the MA. The MA thus appears to lie on top of the tegulum (Figs 13A–C, 75B). The condition in *Anelosimus* (Fig. 17E) is somewhat intermediate (unsurprising given its phylogenetic position), but the attachment of the membrane is to the centre of the MA, so it is here scored as putatively homologous to the Theridiinae condition.
75. *MA form*: (0) unbranched (Fig. 7A, B); (1) two nearly equally sized branches (Fig. 22A, B). *Anelosimus rupununi* and *A. lorenzo* are unique in having a basally branched MA.
76. *MA central region*: (0) entire (Figs 44A, B, 46A, 52A, 58A, 66A, 71A–C); (1) with a distinct apophysis (Figs 39B, C, 75A–C, 79A, B, D). Several members of the Theridiinae have an apophysis centrally on the MA. It varies in

both shape and size, from enormous, e.g. *Theridion frondeum* (Fig. 75A–C), to quite inconspicuous, e.g. *Helvibis* (Fig. 49A, C), and can thus be hard to code. Presumably this condition is not homologous to the branched MA, where the MA is split at the base (see previous character). The apophysis is an outgrowth of the central part of the MA, whereas the branching of the MA is basal.

77. *MA apophysis II*: (0) absent; (1) present. *Theridion frondeum* and *T. longipedatum* (and many other *Theridion* species) have a second apophysis on the MA (Figs 75B, 77B, C).
78. *MA distal tip*: (0) entire (Fig. 28F); (1) hooded (Fig. 34D). Species with a cymbial hook usually have a corresponding hood on the MA tip (Fig. 31F). Although perhaps biologically nonindependent, the two characters show independent variation (they do not have identical distribution); including both, at worst, may add weight to a complex character.
79. *MA hood form*: (0) narrow, pit-like (Figs 31F, 34D); (1) scoop-shaped (Figs 60D, 66B, 67D).
80. *TTA*: (0) absent (Figs 10A, 12A); (1) present (Fig. 34A–D). **G98-18**. An additional sclerite beyond the median apophysis and the conductor has been noted in theridiioids and pimoids (Hormiga, 1994a, 2003). In the analysis of Griswold *et al.* (1998), these features turned out not to be homologous, although further phylogenetic work may show otherwise. In accordance with most previous authors I consider the theridiid locking sclerite to be the MA in all theridiids (see character 71). Coddington (1990a) termed the additional sclerite the theridiid tegular apophysis or TTA. However, data available at the time were sparse, and recent studies of functional aspects of palpal sclerites during copulation (e.g. Knoflach, 1998) and comparative morphology of theridiid palps (pers. observ.) have clarified the issue. Those have revealed that Coddington (1990a) was not consistent in the application of the name. Here I consider the sclerite that locks the palp in the cymbium to be the MA, and TTA is the sclerite that closely associated with the C, E. Both the MA, the TTA are membraneously attached to the tegulum, while the C is always fused to it. A putative homologue of the TTA is present in synotaxids (Figs 1A–C, 88C, see also Agnarsson, 2003c) and on this cladogram the sclerite is a synapomorphy of the synotaxids plus theridioids. The TTA is secondarily lost in *Achaearanea*, some *Theridion* (e.g. *T. grallator* and *T. cochise* (pers. observ.) and *Theridula*).
81. *TTA branches*: (0) unbranched (normal, Fig. 34B); (1) two branches (Fig. 52D). A basally branched TTA is an autapomorphy of *Kochiura rosea* on this cladogram. However, it will likely be important to the relationships of *Kochiura* species.
82. *TTA apex*: (0) entire (Fig. 34B); (1) with a small apophysis (Fig. 67A, B). *Selkirkiella* species usually have a characteristic apical knob (apophysis) centrally on the TTA, apparently a generic synapomorphy.
83. *TTA form*: (0) entire (Fig. 34B); (1) grooved (Fig. 44C); (2) excavate (*Synotaxus*, Fig. 88C).
84. *TTA basal portion*: (0) bulky (Fig. 34B); (1) huge, membranous flap (Figs 37B, 67B). The TTA is usually bulky with rather uniform structure. In *Cerocida*, *Phoroncidia* and *Selkirkiella*, however, the basal portion forms an enormous, fairly membranous flap partly engulfing the E.
85. *TTA distal tip*: (0) entire (Fig. 7B); (1) hooked (Figs 17A, F, 22D). The distal tip of the TTA in many cases is strongly hooked (not merely bent as in, e.g. *Synotaxus*, Fig. 1B). The hook, which often has a ridged surface inside it, may play some role in fixing the bulb in the epigynum (see next character).
86. *TTA surface*: (0) smooth (Fig. 28A, D); (1) ridged (Fig. 31D). In many species conspicuous ridges are present on the TTA (Figs 7A–C, 15B, 17F, 24B, 31D, 34D, 51D, 54A, 56B, 86A), which, like the hook on the tip, may stabilize or fix the bulb in the epigynum (e.g. Knoflach, 1998).
87. *Embolus and TTA*: (0) loosely associated with, or resting in shallow groove on TTA (Fig. 7B); (1) parts of E entirely enclosed in TTA (Figs 37A, B, 44C, 89C). In *Thymoites unimaculata* (Fig. 85A) the embolus is partly enclosed in a fold of the MA, not the TTA.
88. *Embolus spiral tip*: (0) entire (Fig. 7B, C); (1) bifid. The embolic tip in some *Anelosimus* species is bifid or forked (Figs 17D, E, 20E, 24A).
89. *Embolus origin*: (0) retroventral on tegulum (Fig. 17B); (1) retrolateral (ectal), partially or completely hidden by cymbium (Figs 44C, 60A–C, 67B). The E of theridiids originates retroventrally or somewhat retrolaterally on the tegulum, being clearly visible outside the cymbium. In some pholcommatines however, the E origin has shifted to the ectal side of the palp and its base is partially or wholly covered by the cymbial margin. *Phoroncidia* sp.

has an ectal embolus, but the modified cymbium does not hide its base.

90. *Embolus surface*: (0) smooth (Fig. 17A–C); (1) ridged (Figs 20F, 31D, 34E).
91. *Embolus shape*: (0) short to moderately elongate (Fig. 7B); (1) extremely long, > two spirals (Figs 54D, 73A–C).
92. *Embolus spiral width*: (0) thin, much of E spiral subequal to E tip; (1) thick, entire E spiral much broader than tip. The free portion of the embolus (the spiral) is usually narrow and cylindrical (Figs 28B, 62B, 69A–D). In some *Anelosimus*, the spiral is markedly thick, and only the very tip is cylindrical (Figs 17B, C, 20B, 24A). On this cladogram, this condition is a synapomorphy of clade 17.
93. *Embolus spiral*: (0) suboval or round (Fig. 7B); (1) distinctly flattened and with pars pendula. *Latrodectus* spp. are the only theridiids known to me where the embolus spiral is distinctly flattened for nearly its entire length and clearly divided into a hard embolus and a membranous pars pendula carrying the sperm duct (Fig. 54D).
94. *Embolus form*: (0) entire (Fig. 17B); (1) with transverse suture or fracture plane. Although autapomorphic here, the embolus of *Achaearanea tepidariorum* (and many other *Achaearanea* species) has a pronounced transverse suture or fracture plane midway along its length (Fig. 10B), see 40.
95. *Embolus distal rim*: (0) entire (normal, Fig. 17B); (1) deeply grooved. Nearly the entire distal rim of the emboli of *A. rupununi* and *A. lorenzo* is deeply grooved or folded longitudinally (Fig. 22C). The emboli of the sister species *A. rupununi* and *A. lorenzo* are nearly identical, and compared to other theridiids, both unusual and highly characteristic. Putatively a source of multiple synapomorphies, here this similarity is conservatively represented in a single character.
96. *Embolic terminus*: (0) abrupt (Fig. 7B); (1) with apophysis (EA, Fig. 34E). **G98-22**. *Argyrodes* and *Ariamnes* have a long distal embolic apophysis. *Crustulina* and some *Steatoda* have an embolic apophysis that curves towards the embolus, but on this cladogram is not homologous to the argyrodine EA (Fig. 42B–D).
97. *Embolus-tegulum junction*: (0) fixed (Fig. 2B); (1) membranous, flexible (Fig. 7B). A membrane lying between the tegulum and the embolic division (ETM) is found in many araneoids, e.g. tetragnathids, araneids (between the tegulum and the radix) and linyphiids (i.e. the linyphiid column) (Hormiga *et al.*, 1995; Griswold *et al.*, 1998). Hormiga *et al.* (1995) concluded that the linyphiid column was not homologous to the ETM in araneids as it showed independent origin when optimized on their cladogram. Hormiga *et al.* (1995) overlooked this membrane in the theridiid *Steatoda* and Griswold *et al.* (1998) also in *Anelosimus*, *Dipoena* and *Emertonella*. Based on the current analysis, interpretation of the linyphiid column is ambiguous. It may be homologous to the ETM of other araneoids (DELTRAN) or it may be unique (ACCTRAN); the same is true of the ETM within theridiids. As these membranes are quite different, here ACCTRAN is preferred.
98. *Embolic base*: (0) entire, smooth (Fig. 4B, C); (1) lobed. The embolic base in many theridiid species is distinctly lobed, but varies in shape, e.g. *Anelosimus* cf. *jucundus* (Fig. 20C), *Latrodectus* (Fig. 54E), *Theridion frondeum* (Fig. 75B) and *Argyrodes* (Fig. 31D). Sometimes it provides a locking mechanism between the bulb and parts of the tegulum. The coding treats all lobes as putatively homologous. However, the *Theridion* + *Coleosoma* lobe, which locks to the tegular pit, apparently arose independently of other 'lobes.' The latter lock system thus seems unique.
99. *Embolic division b*: (0) absent; (1) present. The emboli of many A*nelosimus* have a large, sometimes heavily ridged basal outgrowth (Figs 15D, 20B–D, 24A, 26A, B, 90C) here labelled the embolic division b (Eb, following Levi, 1956, 1963). In *A. vittatus* the Eb is orientated towards the tibia, rather than the E tip, but presumably this is the same sclerite as labelled Eb in other *Anelosimus*.
100. *Embolus inserted piece*: (0) entire (Fig. 7B); (1) break-off point. *Latrodectus* spp. have a distal swelling on a part of the embolus tip (Fig. 54D) that marks for a break-off point. During copulation the tip of the embolus breaks off and thus plugs the female genital opening (e.g. Knoflach & van-Harten, 2002).
101. *Extra tegular sclerite*: (0) absent (e.g. Fig. 10B); (1) present. The spintharines *Episinus* (Fig. 46B) and *Thwaitesia* (Figs 83D, 90G), and some members of the 'ectal hook clade' (Figs 60C, 91G) have a tegular sclerite closely associated with the TTA, in addition to the ones present in most theridiids (here labelled simply 'extra tegular apophysis', ETA). This cladogram suggests three

(ACCTRAN, here preferred) or more (DELTRAN) origins of this sclerite, but given the relatively sparse taxon sampling, the evidence is too weak to justify specific sclerite names.

102. *Lateral eyes (male)*: (0) juxtaposed (Fig. 73F); (1) separate. **G98-30**. Like araneoids in general, theridiids have juxtaposed lateral eyes. Here separated lateral eyes are autapomorphic in *Tetragnatha* and a synapomorphy of *Latrodectus*.
103. *Median eyes (male)*: (0) flush with carapace (Fig. 19F); (1) alone on tubercle (*Argyrodes*); (2) eye area raised (all eyes on 'tubercle'). All argyrodine cephalic regions have modified heads (see below). *Argyrodes*, *Ariamnes*, *Neospintharus* and *Rhomphaea* have conspicuous tubercles (128, Fig. 30A–D). Median eyes on the tip of a dorsal tubercle is synapomorphic for *Argyrodes* (Figs 32E, F, 94B); in *Phoroncidia* (Fig. 62E) and *Stemmops* (Fig. 73F) the entire eye region is raised.
104. *AME size (male)*: (0) subequal or slightly larger than ALE (Figs 14C, 16A); (1) clearly smaller than ALE.
105. *AME-ALE separation (females)*: (0) >2 AME diameters; (1) = <2 AME diameters. ALE, AME are widely separated in *Tetragnatha* and *Argiope*.
106. *Cheliceral promargin*: (0) toothed; (1) smooth. Most araneoids have teeth on the anterior cheliceral margin, and theridiids are no exception (e.g. Figs 19C, 22E, 27F, 29E, 33G, 35H, 41D, 76E, 78F, 80C). A few theridiids lack promarginal teeth, here a synapomorphy of hadrotarsines (Figs 5B, 8E, F) and *Latrodectus*.
107. *Cheliceral anterior tooth shape*: (0) blunt; (1) pointed, sharp. Cheliceral teeth are usually broad basally and taper gradually towards the tip (Fig. 19C). The spintharines *Thwaitesia* and *Episinus* have characteristically sharp anterior cheliceral teeth (Figs 47F, 84D). *Spintharus*, however, has a unique blunt outgrowth whose homology with anterior teeth of other theridiids is unclear (Fig. 70E, F).
108. *Cheliceral anterior tooth number*: (0) four or more; (1) three; (2) two; (3) one. A reduction to three anterior teeth is here an ambiguous synapomorphy (DELTRAN) of the spineless femur clade (also in *Pimoa*). Further reductions take place within Theridiidae, see also character 111.
109. *Cheliceral proximal tooth*: (0) = < adjacent tooth; (1) much larger than adjacent tooth. In most theridiids, the first, proximal cheliceral tooth is much larger than the adjacent one (Figs 14B, 15E, 40C, 45J). Here the condition is a synapomorphy of Theridiidae minus Hadrotarsinae, but homoplasy occurs, e.g. in Spintharinae. In *Robertus*, uniquely, the second tooth is the larger (Fig. 66F).
110. *Cheliceral posterior (retro) margin*: (0) toothed; (1) smooth. Most araneoids have some posterior cheliceral teeth and they are more common in theridiids (Figs 19D, 29F, 40D, 45I, 60H, 68B) than the literature would suggest (e.g. Levi & Levi, 1962). Nevertheless, many theridiids lack them (Figs 5F, 8F, 55E, 70F). In this cladogram teeth were apparently lost at the base of Theridiidae (clade 53), but regained in more distal theridiids (clade 43), only to be lost again in clade 14 (Fig. 103). *Ameridion* is coded as 'smooth', although a tiny denticle is present.
111. *Cheliceral posterior tooth number*: (0) four or more; (1) three; (2) two; (3) one. Levi & Levi (1962) suggested that, although very variable, the number and shape of cheliceral teeth might be informative. Simple counts are just a first attempt to analyse such variation phylogenetically; homologies are unclear.
112. *Cheliceral furrow*: (0) smooth (Fig. 25F); (1) denticulate. In theridiids cheliceral teeth are usually confined to retrolateral and prolateral sides of the fang, while the area directly under the fang (the furrow) is smooth. On this cladogram denticles in the cheliceral furrow are synapomorphic for argyrodines (Fig. 33H), and an autapomorphy of *Cerocida strigosa* (Fig. 37D).
113. *Cheliceral sexual dimorphism*: (0) subequal; (1) male much larger (*Tetragnatha*, *Enoplognatha*). **G98-33**. In *Tetragnatha* and *Enoplognatha* the male chelicera are grossly enlarged (Fig. 44I), compared to the female.
114. *Cheliceral ectal surface (male)*: (0) smooth; (1) stridulatory. **G98-37**. Male cheliceral stridulatory ridges are synapomorphic for linyphioids (Wunderlich, 1986; Hormiga, 1994a, b, 2000; Hormiga *et al.*, 1995), although they occur sporadically in other families (e.g. Griswold *et al.*, 1998).
115. *Cheliceral anterior base*: (0) evenly rounded (Fig. 5C, D); (1) with a distinct knob (Figs 13F, 41C, 76B, 78G).
116. *Cheliceral apophysis (male)*: (0) absent (Fig. 41C); (1) present (*Enoplognatha*, Fig. 44I).

117. *Cheliceral paturon length*: (0) reaching tip of endites, or nearly so (Figs 13F, 60G, 66D); (1) short, not nearly reaching tip of endites. **G98-35**. Forster *et al.* (1990) and Griswold *et al.* (1998) pointed out that hadrostarsid chelicerae are short and do not reach the coxal endites (Fig. 5C). In this cladogram short chelicerae are a synapomorphy of Hadrotarsinae and an autapomorphy of *Phoroncidia* sp. (Fig. 62E), and *Stemmops* (Fig. 73G).
118. *Cheliceral paturon width*: (0) base wider than palpal coxae and coxae II; (1) base subequal to palpal coxae, narrower than coxae II. Although most theridiids have fairly weak chelicerae compared to typical araneoids, their chelicerae at their widest point (basally) are much wider than the palpal coxae and about as wide, or wider than coxae of leg II (Figs 32E, 50E, 60G, 66D) (coxae I size varies greatly). Hadrotarsines, spintharines and some other theridiids, however, have thin chelicerae where the maximum width only slightly exceeds the palpal coxae and is distinctly less than that of coxae II (Figs 5D, 62E, 84C).
119. *Cheliceral fang length (male)*: (0) much shorter than paturon (normal, Fig. 19C, D); (1) huge, nearly as long as paturon (*Enoplognatha*, Fig. 44I). **G98-34**.
120. *Cheliceral fang shape*: (0) cylindrical (Fig. 19C, D); (1) elongated, sickle-shaped. The classical hadrotarsine fang is long and slender, reaching from the apex of the shortened paturon to the tip of the palpal endites (Forster *et al.*, 1990). Griswold *et al.* (1998) reported this condition in *Emertonella funebris* (Fig. 9F, also *E. gertschi*, Fig. 8E) and *Dipoena nigra*, and on their cladogram it was a synapomorphy of the hadrotarsines. In some other hadrotarsine genera the fang is even more elongated and flattened (Forster *et al.*, 1990: fig. 392), but in *Dipoena nigra* it is less so (Fig. 5F). The colulus in *Dipoena* and the relatively unmodified fang suggest that it is a relatively basal hadrotarsine. On this cladogram the slender cheliceral fang is a synapomorphy of Hadrotarsinae.
121. *Cheliceral hairs*: (0) smooth or weakly serrate; (1) strongly serrate and curved. The hairs along the distal, mesial edge of the cheliceral paturon are strongly serrate and curved in *Synotaxus*, nesticids and hadrotarsine theridiids (Fig. 5B), whereas in other theridiids they are weakly serrate (Figs 27A, F, 68B, 72E). *Cerocida strigosa* autapomorphically has strongly serrate hairs (Fig. 37D).
122. *Cheliceral boss*: (0) present; (1) absent. Griswold *et al.* (1998; character 39) discussed the distribution of the cheliceral boss in araneoids, but did not include its presence or absence in their analysis (including it yields the same tree, pers. observ.). Here the loss of a cheliceral boss is an ambiguous synapomorphy of the spineless femur clade, being absent in all theridioids (Figs 41C, 66D, 79F, 80B, including *Nesticus* and *Steatoda*, *contra* Griswold *et al.*, 1998), and *Synotaxus* and *Pimoa*, but present in *Linyphia*, *Tetragnatha* and *Argiope*.
123. *Carapace texture*: (0) smooth (Figs 5D, 27B); (1) rugose, setal bases elevated (Fig. 71D, E); (2) scaly (Fig. 60F, G); (3) rippled (Fig. 38A); (4) bumpy (Fig. 50E, F). Theridiid taxonomic work often refers to carapace (and/or sternum) 'rugosity'. However, 'rugosity' differs between taxa, e.g. *Cerocida* (Figs 37G, 38A), *Helvibis* (Fig. 50F), and *Pholcomma* (Figs 60E, F, 61A, B). Although autapomorphic here, these conditions will probably be generic synapomorphies. *Steatoda* and *Crustulina*, synapomorphically, have rugosity caused by the elevation of setal bases (Fig. 71D–F). Most theridiid carapaces are relatively smooth (Fig. 30A–D, but see character 126).
124. *Carapace height (male)*: (0) = <0.25–0.5 × length; (1) >0.5 × length (hadrotarsines). Most male, and some female, hadrotarsines have extremely high carapaces (Fig. 5A, cf. Figs 40E, 46F). Here, the high carapace is synapomorphic for Hadrotarsinae.
125. *Carapace coloration*: (0) uniform; (1) longitudinal dark band. The usual theridiid carapace colour is fairly uniform. Some species, however, have one or two distinct, dark, longitudinal, central bands (Fig. 94D).
126. *Carapace shape*: (0) longer than wide; (1) round, nearly as wide, or wider than long. Hadrotarsines typically have a roundish carapace, hardly longer than wide.
127. *Carapace hairiness*: (0) sparsely or patchily hirsute (Figs 40E, F, 48D); (1) uniformly hirsute (Figs 19D, 71D). The latrodectine carapace characteristically is densely hirsute, convergent in derived *Anelosimus*. The character is coded here from SEM images, hairs may have been lost from some specimens in SEM preparations.
128. *Carapace pars stridens*: (0) smooth, or irregular; (1) regular parallel ridges. Various spiders have a prosoma-abdomen stridulation mechanism (for reviews see Legendre, 1963;

Uetz & Stratton, 1982). Typically, pairs of elevated setal bases, here called stridulatory picks (SP; the term plectrum refers to such stridulatory parts in general) bordering the pedicel on the abdomen (Figs 11A, 16B, C) interact with ridges on the posterior margin of the carapace (pars stridens) (Fig. 10D, E). Although underreported, this mechanism is widespread and characteristic of theridiids. In several species with distinct abdominal SPR, no regular pars stridens ridges are present (e.g. *Anelosimus* Fig. 21D, E, and *Chrysso* Fig. 40E, F), similar to species lacking SPR (e.g. *Phoroncidia*, Fig. 62G, and outgroups). Presumably, the rubbing of the SPR against patches of irregularly rugose surface nonetheless produces stridulation. More commonly, clearly parallel regular ridges are present (Figs 1D, E, 32A, 41F, 42G, 44H, 49F, 57A, 58D, 60F, 64E, 66G, 67G, 71F, 75D, 79E, 87B) here a synapomorphy of clade 43, but quite homoplasious. Like the abdominal stridulatory picks, the prosomal ridges are nearly always much less developed in females, than in males (compare G and H in Fig. 42, and F and G in Fig. 71), supporting their role in male courtship.

129. *Pars stridens*: (0) separate (two patches, Fig. 71F); (1) continuous (Figs 36G, 60F). In taxa with regular pars stridens lateral to the pedicel, the two patches may be completely separate or interconnected with one another.
130. *Interocular area*: (0) more or less flush with clypeus (Figs 60G, 66D); (1) projecting beyond clypeus. The eye regions of argyrodine genera (*Argyrodes*, *Ariamnes*, *Neospintharus* and *Rhomphaea*, clade 31) project markedly beyond the clypeus (Figs 30A, C, D, 34F, 94A, B, D, E), in contrast to *Faiditus* (Figs 30B, 94C).
131. *Clypeus*: (0) concave or flat (Figs 60G, 66D, 76B); (1) with a prominent projection. The argyrodines *Argyrodes*, *Faiditus* and *Neospintharus* have a markedly projecting clypeus (Figs 30A, B, D, 94B, C, E); *Carniella* (Fig. 36E, F), and some other pholcommatines, are similar.
132. *Ocular and clypeal region setae distribution* (*male*): (0) sparse (Figs 60G, 76B); (1) in a dense field, or fields. Argyrodines (Figs 30A–D, 34F, 48C), and *Carniella* (Fig. 36E, F) have a dense field of hairs, often modified, on the eye and/or clypeal projections.
133. *Clypeal setae morphology (male clypeal glands)*: (0) as other setae (Fig. 76B); (1) thick and strongly serrate. In many argyrodines, hairs on cephalic modifications are strongly modified to be both thick and deeply serrate. The cephalic modifications and the modified hairs reportedly indicate the presence of clypeal glands (Lopez *et al.* 1980; Lopez & Emerit, 1981; Whitehouse, 1987a; Juberthie & Lopez, 1993). Such hairs occur in *Ariamnes* cf. *attenuatus*, *Neospintharus trigonum* and *Rhomphaea metaltissima* (Figs 30C, D, 34F), but were apparently broken off in both *Argyrodes* species (*A. elevatus*, Fig. 30A), where their presence is indicated by broad setal bases (alternatively they may be absent in these two). However, they are apparently absent in *Faiditus* cf. *chickeringi* (Fig. 30B). All *Argyrodes* species studied in detail have both glands and modified hairs (Legendre & Lopez, 1974, 1975; Lopez & Emerit, 1981; Whitehouse, 1987a; Juberthie & Lopez, 1993) and most likely all argyrodines have clypeal glands. Whitehouse (1987a) showed that the accurate detection of clypeal glands may depend on how animals are prepared for SEM. *Carniella* (Fig. 36E, F) also has a dense field of setae on a clypeal modification, although they do not appear strongly modified, and whether they are glandular or not is unknown.
134. *Labium distal margin*: (0) rebordered; (1) not swollen distally. The presence or absence of a rebordered labium (distinctly swollen distal labial edge) is a classical character featured in most family level identification keys to spiders, and characteristic of many araneoids (see e.g. Kaston, 1978, 1981; Dippenaar-Schoeman & Jocqué, 1997). Theridiidae and *Synotaxus*, however, lack a rebordered labium (Fig. 27C, also e.g. Levi & Levi, 1962). The optimization of an unswollen labial edge is here ambiguous. It could be a synapomorphy of theridioids, secondarily rebordered in nesticids (ACCTRAN), or a synapomorphy of *Synotaxus* on the one hand and Theridiidae on the other (DELTRAN). As the rebordering of the nesticid labium is typical, here the latter optimization is preferred.
135. *Labium-sternum connection*: (0) visible seam (Figs 27C, 68A, 72F); (1) fused (Fig. 61A). A distinct seam is sometimes present between the sternum and the labium. Although much used in keys and taxonomy (e.g. Kaston, 1978, 1981), the presence or absence of a seam is extremely homoplasious within theridiids (CI = 0.07) and thus of limited usefulness at higher systematic levels. Here a fused connection is, for example, an ambiguous

synapomorphy of Theridiinae (ACCTRAN), but is certainly not characteristic of the clade (see Fig. 104).

136. *Labium shape*: (0) subrectangular (Fig. 21B); (1) triangular (Fig. 5A). *Dipoena*, *Emertonella* and *Euryopis* have a distinctly triangular labium. This hadrotarsine synapomorphy is also present in at least *Gmogala* sp. and *Hadrotarsus* sp. (pers. observ.).

137. *Sternum shape*: (0) elongated, longer than wide; (1) subequal or wider than long.

138. *Sternocoxal tubercles*: (0) present; (1) absent. Some araneoids have prominent sternal tubercules opposed to the coxae (e.g. *Nephila*, M. Kuntner pers. comm.). Here such tubercles are as synapomorphy of Argyrodinae, but reversed in *Ariamnes*.

139. *Sternum setal bases*: (0) unmodified, like other setal bases; (1) raised. As on the carapace (character 123), the setal bases of the sternum of *Steatoda* and *Crustulina* are elevated. It is unclear whether the two are independent, but the removal of either has no effect on tree topology.

140. *Pedicel location*: (0) anterior (Fig. 94A–D); (1) medial (Figs 43A, C, 94J, K, 97F). The classical description of theridiid abdomens, is 'higher than long' (e.g. *Achaearanea*) vs. the more common 'longer than high' (Levi & Levi, 1962). This nomenclature implies a difference in abdomen shape that may not exist. Instead the abdomens of *Achaearanea* and several other taxa appear 'high' because the pedicel inserts closer to the middle of the abdominal venter, rather than closer to its anterior apex. This means that the pedicel inserts relatively close to the epigynum (Fig. 43C). This distinction also clarifies the coding of the relative position of the spinnerets (character 203).

141. *Pedicel lyriform organs*: (0) narrow; (1) broad. Most, if not all, spiders (and perhaps other arachnids with a pedicel) have rows of slit sensilla (lyriform organs) on either side of the lorum of the pedicel (Fig. 53G, H) (e.g. Barth & Libera, 1970; Lopez & Juberthie, 1996). Usually the row is fairly uniform in width (Fig. 67H), but in the argyrodines *Ariamnes*, *Rhomphaea* and *Neospintharus* (clade 29) the row is notably broad in the middle so that the central slits are several times wider than those at either end (Fig. 34H).

142. *Abdominal shape*: (0) with paired humps (Fig. 57E); (1) ellipsoid, smooth (Fig. 43A).

143. *Abdominal colour pattern (in alcohol)*: (0) folium or similar pattern; (1) uniform (e.g. tan) or unpigmented. The pigmentation pattern on the abdomen is very variable in theridiids (Figs 94A–J, 95E, 96A, B, 97A–F, 99D–F) and it is hard to separate the variation into discrete character states. Regardless of coloration, a folium can be either present (Fig. 94B–E, G–J) or absent, leaving a uniform tan, grey or nonpigmented abdomen (Fig. 94A, F).

144. *Abdominal folium pattern*: (0) bilateral spots or blotches (Figs 94B, C, 96B); (1) distinct central band. In those taxa where a folium is present, it sometimes forms a distinct band down the centre dorsally (Figs 94G–J, 99E, F).

145. *Dorsal band*: (0) dark with white edging (*Kochiura*, *Anelosimus*, Figs 94G, J, 99F); (1) light with dark edging (Fig. 94H); (2) *Ameridion*, light with white edging (Fig. 94I).

146. *Abdominal dot, pigment*: (0) silver; (1) nonreflective, dull. Amongst theridiids, distinctly silvery pigment occurs in argyrodines and *Thwaitesia* (Fig. 97E).

147. *Abdominal pedicel area (male)*: (0) smooth; (1) sclerotized. The pedicel area on the male abdomen usually bears stridulatory setae; it is often sclerotized compared to abdominal cuticles elsewhere (Fig. 77F) and sometimes the sclerotization completely surrounds the pedicel.

148. *Abdominal pedicel area sclerotization*: (0) continuous; (1) separate (two patches).

149. *Abdominal suprapedicellate nubbins*: (0) absent (Fig. 62F); (1) present (Figs 81E–G, 87A). Suprapedicellate nubbins (presumably stridulatory) occur in all araneoid taxa I examined, apart from *Phoroncidia* (Fig. 62F, see Discussion); it is probably an araneoid synapomorphy. In theridiids these nubbins are between and around the stridulatory picks (Figs 4F, 10F, 11A, 14A, 24D, E, 26D, E, 47A, 48E). Although uninformative here, the character may be informative at some deeper level. Nubbins often surround the pedicel (Figs 47B, 53G, H, 77D)

150. *Stridulatory pick row (SPR)*: (0) absent (Fig. 4F); (1) present (Figs 16B, C, 21A, 24D, E). In addition to abdominal nubbins, many theridiids have, in the same region, modified (raised) setal bases (Fig. 51G) that appear to be stridulatory picks (Figs 16B, C, 21A, 24D, E, 29C, D, 51E, F, 52E, F). Although commonly present in both sexes, they are usually much reduced in the female (cf. Fig. 18B and Fig. 18C) and likely play a role in male courtship. Stridulatory 'ridges' on the male abdo-

men have been known in a few theridiids, but picks appear to be nearly universal within the family, although absent in many hadrotarsines (Fig. 4F), as well as in *Phoroncidia* (Fig. 62F), and *Cerocida* (Fig. 38E). The picks range from distinct and obvious to very slightly modified setae (e.g. *Latrodectus*, Fig. 54F). Hadrotarsines occasionally have modified setae that may be intermediate, as their phylogenetic position implies. Spintharines (Fig. 47A) have weak picks, here interpreted as homologous. The feature is thus sometimes difficult to code unambiguously, and further work is required to resolve the issue. In a typical SPR the most dorsal pair orients mesially and the remainder ectally. The mesially orientated picks have been lost (or inverted) several times, but the ectally orientated picks are absent only in *Selkirkiella*.

151. *SPR form*: (0) weakly keeled (Figs 67F, 74F); (1) strongly keeled and elongate (Figs 16B, C, 24D, E, 42F).
152. *SPR pick number*: (0) three or less; (1) four or more.
153. *SPR ectally orientated picks*: (0) present; (1) absent. All but the most dorsal pick setae usually face ectally (outwards, Fig. 24E). These are absent in *Selkirkiella*, leaving only the most dorsal, mesially orientated pick (Fig. 67F).
154. *SPR insertion*: (0) flush with abdominal surface (Fig. 18D); (1) on a ridge (Figs 32D, 41E, 44G, 72A, B). The picks sometimes insert on a conspicuous ridge above the pedicel.
155. *SPR region*: (0) irregular (Fig. 24D, E); (1) parallel ridges. In *Selkirkiella*, the abdominal stridulatory region has parallel ridges, resembling those on the carapace (Fig. 67F).
156. *SPR mesially orientated picks*: (0) absent (Fig. 32C, D); (1) present (Figs 24E, 29D).
157. *SPR mesially orientated picks relative to sagittal plane*: (0) angled dorsally (Fig. 52E, F); (1) perpendicular or angled ventrally. Usually the uppermost picks point slightly dorsally. In some *Anelosimus* (clade 18) they picks are almost exactly perpendicular or angled downwards relative to the sagittal axis of the body (Figs 18B, D, 21A, 24D, E).
158. *SPR setal bases*: (0) low, gently ridged (Fig. 24E); (1) acute, almost pointed. Picks in *Ameridion* and *Theridula* are sharply pointed, almost tooth-like (Fig. 81F).
159. *SPR*: (0) straight or slightly irregular (Fig. 52E, F); (1) distinctly curved; (2) dorsal picks set apart from others. The row of picks in several *Anelosimus* species (clade 20) is distinctly curved (Figs, 18B, 24D). In some argyrodines the two dorsalmost picks are set apart from the rest (Fig. 32C, D).
160. *SPR dorsal pick spacing*: (0) subequal to ventral pick spacing (Figs 76A, 85C, D); (1) distinctly compressed (Fig. 16B). Within *Anelosimus* (clade, 18) the dorsal stridulatory picks are distinctly compressed (Fig. 16B).
161. *SPR relative to pedicel*: (0) lateral (Figs 32C, 58C); (1) dorsal (Figs 34D, 36H, 49D, E).
162. *Additional stridulatory picks*: (0) absent (Fig. 24D, E); (1) present. The SPR are parallel files lateral or dorsal to the pedicel. In some cases additional setae are found outside this file (Figs 10F, 76A, 77E).
163. *Suprapedicellate dorsal (11 o'clock) proprioreceptor*: (0) absent (Fig. 38E); (1) present (Figs, 18D, 32C). Proprioreceptor setae are present on the appendages of many spiders (Seyfarth, 1985; Barth, 2001). The proprioreceptors are socketed and innervated macrosetae that document the relative position of the appendage (or joint) bearing them. As a joint is flexed, such setae, appropriately positioned, are pressed against a nearby substrate, and this mechanical flexion feeds the nervous system accurate positional information. Theridiids and many other spiders (pers. observ.) have a series of long, flexible, abdominal setae situated around the pedicel, with their fine tips touching the carapace from various directions (Figs 43A, B, 53C). When the abdomen moves relative to the carapace, these hairs will, inevitably, be flexed or extended as they press against the carapace. Although information on the innervation of these setae is lacking, a proprioceptive function seems an obvious interpretation. Their presence on spider abdomens is here reported for the first time (but see Foelix, 1996: fig. 206 and legend). Interestingly, Juberthie & Lopez (1994) suggest a similar function for the setae of the SPR. In the taxa examined here, theridioids are unusual in often having relatively many pairs, and in particular a pair of proprioreceptors dorsal (11 o'clock) to the pedicel, while in other taxa the proprioreceptors are placed mostly lateral to dorsolateral. It should be noted that these setae are quite variable and often hard to see unless in excellent SEM preps. This is a preliminary and speculative effort to include a part of the variation of this complicated character system.

164. *Suprapedicellate ventrolateral (4 o'clock) proprioreceptor*: (0) absent; (1) present (Fig. 18D). In most taxa examined here, setal proprioceptors are present along the entire side of the pedicel, from ventrolateral, to dorsolateral. In most argyrodines and a few other taxa proprioreceptors are restricted to the dorsolateral and dorsal side of the pedicel, thus ventrolateral proprioceptors are lacking (Fig. 64D).
165. *Abdominal suprapedicellate apodemes*: (0) distinctly disk-like, strongly rugose; (1) inconspicuous, weakly rugose or smooth (Figs 4F, 24D, 47A). In many araneoids, abdominal apodemes are distinct, disk-like and rugose. Typically, in theridiids they are inconspicuous, or if sclerotized, their surface is relatively smooth.
166. *Abdominal surface*: (0) smooth; (1) with scuta. **G98-47**. Here only *Pholcomma hirsutum* has abdominal scuta. However, other pholcommatines also have scuta, and the character may be important for pholcommatine relationships.
167. *Sigilla*: (0) conspicuous, deep, contrastingly coloured; (1) inconspicuous, superficial, unicolourous. The abdomen typically bears two to several pairs of dorsal small depressions (sigilla) in longitudinal rows. In most theridiids these sigilla are inconspicuous, but in others the depression is distinct and coloured, usually reddish (see Roberts, 1985: plates 103–127).
168. *Epiandrous gland spigots (fusules)*: (0) present (e.g. Figs 3A–E, 21F, 32G, 44F, 56F, 62H, 86C); (1) absent (Figs 7D, 37F, 69F). Epiandrous glands and associated spigots are restricted to male spiders. They are immediately anterior to the genital furrow and are presumably exclusively used to make the sperm web (or part of it). Epiandrous gland spigots seem to be present, albeit sporadically, in most spider lineages (Marples, 1967; Lopez & Emerit, 1988), including liphistiids (Legendre & Lopez, 1981) making them a potential synapomorphy of spiders. Erigonines seem to lack epiandrous fusules and it has been hypothesized to be one of the synapomorphies of this linyphiid subfamily (Hormiga, 2002; J. Miller, pers. comm.), and they are absent sporadically in theridiids.
169. *Epiandrous spigot arrangement*: (0) in one pair of sockets (Fig. 44F); (1) in a row (Fig. 3B–E). In many orbicularians the epiandrous gland spigots are arranged in irregular transverse rows along the male genital plate (Fig. 3B–E). In, others, e.g. *Tetragnatha extensa* (Fig. 3A), the pimoid *Weintrauboa* (Hormiga, 2003), and many basal theridiids, however, the spigots are tightly arranged in two patches, usually in clear depressed sockets (Figs 4G, 24F, 28G, 44F, 48G, 53D, 72C, 74H). Here, where ACCTRAN optimization is selected, socketed epiandrous spigots are interpreted as synapomorphic for theridiids, with three reversals. A reversal to spigots in rows defines latrodectines (Fig. 55F); with additional homoplasy in *Steatoda* (Fig. 72C) it is autapomorphic in *Ariamnes* and is a synapomorphy for Theridiinae (Figs 49G, 58E, 79G, 82A, 85E). Many theridiines are somewhat intermediate (e.g. Figs 14G, 40A) in that rows are not continuous (a cap in the centre); nevertheless, in these cases individual spigots are still separate (Fig. 40A), rather than tightly grouped (as e.g. in Figs 15F, 19A), and no distinct depression (socket) surrounds them.
170. *Epiandrous gland spigot pair number*: (0) >10 (Fig. 3B–D); (1) <8 (Fig. 4G). Theridioids have comparatively few pairs of fusules, usually eight or fewer, with some reversals to ten or more within Theridiidae. Considerable intraspecific and intrageneric variation has been reported in fusule numbers of some families (e.g. Marples, 1967; Hormiga, 2002, 2003). Intrageneric (Figs 14F, G, 83F, G), and intraspecific variation is also found in theridiids, and some show asymmetric variation as well (Fig. 24F). Here, such variation was not extensively assessed, as accurate counts require SEM; the coding in some cases (based on a single specimen) may thus be somewhat artefactual.
171. *Male seminal vesicula*: (0) small; (1) large and darkened. Knoflach (1998) found that a group of closely related *Theridion* (including the type species *T. pictum*) have large and darkened seminal vesicles compared to other theridiids she studied.
172. *Colulus*: (0) present (Figs 45E, 61F, 74C); (1) absent (Figs 16E, 78A); (2) invaginated (Figs 9D, 63G). **G98-65**, in part. The colulus is generally considered homologous to the cribellum (e.g. Griswold *et al.*, 1998 and references therein). It has been lost frequently in araneoids. Here the loss of a colulus is synapomorphic for *Anelosimus* plus theridiines (clade 25, termed the lost colulus clade). However, a strongly invaginated colular area is a synapomorphy of *Emertonella* plus *Eury-*

opis and autapomorphy of *Phoroncidia* (Fig. 109).

173. *Colulus size*: (0) large and fleshy (Figs 55H, 61F); (1) small, less than half the length of its setae (Fig. 38B). **G98-65**, in part. The araneoid colulus is usually large and fleshy, but Griswold *et al.* (1998; character 65) reconstructed it as reduced or absent in several lineages. Griswold *et al.* (1998) scored only the size of the colulus, where small included absence, and found a 'reduced' colulus uniting *Anelosimus* and the hadrotarsines in their cladogram. However, I view the states of these taxa as nonhomologous; the colulus in *Dipoena nigra*, as in many other *Dipoena*, is certainly larger than half of the length of its setae and a colulus is absent in *Anelosimus*. Here, instead, a small colulus occurs in spintharines, *Cerocida strigosa* and *Kochiura* (Fig. 109).
174. *Colular setae*: (0) present; (1) absent. The colulus usually bears some setae, including a distinctive median pair of long setae (Fig. 55H). Even when the colulus is absent this pair of setae often persists (Figs 25E, 63G). Levi & Levi (1962) termed this condition 'colulus replaced by two setae', a misnomer because if the colulus is present, the setae are also. These setae are lost distally in the lost colulus clade, a theridiine synapomorphy, and autapomorphically in *Euryopis gertschi* (Fig. 109).
175. *Colular setae number (female)*: (0) three or more (Fig. 55H); (1) two (Figs 16E, 38B, 45E). *Crustulina*, *Latrodectus* and *Steatoda* females have three or sometimes more setae, males sometimes only two. Here, the loss of setae other than the central pair is a synapomorphy of the theridioid clade, with a reversal to additional colular setae synapomorphic for Latrodectinae (Fig. 109).
176. *Palpal claw (female)*: (0) present (e.g. Fig. 16G); (1) absent (Fig. 63I). **G98-53**. The absence of a palpal claw here is autapomorphic for *Phoroncidia* (Fig. 63I). However, many hadrotarsines and possibly other *Phoroncidia* species also lack female palpal tarsal claws.
177. *Palpal claw form (female)*: (0) attenuate (Figs 16G, 47E 58G); (1) palmate; (2) semipalmate. **G98-54**. Hadrotarsines have flattened, distally broadened (palmate) female palpal claws (Fig. 9E, see also Hickman, 1943; Wunderlich, 1978; Forster *et al.*, 1990; Griswold *et al.*, 1998). A somewhat similar claw occurs in other theridiid genera (Figs 11D, 87E), here termed semipalmate. The semipalmate claw is distinctly curved and has a strong row of subequally sized denticles. However, it is not flattened as in the hadrotarsines. Here the palmate palpal claw occurs in Hadrotarsinae and the semipalmate claw in *Achaearanea* and *Tidarren*.
178. *Palpal claw dentition (female)*: (0) dense, > half of surface covered by denticles (Figs 2D, 9E, 11D, 12G, 45G, 47E, 58G, 76D, 80D); (1) sparse, <half of surface covered by denticles (Fig. 57D).
179. *Palpal tibial dorsal trichobothria (female)*: (0) numerous, more than six; (1) three to five; (2) one to two (Fig. 74D).
180. *Palpal tarsal setae (female)*: (0) smooth; (1) serrated (Figs 9E, 43E).
181. *Palpal tarsus dorsal setae (female)*: (0) present; (1) absent (Fig. 43E). Theridiids and relatives have relatively asetose appendages (see 183; Griswold *et al.*, 1998). J. Miller (pers. comm.) found the distribution of dorsal tarsal macrosetae to be informative for erigonine phylogeny; here the absence of dorsal macrosetae on the female palpal tarsus is a synapomorphy of the spineless femur clade.
182. *Femur I relative to II*: (0) subequal; (1) robust, clearly larger than femur II.
183. *Femoral macrosetae*: (0) present; (1) absent (Fig. 63F). **G98-59**. Socketed macrosetae are found on the femora of most spiders. Wunderlich (1986) pointed out that the theridioid (nesticid-theridiid) lineage lacked them. Griswold *et al.* (1998) found them absent in cyatholipoids (synotaxids plus cyatholipids) as well, thus constituting the spineless femur clade. The present study corroborates this pattern.
184. *Leg IV relative length (male)*: (0) 3rd longest (typical leg formula 1243); (1) 2nd longest (typical leg formula 1423); (2) longest (typical leg formula 4123). Relative araneoid leg length varies considerably. Leg I is usually the longest, followed either by legs IV or II; leg III is always the shortest. Here leg IV longer than II is primitive for theridiids. However, in some argyrodines, *Kochiura*, and *Anelosimus*, leg IV is shorter than II, and in *Euryopis* leg IV is the longest.
185. *Leg IV relative length (female)*: (0) 3rd longest; (1) 2nd longest; (2) longest. The phylogenetic distribution of leg lengths differs between males and females.
186. *Femur vs. metatarsus length (leg I)*: (0) metatarsus longer; (1) metatarsus shorter (Fig. 63F).

187. *Metatarsus vs. tibia length (leg I)*: (0) metatarsus longer; (1) metatarsus shorter (Fig. 63F). On this cladogram an elongated metatarsus is a synapomorphy of clade 4. *Synotaxus* also has very long metatarsi (Fig. 95D), but other leg segments are equally elongated.
188. *Metatarsal ventral macrosetae*: (0) like other macrosetae; (1) thickened ventrally. Several *Anelosimus* have a row of notably thick macrosetae ventrally on the metatarsus (Fig. 26F). The condition is polymorphic for at least *A. studiosus*.
189. *Metatarsus I trichobothrium position*: (0) proximal (0.3–0.45); (1) distal (0.55–0.7); (2) submedian (0.46–0.54).
190. *Metatarsus III trichobothrium*: (0) present; (1) absent.
191. *Metatarsus IV trichobothrium*: (0) absent; (1) present.
192. *Patella–tibia autospasy*: (0) absent; (1) present. **G98-60**. Among araneoids coxa–trochanter autospasy is the norm and patella–tibia autospasy is synapomorphic for linyphioids (Wunderlich, 1986; Hormiga, 1994b; character 55).
193. *Tarsus IV ventral setae (comb)*: (0) smooth; (1) serrated (theridioid tarsal comb). **G98-62**. A row of stronger, curved serrated setae on tarsus IV is a classic theridiid character (Figs 59A, B, 76C). Some serrated bristles are also present in nesticids and *Synotaxus*. Here the feature is synapomorphic for the spineless femur clade. Allegedly, some *Pholcomma* and several argyrodines lack the comb (Kaston, 1981; Levi & Levi, 1962; Roth, 1993, etc.), but this is incorrect (Figs 25E, F, 32H, 57F), although the comb's presence may not be detected in light microscopy.
194. *Tarsus IV ventral setal surface*: (0) smooth; (1) theridiid grooves. In most theridiids the tarsal comb setae are distinctly curved with deep parallel longitudinal grooves (Fig. 11E, F), features absent in other families, and in Hadrotarsinae (Fig. 6A). In some rare or very small species I have not been able to verify the grooves (e.g. *Carniella*, *Phoroncidia*).
195. *Tarsus IV comb serrations*: (0) simple, straight; (1) curved hooks. Tarsal comb bristle morphology varies greatly. *Synotaxus*, nesticids and various theridiids have simple straight bristles (Figs 5G, 6A, 8B, 14E, 16F, 19E, 23E, F, 63E), while in others the serrations form curved hooks (Figs 11E, F, 12F, 35E–G, 59A, B, 78E, 80E, 84E).
196. *Tarsus IV comb bristle dorsal margin*: (0) straight; (1) distinctly notched. Spintharines have peculiar tarsal comb bristles. Viewed dorsally, the distal part is somewhat ladder-like, having distinct acute dorsal notches, particularly at the very tip (Figs 47D, 70D, 84E; compare to *Achaearanea*, Fig. 11F).
197. *Tarsus I ventral setae*: (0) ungrouped; (1) grouped, flat-tipped (Figs 6B, C, 8C, D). Hadrotarsines synapomorphically have grouped, flat-tipped setae on tarsus I (Figs 6B, C, 8C, D, see also Levi, 1968: fig. 9; Wunderlich, 1978: fig. 3; Forster *et al.*, 1990). The first tarsi of at least some theridiids also have similarly modified setae (Figs 26G, 84F), possibly homologous to those in hadrotarsines. Regardless, tightly grouped modified setae, at least, are a hadrotarsine synapomorphy. Further work is clearly needed to understand the distribution and function of the various setal types on theridiid legs.
198. *Tarsal organ size*: (0) smaller than setal sockets (normal); (1) enlarged. The typical araneoid tarsal organ (all legs and palpi) is about the size of a macrosetal or trichobothrial socket, with the opening clearly smaller than the width of adjacent setae (Figs 1D, 43E). Some theridiids (clade 46) have enlarged tarsal organs in which the circumference is equal to or larger than adjacent setal sockets, and the opening is as large or larger than those of setal or trichobothrial sockets (Figs 11C, 27G, 33F).
199. *Tarsus IV central claw vs. laterals (male)*: (0) short, at most subequal (Figs 66E, 72D); (1) elongate, longer (Figs 19E, 21C, 23D, 32H, 57F, 58F). The middle tarsal claw of all argyrodines is notably long in both sexes (Exline & Levi, 1962). In most male theridiids the central claw is relatively longer than in females and here the central claw longer than laterals is a synapomorphy for clade 33.
200. *Tarsus IV central claw vs. laterals (female)*: (0) equal or shorter; (1) stout and distinctly longer; (2) minute. **G98-63**. In argyrodines the fourth tarsal female (and male) claw is stout and long. It is also set as high on the tarsal tip as the lateral claws (Figs 32H, 57F), whereas normally the central claw inserts much lower than the lateral claws (e.g. Figs 21C, 37E, 45H, 55B). In the hadrotarsines and some other theridiids the central claw (in both sexes) is minute, being less than half the length of the laterals (Figs 8B, C, 74E).

201. *Spinneret insertion*: (0) abdominal apex (Figs 43A, 94F, J); (1) subapical, abdomen extending beyond spinnerets. Although the shift of the theridiid pedicel posteriorly on the abdominal venter (character 140) causes the abdomen to appear to extend beyond the spinnerets (Fig. 94J) this does represent a change in abdomen shape or spinneret insertion position. However, in some taxa the spinneret insertion has moved anteriorly (or the abdomen extended posteriorly; Figs 94A–E, 98F), regardless of the position of the pedicel.
202. *Spinneret sclerotized ring*: (0) absent (Fig. 43A); (1) present (Figs 63B, 74A). *Phoroncidia* and *Stemmops* have an elevated, sclerotized, ridge around the spinneret area.
203. *ALS median surface*: (0) like ectal surface (Figs 59C, 78D, 85G); (1) with parallel ridges (Fig. 7F). **G98-67**. All studied *Hadrotarsus* (and some other hadrotarsines) have series of apparently stridulatory parallel ridges on the ALS median surface (e.g. Forster *et al.*, 1990). Although considered a hadrotarsine synapomorphy by Griswold *et al.* (1998), their distribution is not so simple. Here, only *Euryopis gertschi* and *Emertonella funebris* (clade 51) have these ridges (Figs 7F, 9B). *Dipoena nigra* does not (Fig. 6D, *contra* Griswold *et al.*, 1998), and nor do *D. torva*, *D.* cf. *hortoni*, or *Gmogala* sp. The supposedly distantly related *Chilenodes* (Malkaridae: Palpimanoidea, but see Schütt, 2000, 2002) have similar ridges (Platnick & Forster, 1987).
204. *ALS piriform (PI) spigot bases*: (0) normal; (1) reduced. **G98-69**. As in other members of Griswold *et al.*'s (1998) 'reduced piriform clade', all theridiids have short piriform bases (e.g. Figs 39F, 59D).
205. *ALS piriform field size*: (0) large (over 40 spigots); (1) small (less than 35 spigots). The piriform field of some araneoids, e.g. *Argiope argentata* (Griswold *et al.*, 1998: fig. 48B) is large, containing numerous spigots. In theridiids (e.g. Figs 6D, 7F, 23C, 25B, 35B, 36I, 38C, 78C) and *Synotaxus* (Fig. 1E), however, the piriform spinning field is typically reduced. However, as the number of piriform spigots varies continuously, it is hard to reduce observations to homology statements. Some theridiids, e.g. *Achaearanea*, *Tidarren* and *Enoplognatha* (Figs 45D, 87C) do have a piriform field of 40 spigots or more. Others, such as *Latrodectus* (Fig. 55C) have approximately 35. For the taxa included here, 35 spigots is a convenient, although arbitrary, limit.
206. *PLS flagelliform spigot length*: (0) subequal to PLS CY; (1) longer than PLS CY (Figs 68E, 78B, 82D, 87D).
207. *PLS post CY base*: (0) normal; (1) enlarged. **G98-75**. The PLS posterior and mesial CY spigots are usually about the same size (e.g. Fig. 11B), but in a few taxa the former is obviously larger and longer (Coddington, 1989; Hormiga, 1993, 1994a, b; Hormiga *et al.*, 1995). Hormiga (1994a; character 58, fig. 146) and Griswold *et al.* (1998) showed that the enlarged state is a synapomorphy of linyphioids, convergently present in some symphytognathoid taxa as well.
208. *PLS, PMS CY spigot bases*: (0) not modified, subequal or smaller than ampullates (Fig. 11B); (1) huge and elongated, much larger than ampullates. All the argyrodine genera have distinctively shaped, grossly enlarged CY spigot bases (Figs 33B, 35A, 57C, 65C), here an unambiguous argyrodine synapomorphy.
209. *CY shaft surface*: (0) smooth (Figs 38D, 43G); (1) grooved. The argyrodine CY shaft is distinctly ridged (Figs 33B, 35A, 57C, 65C).
210. *PLS CY spigot number*: (0) two (Fig. 11B); (1) one. **G98-74**. *Cerocida strigosa* apparently has only one PLS CY (Fig. 38D). Although autapomorphic here, it may be an important feature of future work on *Cerocida* or Pholcommatinae.
211. *PLS AC spigot number*: (0) five or more (Fig. 29B); (1) four or less (Fig. 8A). The plesiomorphic araneoid PLS has numerous AC spigots, but the number has been reduced repeatedly, e.g. in pimoids (Hormiga, 1994a: character 60), nesticids, within hadrotarsines (*Euryopis*, Figs 8A, 9B), and within the Pholcommatinae (e.g. *Pholcomma*, Fig. 61E). Most taxa with a reduced field have one to three AC, but *Phoroncidia* has four (Fig. 63C, D).
212. *PLS flagelliform spigot*: (0) present (Fig. 11B); (1) absent. **G98-77**. The loss of PLS flagelliform (FL) gland spigot is a hadrotarsine synapomorphy (*Dipoena nigra*, Fig. 6D, F; *D. torva*, Fig. 6E; *Euryopis*, Figs 8A, 9C; *Gmogala* sp., pers. observ.; *Hadrotarsus* sp., pers. observ.). *Thwaitesia* (Fig. 84A, B) and basal argyrodines (*Argyrodes*, Fig. 33B; *Faiditus*, Fig. 48F; *Neospintharus*, Fig. 57C) also lack the FL. Spigot loss should track gland loss. Kovoor & Lopez (1983) found no flagelliform glands in

Argyrodes argyrodes, *Rhomphaea* or *Ariamnes*. The latter two do have just two of the triplet spigots, but morphology clearly suggests that an aggregate, not an FL, is lost (Figs 35A, 65A, C). This interpretation requires the regaining of the FL spigot in *Rhomphaea* or *Ariamnes* (Fig. 103). Although the histological interpretation is more parsimonious, it would be inconsistent to code an apparent flagelliform spigot as an aggregate. Histology and morphology conflict here and only further research can resolve it.

213. *PLS AG spigot number (female)*: (0) two (Fig. 11B); (1) one. The argyrodine genera *Ariamnes* (Fig. 35A) and *Rhomphaea* (Fig. 65C) share the loss of one of the two AG spigots in the female (clade 28, note that male *Dipoena nigra* may have only one, Fig. 6F). Forster *et al.* (1990: 97) indicate the absence of AG also in *Neospintharus trigonum* (their fig. 358). However, what they have illustrated resembles a *Rhomphaea* much more than *N. trigonum* (cf. Fig. 57C). *Achaearanea wau* (Fig. 12D) also appears to have only a single AG; the condition in its sister species *A. vervoorti* is unknown.

214. *PLS AG spigot size*: (0) circumference at base subequal to or less than CY; (1) circumference at base distinctly greater than CY (Fig. 11B). **G98-78**. The enlarged and modified PLS AG spigots in theridiids and nesticids were pointed out by Coddington (1989) and stressed by Forster *et al.* (1990). Griswold *et al.* (1998) scored *Pimoa* as having normal AG. However, if 'huge' means '… the diameter of … AG spigots is much greater than any other spigot elsewhere on the spinneret' (Griswold *et al.*, 1998: 42), then *Pimoa* does indeed have enlarged AG spigots (Hormiga, 1994a: e.g. fig. 83); the other pimoid genus, *Weintrauboa*, however, does not (Hormiga, 2003). Here enlarged AGs are an ambiguous synapomorphy of clade 59 (ACCTRAN), convergent in reversed *Linyphia*.

215. *PLS anterior AG spigot shape*: (0) normal, round; (1) flattened. Theridiids have distinctly flattened anterior AG shafts (Figs 7F, G, 8A, 9A–C, 11B, 12D, 25C, 43G, 53B, 74J, 78B, 87D instead of the more typical round shape (Fig. 1F). *Dipoena nigra* males have one very slightly flattened AG (Fig. 6F), likely also in females.

216. *PLS posterior AG spigot shape*: (0) round; (1) flattened (Fig. 11B). In contrast to most theridiids, only one of the two AGs is flattened in *Cerocida* (Fig. 38D), *Pholcomma* (Fig. 61C–E), *Robertus* (Fig. 66H), *Selkirkiella* (Fig. 68E), and probably *D. nigra* (Fig. 6D). The posterior AG is unmodified (and only slightly modified in *Enoplognatha* (Fig. 45B, C), an intermediate given its phylogenetic position (Fig. 102). In *Carniella* (Fig. 36I) both are unmodified. In *Pholcomma* the anterior one is very slightly flattened. These seem to represent secondary loss of spigot modification within pholcommatines, reaching its maximum in *Carniella*. Here flattened posterior AG spigots are an ambiguous synapomorphy of Theridiidae (ACCTRAN).

217. *PLS aggregate gland form*: (0) entire; (1) lobed. Apstein (1889) was probably the first to study silk glands in detail in a comparative framework. He studied a range of families, and pointed out that theridiids and *Nesticus* uniquely have lobed PLS AG glands. Kovoor (1977) and Kovoor & Lopez (1988) provided corroborating data (see also Nielsen, 1932; Coddington, 1986c, 1989; Forster *et al.*, 1990; Griswold *et al.*, 1998). Apstein (1889: 41, 60) found lobed aggregate glands in *Theridion sisyphium*, *Enoplognatha ovata*, *Steatoda bipunctata*, *S. albomaculata*, *S. phalerata*, *Episinus truncatus*, *Crustulina guttata*, *Euryopis flavomaculata* and *Nesticus cellulanus*, but not in *Tetragnatha extensa* or *Linyphia triangularis*. Here I code lobed PLS MAP glands as present in genera mentioned by Apstein (assumed if Apstein's study species is not in my matrix). Lobed glands also occur in *Latrodectus mactans* (Kovoor, 1977) and *Steatoda grossa*, *Argyrodes argyrodes* and *A. elevatus* (Kovoor & Lopez, 1983) Here the feature is optimized as synapomorphic for the theridioids (DELTRAN). Studying *Synotaxus* is important for accurate optimization of this feature. Interestingly, Apstein (1889: 61) briefly mentioned two lobed glands in *Steatoda*, *Episinus*, *Crustulina*, *Euryopis* and *Nesticus*, but only one in '*Theridium*' which included *Enoplognatha* and *Theridion*. Although too vague to be incorporated as a character here, the reduction to a single lobed PLS AG gland is at least a putative synapomorphy of clade 43.

218. *PLS theridiid type AG position*: (0) more or less parallel; (1) end-to-end. When the PLS AG spigots are flattened, their relative orientation becomes informative. In most theridiids they are organized 'end-to-end' (Figs 11B, 18F, 23A, 47C, 48F, 50A, B, 59E, 70B, 78B, 80A, 84B, 87D). In Latrodectinae and Phol-

comminae (where applicable) the AG are not end-to-end but nearly parallel (Figs 43F, G, 45A–C, 55D, 63D, 72H, 74B, 82D). The orientation of the spigots can only be addressed when they are flat and thus this character is coded as inapplicable for taxa where both AGs are round, or only one of them is flattened.

219. *PLS AG, FL (male)*: (0) absent; (1) present. Adult male araneoids typically lack the triplet (AGs plus FL), and thus the ability to produce sticky silk (Figs 33D, 39G, 53A, 76G, 78D). Adult males of several araneoid lineages, however, retain these spigots such as cyatholipids (Griswold, 2001) and erigonine linyphiids (Cushing, 1995; Hormiga, 2000). Male hadrotarsines (Figs 6F, 9C), argyrodines minus *Argyrodes* (Figs 48F, 65E), and a pholcommatine subclade (clade 38) (Figs 36I, 61D, E, 63D, 74I) also retain at least a part of the triplet (usually AGs, sometimes also FL). The triplet is scored as present if any of the triplet spigots are functional (e.g. female and male *Dipoena* lack the FL, but in both AGs are present).

220. *PMS mAP nubbins*: (0) present (Fig. 1F); (1) absent (Figs 14D, 16D, 23B, 25D). **G98-71**. PMS mAP spigot nubbins (Fig. 1F) are an araneoid synapomorphy (Coddington, 1990b; Griswold *et al.*, 1998). The latter (character 71) mapped nubbin loss as a synapomorphy of the 'araneoid sheet web weaver clade', but regained in nesticids and *Synotaxus*. Here nubbin loss is, controversially, synapomorphic for linyphioids on one hand and theridiids on the other.

221. *PMS CY spigot base*: (0) distinct (Fig. 33C); (1) indistinct, absent (Fig. 1G).

222. *PMS AC spigot number*: (0) five or more; (1) four; (2) three; (3) two; (4) one; (5) none. **G98-70**, in part. Coddington (1989) and Griswold *et al.* (1998) hypothesized that a dense brush of AC spigots on the PMS was probably the primitive condition in Orbiculariae. Most derived araneoids, however, have exactly three AC spigots on the PMS. Coddington (1989) commented that the different numbers of PMS AC spigots in theridiids might be informative and this study supports that view. On this cladogram, exactly four PMS AC spigots defines Latrodectinae (Figs 43F, 55G, see also Coddington, 1989: fig. 28). Here, two PMS AC spigots are a theridiid synapomorphy (e.g. Figs 18G, 33C, 65D, 70C). *Pholcomma* has a single PMS AC spigot (Fig. 61D), while the related *Carniella* has none (Fig. 36I, also absent in *Pimoa rupicola*). Intraspecific variation in AC spigot numbers occurs in Pimoids (Hormiga, 1994a), but I did not record any in the theridiids I examined (left and right side were symmetrical in all specimens examined, males and females had equal numbers of AC spigots).

223. *PMS minor ampullate (mAP) spigot shaft length*: (0) short, subequal to CY shaft, or shorter (Fig. 7C); (1) clearly longer than any CY shaft. Long PMS mAP spigot shafts are here synapomorphic for clade 27 (Figs 18E–G, 23B, 25D, 27E, 87D), but the feature is quite homoplasious.

224. *Prey-catching web*: (0) present (Fig. 100A–F); (1) absent. Few hadrotarsines are known to build prey-catching webs (webs that trip or entangle prey). *Dipoena tristis* (see Wiehle, 1937) and *D. torva* (see Roberts, 1995) are exceptions. Supposedly, most are wandering ant specialists (e.g. Levi, 1954 1963; Carico, 1978) Very little is known of theridiid webs in general. Although some are probably webless, other studied theridiids do build prey-catching webs, or are able to do so (e.g. Nielsen, 1932; Whiele, 1937; Holm, 1939; Benjamin & Zschokke, 2003). Argyrodines in general do not build typical prey-catching webs (e.g. Eberhard, 1979; Whitehouse, 1986, 1987b; Whitehouse & Jackson, 1993), but they do build silken structures into the structure of the webs of other spiders that catch prey. Some kleptoparasitic argyrodines facultatively build sticky traps that have been described as 'inefficient' (e.g. Whitehouse, 1986). *Ariamnes* builds non-sticky lures (Eberhard, 1979) in which a simple line web is used as substrate by other male spiders and nematocerous flies, which it then ambushes. *Rhomphaea* uses a similar ambush strategy, throwing sticky lines over approaching spiders (Whitehouse, 1987b).

225. *Web form*: (0) orb; (1) linyphioid-like knockdown sheet web (Fig. 99C); (2) chicken-wire, rectangular orb (*Synotaxus*, Fig. 95A); (3) cobweb (Figs 97G, 99A, B, 100A–F, 101A–E); (4) Spintharine H-web (Fig. 97A); (5) network mesh web, with foraging field below (e.g. *A. rupununi*); (6) dry line-web; (7) gumfoot line-web (*Phoroncidia*, Fig. 97B–D). **G98-80**. Objective coding of the wide variety of sheet and tangle web architecture remains problematic. Orb webs are well defined, both structurally and behaviourally (Robinson & Robinson, 1973, 1975; Eberhard, 1982, 1990; Coddington, 1986b; Hormiga *et al.*, 1995).

The *Synotaxus* chickenwire-like web (Fig. 95A) or 'rectangular orb' is likewise distinctive and constructed in well-defined behavioural units (Eberhard, 1977, 1995). Linyphioid sheet webs typically have a planar, horizontal sheet, sometimes sticky. Many, especially nonlitter dwelling linyphioids, have a mesh of nonsticky knock-down threads above the sheet intercepting prey in flight, which then gets trapped on the sheet (e.g. Benjamin *et al.*, 2002). Some social *Anelosimus* webs are architecturally and functionally similar to linyphiid sheets, albeit typically dome-shaped (Fig. 99C). Cobweb is here considered to be a three-dimensional mesh, with or without gumfoot lines, whose catching area is not limited to a single plane (Figs 97G, 99A, B, 100A–F, 101A–E). Some have sticky silk in the mesh, while others have a central (Fig. 100A–F) or peripheral (Fig. 96C–F, and legend) retreat from which gumfoot lines radiate. In either case, the area where prey gets stuck is three-dimensional. A few theridiids apparently build cobwebs without sticky silk, while others do not build cobwebs, but rather linyphioid-like sheets. Spintharines typically build a highly modified H-shaped web with only two gumfoot lines (Fig. 97A, see also Holm, 1939; Ikeda *et al.*, 1983; Roberts, 1995: 261), here not considered a 'cobweb', as it is planar. A few theridiids build 'line-webs', a few nonsticky lines that serve to lure rather than snare prey, e.g. *Ariamnes* (see Eberhard, 1979) *Rhomphaea* (see Whitehouse, 1987b), *Thwaitesia* spp. (pers. observ.). *Phoroncidia* makes a 'gumfoot line-web', a single gumfoot line (occasionally a few lines) that it holds on to (Fig. 97B–D, see also Eberhard, 1981). Some social theridiids build a mesh network without knockdown threads, but instead forage below the 'sheet' (Levi *et al.* 1982; Lubin, 1982, 1995; Avilés & Salazar, 1999).

226. *Sticky silk in web*: (0) present; (1) absent.

227. *Sticky silk placement*: (0) in sheet or tangle (Fig. 95A); (1) on gumfoot lines (Figs 96E, F, 97B–D, 101A, B, D). Araneoid webs typically contain viscous globules on silk lines of the sheet. *Linyphia* makes such sheets, but the sticky silk desiccates quickly and may not function as in orbs or gumfoots (Benjamin *et al.*, 2002). In contrast, nesticids and many theridiids place the sticky globules on the tips of lines radiating from their mesh retreat or web centre, which attach to the substrate (gumfoot lines). In this cladogram the presence of gumfoot lines is a synapomorphy of theridioids, although repeatedly lost. Gumfoot line construction seems to constitute a unique, stereotyped behaviour (Benjamin & Zschokke, 2003). However, some theridiid web building behaviours are shared with other araneoids. For example, *Achaearanea tepidariorum* attaches sticky silk lines to dry lines in a manner typical of orb-weavers (Eberhard, 1982). Cutler (1972) found gumfoot lines in *Coleosoma floridanum*, but Benjamin & Zschokke (2003), indicate that the sticky silk is confined to the sheet. This discrepancy is here represented by coding *C. floridanum* as polymorphic for this character. [Note added in proof: Benjamin & Zschokke's observation was a lapsus (S. P. Benjamin, pers. comm.). *C. floridanum* has gumfoot lines.]

228. *Wrap-bite attack*: (0) present; (1) absent. **G98-92**. Some araneoid spiders wrap prey before biting, while others bite first (Robinson, 1975; Eberhard, 1982). The wrap-bite attack is apparently synapomorphic for orbicularians (Griswold *et al.*, 1998) although lost in lineages such as linyphiids and pimoids. Here the attack is a synapomorphy of clade 57.

229. *Sticky silk wrap attack*: (0) absent; (1) present. **G98-93**. Theridiioids have a modified form of the wrap-bite attack in which sticky silk is employed (Whitehouse, 1987b; Forster *et al.*, 1990; Griswold *et al.*, 1998; Vakanas & Krafft, 2001). Nielsen (1932: 188) stated: 'They [*Theridium*, including various theridiids] never attack their victim with the chelicerae before it is properly entangled in viscous threads. This is done by the spider turning its back to the victim and throwing threads over it by means of the tarsi of the posterior legs. The viscid matter may at first drip from these threads, which are subsequently more sparingly provided with it.' Although presumed to be the rule for theridioids, relatively few observations have been published. *Synotaxus* is assumed to be similar (from a single observation on *S. turbinatus*; Griswold *et al.*, 1998). Here the SS wrap attack is an ambiguous synapomorphy of the spineless femur clade (DELTRAN), because only *Argiope* wrap attacks do not involve SS, while *Tetragnatha* and linyphioids do not wrap attack at all.

230. *Egg sac surface*: (0) spherical to lenticular (Fig. 95B, C, E); (1) stalked (Figs 88E, 98D). Among theridiids, argyrodines are unusual

in having a distinctly stalked egg sac that they usually hang on vegetation, or in webbing in their host's web (Fig. 98C, D).

231. *Egg case structure*: (0) suboval or roundish (Figs 95B, C, E, 101G); (1) basal knob (Fig. 98C, D); (2) rhomboid; (3) elongated (Fig. 98E); (4) Spiky. Exline & Levi (1962: figs 1–5) illustrate the types of egg sac found in the Argyrodines (see also Chikuni, 1989: 34–35), and these appear to be informative at the genus level. In addition to being stalked, *Argyrodes*, *Faiditus* and *Neospintharus* egg sacs have 'basal', cylindrical knobs (Fig. 98C, D); those of *Rhomphaea* are similar but rhomboid. Many *Ariamnes* egg sacs are thin and extremely elongated (Fig. 98E); others are like those of *Rhomphaea*. *Latrodectus geometricus* egg sacs are spiky.

232. *Egg sac, outermost fibres*: (0) fine, densely woven; (1) thick, coarsely spun. In at least some spintharines the outermost fibres of the egg sac are loosely woven, e.g. *Thwaitesia* (Fig. 88C) and *Episinus*, compared to many other theridiids where all fibres are densely spun and thus the egg sac surface appears smooth (Fig. 88A, E, G) (Roberts, 1995). There appear to be no observations for *Spintharus*.

233. *Egg sac fibre ultrastructure*: (0) smooth (Fig. 88A, B, E–H); (1) spiny (Fig. 88C, D). The egg sacs of spiders protect the eggs against predation and parasitism (Austin, 1985; Foelix, 1996). Presumably, most egg sac fibres are smooth (Fig. 88B, F, H), but *Thwaitesia* has unique spiny fibres in (at least) the outer layer of the sac (Fig. 88D). This morphology seems obviously defensive, although direct observation of their function is lacking. The character scoring is assumed for *T. margaritifera* based on *Thwaitesia* sp. from Madagascar, for *Argyrodes argyrodes* and *A. elevatus* based on *Argyrodes* sp., and for *Theridion pictum* and *T. varians* based on *Theridion* sp. Although data remain very sparse, the feature is included here to emphasize this fascinating feature of *Thwaitesia*, and to stimulate further work on egg case ultrastructure.

234. *Web construction*: (0) solitary; (1) communal. The participation of several individuals (whether juvenile or adult) in web construction is one of the features that define web-sharing sociality.

235. *Sex ratio*: (0) roughly equal <2 × female-biased; (1) >3 × female-biased. Social theridiids characteristically have female-biased sex ratios, unlike the vast majority of spiders (e.g. Avilés & Maddison, 1991; Avilés *et al.*, 2000). Unbiased sex ratios can be inferred from museum collections and are here presumed in the absence of contrary evidence. Sex ratio bias seems to increase with the level of sociality. Interestingly, Stiles & Coyle (2001) reported slightly biased sex ratios in *Theridion frondeum* and two *Rugathodes* species (about 1.9 females per male). At least two of these show maternal care beyond the egg sac stage, and such slight sex ratio biases may well be common in species showing extensive maternal care.

236. *Male palp amputation*: (0) both palps present before (and after) final moult; (1) one palp amputated prior to final moult. *Tidarren* and *Echinotheridion* males amputate one palp (left or right randomly) prior to the final moult so that the adult has only a single functional palp (Branch, 1942; Knoflach & van-Harten, 2000, 2001; Knoflach, 2002). Only *Tidarren* is included in this study, but future inclusion of *Echinotheridion* will demonstrate if this remarkable behaviour in the two genera is homologous.

237. *Initial palpal insertions*: (0) transfer sperm; (1) pseudocopulation. In *Linyphia* and some distal theridiines, the first palpal insertion is a pseudocopulation, not involving sperm transfer (Helsdingen, 1983; Knoflach, 1998)

238. *Palpal insertions*: (0) ipsilateral; (1) contralateral. During mating the male spider may insert its palp either to a corresponding epigynal opening (ipsilateral) or to the opposite one (contralateral). Presumably, ipsilateral insertions are the norm in orbiculariarian spiders (Gerhard, 1921–33; Helversen, 1976; Huber & Senglet, 1997; Knoflach, 1998). Huber (1993) found ipsilateral insertions in *Nesticus cellulanus* (assumed here for *N. silvestrii*), and Gerhardt for many basal theridiids. However, *Tetragnatha* spp. (e.g. *T. extensa*) and *Leucauge* use contralateral insertions (Huber & Senglet, 1997), as do *Theridion varians*, *T. pictum*, and *Coleosoma floridanum* (Knoflach, 1998). *Tidarren cuneolatum*, which has only one palp, uses ipsilateral insertions only when mating with a previously mated female plugged on the contralateral side (Knoflach & van-Harten, 2000).

239. *Sperm induction*: (0) independent of copulation; (1) during copulation sequence. Male spiders typically charge their palps with sperm prior to entering the female web, while in others sperm induction is a part of the cop-

ulation sequence (e.g. Gerhardt, 1921–33). Data for *Tetragnatha extensa*, *Linyphia triangularis*, *Nesticus cellulanus*, *Steatoda* (4 species) and *Enoplognatha ovata* are from Gerhardt (1921–33, as summarized by Huber, 1998). Data for *Dipoena*, *Euryopis*, *Latrodectus*, *Achaearanea tepidariorum*, *Tidarren sisyphoides*, *Kochiura aulica* are from Knoflach (1998) and Knoflach & van-Harten (2000). Here, induction by *Nesticus silvestrii* is assumed, based on *N. cellulanus*, by *Steatoda grossa,* based on Gerhard's four *Steatoda* species, by *Dipoena*, *Euryopis* and *Latrodectus*, based on congeners observed. The logical interdependence (if any) of this character and character 237 is not clear.

240. *Mating thread*: (0) present; (1) absent. In some theridiids, as in many other araneoids, the male constructs a special thread in the female web on which mating takes place (e.g. Gerhardt, 1921–33; Knoflach, 1998). In others, mating takes place on threads of the female web.
241. *Bulbal movements during insertion*: (0) no rhythmic movements; (1) rhythmic expansion of haematodocha.
242. *Male position during deposition of sperm on sperm web*: (0) below; (1) above.

APPENDIX 2

SIMON'S (1894) TRIBAL GROUPS

Four of Simon's (1894) groups contained only taxa that now are in other families and are not shown. Some names appear twice, or more, as several genera Simon dealt with are currently in synonymy.

Assignee: *Crustulina, Craspedisia, Enoplognatha, Steatoda, Robertus*
Hetschkieae: *Cerocida, Helvibis, Hetschkia*
Dipoeneae: *Dipoena, Latrodectus, Thymoites*
Phoroncidieae: *Dipoena, Enoplognatha, Episinus, Phoroncidia*
Argyrodeae: *Argyrodes, Ariamnes, Rhomphaea*
Spinthareae: *Spintharus*
Theridieae: *Achaearanea, Cephalobares, Molione, Theridion, Theridula, Thymoites*
Propostireae: *Propostira*
Episineae: *Episinus, Tomoxena, Thwaitesia, Chrysso, Chrosiothes*
Euryopeae: *Audifia, Euryopis, Coscinida, Dipoena*
Moneteae: *Moneta*
Theonoeae: *Theonoe*
Histogonieae: *Histagonia, Wirada*
Pholcommateae: *Pholcomma, Styposis*

APPENDIX 3

LIST OF SPECIMENS EXAMINED

Same data for both sexes if not specified. Detail of information reflects information on label, lack of dates, collector etc. indicates that this information was missing on label.

Araneidae
Argiope argentata (Fabricius). Male: Venezuela, Bolivar, 20.iii.1982, Hevel (NMNH). Female: Argentina, Formosa, Arroyo Guaycolec, 25.iv.1989, Pereira (NMNH).

Tetragnathidae
Tetragnatha extensa (Linnaeus). Russia, Sakhalin Island. Aniva Dist. Novoaleksandrovka, vi.1990, Basarukin (NMNH).

Linyphiidae
Linyphia triangularis (Clerck). Denmark, Hestehaven, 30.viii.1994, Coddington *et al.* (NMNH).

Pimoidae
Pimoa breviata Chamberlin & Ivie. USA, California, Humboldt Co. 18.vii.1990, Hormiga (NMNH).
Pimoa rupicola (Simon). France (NMNH).

Nesticidae
Eidmanella pallida (Emerton). Trinidad, 1988, Coddington (NMNH).
Nesticus reclusus Gertsch. Male: USA, TN: Sevier CO. GSMNP, N & E of Grotto Falls 19.iv.1997, Coyle. Female: as male, except col. 4.viii.1997, Davis (NMNH).

Synotaxidae
Synotaxus monoceros, Guyana, Bartika, 27.vii.1999, Agnarsson & Kuntner (NMNH).
Synotaxus sp., Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999. Coddington *et al.* (NMNH).

Theridiidae
Achaearanea tepidariorum. Male: USA, NC, Macon Co. Highlands biological station, 15.vii.1998, Agnarsson (NMNH). Female: USA, NC, Macon Co. Highlands biological station, 12.vii.1998, Agnarsson (NMNH), USA, SC, Lexington Co. 13.ix.1998, Reeves (NMNH).
Achaearanea vervoorti. New Guinea (MCZ).
Achaearanea wau Levi, Lubin & Robinson. New Guinea, Marobe province, Wau Ecological Institute, 13.vi.1979, Lubin (MCZ).
Ameridion cf. *petrum*. Costa Rica, Cartago, Reserva forestal de Rio Macho, 2850m. 22–26.iii.1999, Zujko-Miller (NMNH).
Ameridion sp. Costa Rica, Cartago, Cerro de la Muerte, 3250m 25.iii.1999, Zujko-Miller (NMNH).

Anelosimus analyticus Chamberlin. Mexico, Sonora, Guaymas, 26.vi.1939, Davis (NMNH).
Anelosimus eximius (Keyserling). Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 15.vii.1999, Agnarsson (NMNH).
Anelosimus jucundus (O. P.-Cambridge), (male holotype and paratype), Mexico, Omilteme, Godman & Salvin, BM1905.4.28.1811-30 (part) (BMNH).
Anelosimus cf. *jucundus* (O. P.-Cambridge). Mexico, San L. Potosi, Salto falls, 6.ii.1967 (NMNH)
Anelosimus lorenzo Fowler & Levi. Paraguay, St. Luis, x.1908 (MCZ); female paratypes: Paraguay, San Lorenzo, 25.vii.1976, Fowler, 1980.3.20.1-3 (BMNH).
Anelosimus pulchellus (Walckenaer). Italia, Lazio, Mt. Circeo, 16–17.v.1962, Levi (MCZ).
Anelosimus saramacca Levi. Female paratype: Surinam, Voltzberg-Raleigh vallen Nature Reserve, Saramacca province, 04°32′N 56°32′W, ii.1982, Smith-Trail (BMNH).
Anelosimus studiosus (Hentz). No collection data (NMNH).
Anelosimus rupununi Levi. Brazil: Mato Grosso; Cachoeirinha, Chapada dos Guimaraes, 5.xii.1990 (NMNH).
Anelosimus vittatus. Slovenia, Sempas, 1998, Kuntner *et al.* (NMNH).
Anelosimus sp. 1. Tanzania, Iringa District, Uzungwa Scarp forest, 17–27.v.1997, Scharff *et al.* (NMNH).
Anelosimus sp. 2. Tanzania, Iringa District, Uzungwa Scarp forest, 17–27.v.1997, Scharff *et al.* (NMNH).
Argyrodes argyrodes Walckenaer. Croatia, Murter Island, 2.ix.1999, Bedjanic (NMNH).
Argyrodes bonadea (Karsch). China, Soochow, Gist Gee (NMNH).
Argyrodes elevatus Taczanowski. USA, Texas Bastrop Co. 13 miles SSE of Elgin.15.viii.1968, Vogel (NMNH).
Argyrodes fur Bösenberg & Strand. China, Soochow, Gist Gee (NMNH).
Argyrodes nephilae Taczanowski. Bermuda, Hamilton Parish, Skelly Bay, Mangrove swamp, 20.xi.1987, Hilburn (NMNH).
Argyrodes pluto Banks. [Label poor, presumably USA.] USA, VA, 21.vi.1913 (NMNH).
Ariamnes attenuata O. P.-Cambridge. Male: Venezuela, Alto Mavaca base camp, upper Rio Mavaca, 31.i.1989, Polhemus (NMNH). Female: Peru, Madre de Dios, Pakitza, 2.x.1987, Silva & Coddington (NMNH).
Ariamnes longissimus Keyserling. Male: Brazil (Marx Collection) (NMNH).
Ariamnes sp. Madagascar, Périnet Special Reserve (Parc National Andasibe Mantadia), Toamasina Province, 900–1000m, 18°56′S, 48°25′E, 7–8.v.2001, Agnarsson & Kuntner (NMNH).
Carniella siam Knoflach. Male: Thailand, Doi Inthanon N.P., 25.ix.1999, 2430m, Dankittipakul (NMNH). Female coded from Knoflach (1996).
Cerocida strigosa (Simon). Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).
Chrosiothes cf. *jocosa*. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).
Chrysso cf. *nigriceps*. Colombia, Boyacá, S.F.F. Iguaque, near margin of Laguna Iguaque, 5–8.ii.1998, Hormiga *et al.* (NMNH).
Coleosoma floridanum Banks. Male: no locality data; label states: 2870 (INBio). Female: Bermuda, Smith's Parish, 16–22.v.1988, Sierwald (NMNH).
Crustulina guttata (Wider). Slovenia SIF, N, 13.vii.1999 (NMNH).
Crustulina sticta O. P.-Cambridge. USA, WV, Berkeley Co. 17–23.vii.1986, Martinat (NMNH).
Dipoena nigra Emerton. Male: USA, Massachusetts, Barnstable Co. 18.vii.1989, Edwards (NMNH). Female: as male but col. 8.viii.1990 (NMNH).
Dipoena cf. *hortoni*. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).
Dipoena torva (Thorell). Male Slovenia, Tabor, 28.vii.1998, Kuntner *et al.* (NMNH) Female: Slovenia, Sembpas 1998, Kuntner *et al.* (NMNH).
Emertonella funebris (Hentz). Male: USA, WV, Monongalia Co. 12–19.vii.1989, Jennings, (NMNH).
Enoplognatha latimana Hippa & Oksala. Male: Germany, Stellin, 20.vii.1898 (NMNH). Female: USA, Washington, Lewis Co., 15.viii.1984, Holt (NMNH).
Enoplognatha ovata (Clerck). USA, Massachusetts, Barnstable Co., 1.vii.1989, Edwards (NMNH).
Episinus amoenus Banks. USA, Georgia, Rabun Co., 2.vi.1993, Dellinger (NMNH).
Episinus maculipes Cavanna. Slovenia, Sembpas, 1998, Kuntner *et al.* (NMNH).
Euryopis gertschi Levi. Male: USA WV, Berkeley Co. 6–13.vi.1986, Martinat (NMNH). Female: as male but col. 20–27.vi.1986 (NMNH).
Faiditus americanus (Taczanowski). Male: Peru, Madre de Dios, Reservada Tambopata, 22.vii.1986, Rypstra (NMNH).
Faiditus amplifrons (O. P.-Cambridge). Peru, Madre de Dios, Zona Reservada de Manu, Rio La Torre and Rio Tambopata, 12°50′S, 69°17′W, viii–xii.1979, Rypstra (NMNH).
Faiditus cancellatus (Hentz). USA, SC, Pickens Co., Wildcat picnic area near Lake Issaqueena, 700 m, 34°45.53N 82°52.24W, 18.vii.1998, Wang (NMNH).
Faiditus cf. *caudatus*. Colombia, Iguaque, 5°42′5.3″N 73°27′20.1″W, 2850–3000m, 5.ii.1998, Hormiga *et al.* (NMNH)

Faiditus cf. *chickeringi*. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15 vii. 1999, Coddington *et al.* (NMNH).

Faiditus spinosus Keyserling. Peru, Madre de Dios, Zona Reservada de Manu, Rio La Torre and Rio Tambopata, 12°50′S, 69°17′W, viii–xii.1979, Rypstra (NMNH).

Faiditus ululans (O. P.-Cambridge). Peru, Madre de Dios, Reservada Tambopata, viii.1987, Cangialosi (NMNH).

Gmogala sp. Australia, W. A., Bushmead, Ridge hill Road. 16.iv.–17.vi.1996, Harvey (NMNH).

Hadrotarsus sp. Australia, W. A., Pintharuka, 23.v.–17.ix.1996, Harvey (NMNH).

Helvibis germaini Simon. Male: Bolivia, Dpto. Beni, Est. Biol. Beni, Zone 1, Plot 04, *c.* 14°47′S; 66°15′W, *c.* 225 m, 8–14.xi.1989, Coddington (NMNH).

Helvibis cf. *longicaudatus*. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).

Kochiura rosea Nicolet. Juan Fernandez Islands, Mas Afuera, Quebrada Vaca, 22.iii.1962, Malkin (MCZ).

Kochiura aulica (C. L. Koch). France (NMNH).

Latrodectus geometricus C. L. Koch. Madagascar: Berenty reserve, 2.v.2001, Agnarsson & Kuntner (NMNH).

Latrodectus mactans (Fabricius). Male: USA, Colorado, El Paso Co. 25.ix.1965, C.Bucy (NMNH). Female: USA, VA, Mt. Vernon, 22.v.1911 (NMNH).

Latrodectus variolus Walckenaer. Female: USA, SC, Pickens Co., Wildcat picnic area near Lake Issaqueena, 700 m, 34°45.53N 82°52.24W, 18.vii.1998, Klawinski (NMNH).

Neospintharus concisus (Exline & Levi). Female: Mexico, Veracruz, Fortin de Las Flores, 15.viii.1992 (NMNH).

Neospintharus furcatus (O. P.-Cambridge). Male: USA, Texas, Travis Co., Bull Creek, 8.5 miles NNW of Austin, 22.viii.1968, Vogel (NMNH).

Neospintharus trigonum (Hentz). Male: USA, Georgia, Rabun Co. 1993, Dobyns
(NMNH). Female: USA, SC, Pickens Co. 18.vii.1998, Agnarsson (NMNH).

Neottiura bimaculata (Linnaeus). Slovenia, approx. 500m north of Cmice, 220–260 m, 27–29.vii.1998, Kuntner (NMNH).

Nesticodes rufipes (Lucas, 1846). Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).

Pholcomma hirsutum Emerton. USA, NC, Macon Co. Highlands biological station, 15.vii.1998, Agnarsson (NMNH).

Phoroncidia sp. Tanzania, Iringa District, Uzungwa Scarp forest, 17–27.v.1997, Scharff *et al.* (NMNH).

Phoroncidia cf. *moyobamba*. Male: Tobago, St. Paul Parish, King's Bay R. Dam, 1.2 miles. SW of Speyside, *c.* 290 m, *c.* 11°17′N 60°34′W, 10–17.v.1991, Hormiga *et al.* (NMNH).

Rhomphaea fictilium (Hentz). Male: [label hardly legible, presumably from USA] ?Mason, Sa, viii.1887, ?Underwood (NMNH). Female: USA, VA, Great Falls, 17.vi.1913, Hentz (NMNH).

Rhomphaea projiciens O. P.-Cambridge. Male: Peru, Madre de Dios, Zona Reservada de Manu, Puesto de Vigil, Pakitza, Zone 1 trail, 11°58′S, 71°18′W, 3.x.1987, Silva & Coddington (NMNH). Female: Mexico, Veracruz, Fortin de las Flores, 10.ix.1992 (NMNH).

Rhomphaea metaltissima Soares & Camargo. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15 vii. 1999, Coddington *et al.* (NMNH).

Robertus frontatus (Banks). Male: USA, WV, Monongalia Co., 10–17.vii.1987, Jennings (NMNH). Female: USA, NC, Macon Co., 20.vii.1998, Agnarsson (NMNH).

Robertus neglectus (O. P.-Cambridge). Denmark, Hestehaven, Ronde, 22 km NE of Arhus, 56°17.46′N, 10°28.50′E, 30.viii.1994, Coddington *et al.* (NMNH).

Rugathodes sexpunctatus (Emerton). Female: USA, Washington, Island Co., Lake Pondilla, 48.227°N, 122.765°W, 16.vi.1987, Crawford (NMNH)

Selkirkiella alboguttata Berland. Male (paratypes of *A. portozuelo* Levi): Chile, Juan Fernandes Islands, Quebrada Demajuana, 5.iv.1962, Malkin (AMNH). Female (paratype of *A. portozuelo* Levi): Chile, Juan Fernandez Islands, El Camote, 25.iv.1962, Malkin (AMNH).

Selkirkiella attrita (Nicolet). Chile: Reg. X. Osorno Prov. , P. N. Puyehue, 700m, 12.xii.2000–2.i.2001, Miller *et al.* (NMNH).

Selkirkiella magallanes. Chile: Magallanes: Camerón, S. Bahía Inutil, Tierra del Fuego, 14.xi.1960, l. Peña (AMNH); male and female paratypes: Chile, Magallanes: Camerón, S. Bahía, inutil, T. del Fuego, 14.xi.1960, Peña (BMNH).

Selkirkiella cf. *magallanes*. Chile: Reg. X. Osorno Prov., P. N. Puyehue, 700m, 12.xii.2000–2.i.2001, Miller *et al.* (NMNH).

Spintharus flavidus Hentz. Costa Rica, Cartago, RF de Rio Macho, 22–26.iii.1999, Miller (NMNH).

Steatoda americana (Emerton). USA, WV, Berkeley Co. 30.v.– 06.vi.1986, Martinat (NMNH).

Steatoda bipunctata (Linnaeus). Slovenia, Sempas, 1998, Kuntner *et al* (NMNH).

Steatoda grossa (C. L. Koch). Male: Brazil, Paraná, 26.xi.1985, Henny (NMNH). Female: USA, CA, Chula Vista, 7.xii.1970, Re (NMNH).

Stemmops bicolor O. P.-Cambridge. Peru, Cuzco Dept, (AMNH).

Stemmops cf. *servus*. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15 vii.1999, Coddington *et al.*, (NMNH).

Stemmops sp. Argentina, Misiones, P. Nac. Igazu, area Cataratas, 11–16.xii.1999, Ramirez & Lopardo (NMNH).

Styposis cf. *selis*. Argentina, Misiones, P. Nac. Igazu, area Cataratas, 11–16.xii.1999, Ramirez & Lopardo (NMNH).

Styposis sp. Colombia, Iguaque, 5°41′20″N 73°26′7.0″W, 3450–3650 m, near margin of Lake Iguaque, 6–8.ii.1998, Hormiga *et al.* (NMNH).

Tekellina sp. Female: Bolivia, Dpto. Beni, Est. Biol. Beni, Zone 1, Plot 04, *c.* 14°47′S; 66°15′W, *c*. 225m. 8–14.xi.1989, Coddington *et al.* (NMNH).

Theridion cochise Levi. USA, Arizona, Pima Co. Santa Rita Mts., 30.ix.2000, Bodner (NMNH).

Theridion frondeum Hentz. Male USA, SC, Pickens Co. Eastatoe, 17.viii.1961, Carico (NMNH). Female USA, MD, Montgomery Co., 30.v.1985, Smith. (NMNH).

Theridion longipedatum Roewer. Colombia, Cauca, PN Purace, 5.x.1992, 2950 m, Florez (ICN).

Theridion pictum (Walckenaer). Male: coded from literature. Female, Russia, NE Siberia, River 12–19.viii.1992, Marusik (NMNH).

Theridion varians Hahn. Slovenia, 23.vii.1999, (NMNH).

Theridula emertoni Levi. Male: USA, NC, Macon Co., 19.vii.1988, (NMNH).

Theridula opulenta (Walckenaer). Male: USA, Georgia, Rabun Co, 28.v.1993, Bond *et al.* (NMNH). Female, USA, SC, Pickens Co., 18.vii.1998, Agnarsson (NMNH).

Thwaitesia margaritifera O. P.-Cambridge. Australia, Mt. Coottha, 1.iii.2000 (NMNH).

Thwaitesia sp. Guyana, Upper Essequibo Reg; 4.42km S of Gunn's Strip, 7–15.vii.1999, Coddington *et al.* (NMNH).

Thymoites anserma Levi. Colombia, Agua Bonita, 4°25′88″N, 74°19′42″W, 2400–2560 m. 1.ii.1998, Hormiga (NMNH).

Thymoites unimaculatum (Emerton). USA, Florida, Orange Co., Corey (NMNH).

Tidarren sisyphoides (Walckenaer). USA, Arizona, Molino Basin, 16.vi.2001, Bodner (NMNH).

Tidarren haemorrhoidale Bertkau. Female: Peru, Cusco, Machupicchu ruins, bamboo/cloud forest, 16.x.1987, Coddington (NMNH).

Wamba crispulus (Simon). Female: USA, Massachusetts, Barnstable Co., Hatchville, 31.vii.1989, Edwards (NMNH).

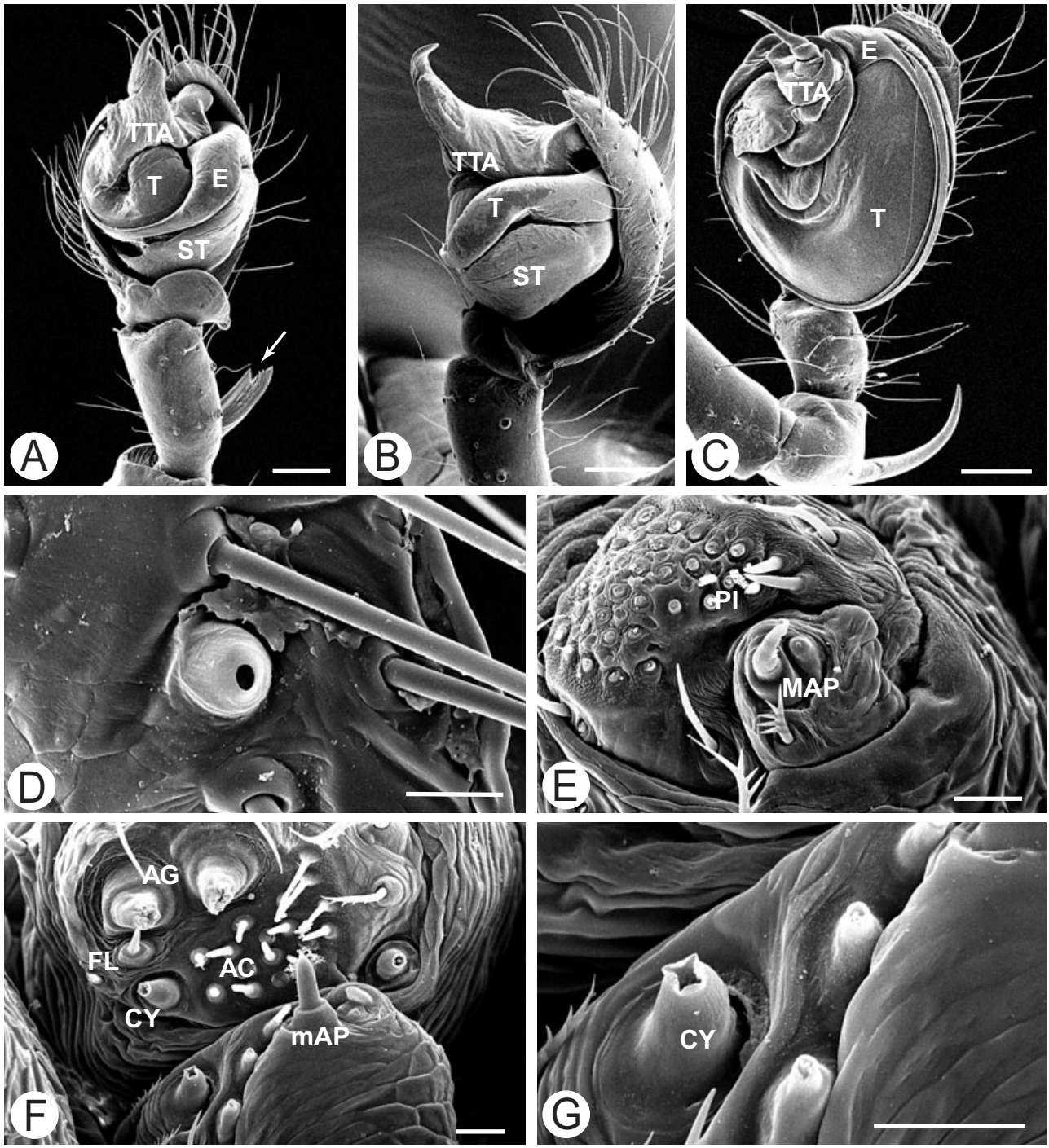

Figure 1. S*ynotaxus*. A, B, *S. monoceros* male palp. Character numbers and states typeset in bold here and in subsequent captions. A, ventral; note spur on patella (arrow) (**20-1**). B, ectal. C, D, *S. waiwai* male palp. C, ventral. D, tarsal organ, with a small opening (**198-0**). E–G, *Synotaxus waiwai*, spinnerets. E, ALS. F, PLS and PMS; note large (**214-1**) but not flattened AGs (**215-0**, **216-0**). G, CY, the fusule bears no distinct base (**221-1**). Scale bars: A–C, 100 μm; D–G, 10 μm.

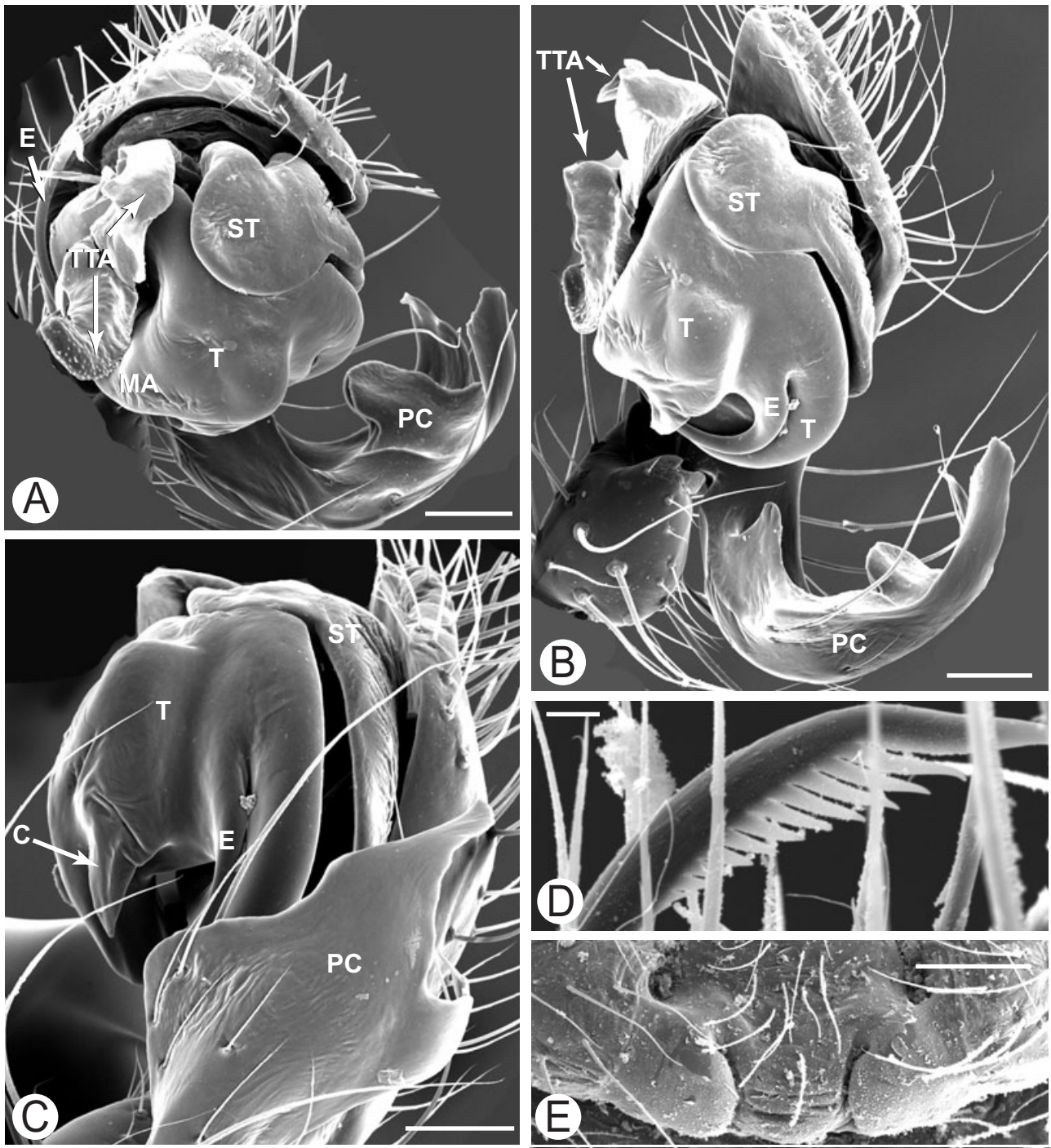

Figure 2. *Nesticus reclusus*. A–C, male palp. A, ventral; note huge PC (**30–5**). B, ectal. C, ectal side from below; note tegular apophysis (paramedian apophysis *sensu* Huber, 1993), which is here hypothesized to be homologous to the conductor (**62-0**). It is positioned caudally on the tegulum near where E originates. D, female tarsal claw. E, epigynum. Scale bars: A–C, E, 100 μm; D, 20 μm.

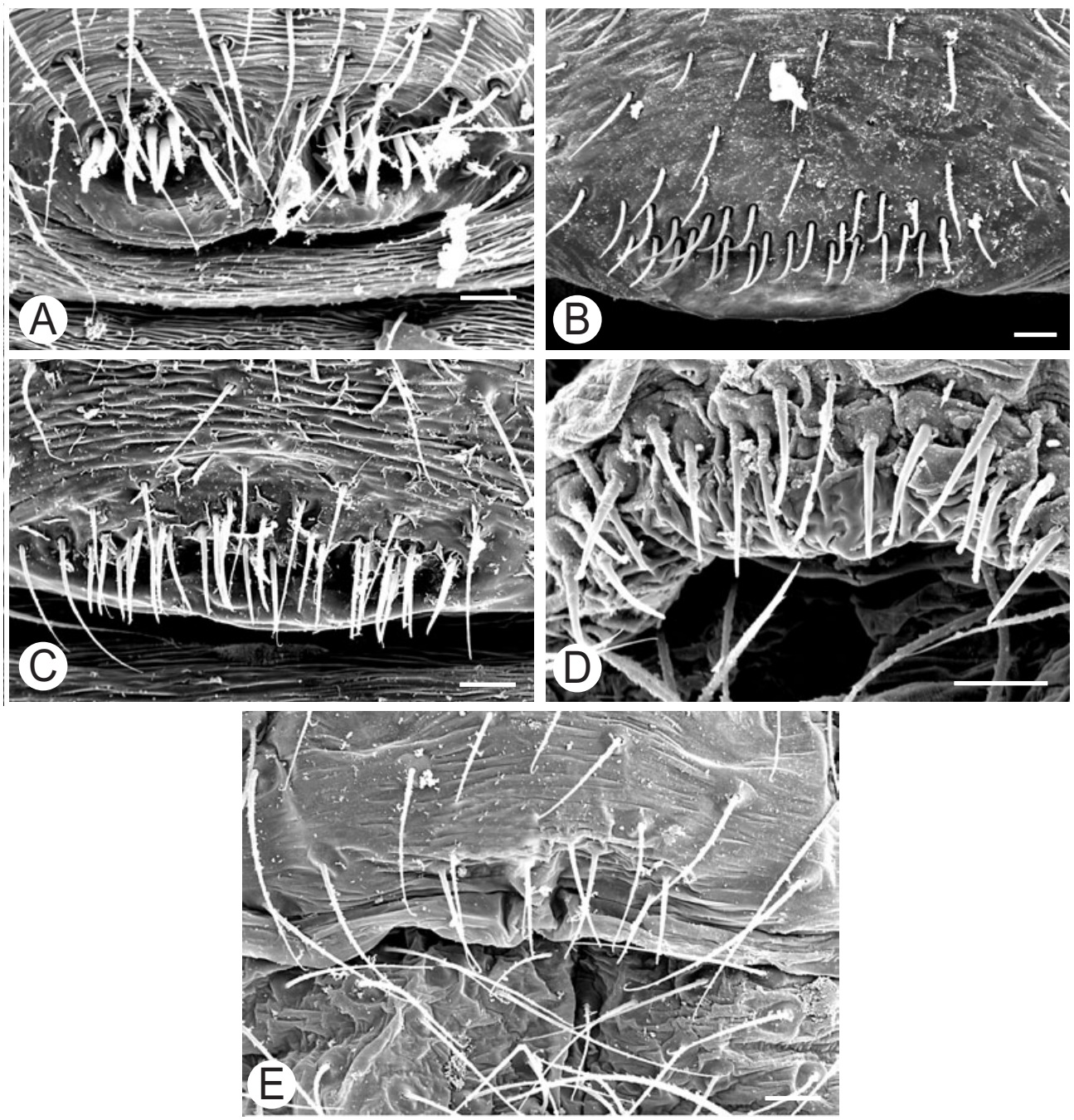

Figure 3. Epiandrous gland spigots (**168–170**). A, *Tetragnatha extensa*. B, *Pimoa breviata*. C, *Linyphia triangularis*. D, *Synotaxus monoceros*. E, *Eidmanella pallida*. Scale bars: 20 μm.

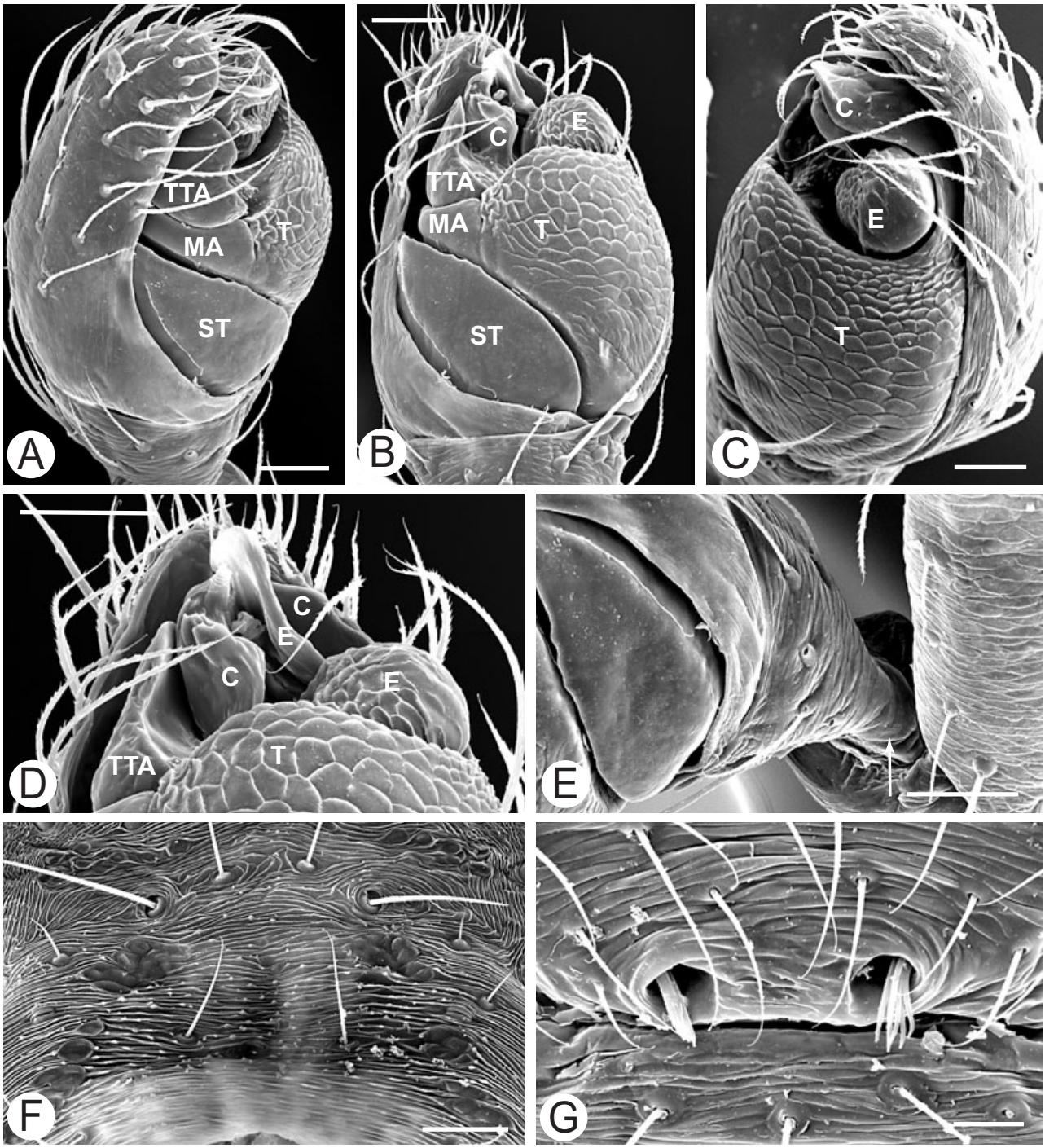

Figure 4. *Dipoena nigra*, male. A–D, palp. A, mesial. B, ventral. C, ectal. D, ventral close; the scaly texture of the tegulum is unique to this species among the taxa explored here. E, apical view of tibia and base of palpus; note broad tibial tip (**14-1**), compared to the extremely narrow base which connects to the much broader patella (arrow). F, area above pedicel on abdomen. G, epiandrous gland spigots. Scale bars: A–F, 50 μm; G, 20 μm.

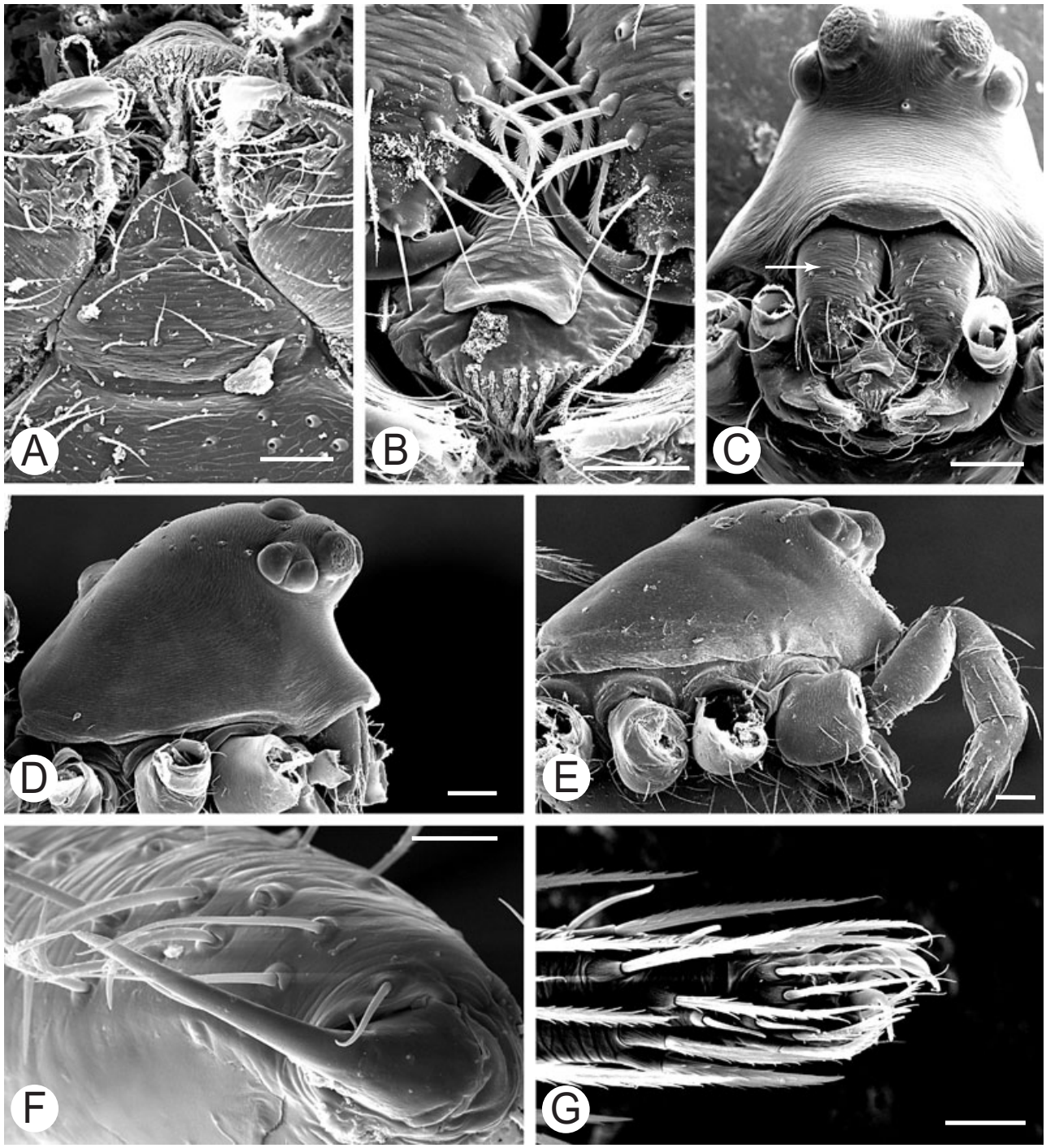

Figure 5. *Dipoena nigra*. A, female labium; the triangular shape is a synapomorphy of Hadrotarsinae (**136-1**). B, tip of male chelicera; note plumate hairs (**121-1**). C, D, male prosoma. C, front view, the short cheliceral paturon (arrow) is a synapomorphy of Hadrotarsinae (**117-1**). D, side view of the elevated prosoma (**124-1**). E, female prosoma side view, less elevated than in male; note also the short and thick segments of the palp. F, female cheliceral fang, both promargin (**106-1**) and retromargin (**110-1**) without teeth. G, tip of male fourth tarsus. Scale bars: A, B, 50 μm; C–E, 100 μm; F, G, 10 μm.

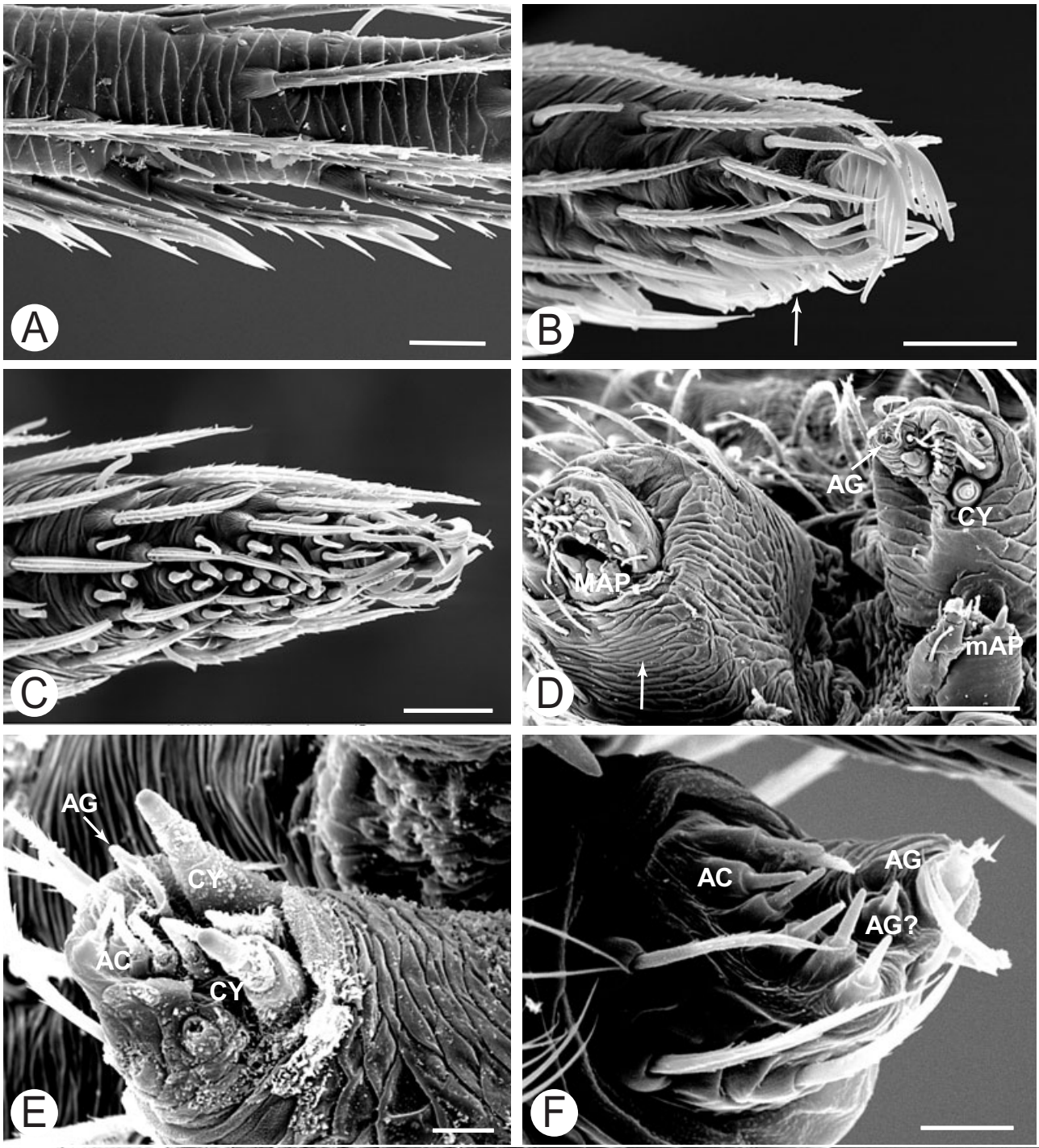

Figure 6. *Dipoena nigra*. A, serrated bristles of tarsal comb (**193-1**, **194-0**, **195-0**); compare to the characteristic theridiid tarsal comb, e.g. *Achaearanea* (Fig. 11E, F). B, C, tip of tarsus I female. B, note presence of grouped flat tipped setae ventrally (arrow), a Hadrotarsinae synapomorphy (**197-1**). C, ventral view. D, female spinnerets, FL is probably absent (**212-1**), the size and shape of the AGs is uncertain, but probably one is enlarged and flattened (**215-1**, see male in F); note also the absence of stridulatory ridges on ALS (arrow, **203-0**), previously thought to be a hadrotarsine synapomorphy. E, *Dipoena torva* female PLS, with a small AG, lacking FL. F, male PLS has a functional (**219-1**), flattened AG, the second non-AC spigot is morphologically similar to FL, but given the condition in the female is probably an AG. Scale bars: A–C, 20 μm; D, 50 μm; E, F, 10 μm.

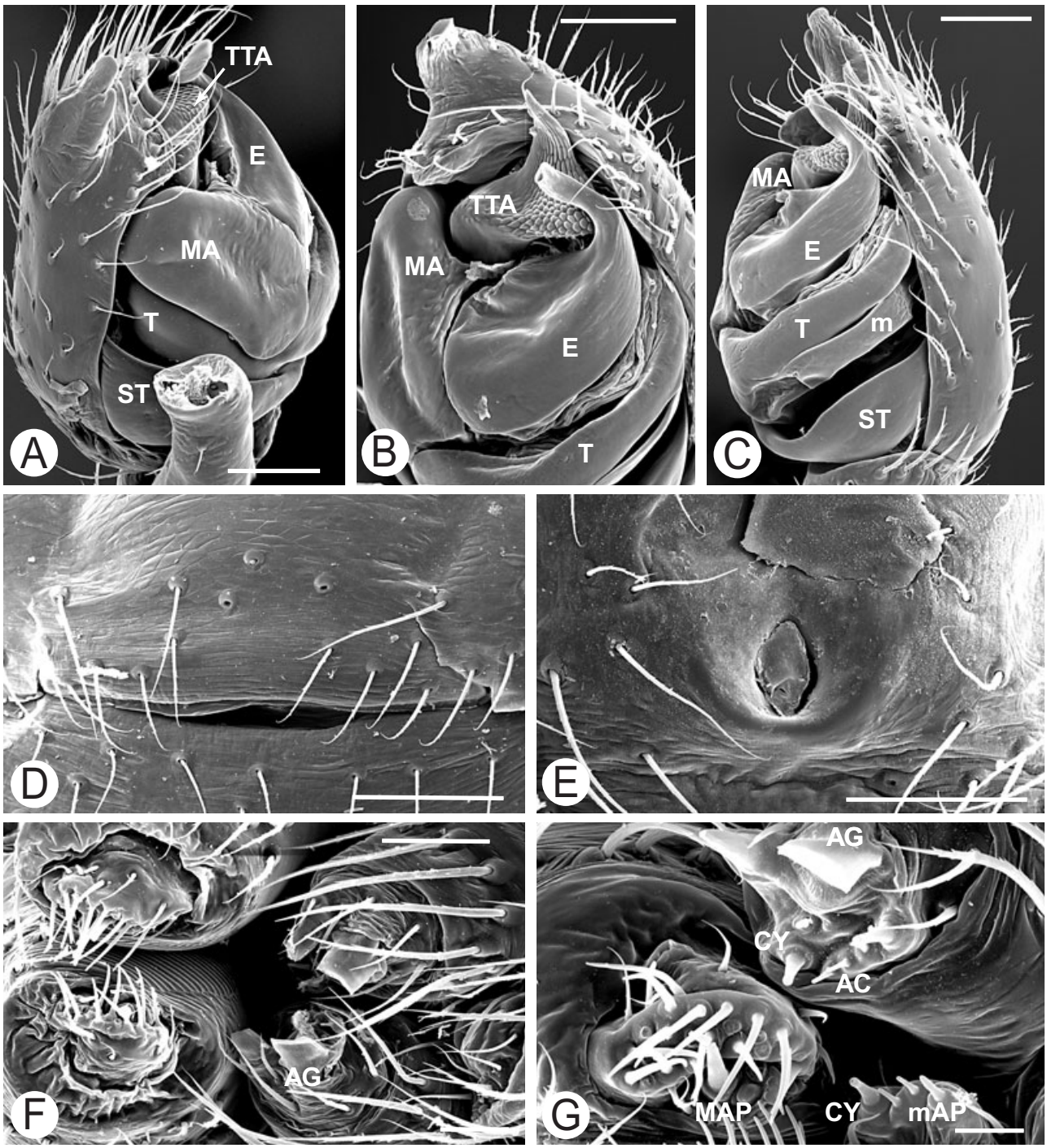

Figure 7. *Euryopis gertschi*. A–C, male palp. A. mesial. B, ventral; note absence of a conductor (**62-1**). C, ectal, the apparent sclerite basal to the tegulum is a membrane (m). D, male genital furrow, epiandrous gland spigots absent (**168-1**). E, epigynum. F, male spinnerets; note presence of functional AG (**219-1**). G, female left spinning field. Scale bars: A–E, 100 μm; F, 50 μm; G, 20 μm.

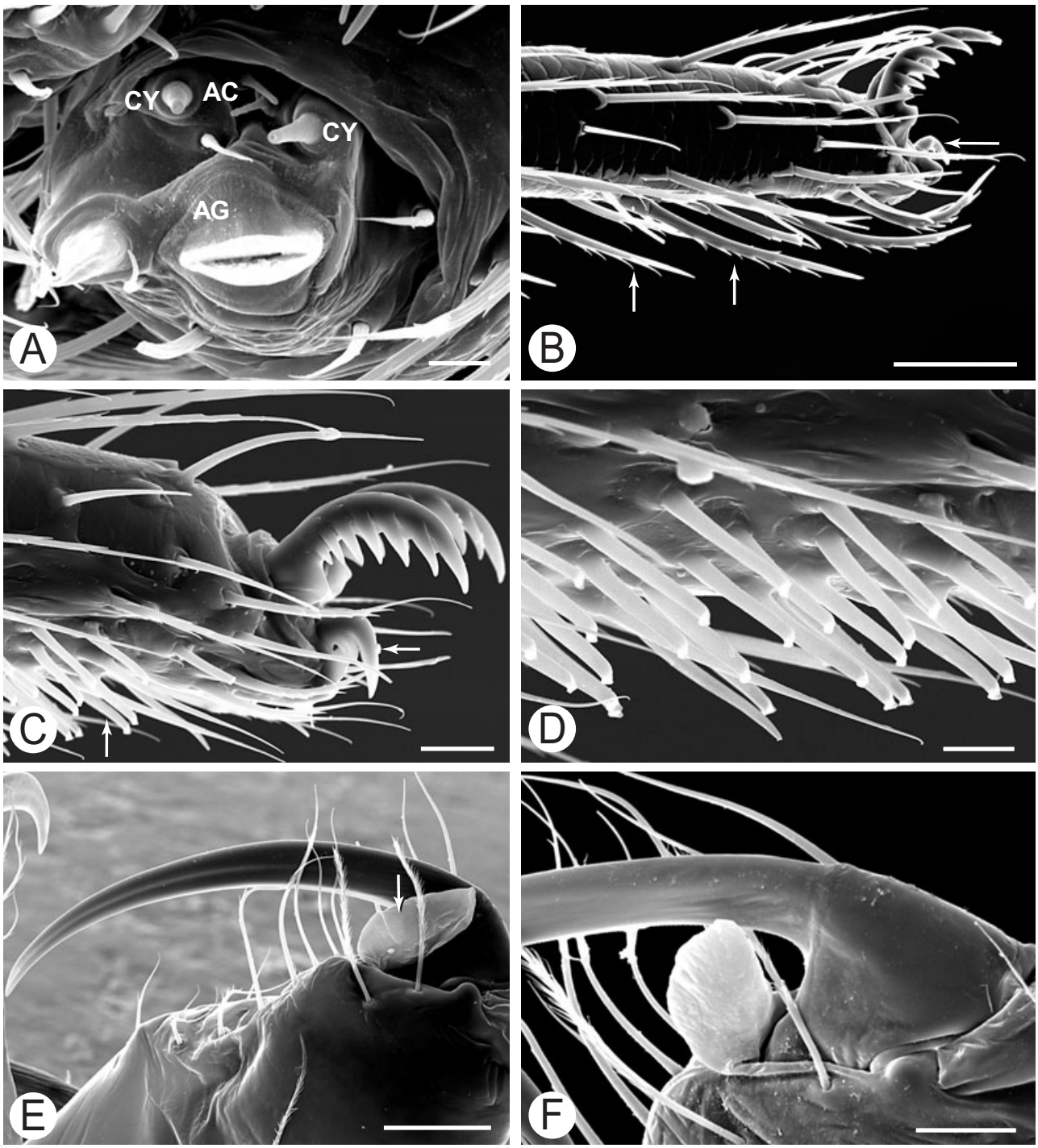

Figure 8. *Euryopis gertschi*. A, female PLS; note absence of FL (**212-1**). B, tip of male tarsus IV; note short central claw (upper arrow, **200-2**) and serrated setae of the hadrotarsine tarsal comb (lower arrows, **193-1**, **194-0**, **195-0**). C, tip of female tarsus I; note short central claw (upper arrow) and grouped flat tipped setae ventrally (lower arrow, **197-1**). D, ventral view of flat tipped setae, probably sense chemicals (taste) by touch. E, long and slender hadrotarsine cheliceral fang (**120-1**); note unusual outgrowth at base (arrow). F, details of cuticular outgrowth at base of male fang; this is the only species in which I have seen this structure, and its function (if any) is unknown. Scale bars: A, D, 10 μm; B, E, 50 μm; C, F, 20 μm.

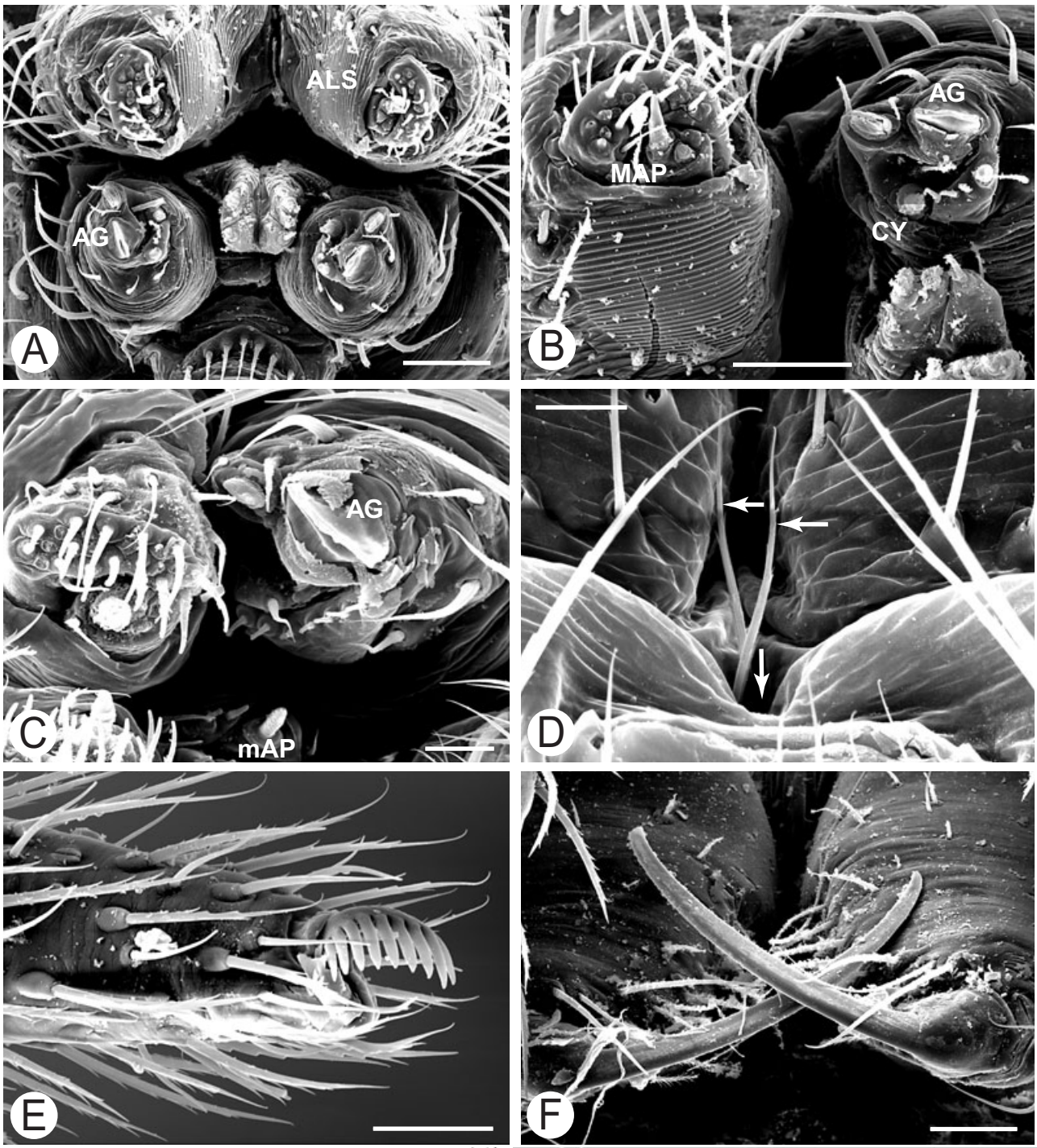

Figure 9. *Euryopis* and *Emertonella*. A–D, spinnerets. A, B, female *Euryopis flavomaculata*. A, all. B, ditto, left spinning field; note ridges on ALS (**203-1**) and the absence of FL on PLS (**212-1**). C, D, *Emertonella funebris* male. C, left field; note presence of functional AG (**219-1**). D, colular setae; note invagination of the colular area (vertical arrow, **172-2**), and the pair of long colular setae (horizontal arrows). E, *E. flavomaculata* palpal claw; the palmate condition (**177-1**) is a synapomorphy of Hadrotarsinae. F, ditto, cheliceral fangs. Scale bars: A, B, E, F, 50 μm; C, D, 20 μm.

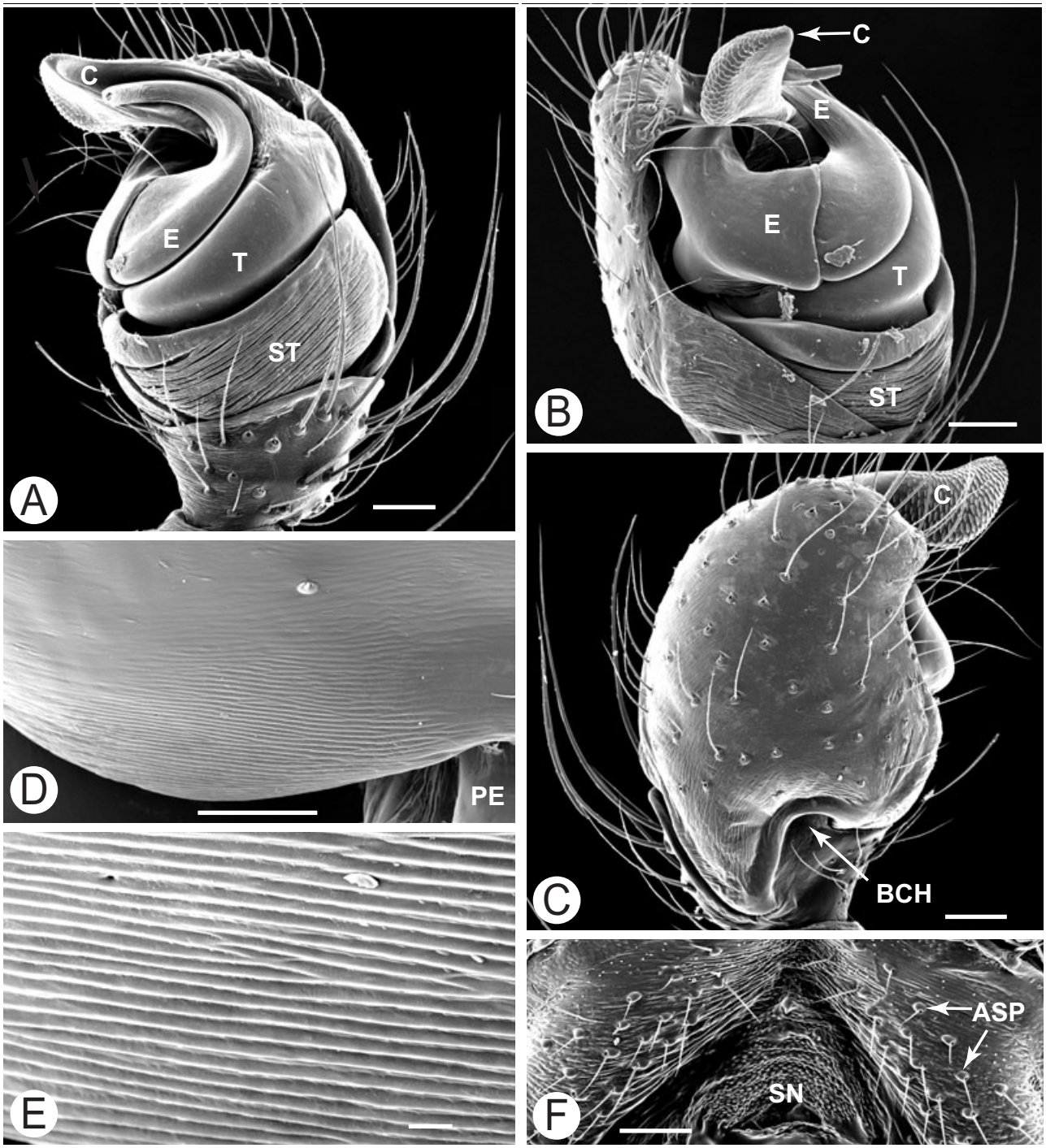

Figure 10. *Achaearanea tepidariorum*. A–C, male palp. A, ventral. B, retrolateral; note split in the embolus (**94-1**). C, dorsal, the BCH (**23-1**) is a putative synapomorphy of *Achaearanea*. D, E, dorsal portion of male prosoma, showing stridulatory ridges (**128-1**) near the pedicel (PE). F, male abdomen, showing SPR (**150-1**) and nubbins (SN, **149-1**) around the pedicel, the additional stridulatory picks (ASP) are found in *Achaearanea* and some other theridiines (**162-1**). Scale bars: A–D, F, 100 μm; E, 10 μm.

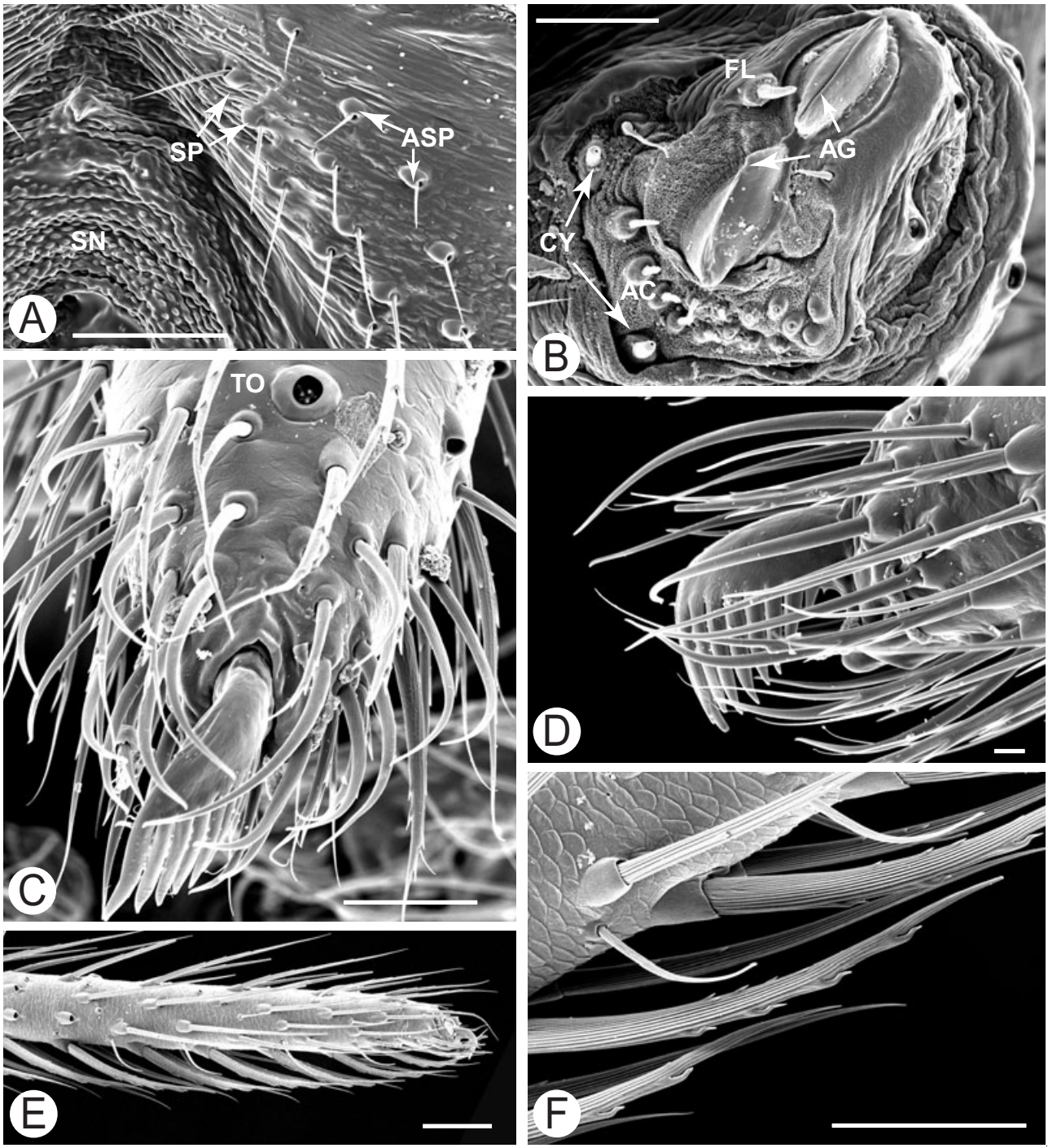

Figure 11. *Achaearanea tepidariorum*. A, male SPR and nubbins. B, female PLS. C, D, female palpal claw, showing semi palmate condition (**177-2**). E, F, female fourth tarsus. E, theridiid tarsal comb (**193-1**). F, individual setae of the tarsal comb with longitudinal grooves (**194-1**), and hooked comb condition (**195-1**). Scale bars: A, E, F, 100 μm; B, C, 50 μm; D, 10 μm.

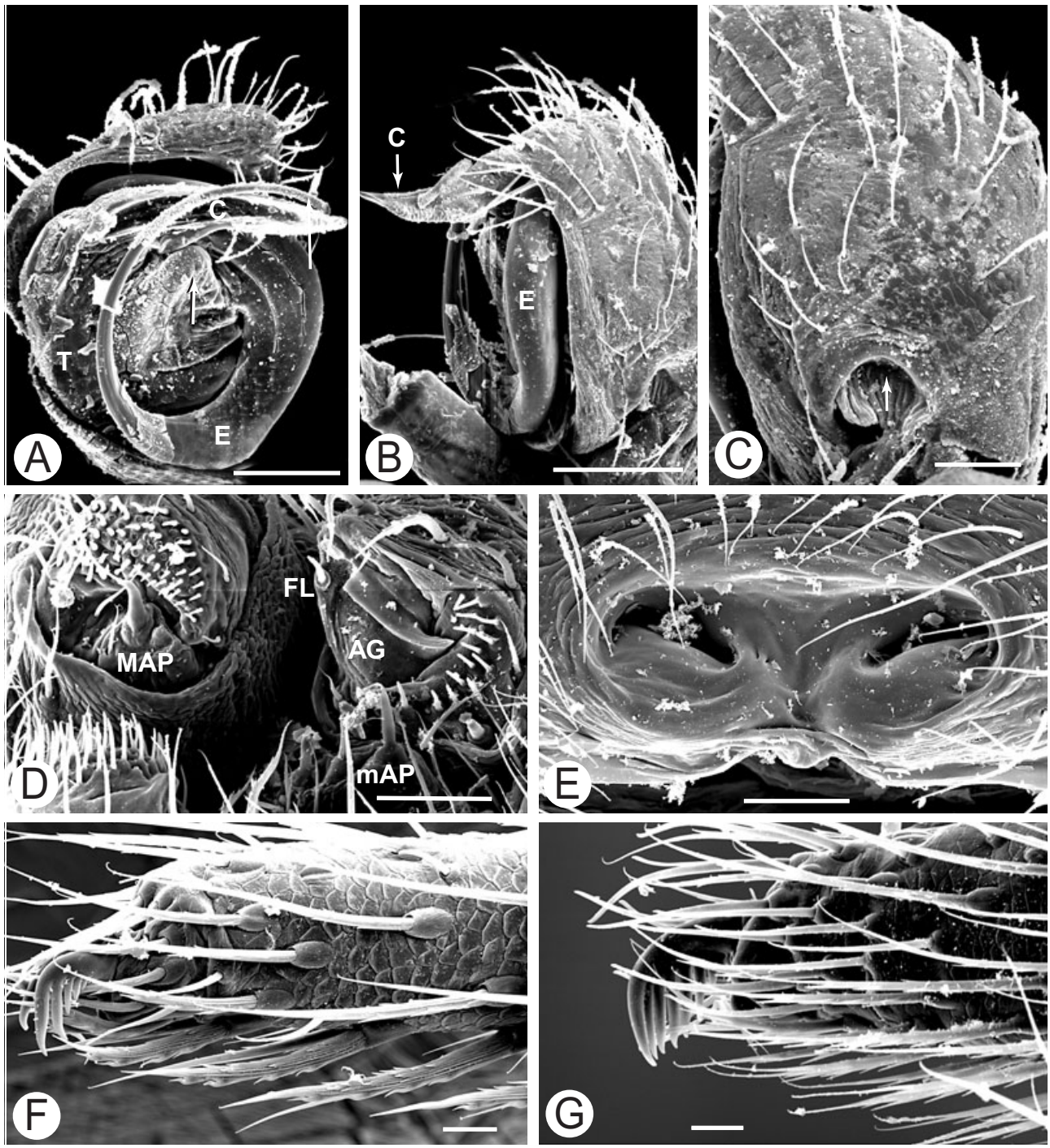

Figure 12. *Achaearanea wau.* A–C, male palp. A, ventral. B, ectal. C, dorsal; note cymbial modification (arrow, **23-1**). D, female spinnerets. E, epigynum. F, fourth tarsal claws and comb. G, palpal claw. Scale bars: A–C, 100 μm; D, E, 50 μm; F, G, 20 μm.

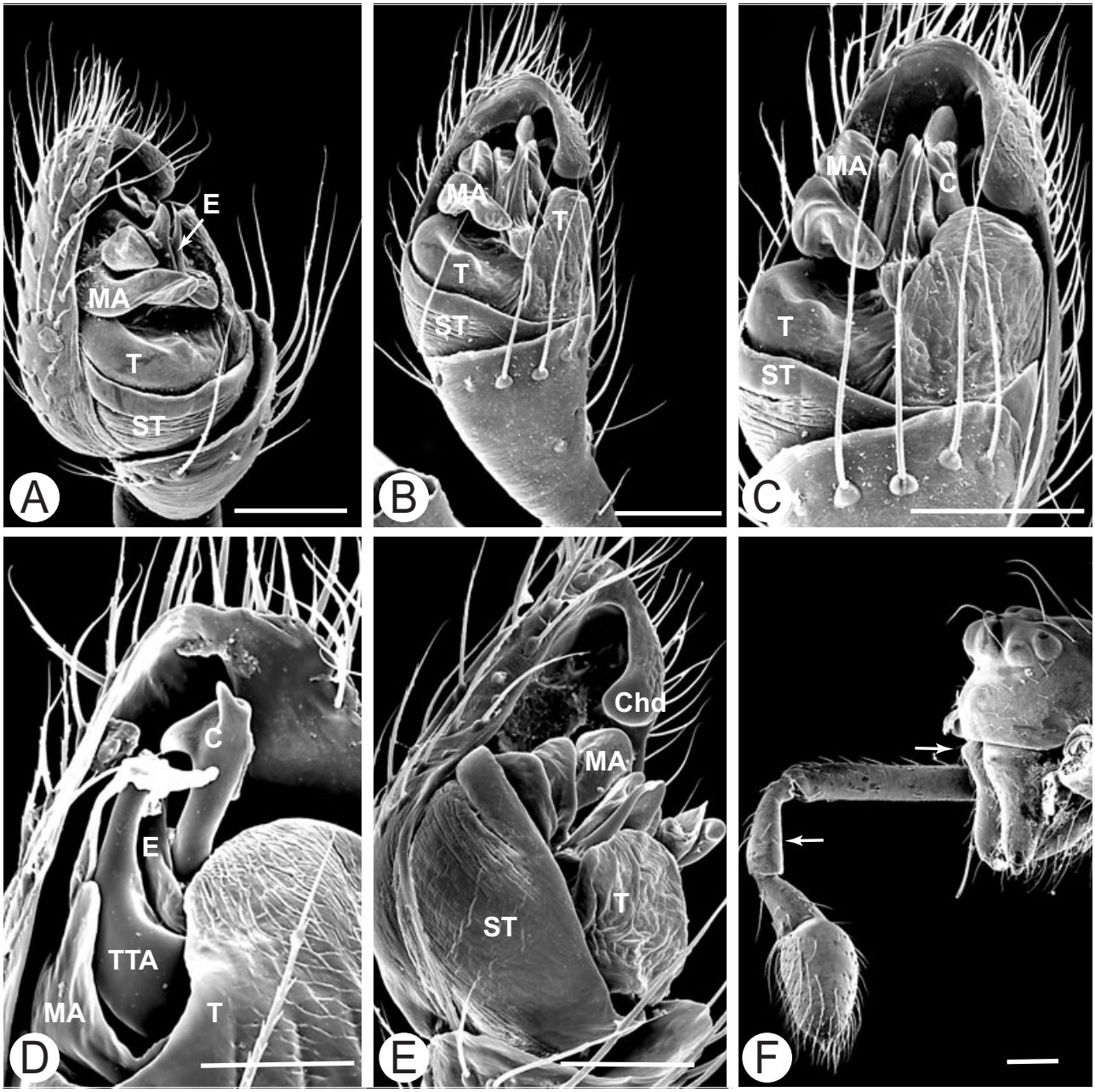

Figure 13. *Ameridion*, male. A–C, *Ameridion* nr. *petrum*, palp. A, mesial. B, ventral; note elongated tibia. C, ventral close-up. D, E, *Ameridion* sp. palp. D, mesial. E, expanded; note cymbial outgrowth containing Chd (**22-1**). F, *Ameridion* nr. *petrum*, prosoma and left palp; note basal cheliceral knobs (upper arrow, **115-1**) and a relatively long palpal tibia (lower arrow). Scale bars, A–C, E, F, 100 μm; D, 50 μm.

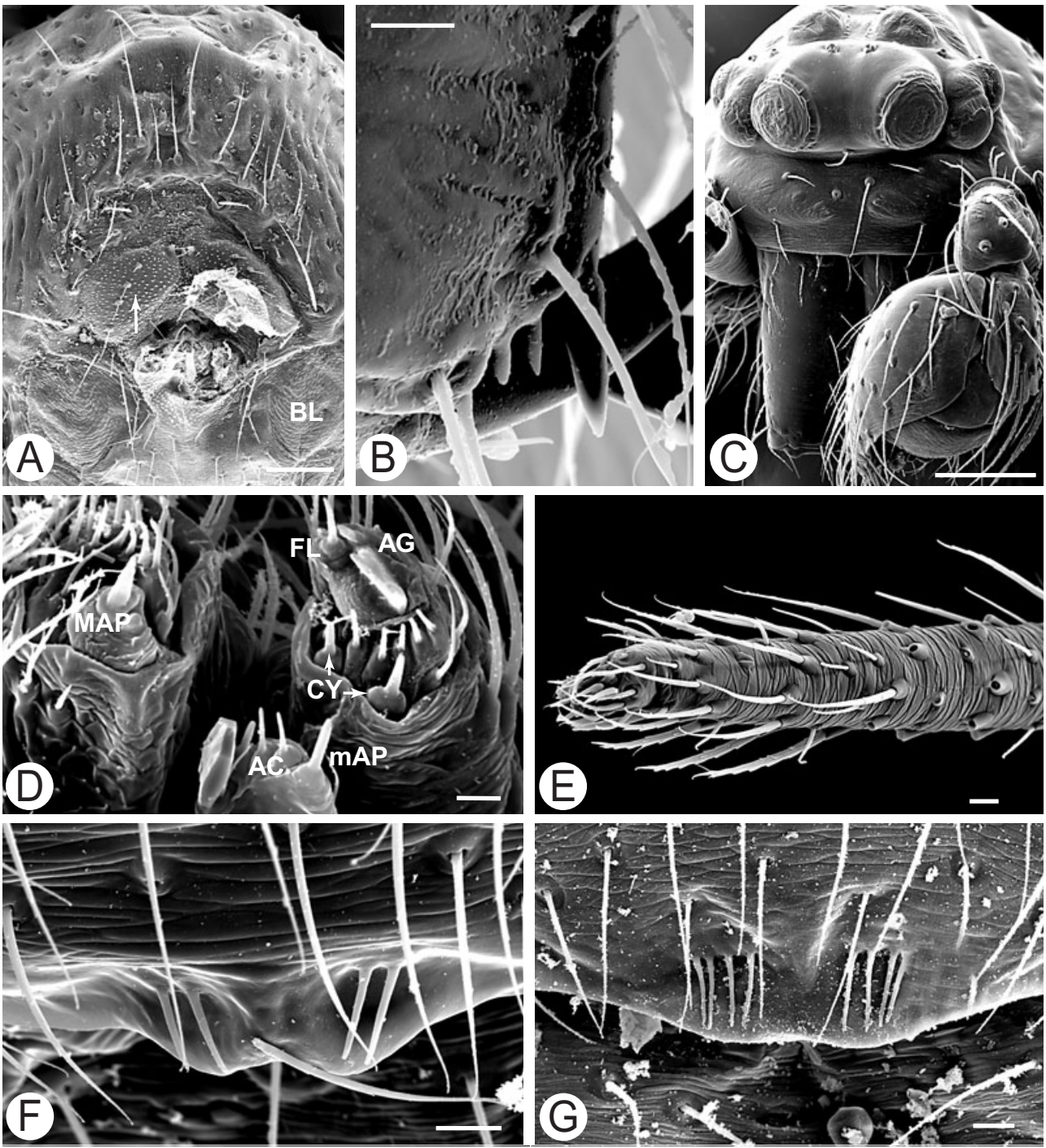

Figure 14. *Ameridion* nr. *petrum*. A, ventral side of abdomen; note SPR (arrow, **150-1**). B, promarginal cheliceral teeth (**106-0**). C, front view of male prosoma; note enlarged AM eyes. D, female spinning field. E, female fourth tarsus. F, epiandrous gland spigots. G, *Ameridion* sp., epiandrous gland spigots. Scale bars: A, C, 100 μm; B, D–G, 10 μm.

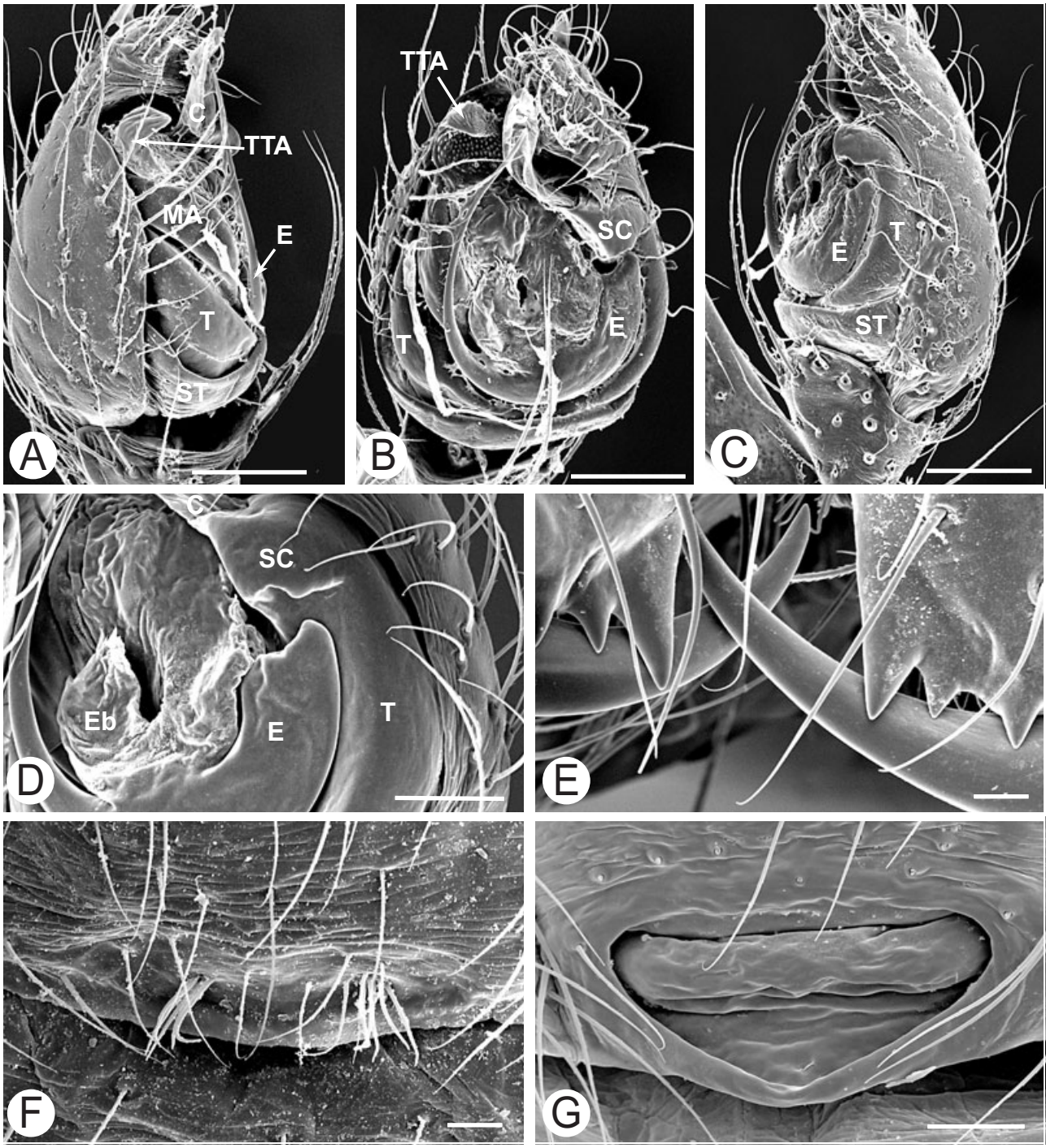

Figure 15. *Anelosimus analyticus*. A–D, male palp. A, mesial. B, ventral. C, ectal. D, details of E and T. E, female cheliceral promargin. F, epiandrous gland spigots. G, epigynum. Scale bars: A–C, 100 μm; D, G, 50 μm; E, F, 20 μm.

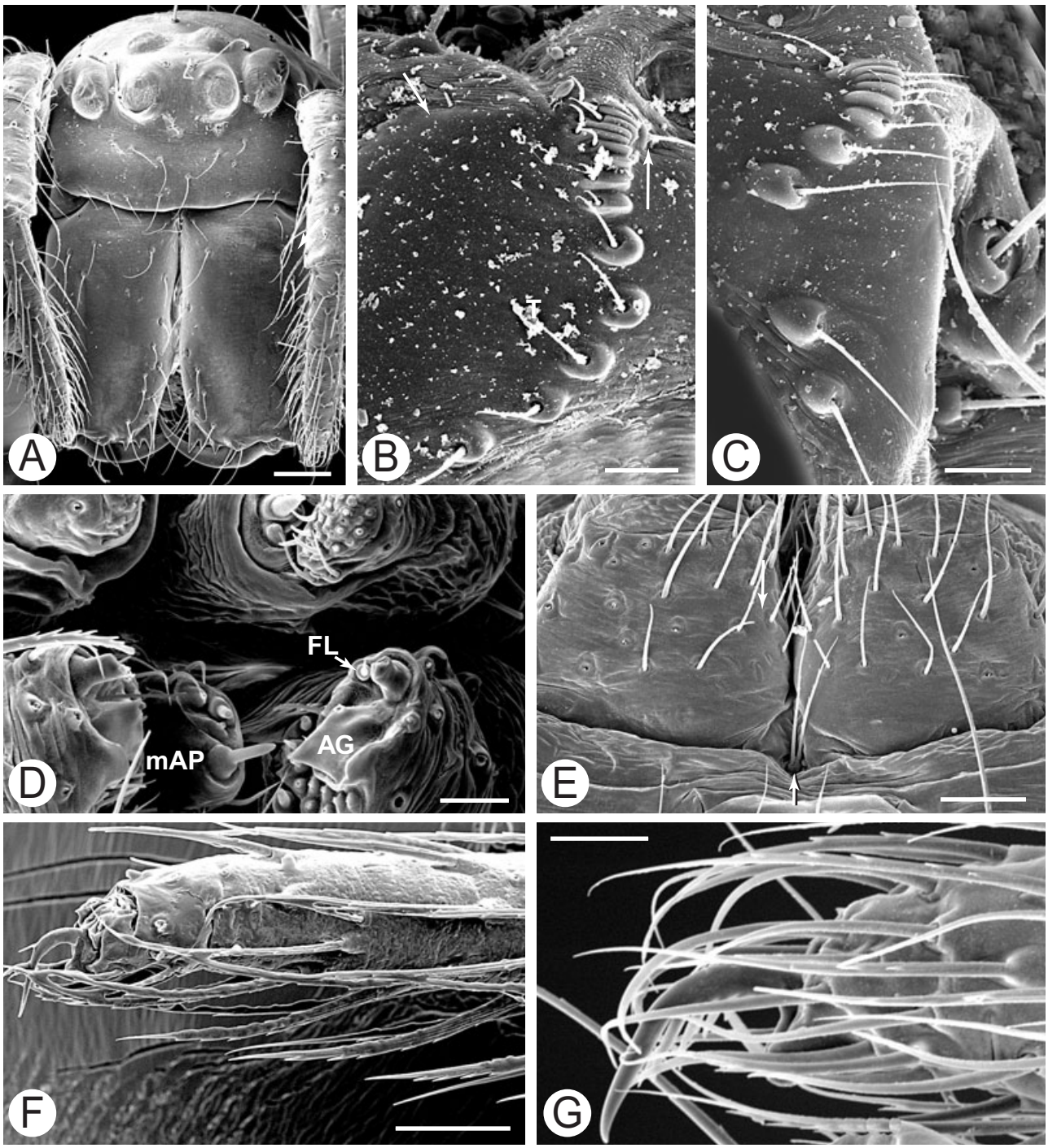

Figure 16. *Anelosimus analyticus*. A, female prosoma, front view. B, C, male stridulatory picks. B, left side; note inverse position of top spine (arrow). C, right side, same animal. D, E, female spinnerets. D, left field. E, colular setae (arrow). F, female tarsal comb. G, details of the comb's serrated bristles. Scale bars: A, 100 μm; B–D, G, 20 μm; E, F, 50 μm.

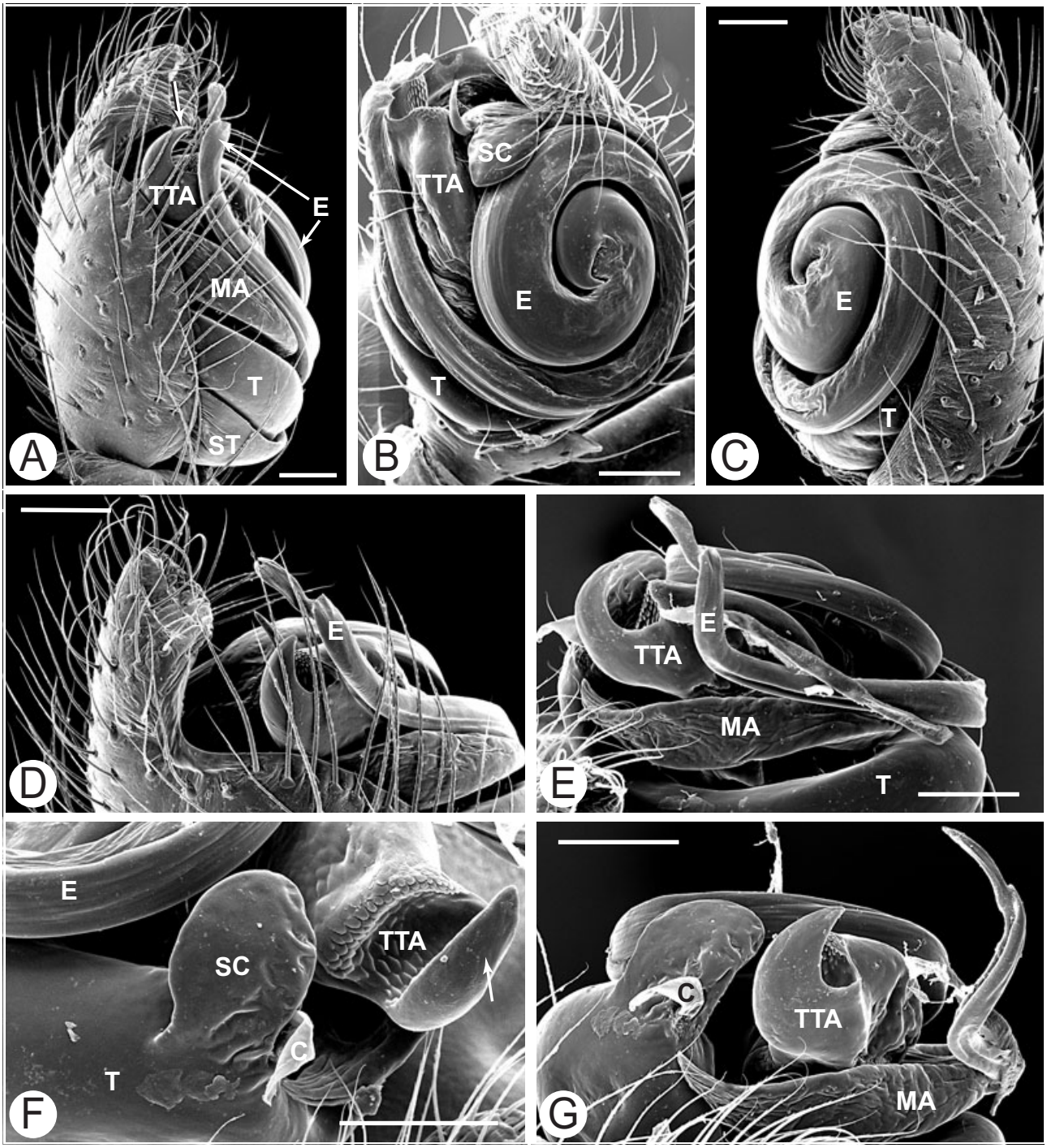

Figure 17. *Anelosimus eximius*, male palp. A, mesial; note hooked TTA tip (arrow, **85-1**). B, ventral. C, ectal. D, mesial tip of palp. E, view of expanded palpal sclerites. F, details of SC (**70-1**) and TTA with a hooked tip (arrow). G, conductor rising out of the side of the SC, the SC was interpreted as the C by Levi & Levi (1962) and Coddington (1990a). Scale bars: A–G, 100 μm.

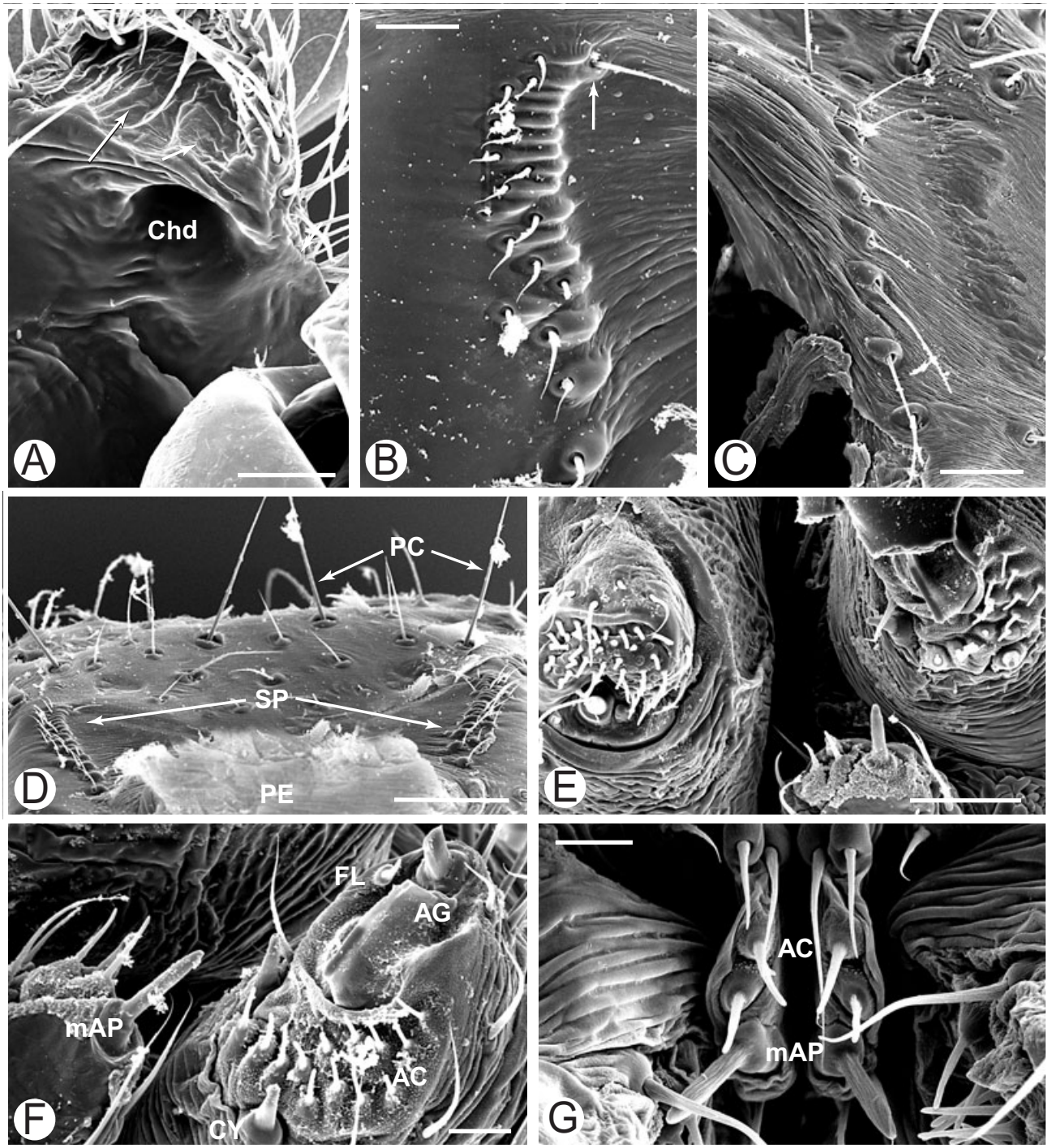

Figure 18. *Anelosimus eximius*. A, tip of cymbium of the expanded palp; note depressed tip (arrow), the light sclerotization of the cymbial tip is a synapomorphy of *Anelosimus* (**26-1**). B, male SPR; curvy rows (**159-1**) are characteristic of some *Anelosimus*. C, the much less pronounced female picks. D, male SPR area; note also proprioreceptic setae (PR, left arrow points toward a dorsal (11 o'clock) proprioreceptor, **163-1**). E, female spinnerets. F, female PLS and PMS. G, male PMS. Scale bars: A–D, 50 μm; E–G, 20 μm.

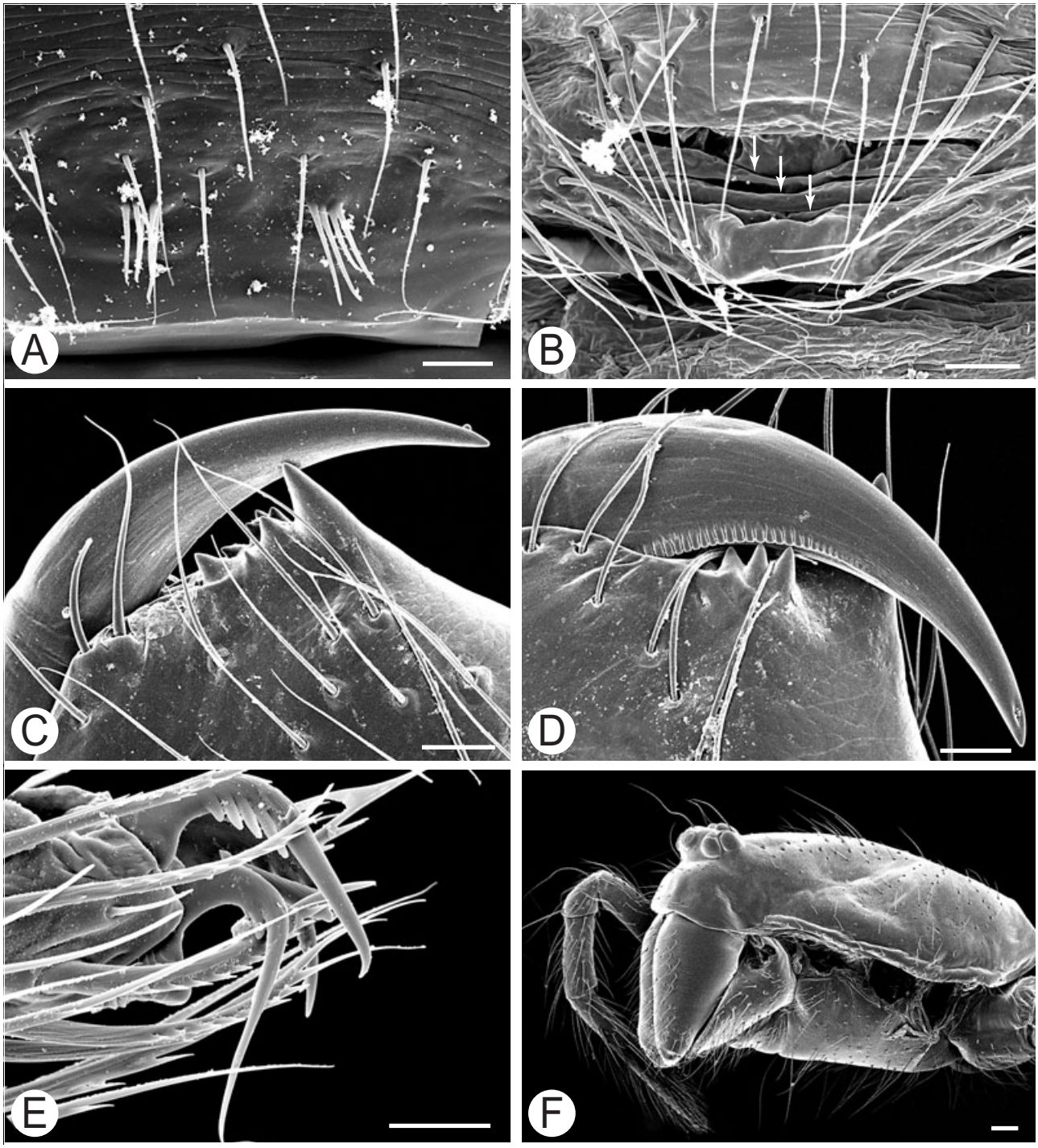

Figure 19. *Anelosimus eximius*. A, epiandrous gland spigots. B, epigynum; note ridges on epigynal plate (arrows, **3-1**). C, prolateral cheliceral margin. D, retrolateral cheliceral margin. E, male fourth tarsal claws. F, female prosoma. Scale bars: A, C–E, 20 μm; B, 50 μm; F, 100 μm.

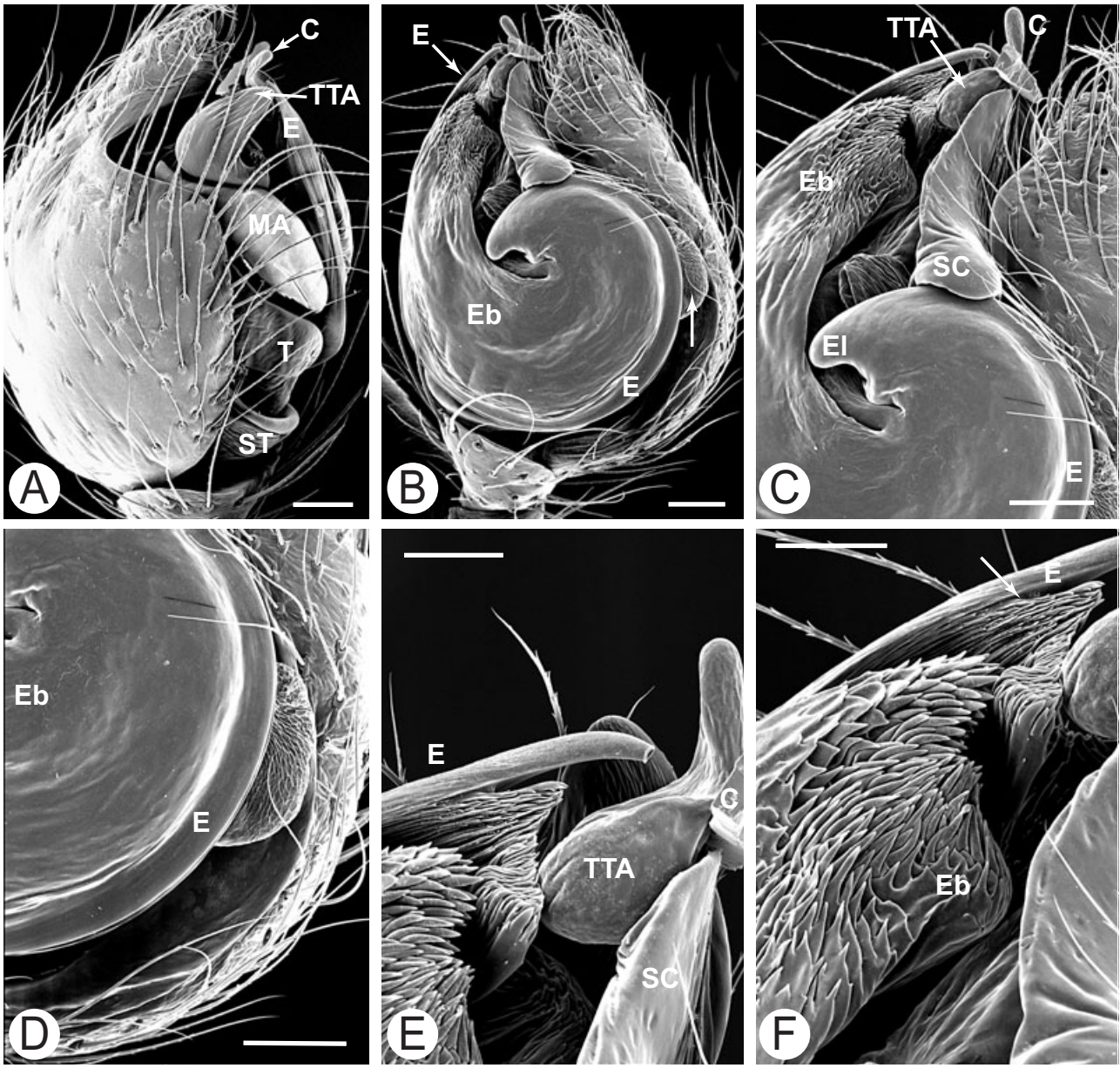

Figure 20. *Anelosimus* cf. *jucundus*, male palp. A, mesial; note deep cymbial incision, an *Anelosimus* synapomorphy (**25-1**). B, ventral; note ectal outgrowth of the tegulum (arrow, closer view in D, **46-1**). The embolus spiral is split along nearly its entire length, forming a thin sclerotized part containing the duct (the E) and the large embolic division b (Eb, **99-1**). C, distal tip, ventral. D, details of basal portion of E, the tegular outgrowth unique to *A.* cf. *jucundus*. E, apical part. F, details of ridge on E, Eb; note forked E tip (arrow, **88-1**). Scale bars: A–D, 100 μm; E, F, 50 μm.

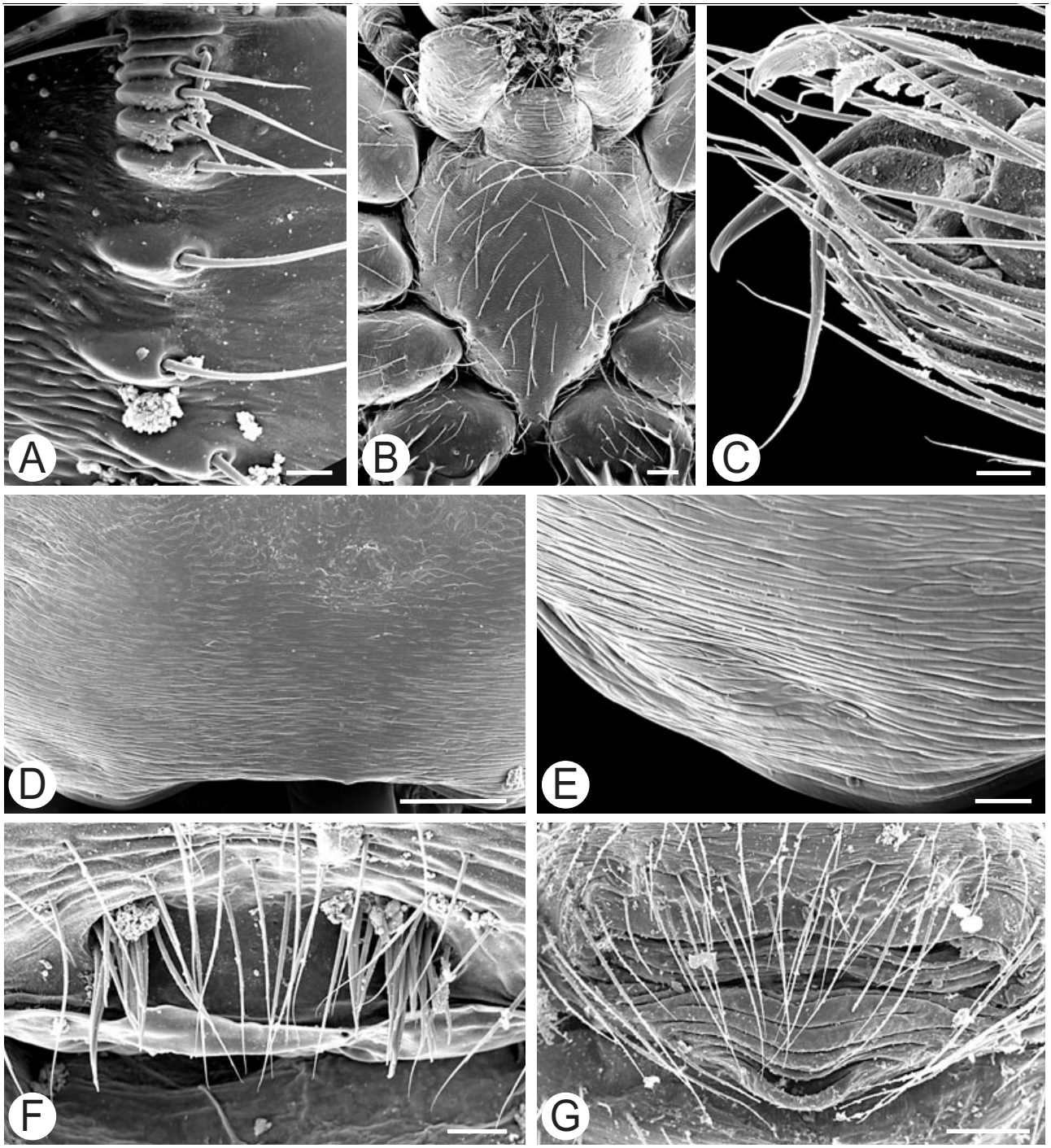

Figure 21. *Anelosimus* cf. *jucundus*. A–F, male. A, SPR. B, sternum. C, fourth tarsal claws. D, posterior margin of prosoma, lacking regular stridulatory ridges, but with patches of irregular rugosity (**128-0**). E, details of the irregular, possibly stridulatory, surface. F, epiandrous gland spigots. G, epigynum. Scale bars: A, C, 50 μm; B, D, G, 100 μm; E, F, 20 μm.

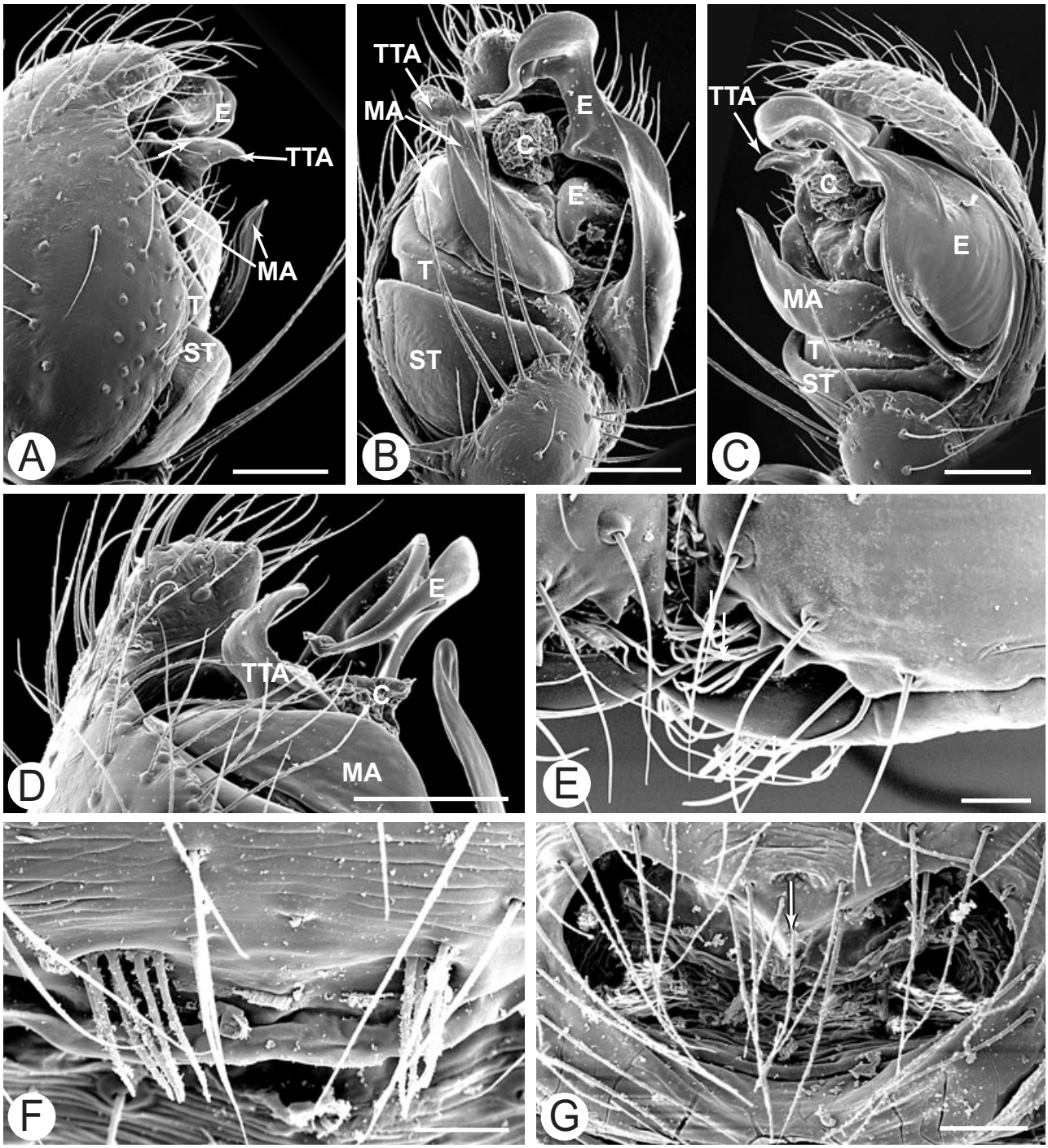

Figure 22. *Anelosimus rupununi*. A–D, male palp. A, mesial; note bifurcated MA (**75-1**). B, ventral. C, ectal. D, distal tip. E, cheliceral promarginal teeth. F, epiandrous gland spigots. G, epigynum; note acute upper wall of bursa (arrow, **6-1**). Scale bars: A–D, 100 μm; G, 50 μm; E, F, 20 μm.

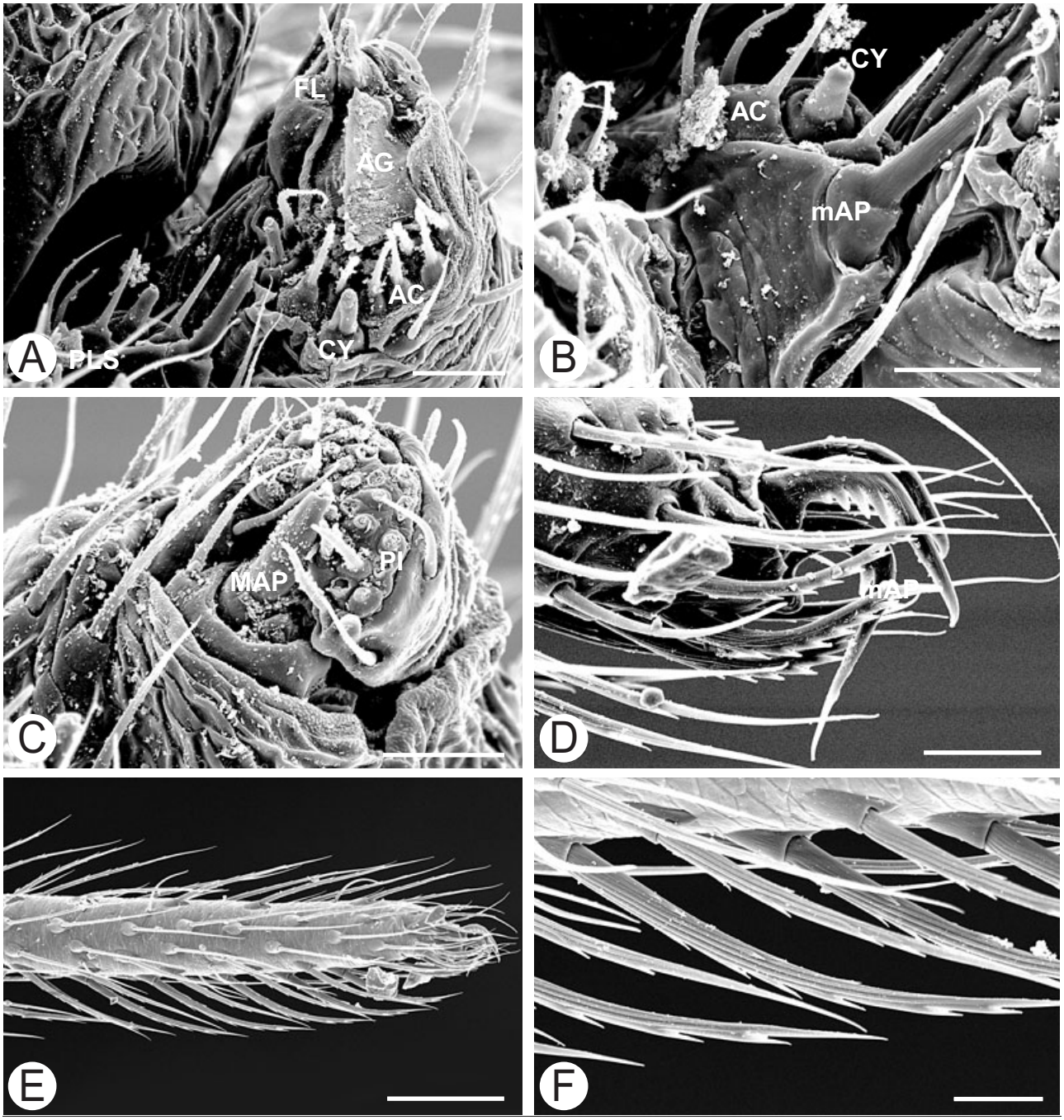

Figure 23. *Anelosimus rupununi*, female. A, PLS. B, PMS. C, ALS. D, fourth tarsal claws. E, tarsal comb on fourth tarsus. F, details of serrated setae. Scale bars: A–D, F, 20 μm; E, 100 μm.

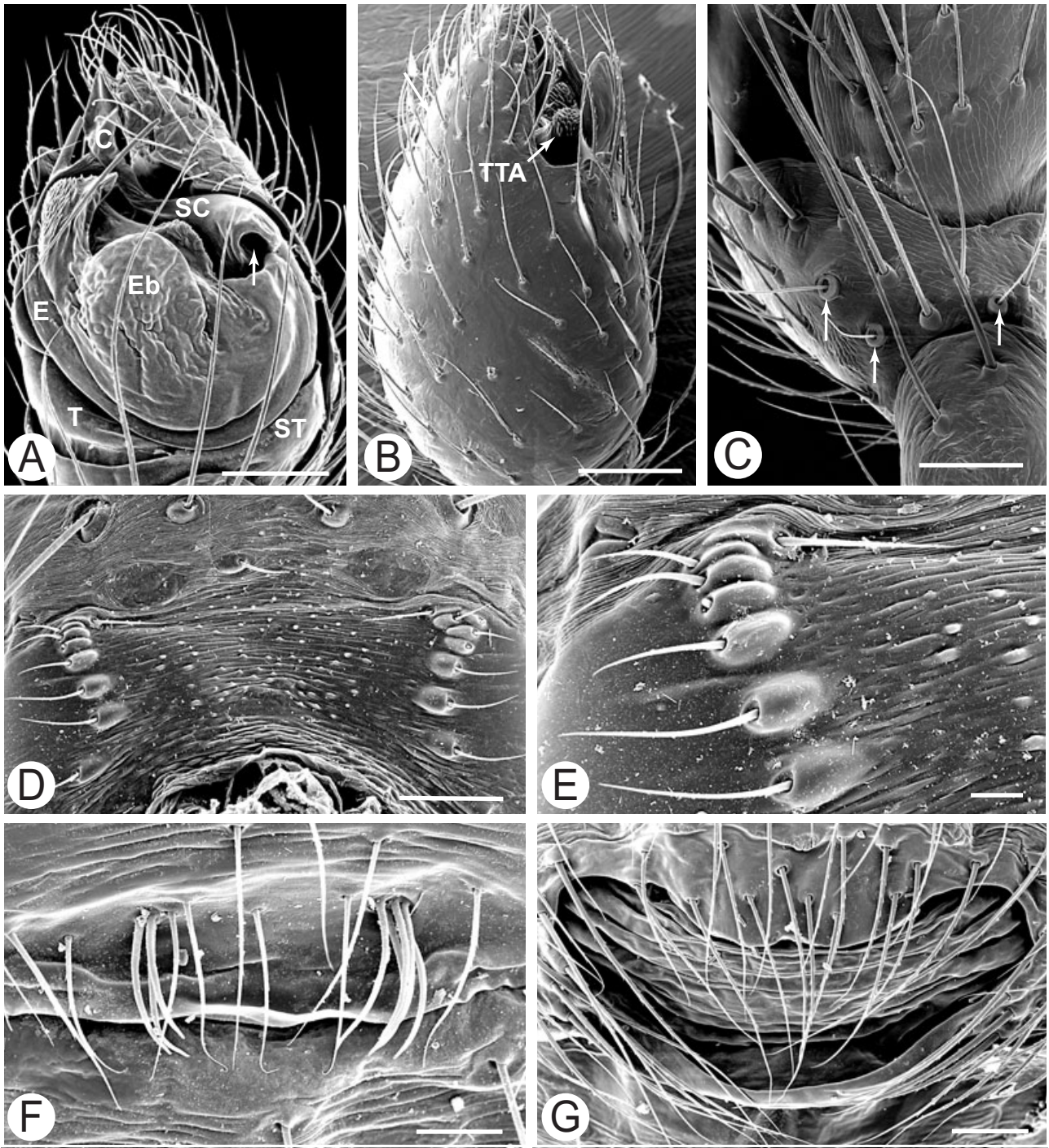

Figure 24. *Anelosimus studiosus*. A–C, male palp. A, ventral. B, dorsal. C, tibia; note three trichobothria (arrows, **18-1**, **19-1**). D, male abdominal stridulatory picks. E, details. F, epiandrous gland spigots. G, epigynum. Scale bars: A–C, 100 μm; D, G, 50 μm; F, 20 μm; E, 10 μm.

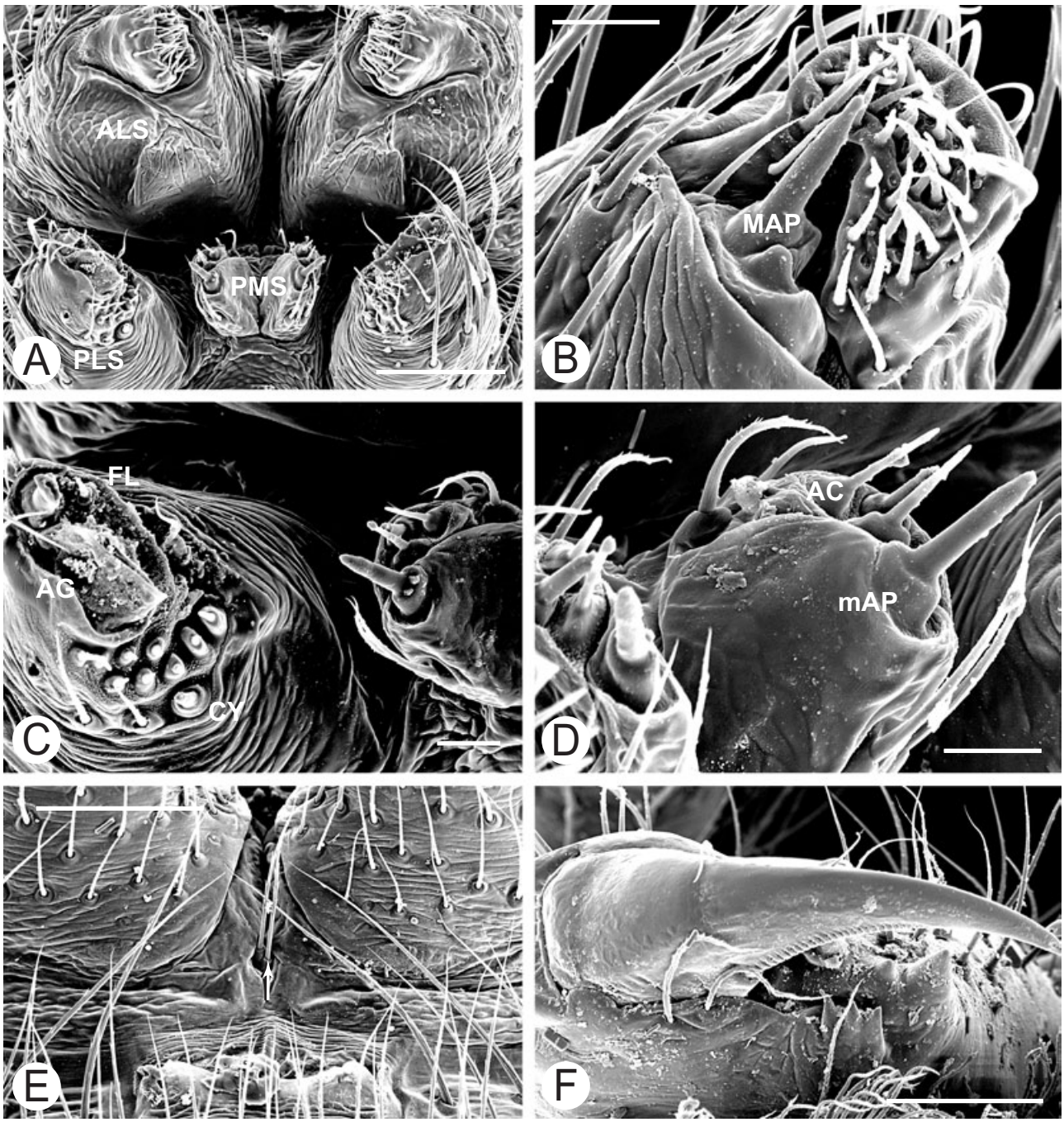

Figure 25. *Anelosimus studiosus*, female. A, spinnerets. B, ALS. C, PLS. D, PMS. E, colular setae (arrow); note absence of colulus (**172-1**). F, cheliceral teeth. Scale bars: A, E, F, 100 μm; B–D, 20 μm.

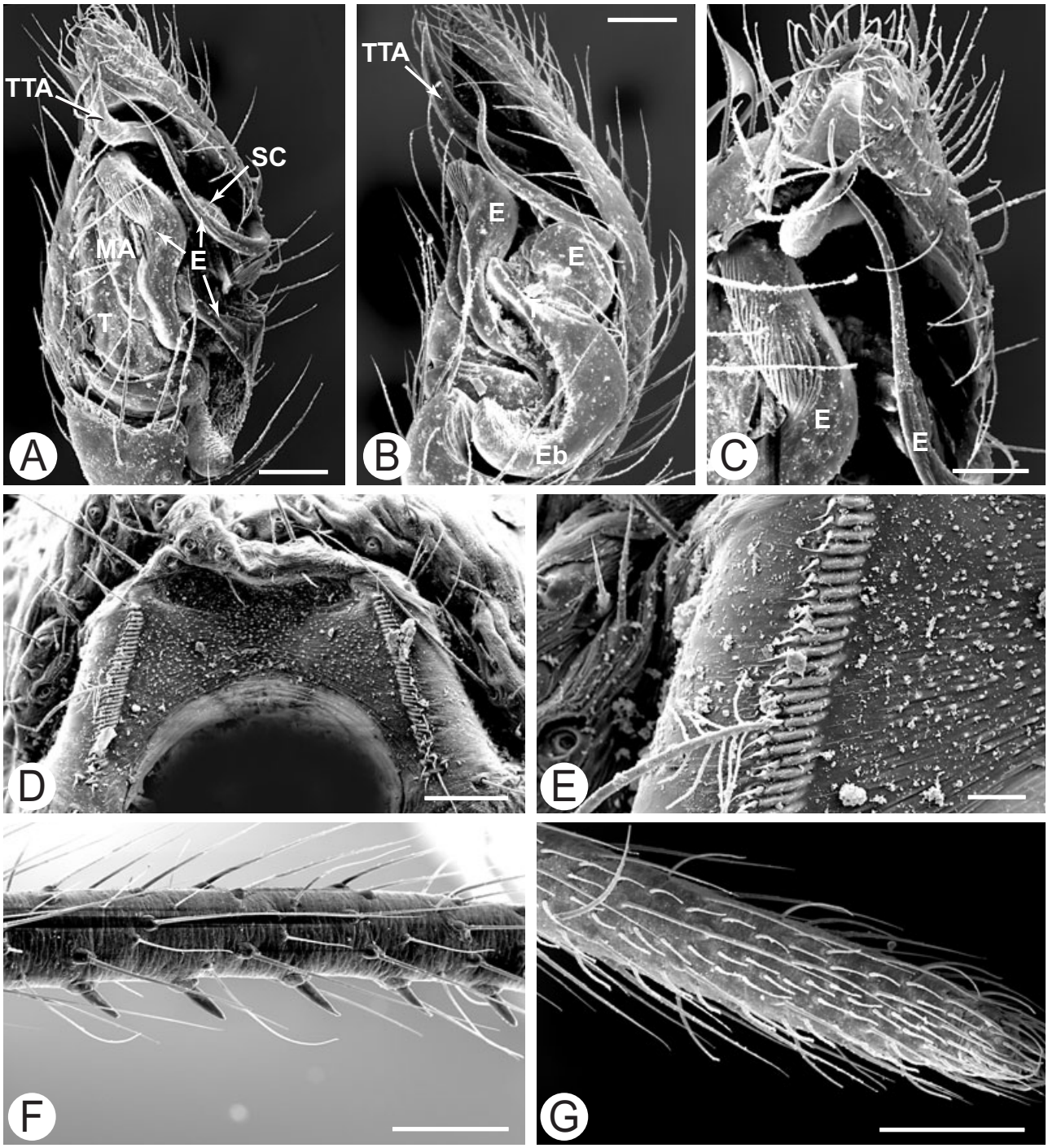

Figure 26. *Anelosimus vittatus*, male. A–C, palp. A, ventral. B, ectal. C, close-up of E, TTA. D, E, male SPR. D, view above the pedicel. E, details of a single row. F, metatarsus I. The sturdy ventral setae are found in many *Anelosimus*. G, tarsus I ventral. Scale bars: A–D, F, G, 100 μm; E, 20 μm.

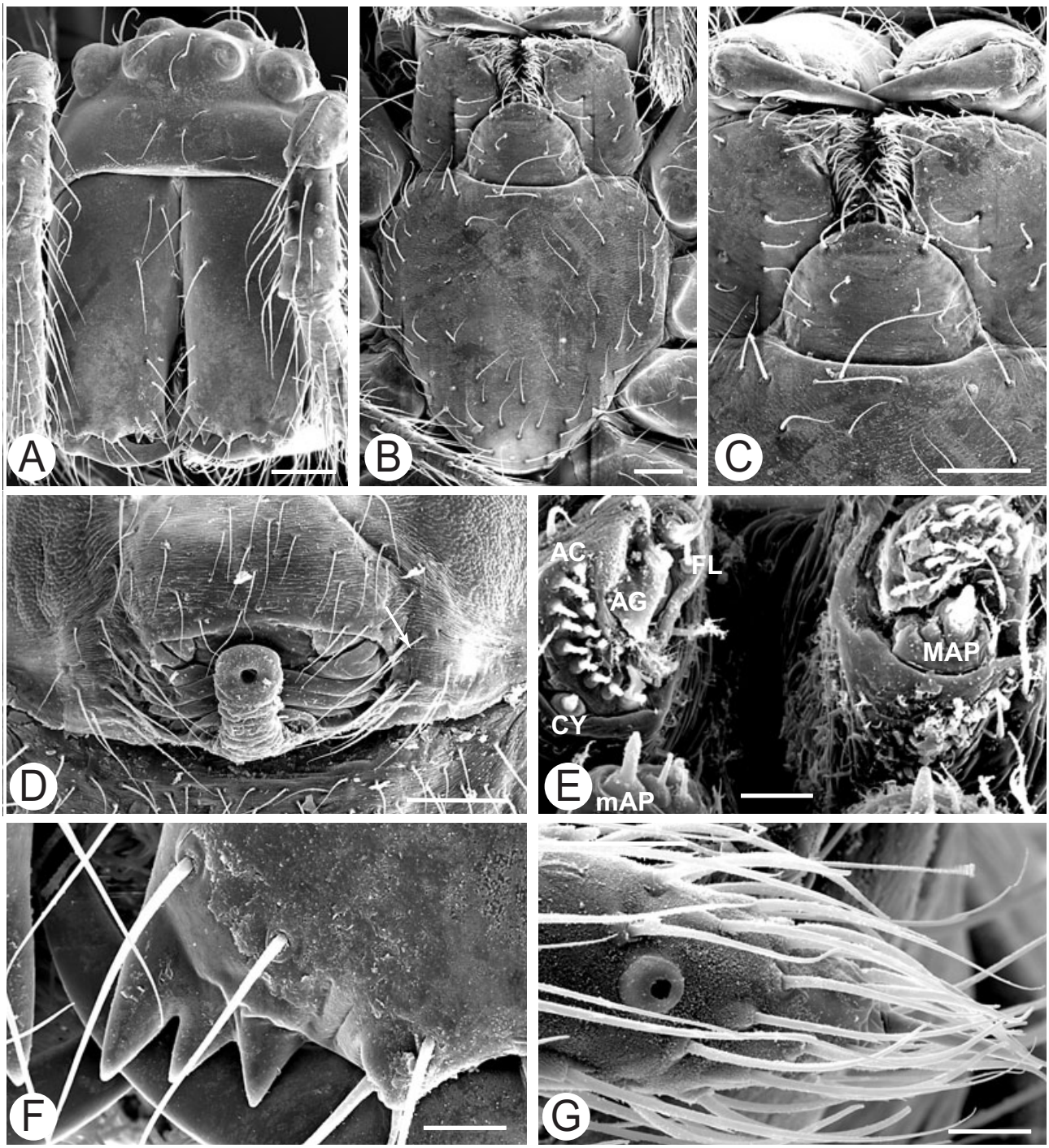

Figure 27. *Anelosimus vittatus*, female. A–C, prosoma. A, front. B, sternum. C, labium. D, epigynum; note scape (**1-1**), here unique to *A. vittatus* and *A. pulchellus*, but also present in *A. ethicus* (pers. observ.). E, spinnerets. F, cheliceral promarginal teeth. G, tarsal organ on palpus, a tarsal organ much larger than setal bases and with broad opening (**198-1**) is a synapomorphy of theridiids minus Hadrotarsinae and Latrodectinae (enlarged tarsal organ clade). Scale bars: A–D, 100 μm; E–G, 20 μm.

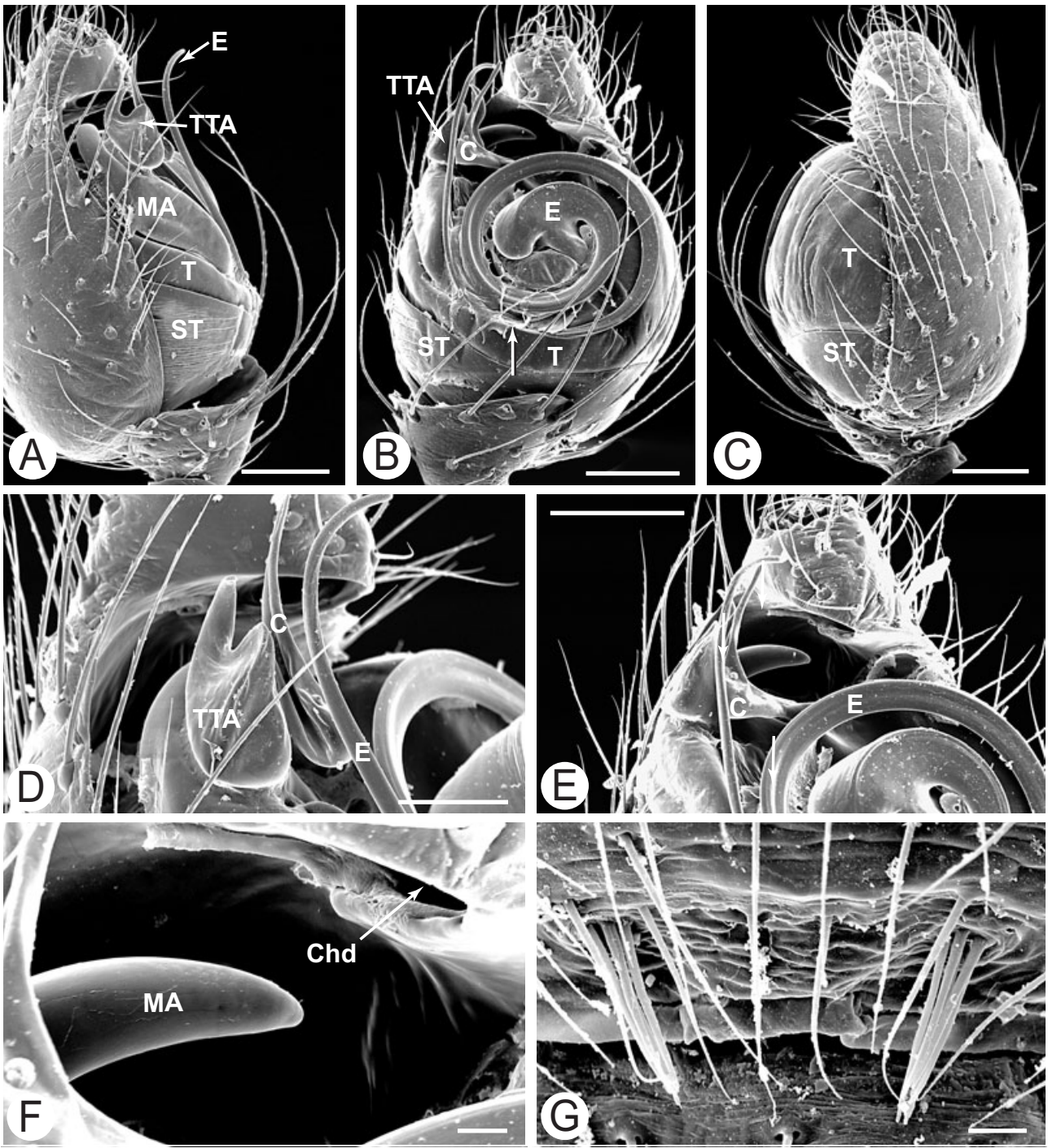

Figure 28. *Anelosimus* sp., male from Tanzania. A–F, palp. A, mesial, B, ventral, a unique groove in the tegulum (arrow, **47-1**) is a synapomorphy of the two Tanzanian *Anelosimus* species included here. C, ectal. D, details of TTA and C. E, ventral, distal portion. F, details of the bulb-cymbium lock mechanism, the MA tip is without a hood (**78-0**), but fits into the hood in the cymbium (Chd, **33-1**). G, epiandrous gland spigots. Scale bars: A–C, E, 100 μm; D, 50 μm; F, G, 10 μm.

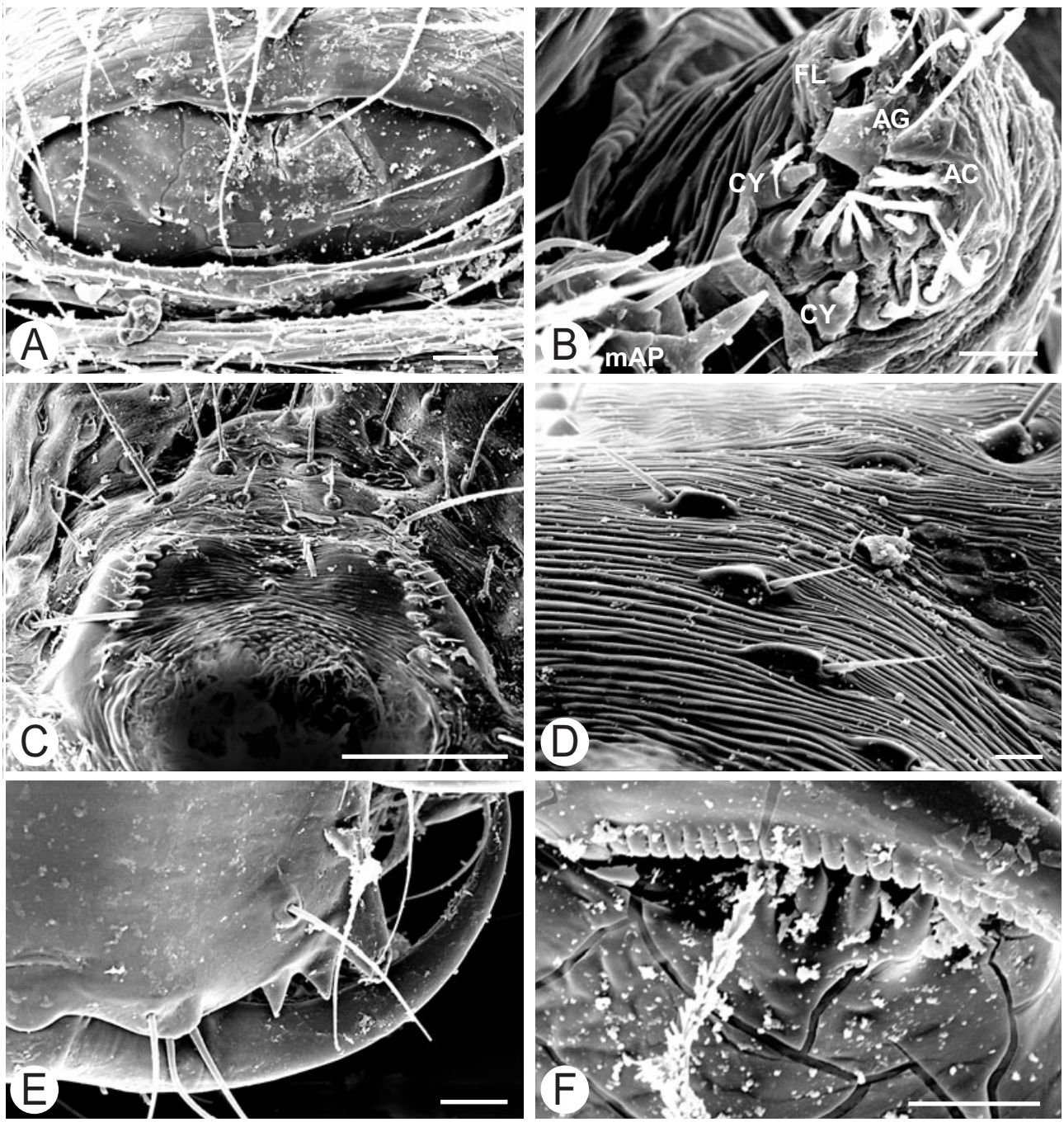

Figure 29. *Anelosimus* sp. (Tanzania). A, epigynum. B, PLS and PMS. C, D, male SPR. C, view above the pedicel. D, details. E, F, female cheliceral teeth. E, promargin. F, retromargin. Scale bars: A, B, E, F, 20 μm; C, 100 μm; D, 10 μm.

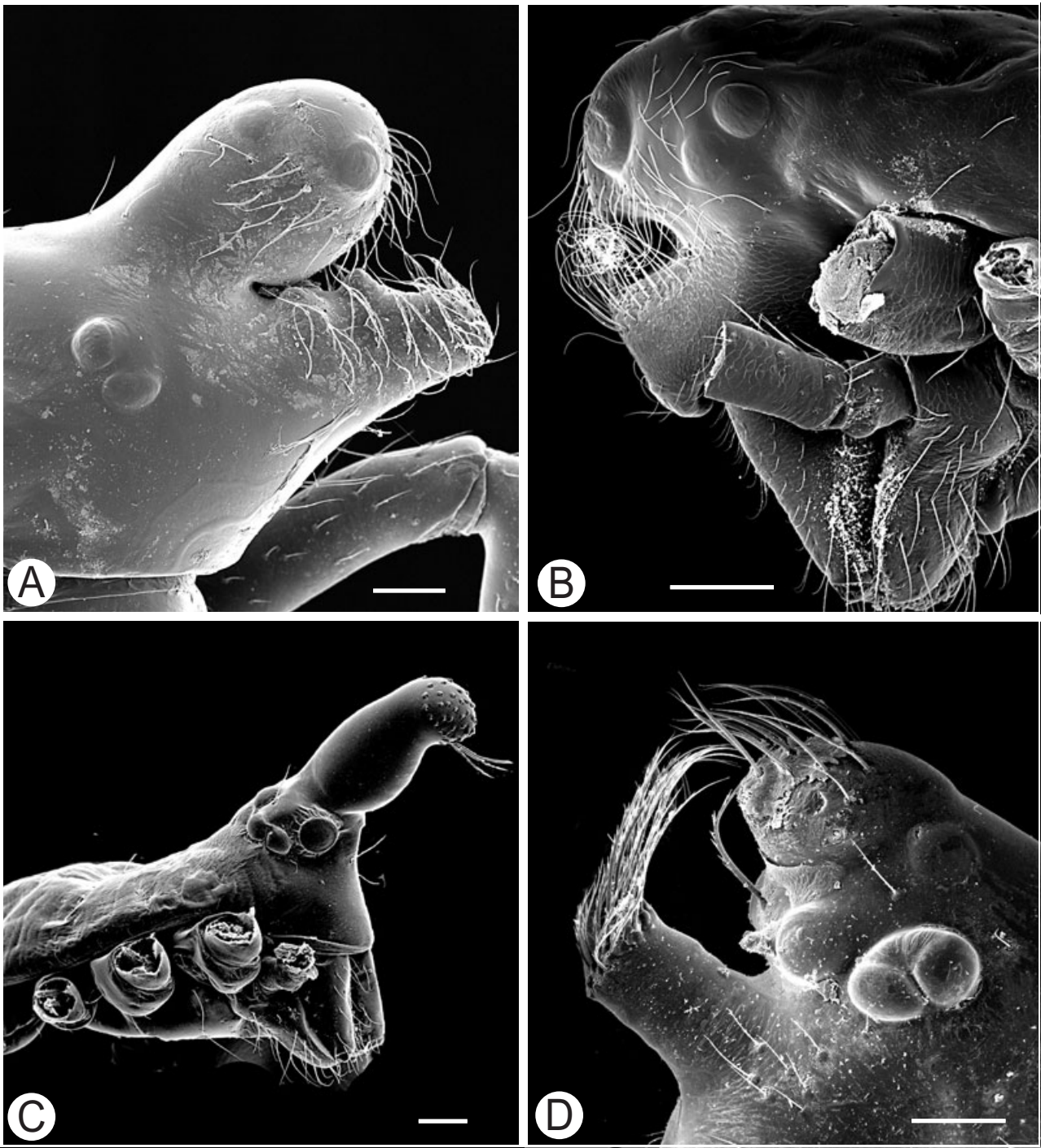

Figure 30. Argyrodinae male prosoma modifications. A, *Argyrodes elevatus*. B, *Faiditus* cf. *chickeringi*. C, *Rhomphaea metaltissima*. D, *Neospintharus trigonum*. Scale bars: 100 μm.

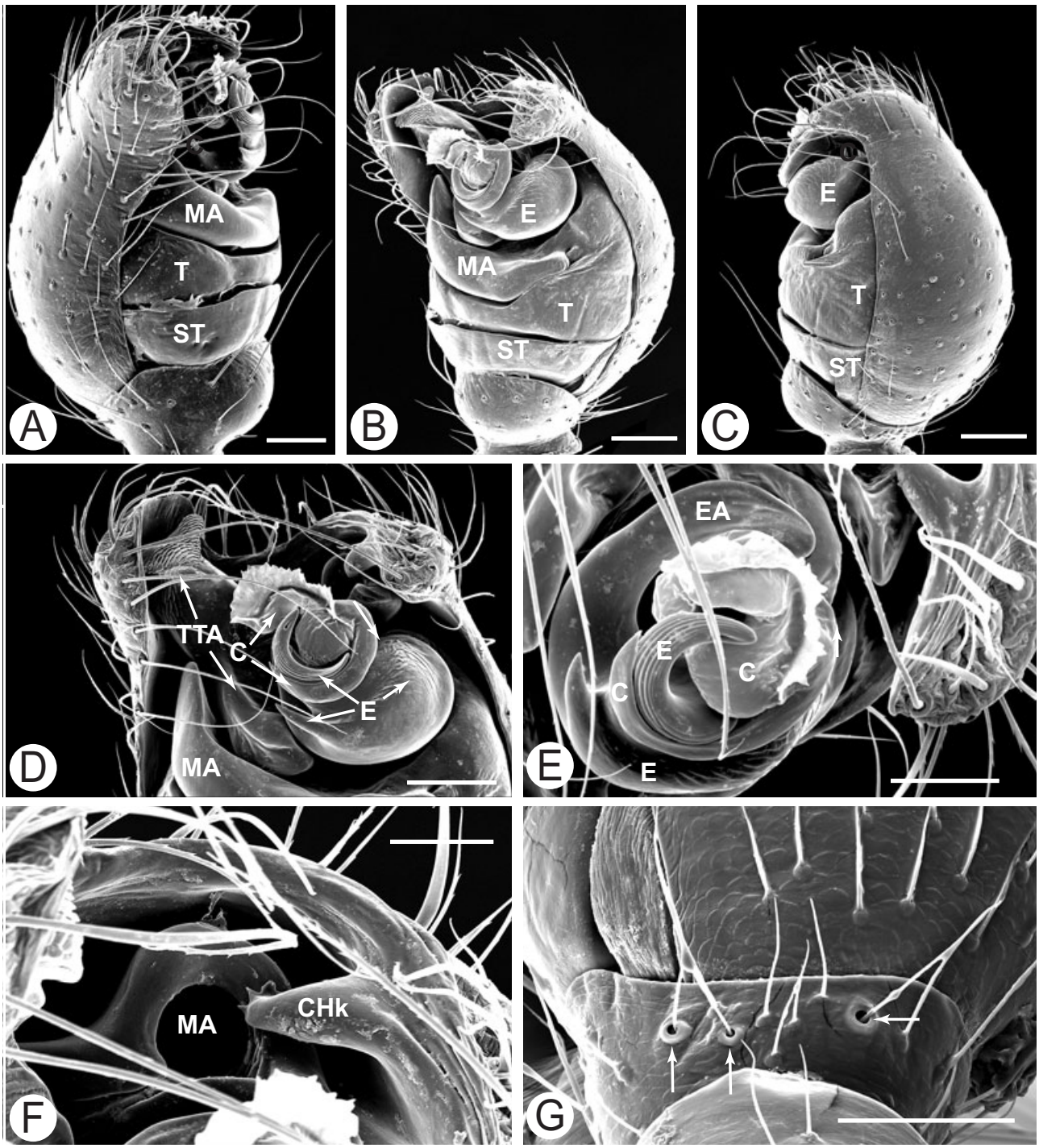

Figure 31. *Argyrodes*, male palps. A–F, *A. argyrodes*. A, mesial. B, ventral. C, ectal. D, embolic division; note complex interactions of C, embolus. E, close look at the embolus and C. F, the BC-lock system; a hood on the MA tip (**78-1**) fits the hook on the cymbium (**33-0**). G, *A. elevatus* tibia; note trichobothria. two retrolateral (vertical arrows, **18-1**) and a single prolateral (horizontal arrow, **19-1**). Scale bars: A–C, 100 μm; D–G, 50 μm.

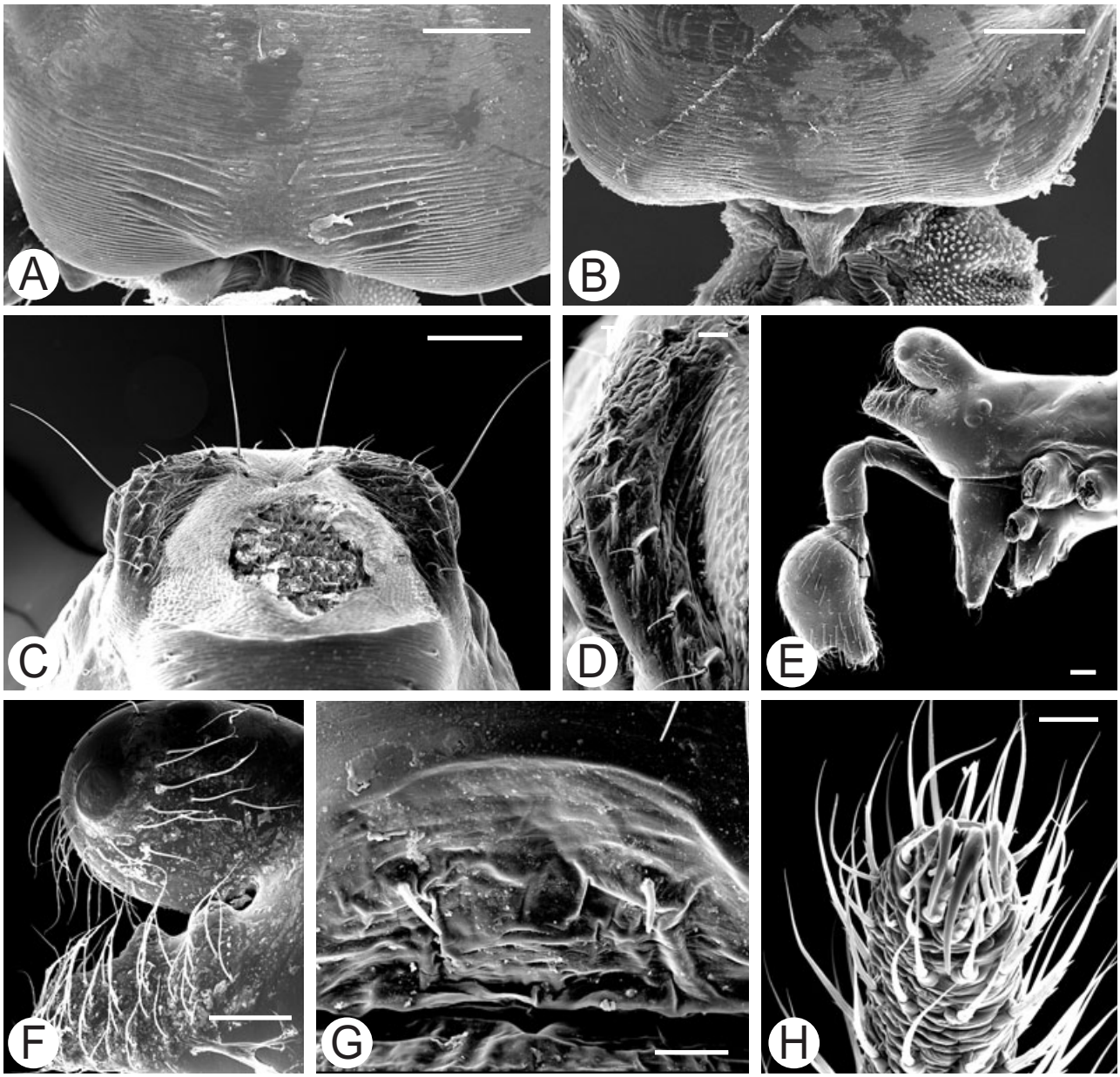

Figure 32. *Argyrodes*. A, B, *A. elevatus*. A, male prosomal stridulatory ridges (**128-1**). B, ditto, female. C–F, *A. argyrodes* male. C, proprioreceptors (long setae) and SPR (short setae) around pedicel on abdomen. D, close-up of SPR; note that all the setae are orientated ectally (**153-0**), none towards the axis of the animal (mesially, **156-0**). E, prosoma. F, close-up of clypeal modification (**130-1, 131-1, 132-1**. G, epiandrous gland spigots. H, fourth tarsal claws; note elongated unpaired claw (**199-1**). Scale bars: A–C, E, F, 100 μm; D, G, H, 20 μm.

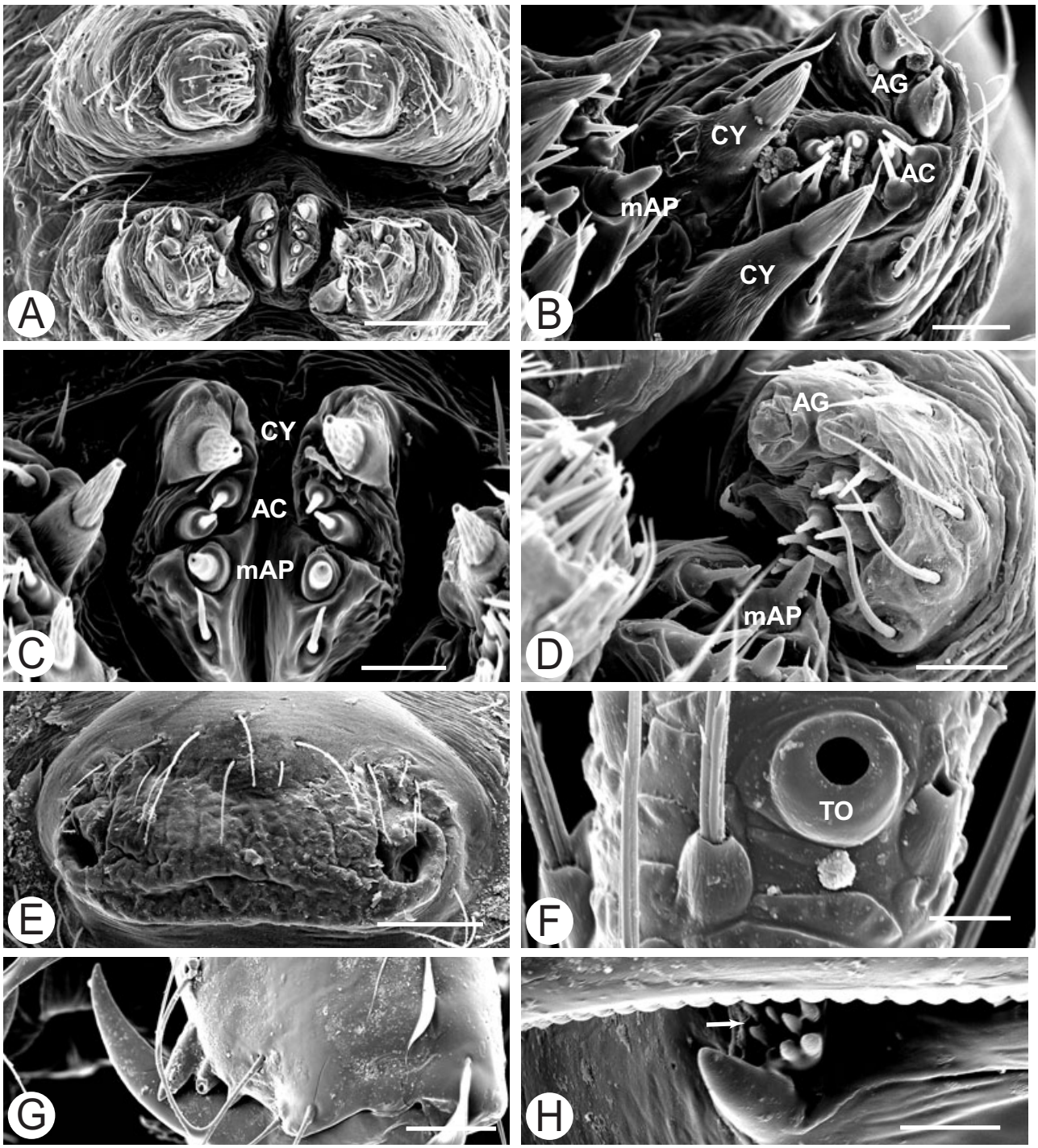

Figure 33. *Argyrodes argyrodes*. A–C, female spinnerets. A, all. B, PMS and PLS; note huge CY (**208-1**) with distinctly grooved bases (**209-1**), and absence of FL (**212-1**). C, PMS. D, male PMS and PLS, dysfunctional AG (**219-0**), but no FL scar. E, epigynum. F, tarsal organ (TO); note size relative to setae, enlarged TOs (**198-1**) are a synapomorphy of the enlarged tarsal organ clade. G, cheliceral promarginal teeth. H, cheliceral retromarginal teeth; denticles in the fang furrow (arrow) are a synapomorphy of Argyrodinae (**112-1**). Scale bars: A, E, 100 μm; B–D, H, 20 μm; F, 10 μm; G, 50 μm.

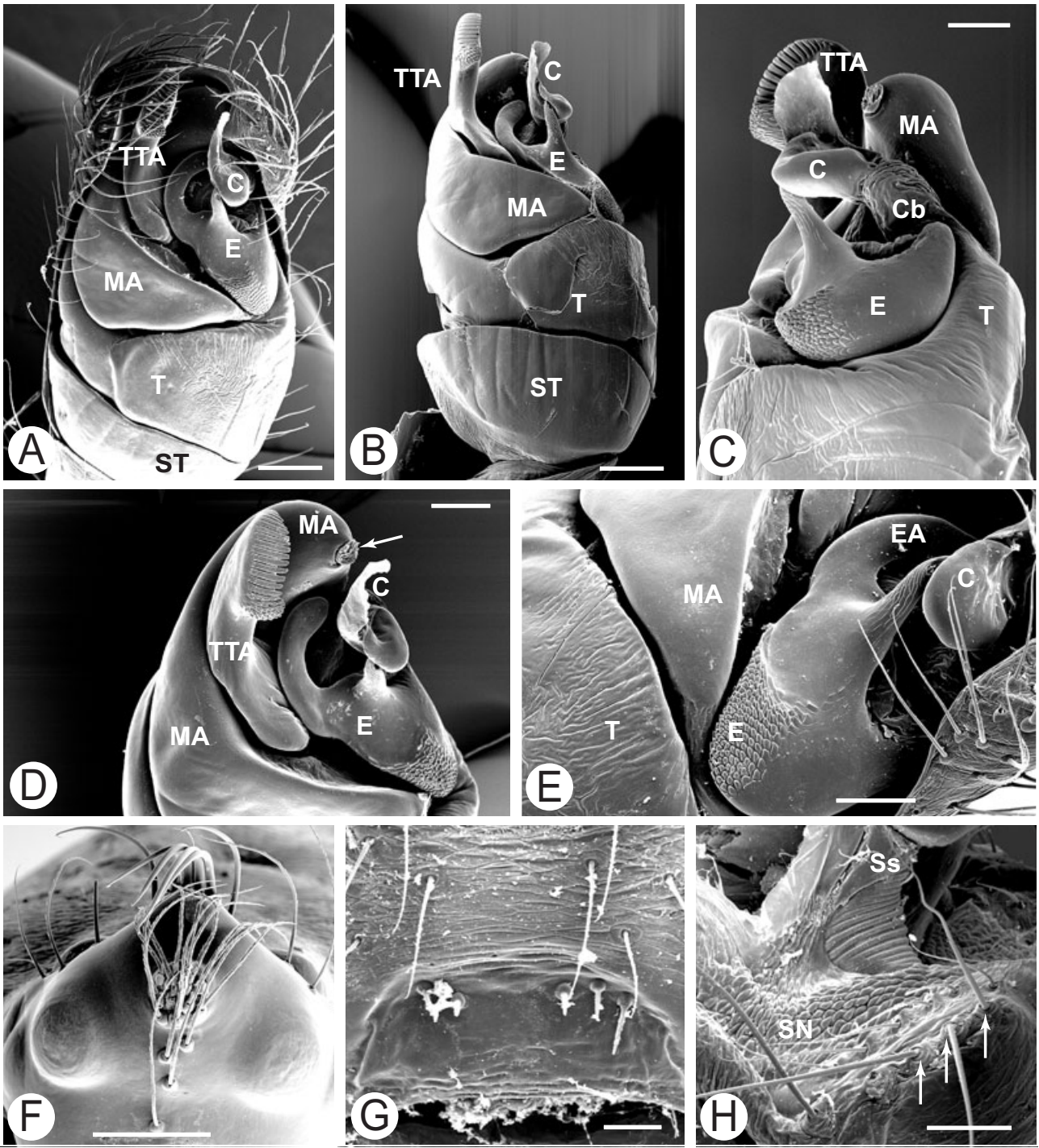

Figure 34. *Ariamnes* nr. *attenuatus*. A–E, male palp. A, ventral. B–E, bulb removed from cymbium. B, ventral. C, ectal. D, ventral close-up; note hooded tip of the MA (**78-1**) with a broken-off cymbial hook (arrow, **33-0**), showing the locking system is active in the unexpanded palp (**31-1**). E, close-up of embolus; note embolic apophysis (EA, **96-1**) and ridges on embolus base (**90-1**). F, modified prosoma (**130-1**), clypeal glands and setae (**132-1, 133-1**). G, epiandrous gland spigots. H, female pedicel area; note broadened slit sensilla (Ss, **141-1**), stridulatory nubbins (SN, **149-1**) and setal proprioreceptors (arrows). Scale bars: A, B, F, 100 μm; C–E, H, 50 μm; G, 20 μm

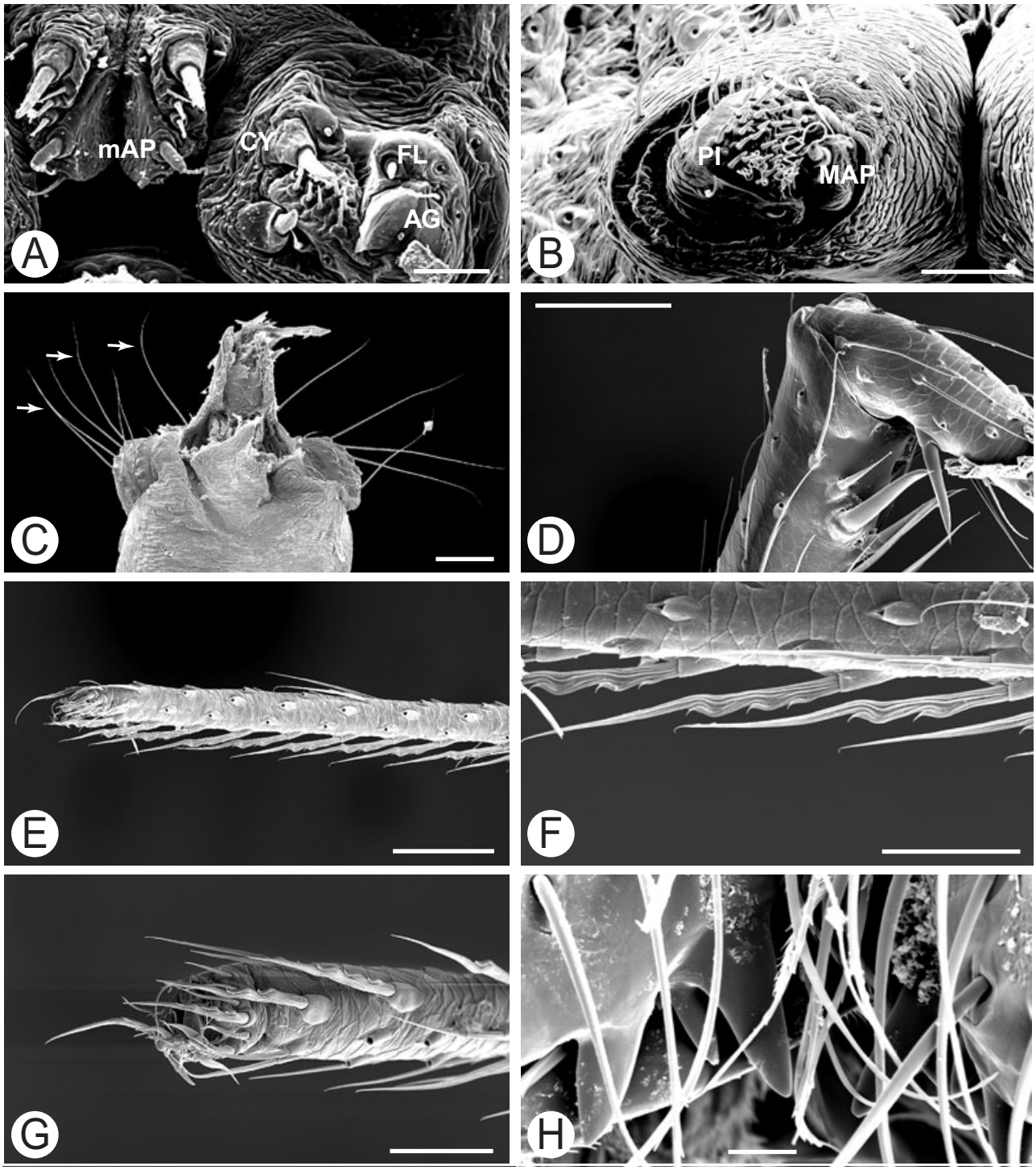

Figure 35. *Ariamnes* nr. *attenuatus*. A, B, female spinnerets. A, PLS and PMS, apparently a FL and a single AG are present (or possibly two highly dimorphic AGs). B, ALS. C, setal proprioreceptors (arrows point to a few). D, male first leg; note sturdy setae on the metatarsus. E, female fourth tarsal comb. F, serrated bristles of the tarsal comb. G, tip of fourth tarsus; note position of the comb relative to the tarsal claws. H, cheliceral promarginal teeth. Scale bars: A, B, F, G, 50 μm; C–E, 100 μm; H, 10 μm

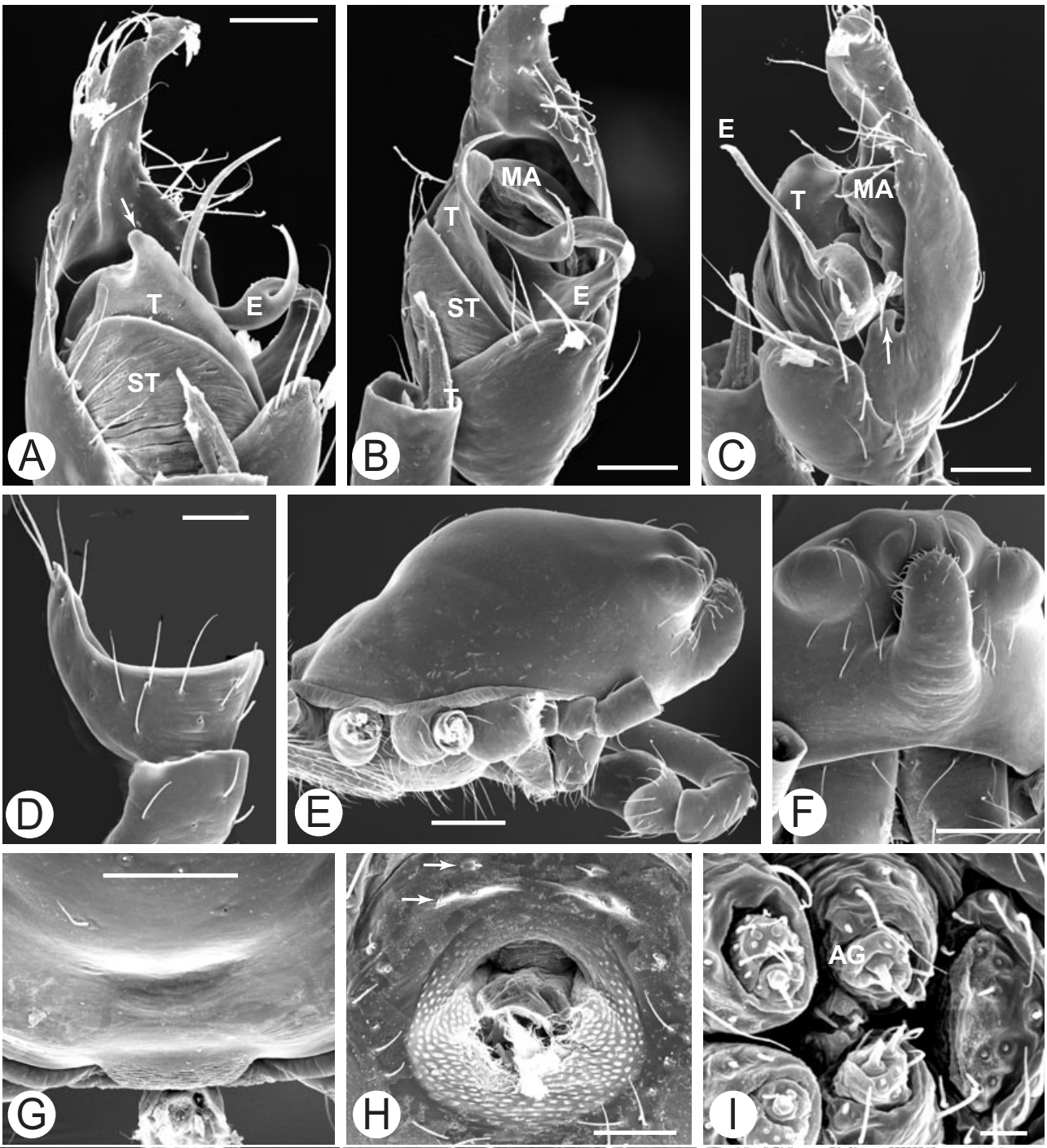

Figure 36. *Carniella siam*, male. A–D, palp. A, mesial; note knob on tegulum that may be the remains of the conductor (arrow). B, ventral. C, ectal; note basal cymbial hook (arrow, **32-0**). D, tibia. E, prosoma. F, clypeus. G, dorsal posterior part of prosoma; note stridulating ridges (**128-1**). H, area around pedicel on abdomen; note pairs of SPR (arrows), and nubbins. I, spinnerets; note presence of AG, FL (**219-1**). Scale bars: A–D, H, 50 μm; E–G 100 μm; I, 10 μm.

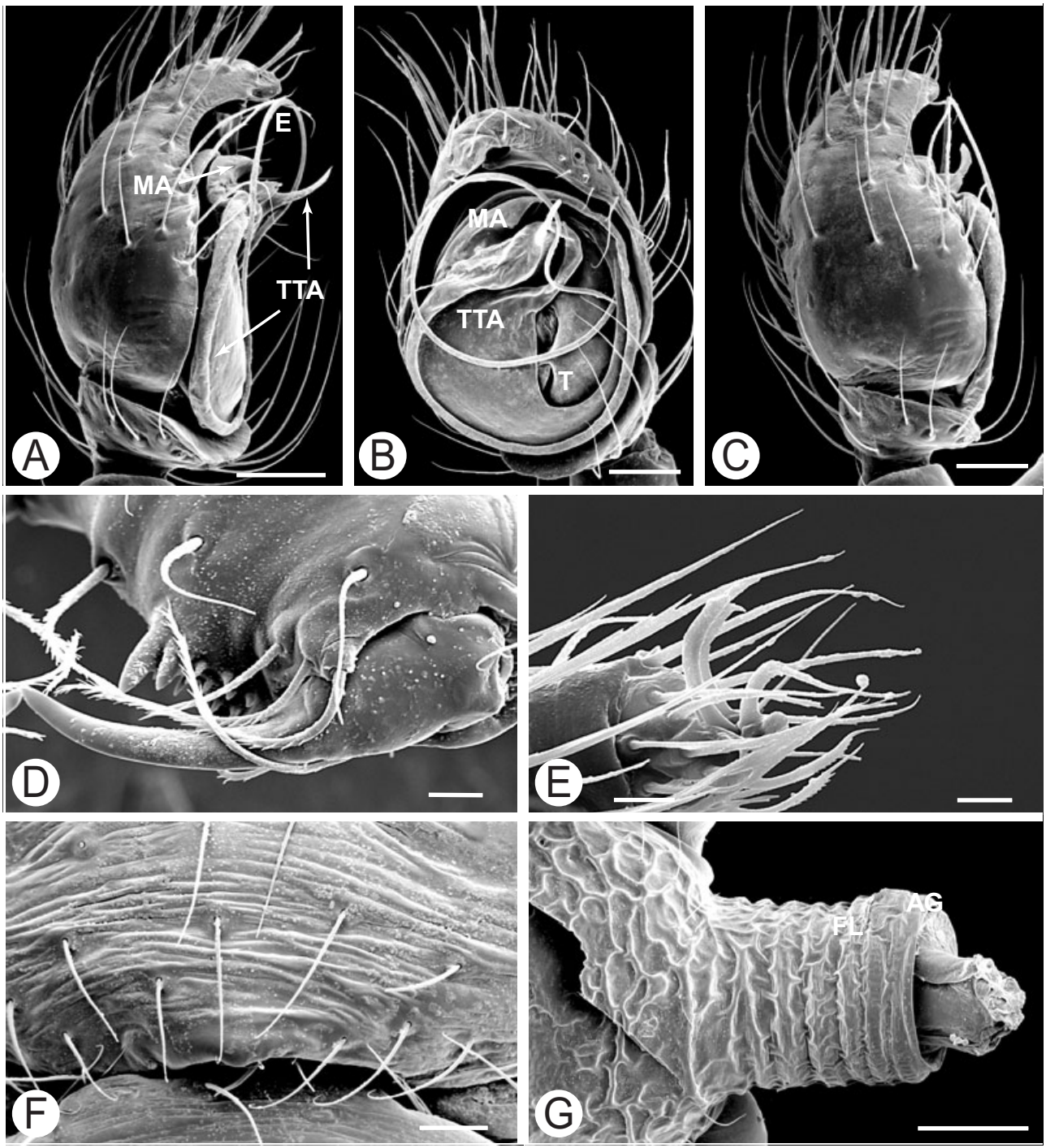

Figure 37. *Cerocida strigosa*, male. A–C, palp. A, mesial. B, ventral; note enormous TTA (**84-1**), C, dorsal. D, cheliceral fang and teeth. E, fourth tarsal claws, the edentate, thin claws are unusual. F, genital furrow, epiandrous gland spigots absent (**168-1**). G, posterior tip of prosoma, the cylindrical extension presumably mimics an ant's thorax. Scale bars: A–C, 50 μm; D, E, 10 μm; F, 20 μm; G, 100 μm.

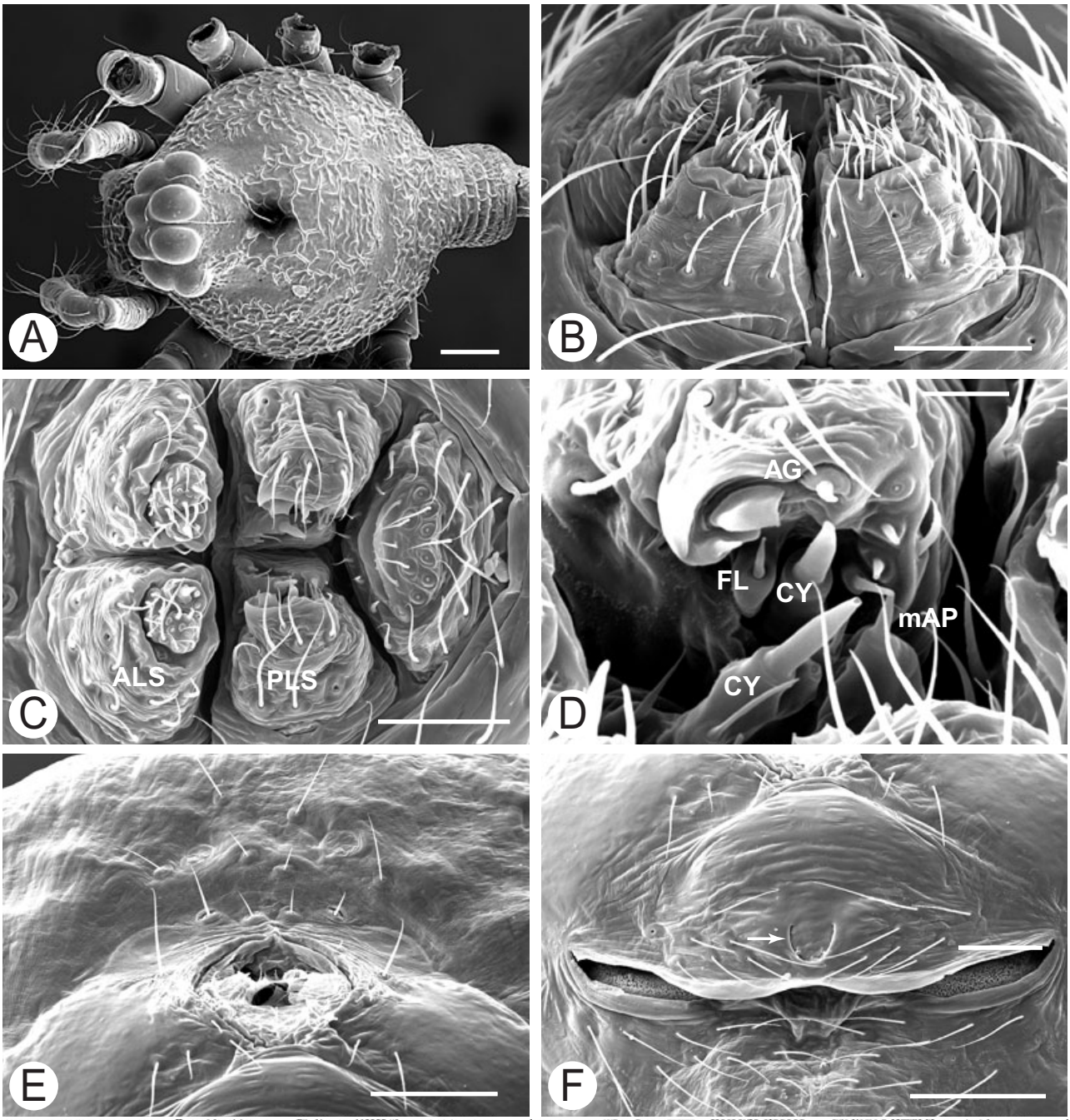

Figure 38. *Cerocida strigosa*, female. A, prosoma. B–D, spinnerets. B, a small colulus (**173-1**), bearing two (**175-1**) long setae. C, all. D, PMS and PLS; note dimorphism of AGs. E, pedicel area of abdomen; note reduced number of proprioreceptors and absence of stridulatory picks (**150-0**, male is similar). F, epigastric furrow, the small epigynum (arrow) has a slit-like opening (**5-1**). Scale bars: A, E, F, 100 μm; B, C, 50 μm; D, 10 μm.

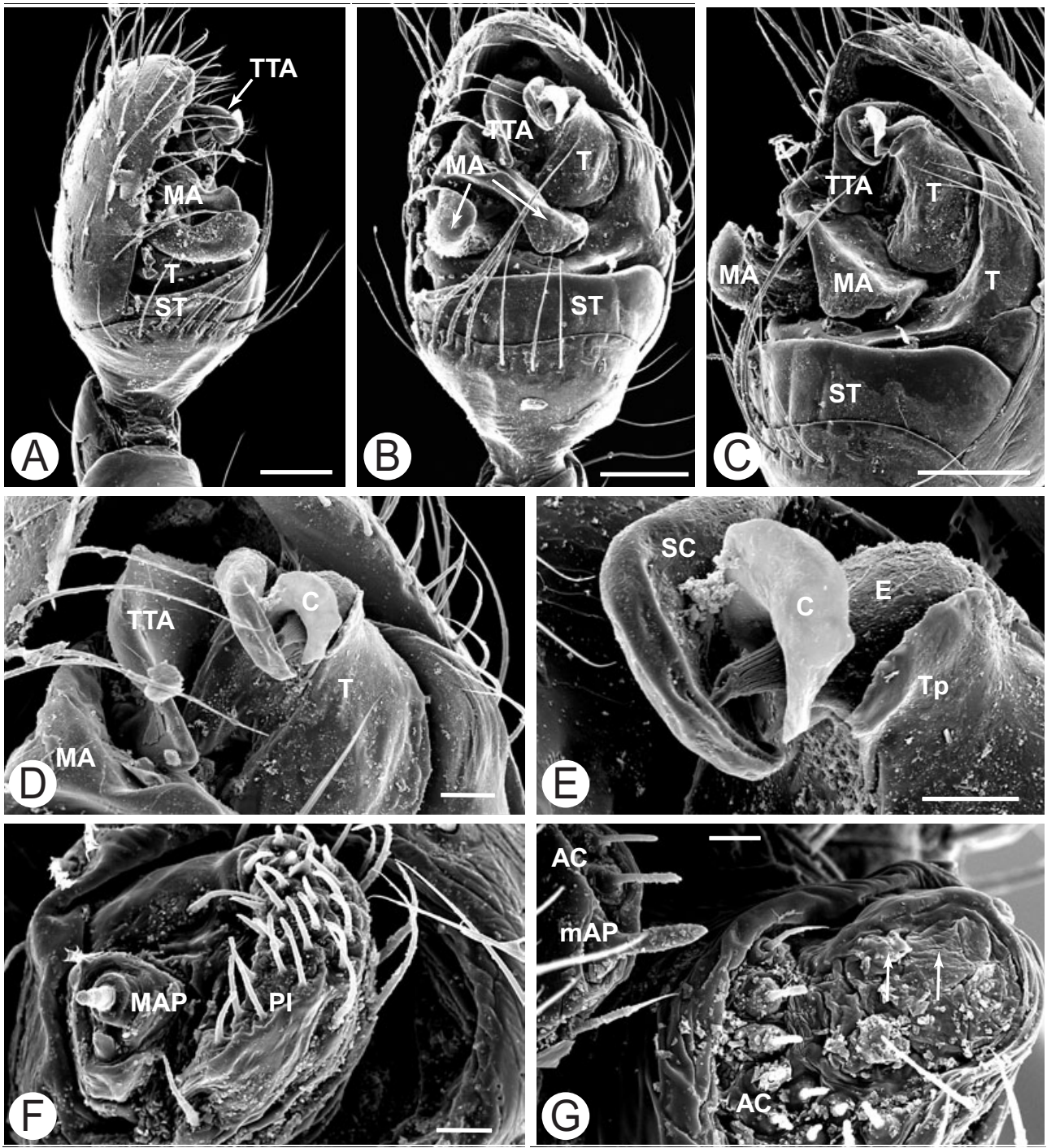

Figure 39. *Chrysso nigriceps*, male. A–E, palp. A, mesial; note bifurcated MA (**76-1**). B, ventral. C, ectal. D, ventral close-up. E, interactions of T, E, and C; note presence of a pit in the tegulum (Tp, **49-1**), in which the E base fits (**50-0**), and the SC (**70-1**) out of which the C rises. F, ALS. G, PMS and PLS, arrows indicate scars of the nonfunctional AG (**219-0**). Scale bars: A–C, 100 μm; D, E, 20 μm; F, G, 10 μm.

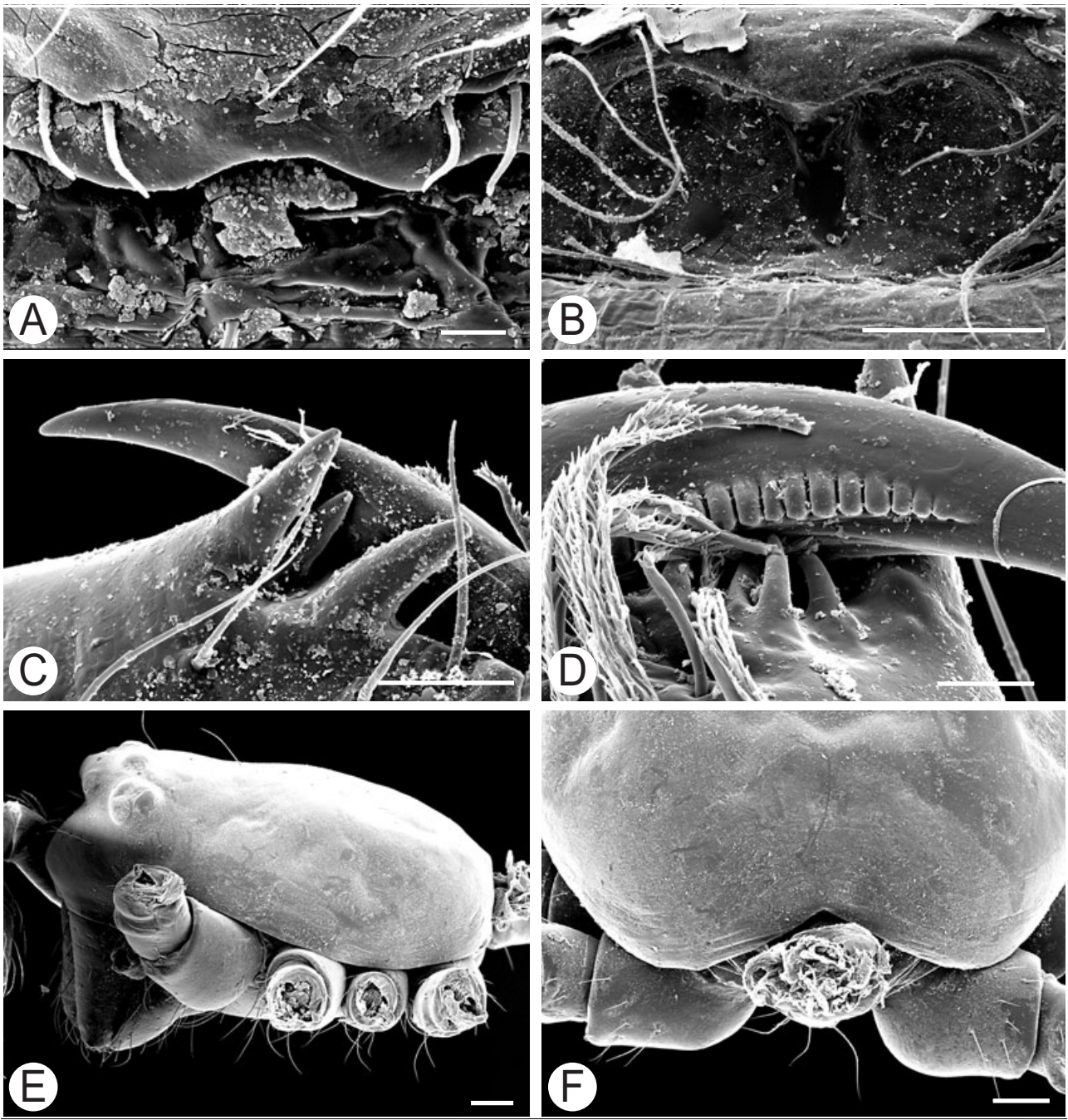

Figure 40. *Chrysso nigriceps*. A, epiandrous gland spigots. B, epigynum. C, prolateral cheliceral teeth. D, retrolateral teeth. E, F, male prosoma. E, lateral view. F, posterior tip. Scale bars: A, 10 μm; B, C, 50 μm; D, 20 μm; E, F, 100 μm.

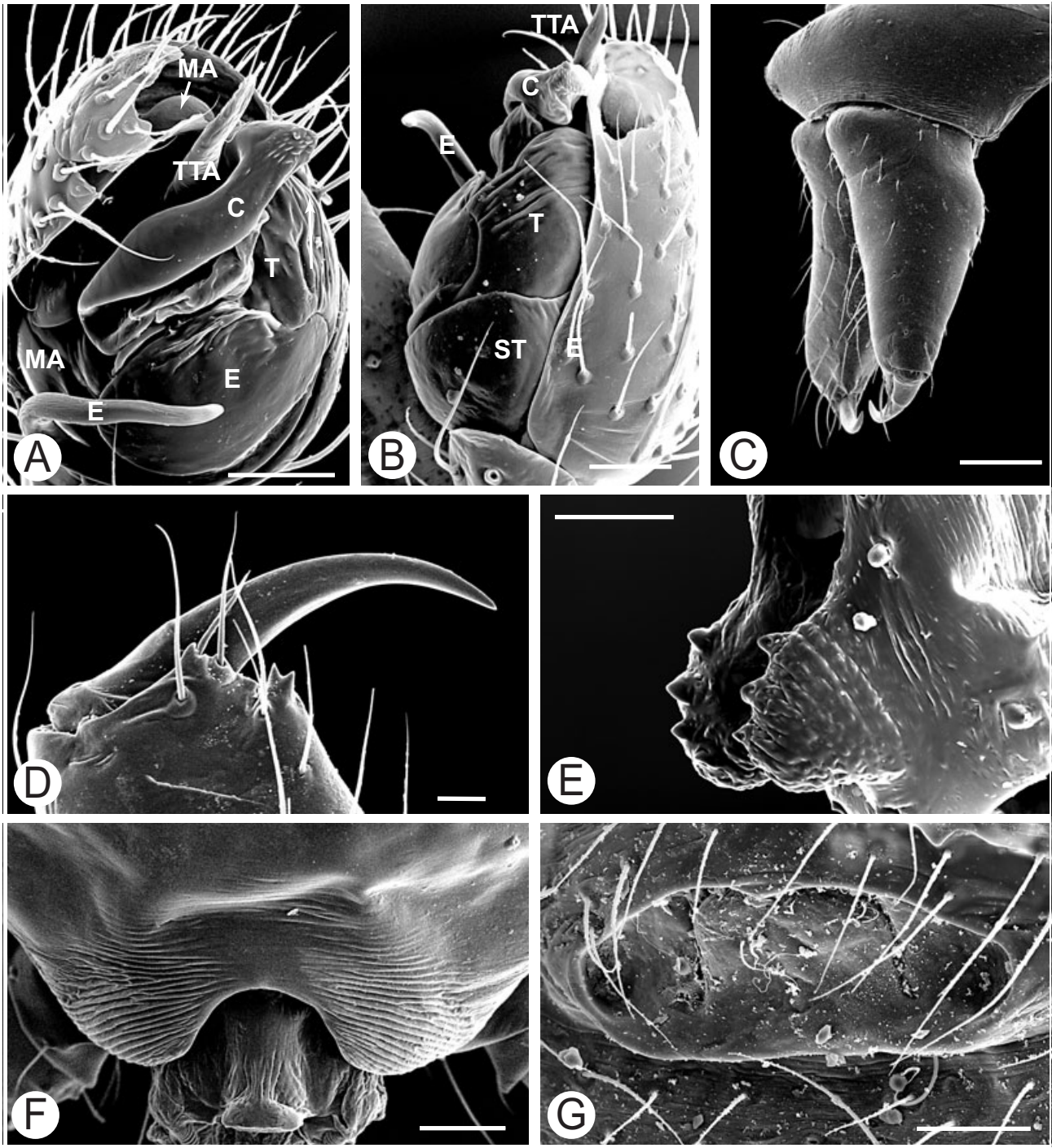

Figure 41. *Coleosoma floridanum*. A, B, male palp. A, ventral. B, ectal. C, chelicera. D, prolateral cheliceral teeth. E, abdominal SPR. F, prosomal stridulatory ridges. G, epigynum. Scale bars: A, B, E–G, 50 μm; C, 100 μm; D, 20 μm.

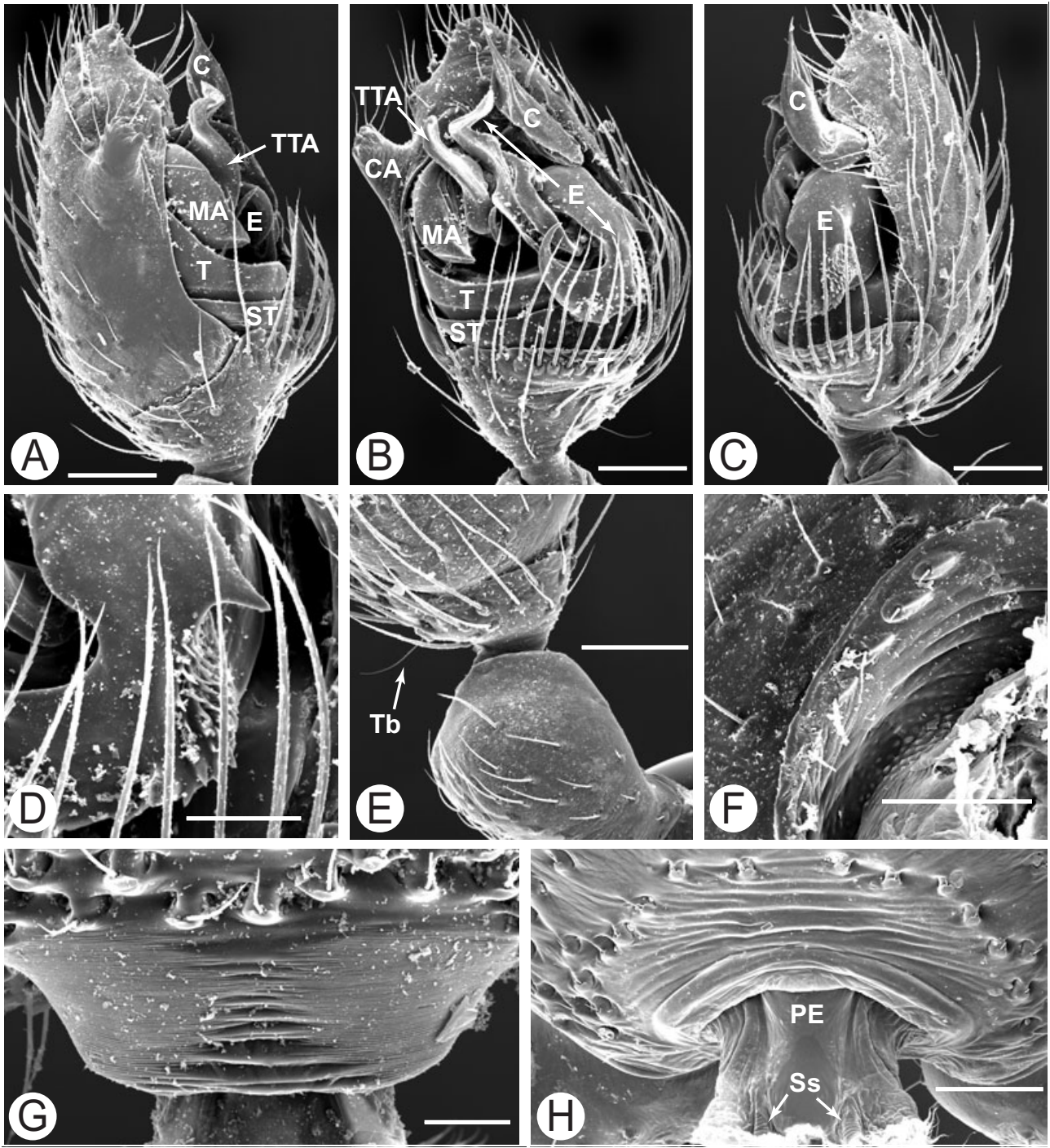

Figure 42. *Crustulina guttata*. A–E, male palp. A, mesial. B, ventral; note cymbial apophysis (CA, **24-1**). C, ectal. D, embolus base with apophysis and ridges. E, femur and tibia with a single trichobothrium (**18-2**, **19-2**). F, male SPR. G, male prosomal stridulatory ridges. H, *Crustulina sticta* female SPR; note pair of lyriform organs (rows of slit sensilla) at side of pedicel (**141-0**). Scale bars: A–C, E, F, 100 μm; D, G, H, 50 μm.

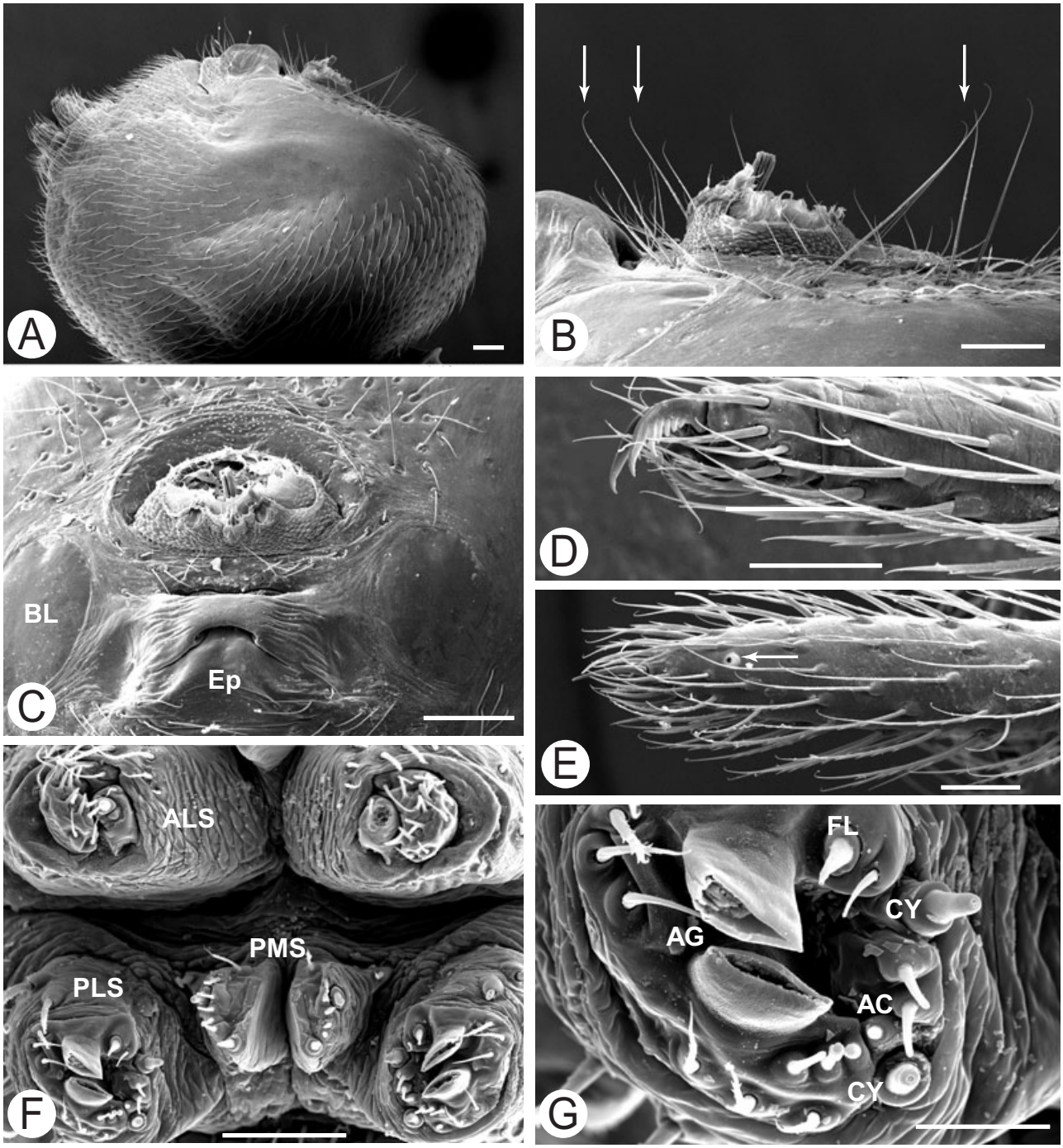

Figure 43. *Crustulina sticta*, female. A, abdomen, white box shows area enlarged in B. B, close-up of abdominal proprioreceptors (arrows); note setae of the modified SPR (see also in C) carry much shorter setae. C, anterior ventral abdomen, showing pedicel area, Ep and BL. D, tip of fourth tarsus. E, palpal tarsus; note small TO (arrow, **198-0**), and serrated bristles ventrally. F, spinnerets. G, PLS. Scale bars: A–C, F, 100 μm; D, E 50 μm; G, 20 μm.

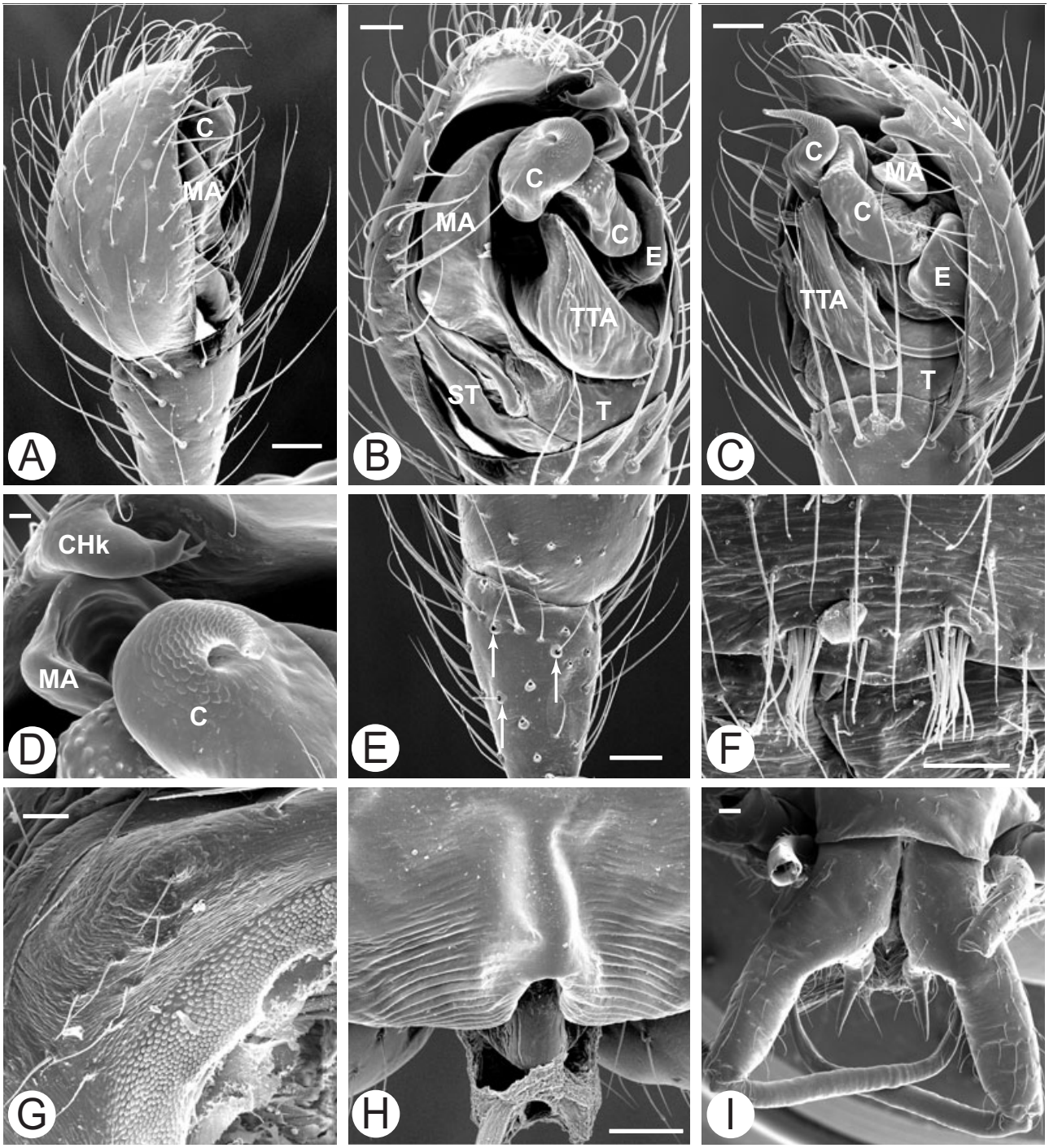

Figure 44. *Enoplognatha ovata*, male. A–E, palp. A, mesial. B, ventral. C, ectal. D, BC-lock mechanism. E, dorsal tibia with three trichobothria (arrows). F, epiandrous gland spigots. G, ridged stridulatory picks. H, stridulatory ridges on prosoma. I, chelicera. Scale bars: A, E, G–I, 100 μm; B, C, F, 50 μm; D, 10 μm.

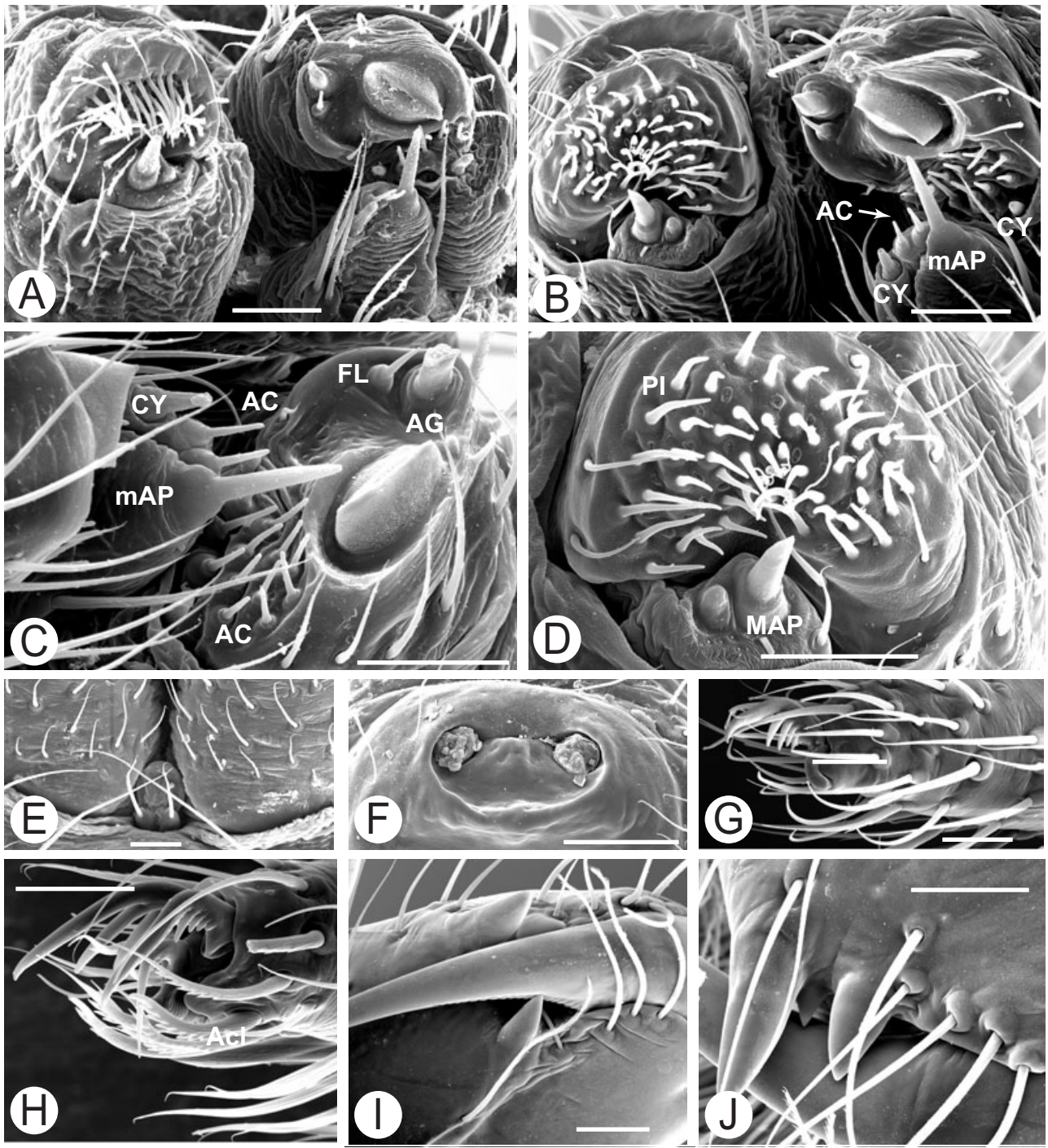

Figure 45. *Enoplognatha*, females. A, G–J, *E. ovata*. B-F, *E. latimana*. A, spinnerets. B, spinnerets. C, PLS and PMS. D, ALS. E, colulus. F, epigynum, the round, wide openings plugged. G, palpal claw. H, fourth tarsal claws. I, cheliceral retrolateral margin. J, cheliceral prolateral margin. Scale bars: A–E, 50 μm; F, 100 μm; G–J, 10 μm.

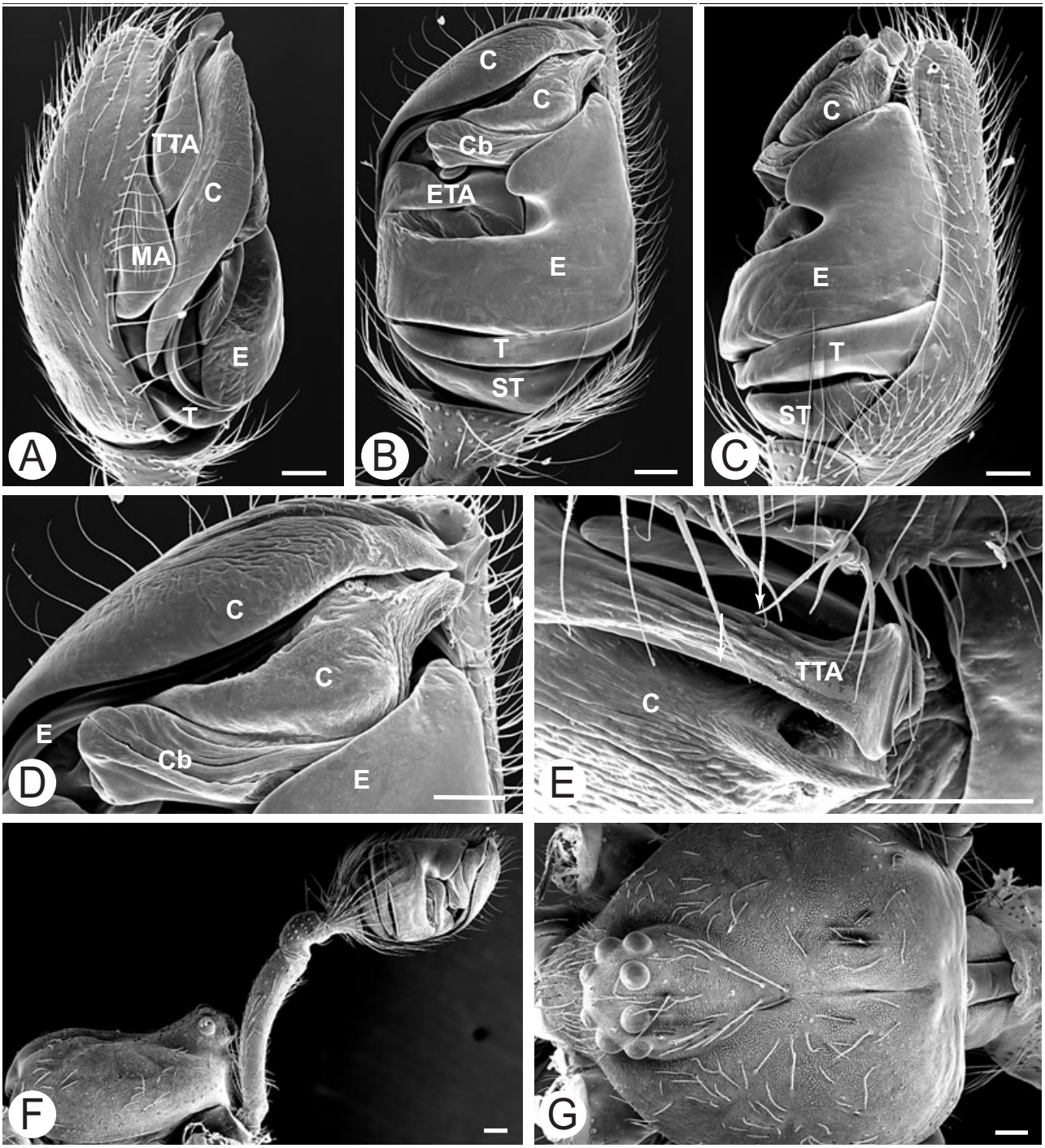

Figure 46. *Episinus maculipes*, male. A–E, palp. A, mesial. B, ventral. C, ectal. D, close-up ventral. E, apical. F, prosoma with palp; the palp of *Episinus*, almost as large as the prosoma, is one of the relatively largest sperm transfer organs in the animal kingdom. G, prosoma dorsal view. Scale bars: 100 μm.

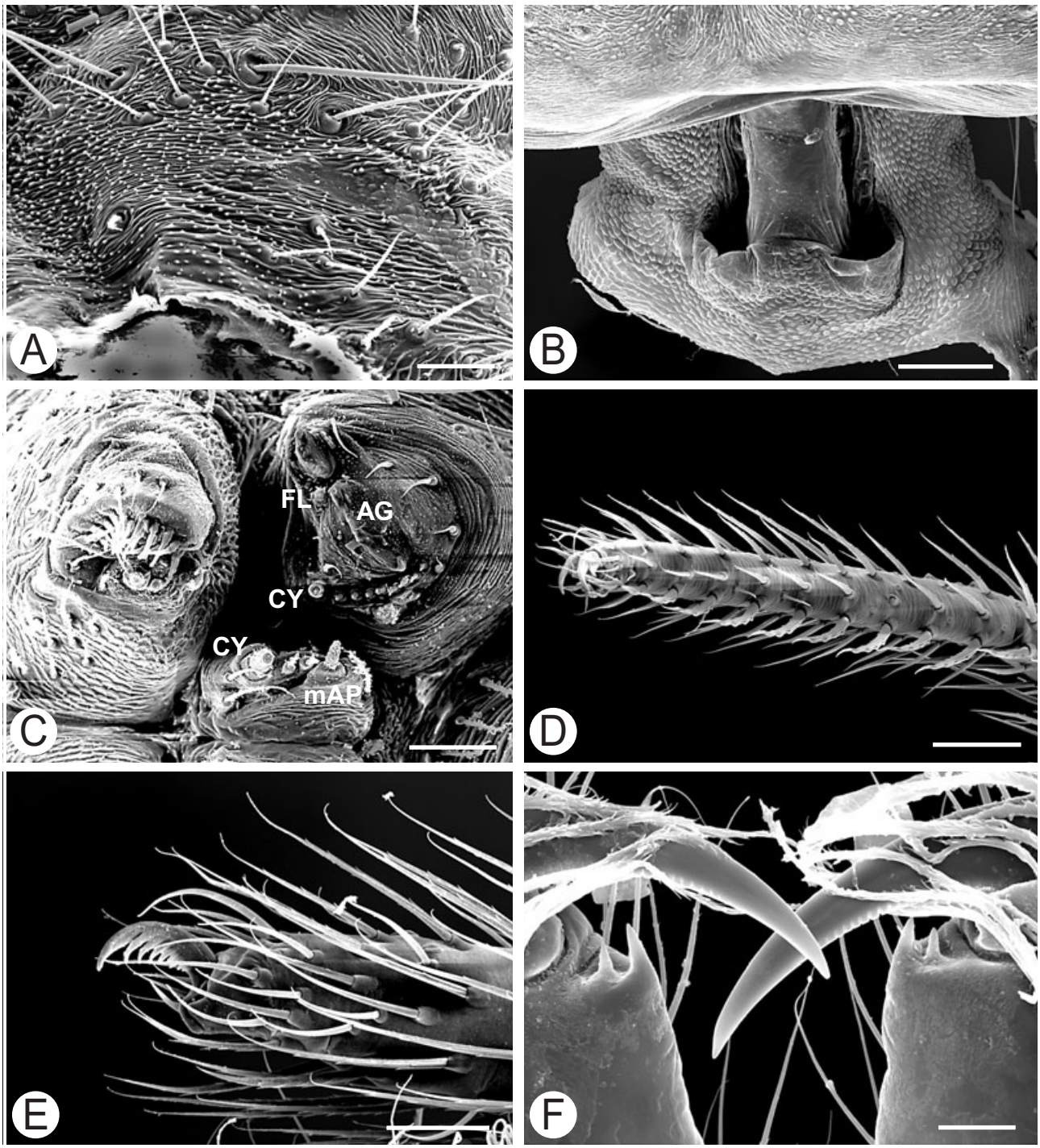

Figure 47. *Episinus maculipes*. A, B, male. A, abdominal stridulatory picks and nubbins. B, pedicel. C–F, female. C, spinnerets. D, fourth tarsus. E, palpal claw. F, cheliceral teeth. Scale bars: A, F, 20 μm; B, D, 100 μm. C, E, 50 μm.

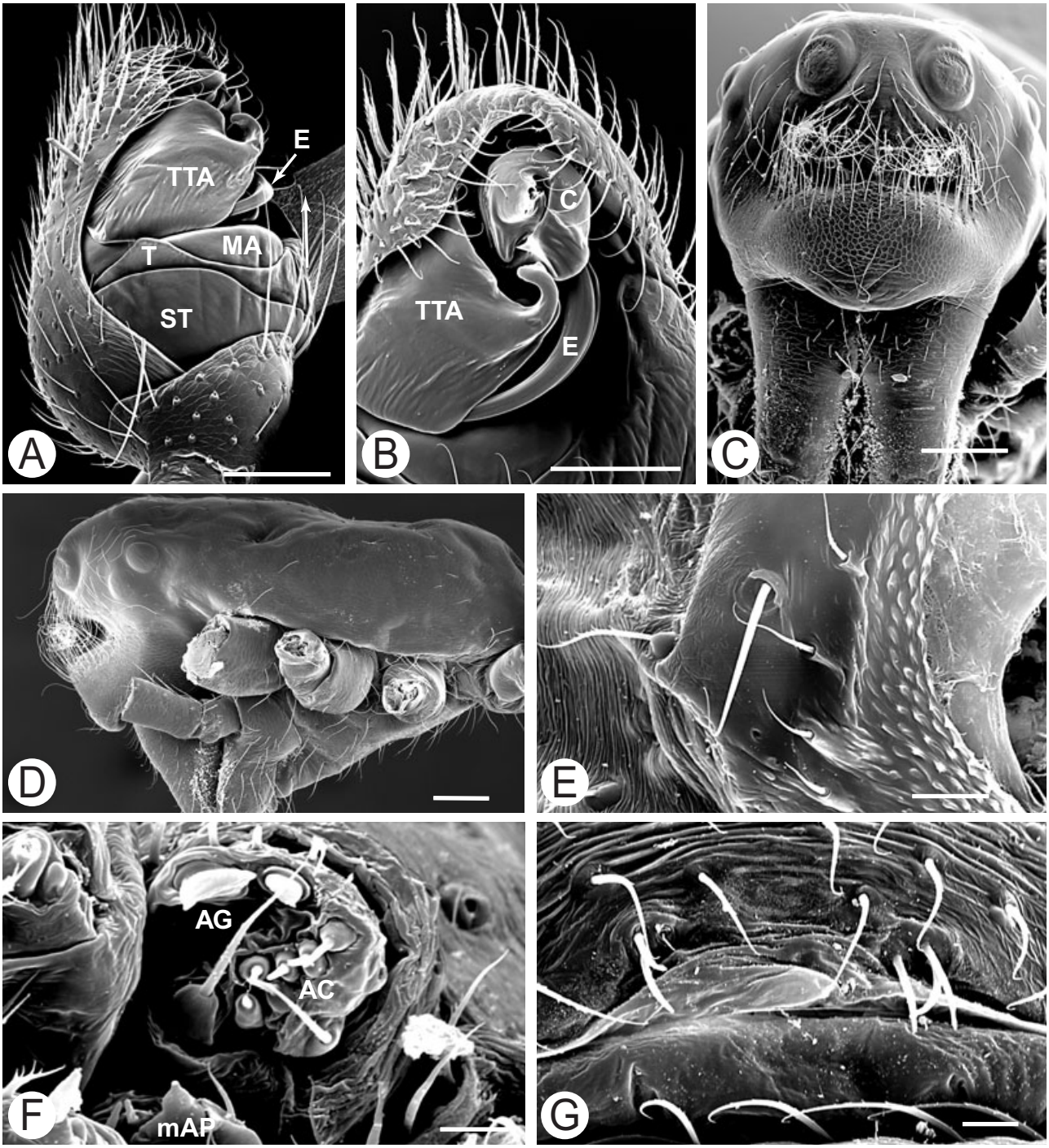

Figure 48. *Faiditus* cf. *chickeringi*, male. A, B, palp. A, mesial. B, ventral. C, D, prosoma. C, front. D, side. E, stridulatory picks and nubbins. F, PMS. G, epiandrous gland spigots. Scale bars: A–D, 100 μm; E, 20 μm; F, G, 10 μm.

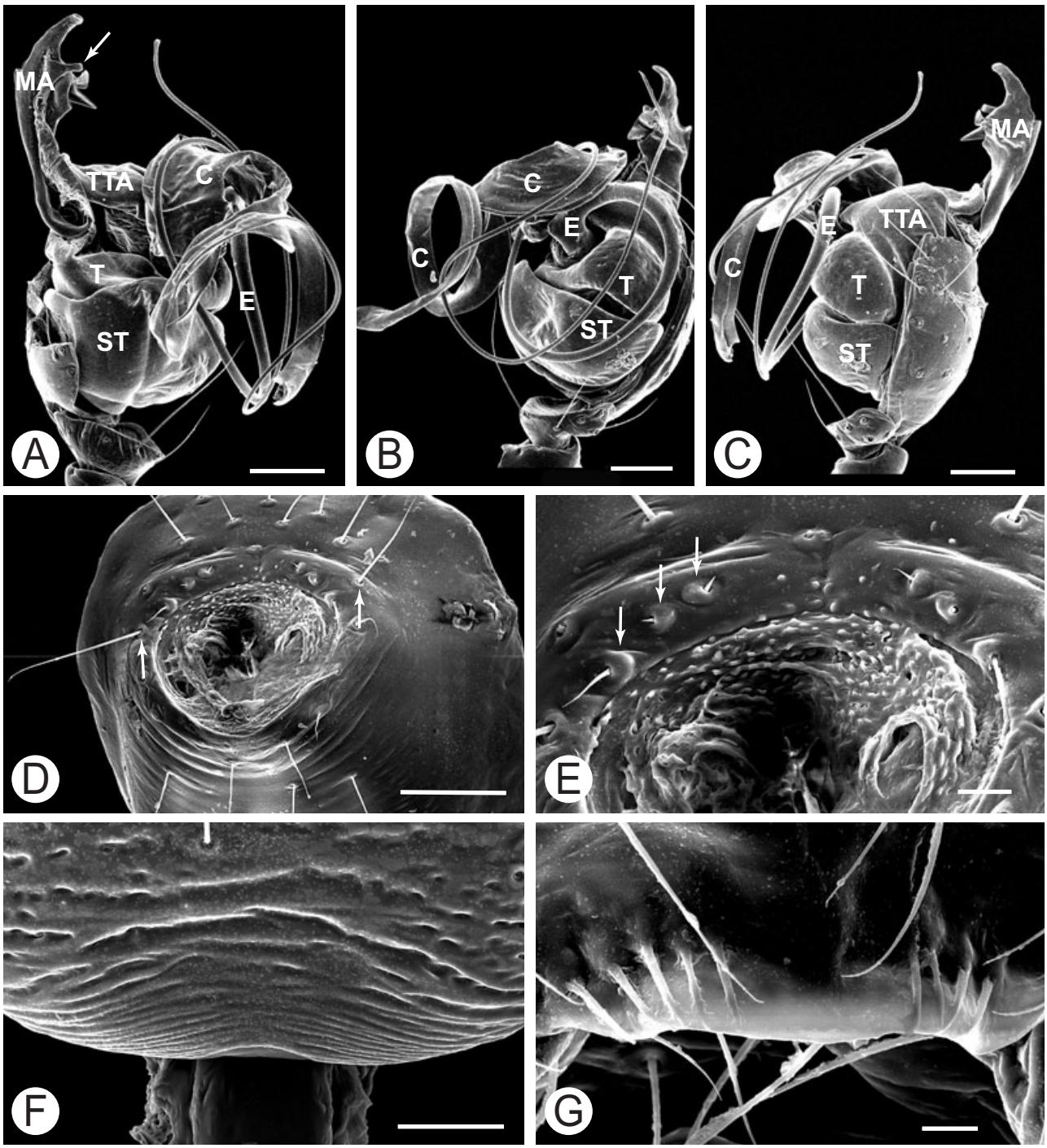

Figure 49. *Helvibis* cf. *longicaudatus*, male. A–C, expanded palp. A, mesial; note small apophysis on the MA (arrow, **76-1**). B, ventral; note extremely elongated and complicated conductor (**63-1, 66-2**). C, ectal. D, area around pedicel on abdomen; note setal proprioreceptors (arrows). E, ditto, SPR (arrows). F, prosomal stridulatory ridges. G, epiandrous gland spigots. Scale bars: A–D, 100 μm; E, 20 μm; F, 50 μm; G, 10 μm.

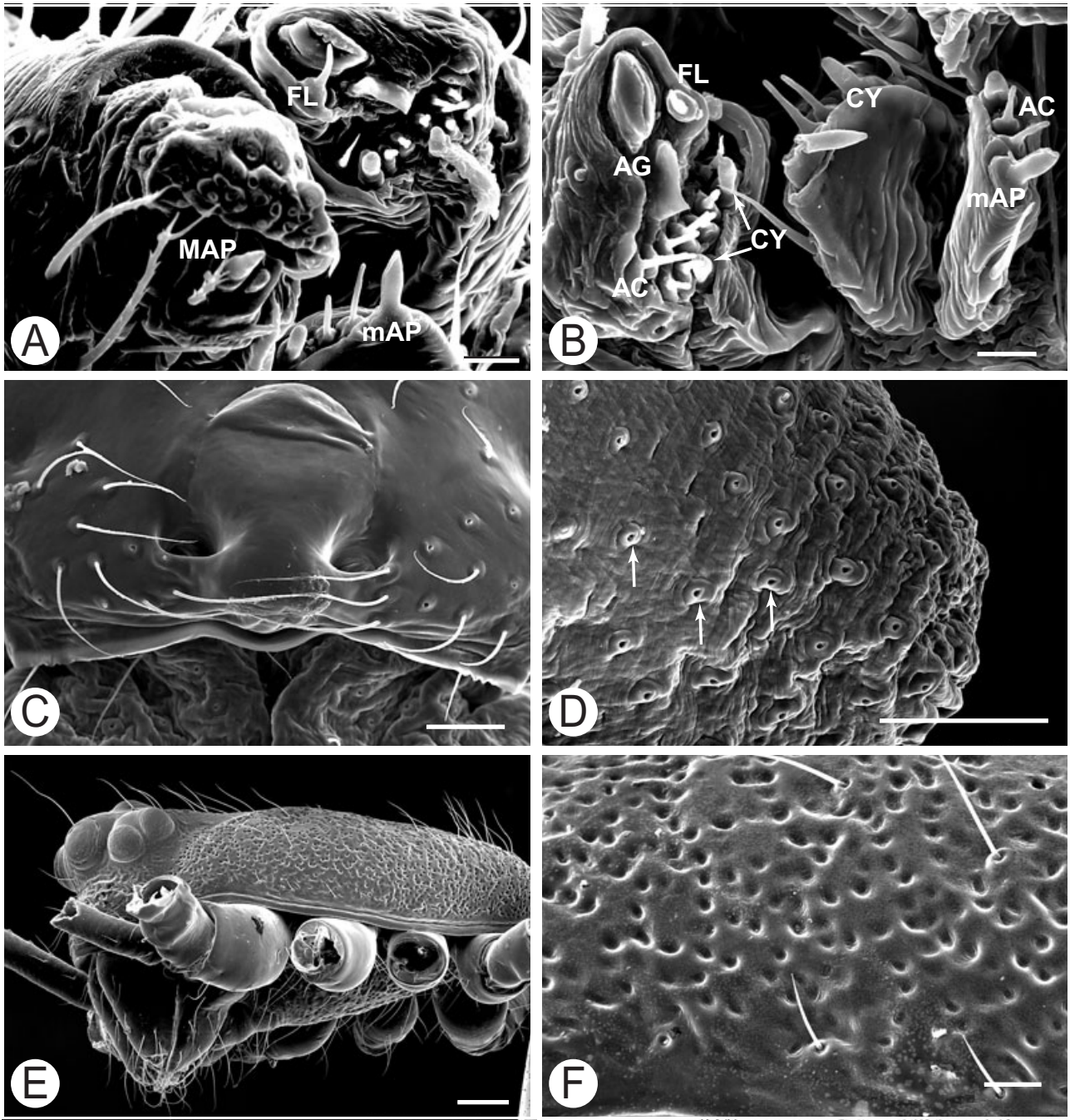

Figure 50. *Helvibis* cf. *longicaudatus*, female. A, B, spinnerets. A, left field. B, PMS and PLS. C, epigynum. D, posterior end of abdomen; note shape of setal bases (arrows). E, the rugose prosoma. F, details of the prosomal pits (**123-4**). Scale bars: A, B, 10 μm; C, 50 μm; D, E, 100 μm; F, 20 μm.

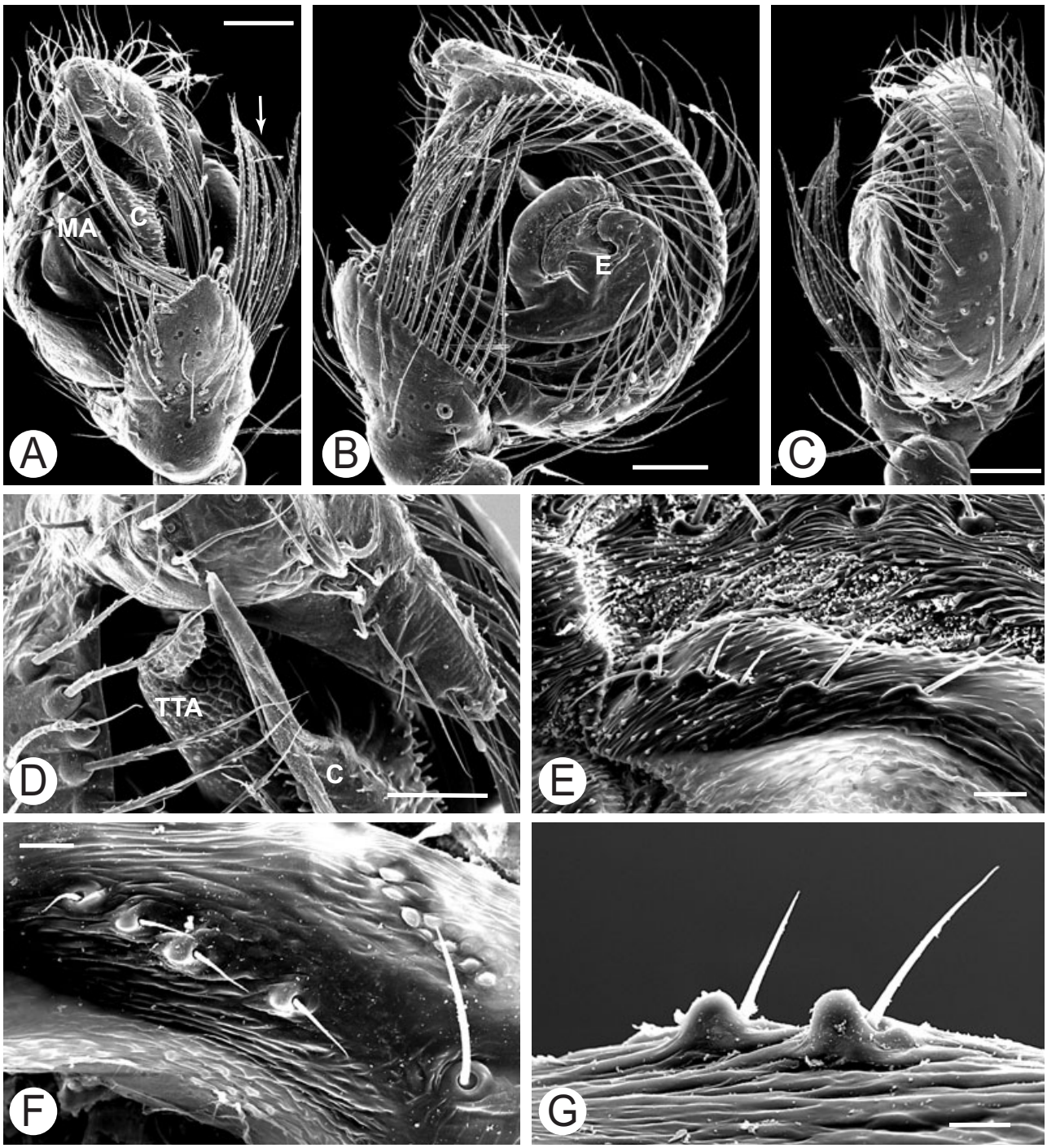

Figure 51. *Kochiura*. A–E, *K. aulica*. A–D, male palp; note shape of tibia (**14-1, 15-1, 17-1**) and extremely pronounced row of strong tibial setae (arrow, **16-1**). A, mesial. B, ventral. C, ectal. D, mesial close-up of C, TTA. E, SPR. F, G, *K. attrita* SPR. F, left field. G, details of setae; note modified bases (**151-1**). Scale bars: A–C 100 μm; D, 50 μm; E, F, 20 μm; G, 10 μm.

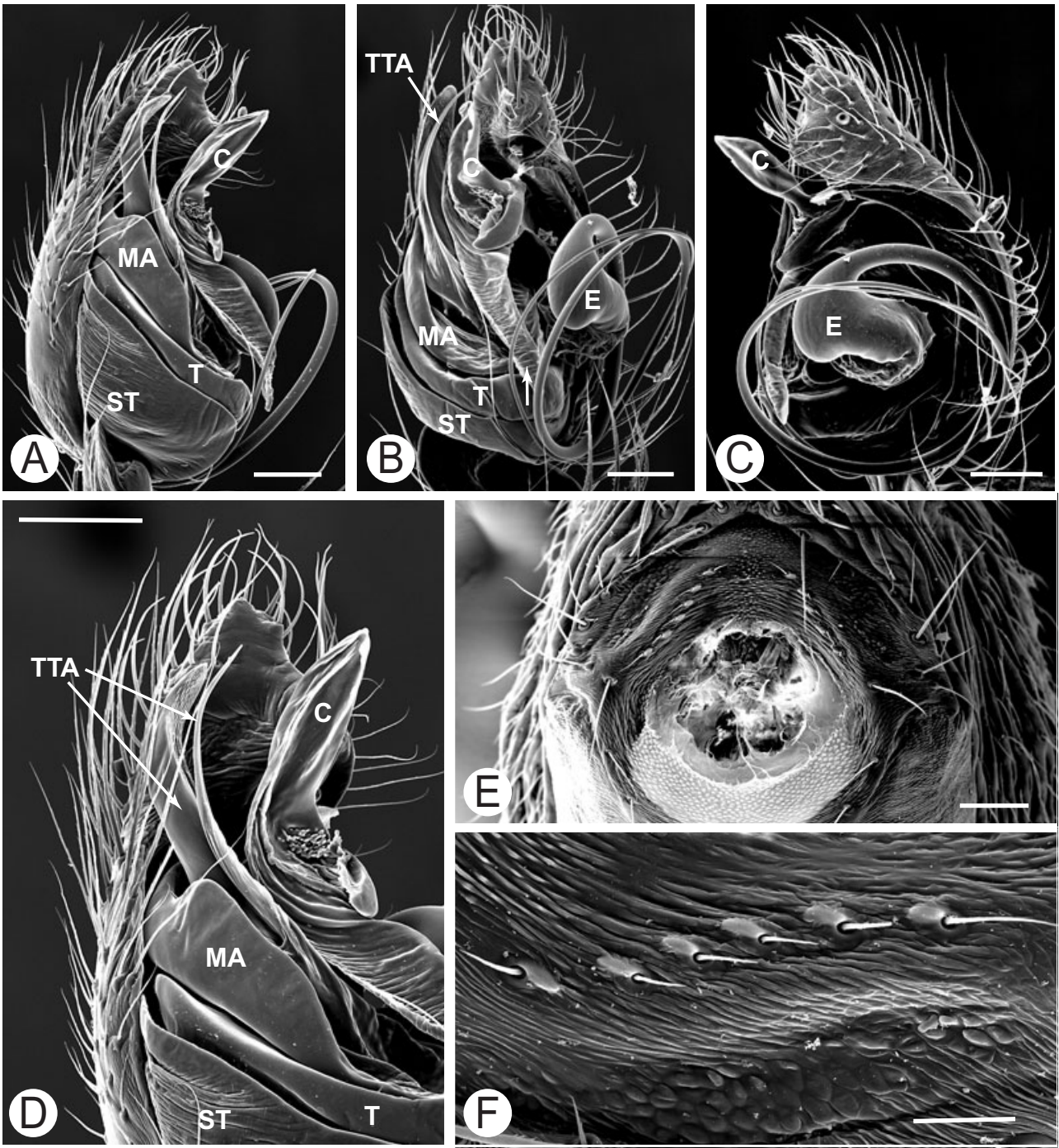

Figure 52. *Kochiura rosea*. A–D, male palp. A, mesial. B, ventral; note extremely elongated conductor, with a narrow base (lower arrow, **63-1**) and broadened distally. C, ectal. D, details of palpal tip; note bifurcated TTA (**81-1**). E, area around pedicel on abdomen. F, SPR. Scale bars: A–C, 100 μm; D, 50 μm; E, 20 μm; F, 10 μm.

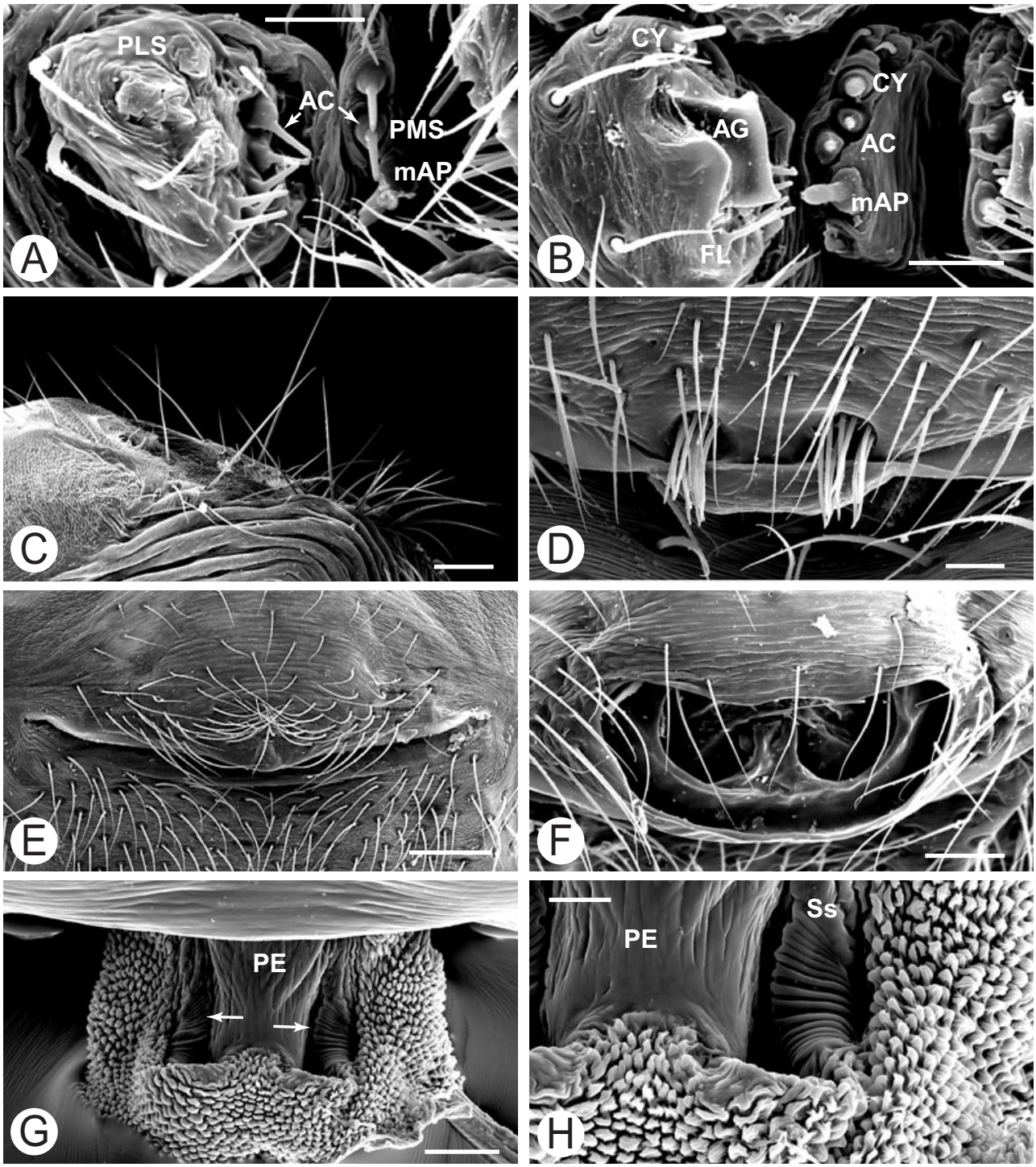

Figure 53. *Kochiura*. A, C–H, *K. rosea.* A, male PLS and PMS. B, *K. attrita* female PLS and PMS. C, setal proprioreceptors on abdomen. D, epiandrous gland spigots. E female genital furrow. F, epigynum. G, pedicel, paired rows of Ss forming lyriform organs (arrows), and stridulatory nubbins. H, details of pedicel. Scale bars: A, B, D, H, 20 μm; C, E, 100 μm; F, G, 50 μm.

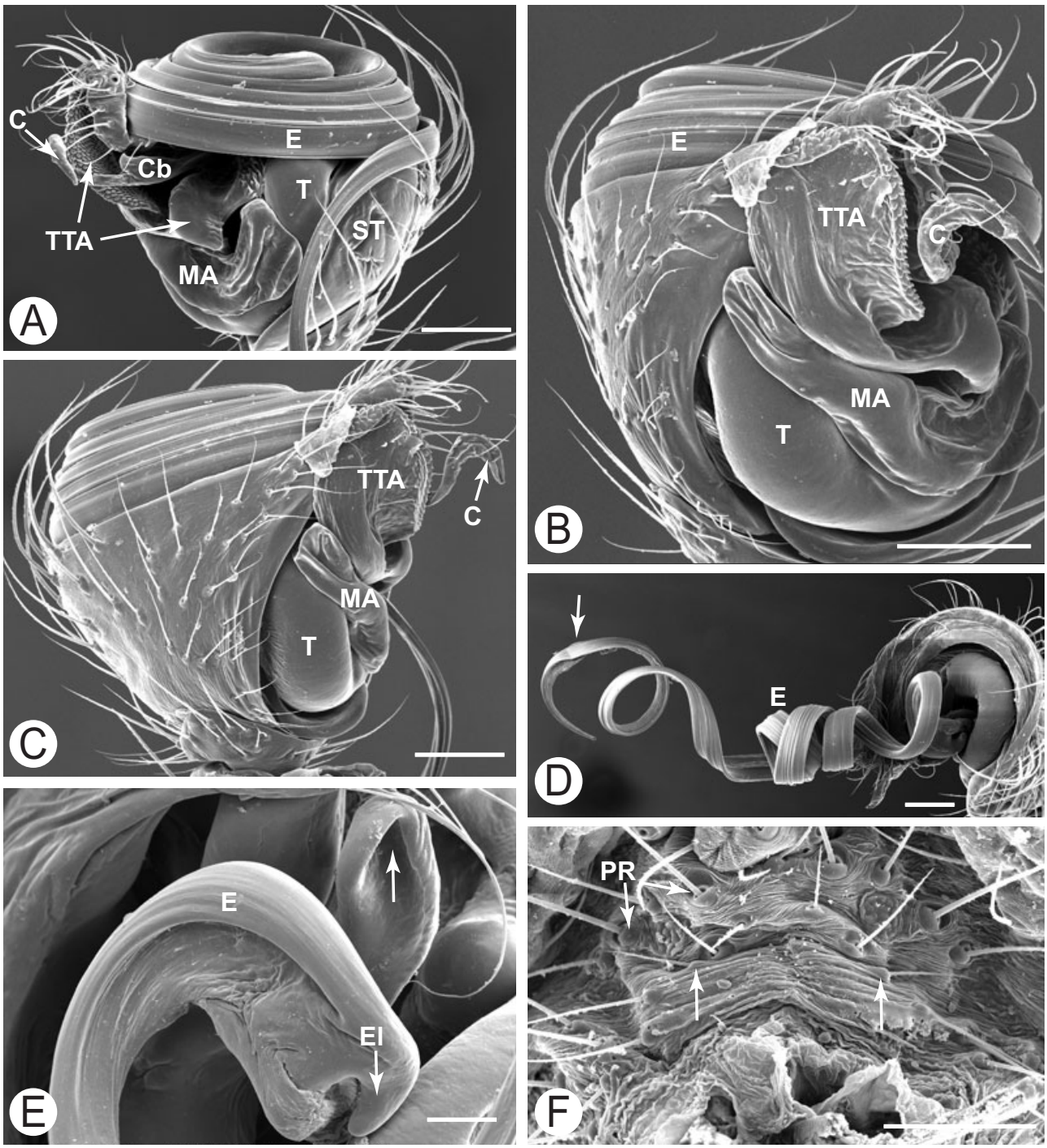

Figure 54. *Latrodectus*. A–C, F, *L. geometricus*. A, B, palp mesial. C, palp dorsal. D, E, *L. mactans*, male palp. D, expanded, ectal view, arrow indicates a break-off point on the embolus which is broken off during mating and left in the epigynum (**100-1**). E, embolus-conductor base lock mechanism; in the unexpanded palp the El (**98-1**) fits in the pit (arrow) of the C (**68-1**). F, area above the pedicel on the abdomen, showing stridulatory picks (arrows) and bases of PR. Scale bars: A–D, F, 100 μm; E, 50 μm.

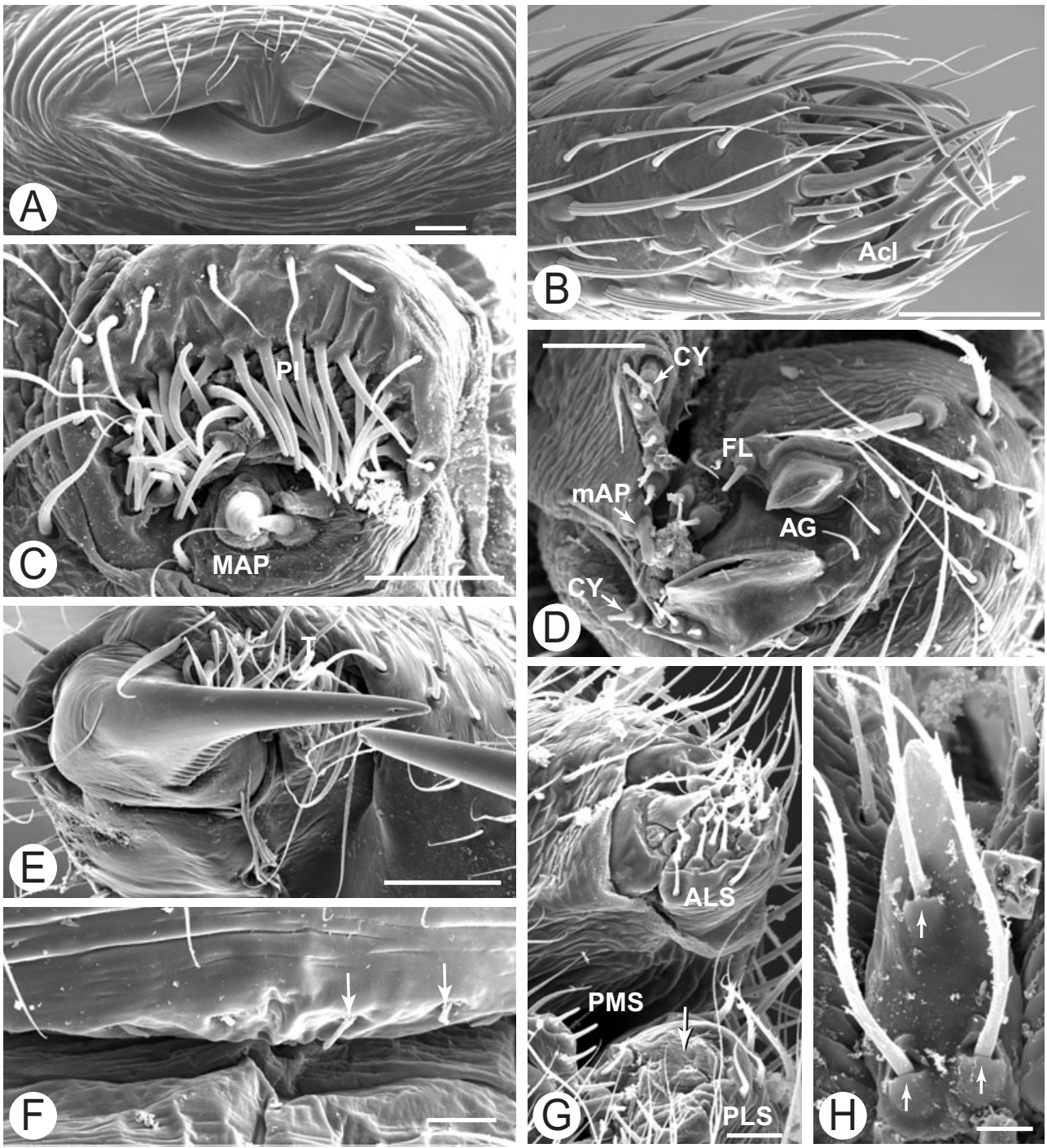

Figure 55. *Latrodectus geometricus*. A–E, female. A, epigynum. B, fourth tarsal claws and accessory claws (Acl). C, ALS. D, PMS and PLS. E, cheliceral claws. F–H, male. F, epiandrous gland spigots (arrows). G, right spinning field, the triplet is nonfunctional (arrow, **219-0**). H, details of a fleshy, triangular colulus (**172-0**, **173-0**), bearing two basal and one central setae (arrows, **174-0**, **175-0**). Scale bars: A, B, E, 100 μm; C, D, 50 μm; F, G, 20 μm; H, 10 μm.

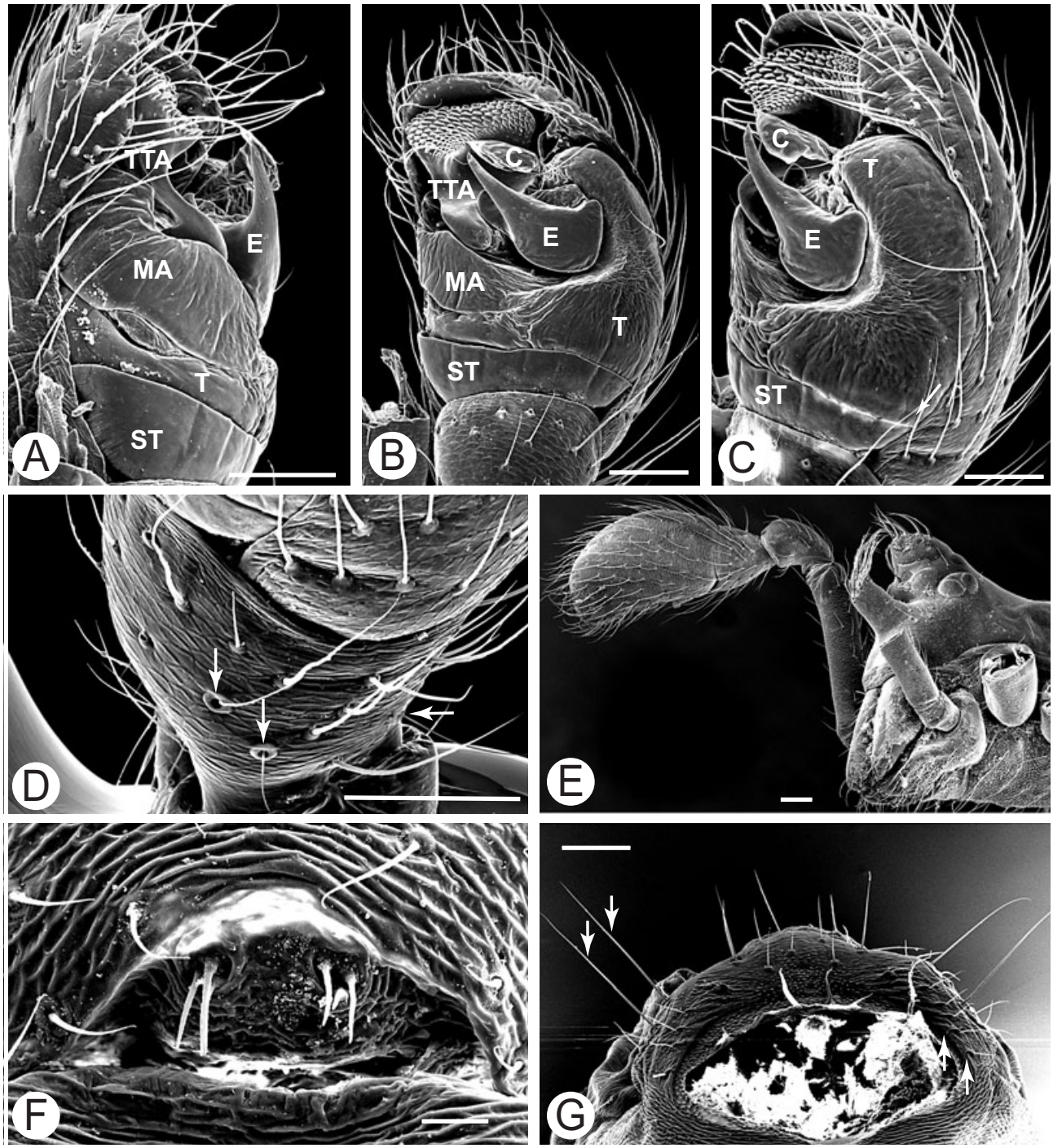

Figure 56. *Neospintharus trigonum*, male. A–D, palp. A, mesial. B, ventral. C, ectal. D, tibia, with two retrolateral (vertical arrows, **18-1**) and one prolateral (horizontal arrow, **19-1**) trichobothria. E, anterior part of the modified prosoma (**130–133**). F, epiandrous gland spigots. G, SPR (lower arrows) and setal proprioreceptors (upper arrows). Scale bars: A–E, G, 100 μm; F, 20 μm.

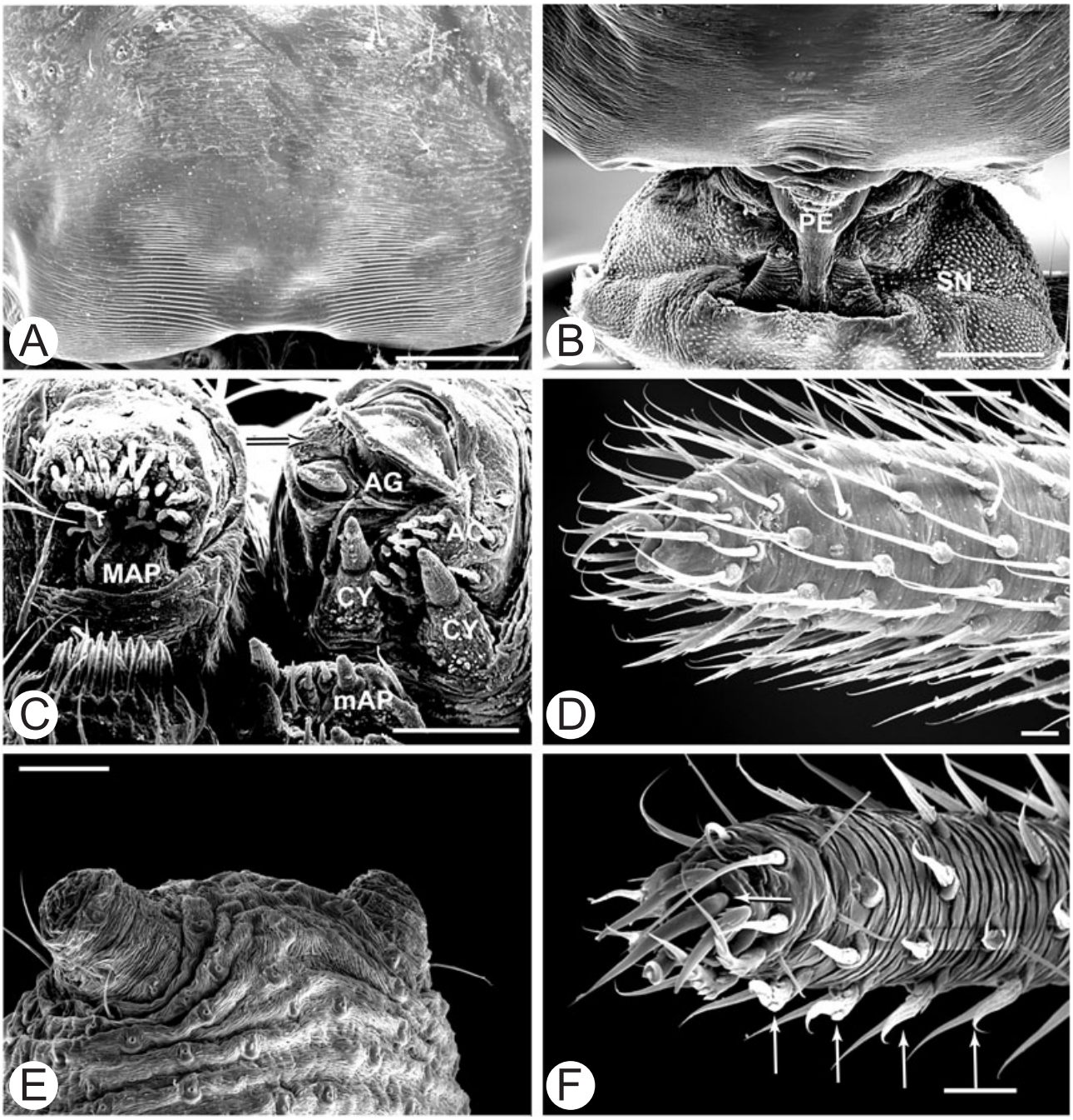

Figure 57. *Neospintharus trigonum*. A, prosomal stridulatory ridges. B, ditto, female; note broadened pair of slit sensilla on either side of PE (**141-1**) and extensive field of SN. C, female left spinning field; note absence of FL (arrow, **212-1**). D, female palpal tarsus; note sparsely dentate claw (**178-1**). E, dorsal view of abdominal humps, also present in *Faiditus* (**142-0**). F, female fourth tarsus; note elongated and elevated central claw (horizontal arrow, **200-1**) and the presence of at least a few serrated bristles (vertical arrows). Scale bars: A, B, E, 100 μm; C, 50 μm; D, F, 20 μm.

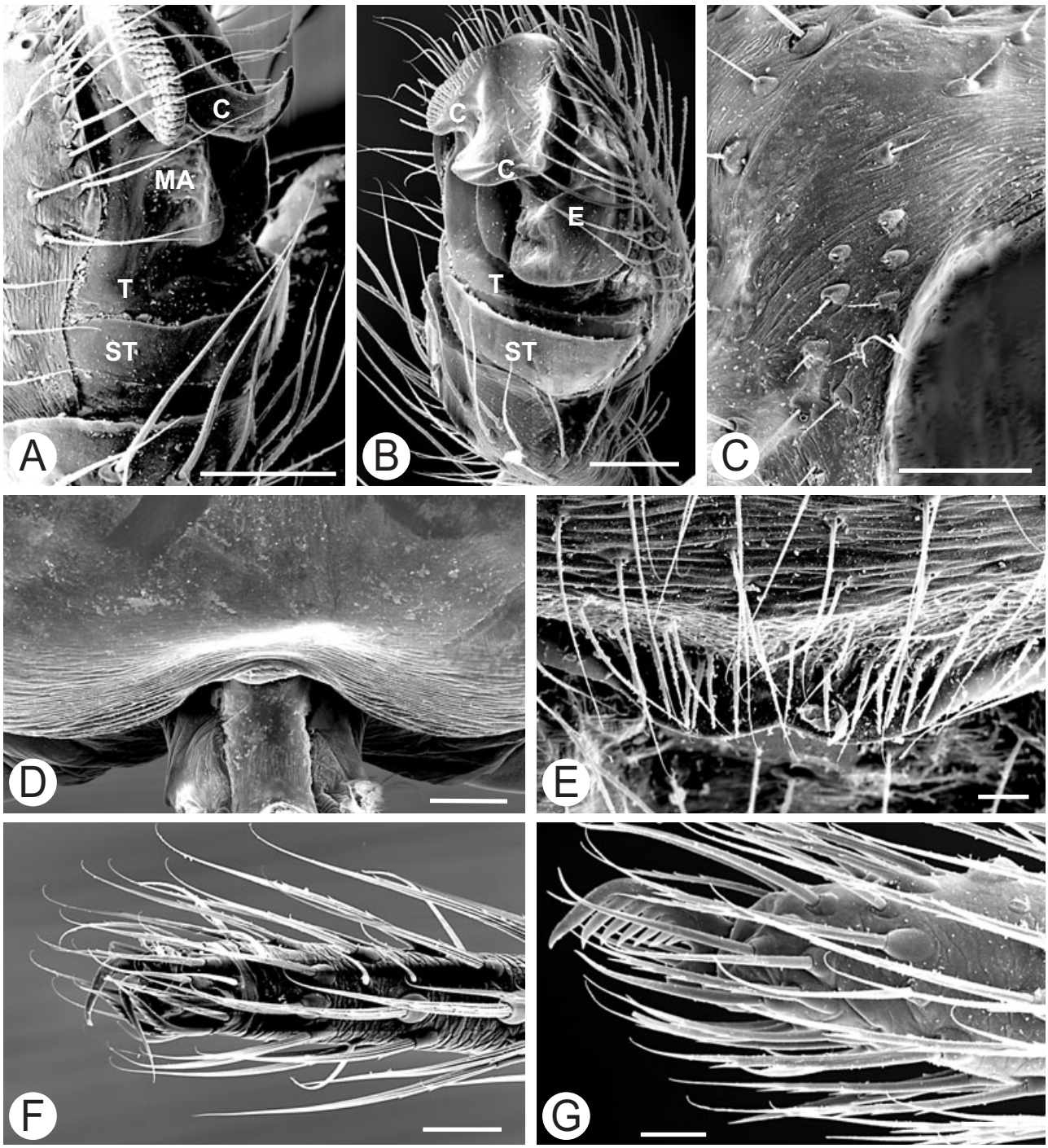

Figure 58. *Nesticodes rufipes.* A, B, male palp. A, mesial. B, ventral. C, stridulatory picks (pedicel area artificially shaded). D, stridulatory ridges. E, epiandrous gland spigots. F, male fourth tarsal claws. G, female palpal claw. Scale bars: A–D, 100 μm; E–G, 20 μm.

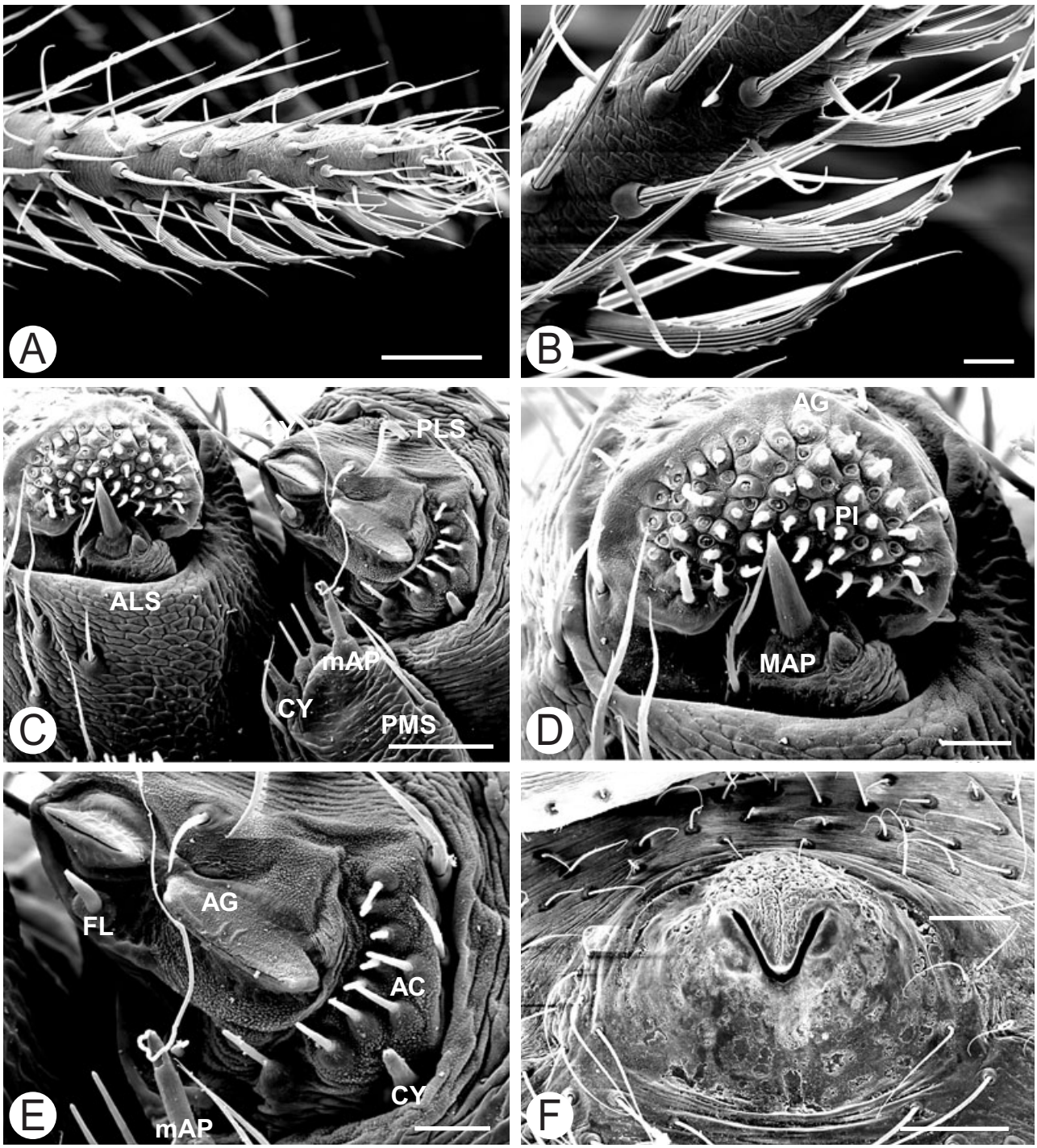

Figure 59. *Nesticodes rufipes*, female. A, tarsal comb. B, serrated setae of tarsal comb. C–E, spinnerets. C, left field. D, ALS. E, PLS. F, epigynum. Scale bars: A, 100 μm; B, 10 μm; C, 50 μm; D, E, F, 20 μm.

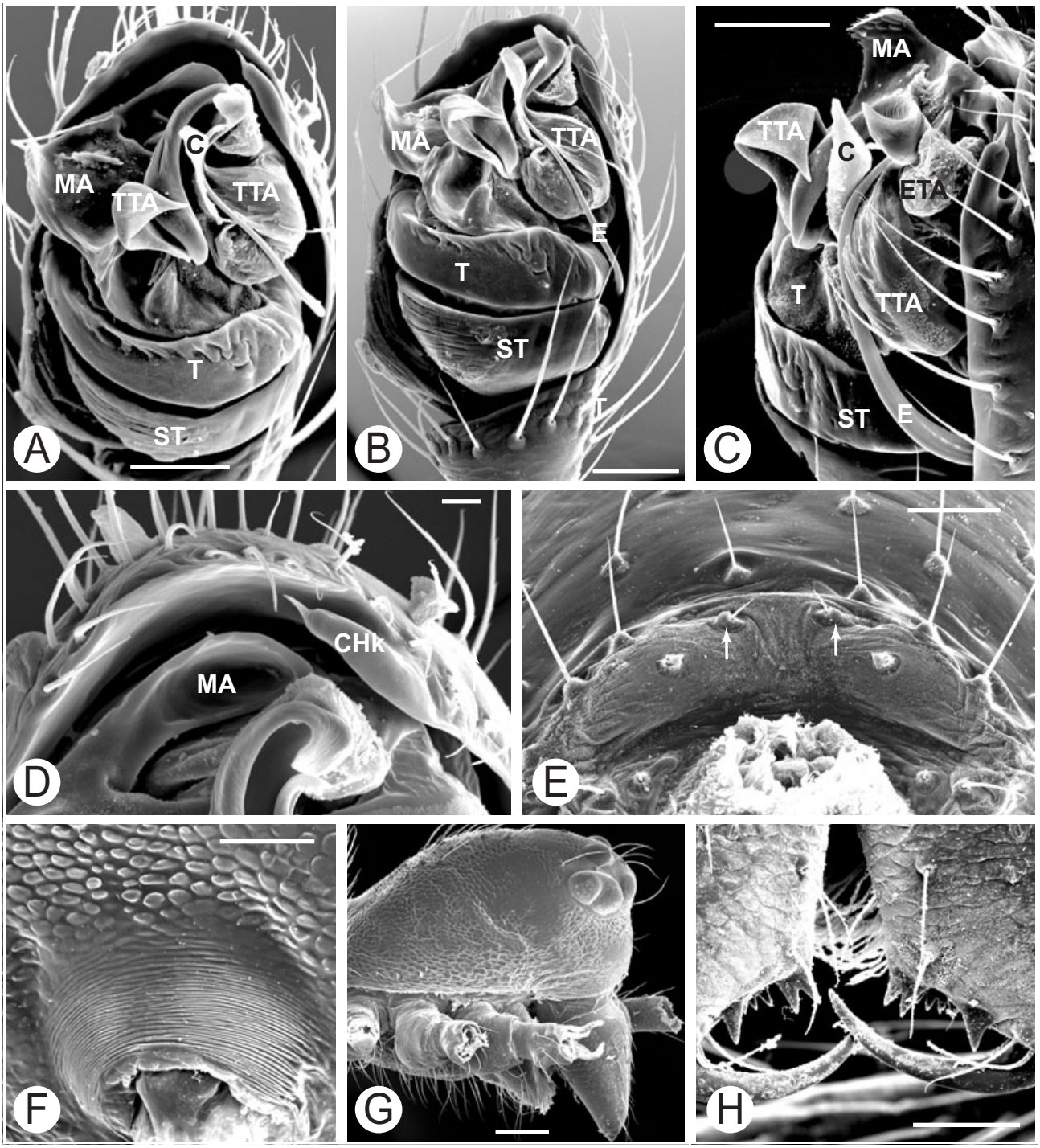

Figure 60. *Pholcomma hirsutum*, male. A–D, palp. A, mesial. B, ventral. C, ectal. D, CB-lock mechanism; note scoop shaped hood of MA (**79-1**) and tapering tip of cymbial hook (CHk, **37-1**). E, pedicel area of abdomen; note a pair SP (arrows). F, stridulatory ridges of the prosoma. G, prosoma. H, cheliceral teeth. Scale bars: A–C, E, F, H, 50 μm; D, 10 μm. G, 100 μm.

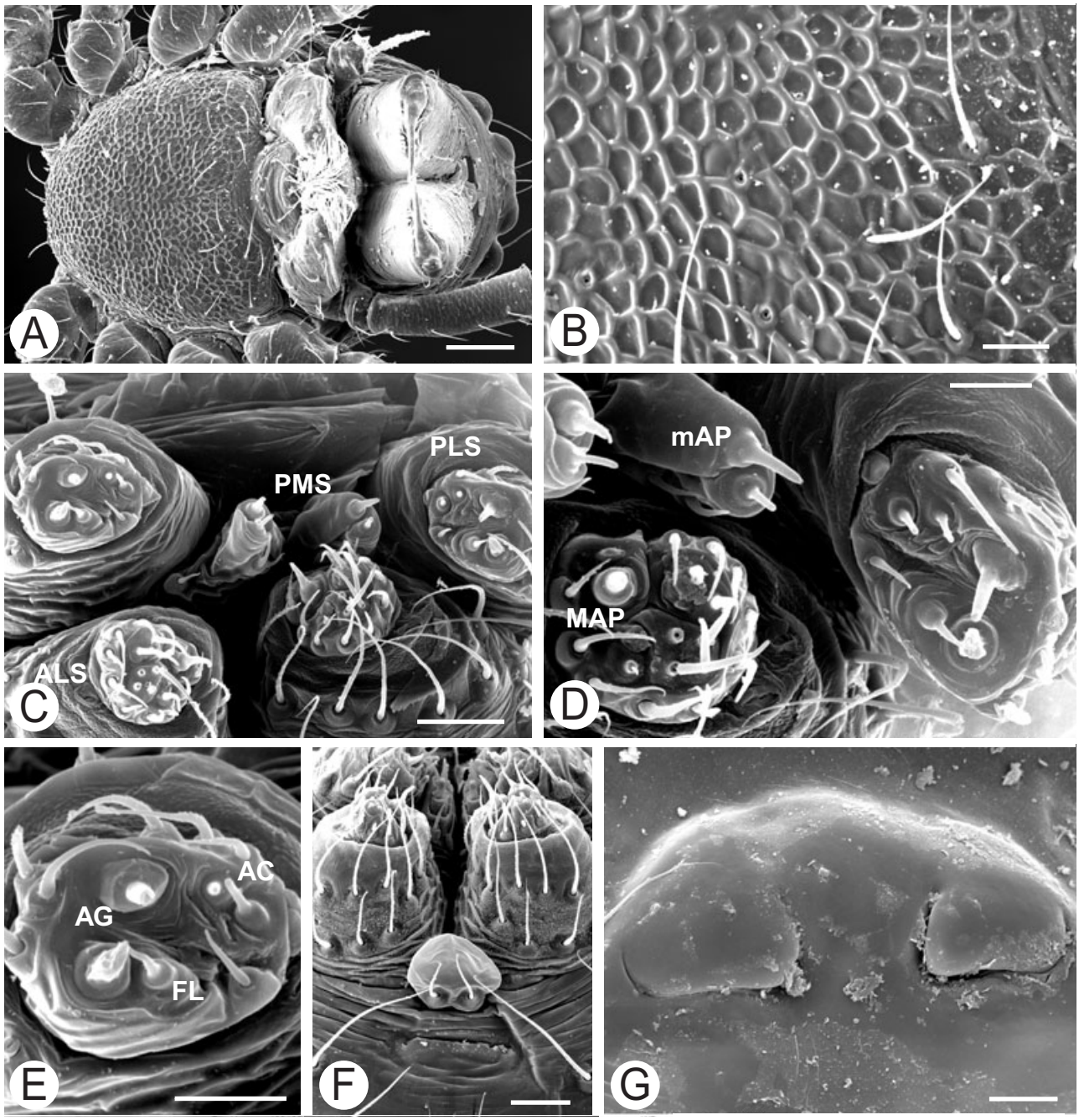

Figure 61. *Pholcomma hirsutum*. A–F, male. A, sternum. B, close-up of sternal 'scaly ridges' (**123-3**). C–F, spinnerets. C, all (female spinnerets are identical, except for the presence of CY). D, left field. E, PLS; note functional araneoid triplet (**219-1**). F, 'leaf shaped' colulus, a putative synapomorphy of *Pholcomma* and relatives. G, epigynum. Scale bars: A, 100 μm. B, D, E, G, 10 μm. C, F, 20 μm.

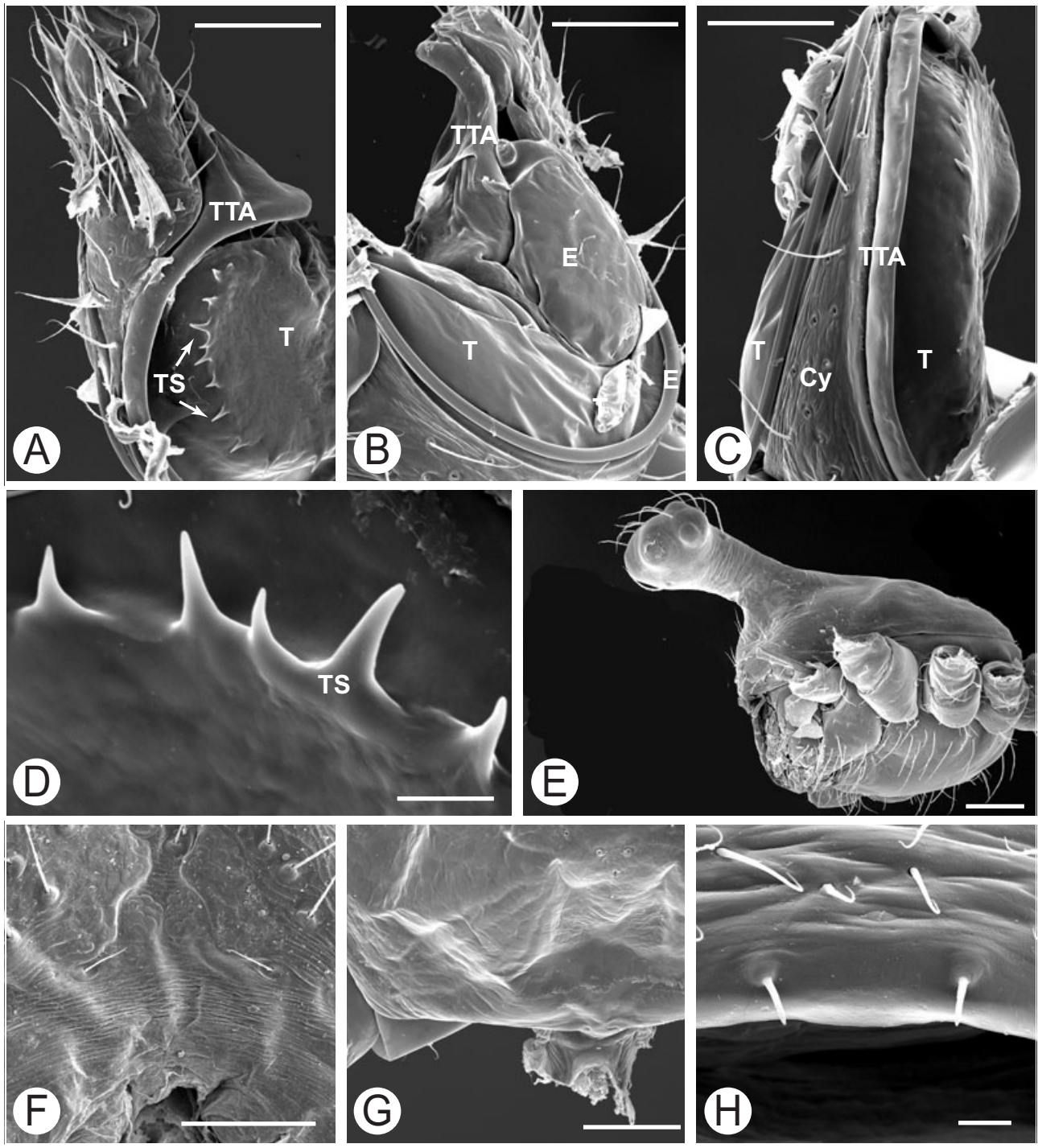

Figure 62. *Phoroncidia* sp., male. A–D, palp. A, mesial; note spines on tegulum, such spines are also present in *Sternodes foraminatus* Butler (see Moran, 1986), originally in Palpimanidae, later made the type of Sternodidae (Moran, 1986) and then transferred to Malkaridae by Platnick & Forster (1987). *Sternodes* shares several additional features with *Phoroncidia*. B, ventral. C, dorsal. D, close-up of tegular spines (TS). E, prosoma, head shape is typical for males of this genus (**103-2**). F, stridulatory area of abdomen, highly reduced. G, posterior end of prosoma, no stridulatory ridges visible (**150-0**). H, epiandrous gland spigots. Scale bars: A–C, E–G, 100 μm. D, H, 10 μm.

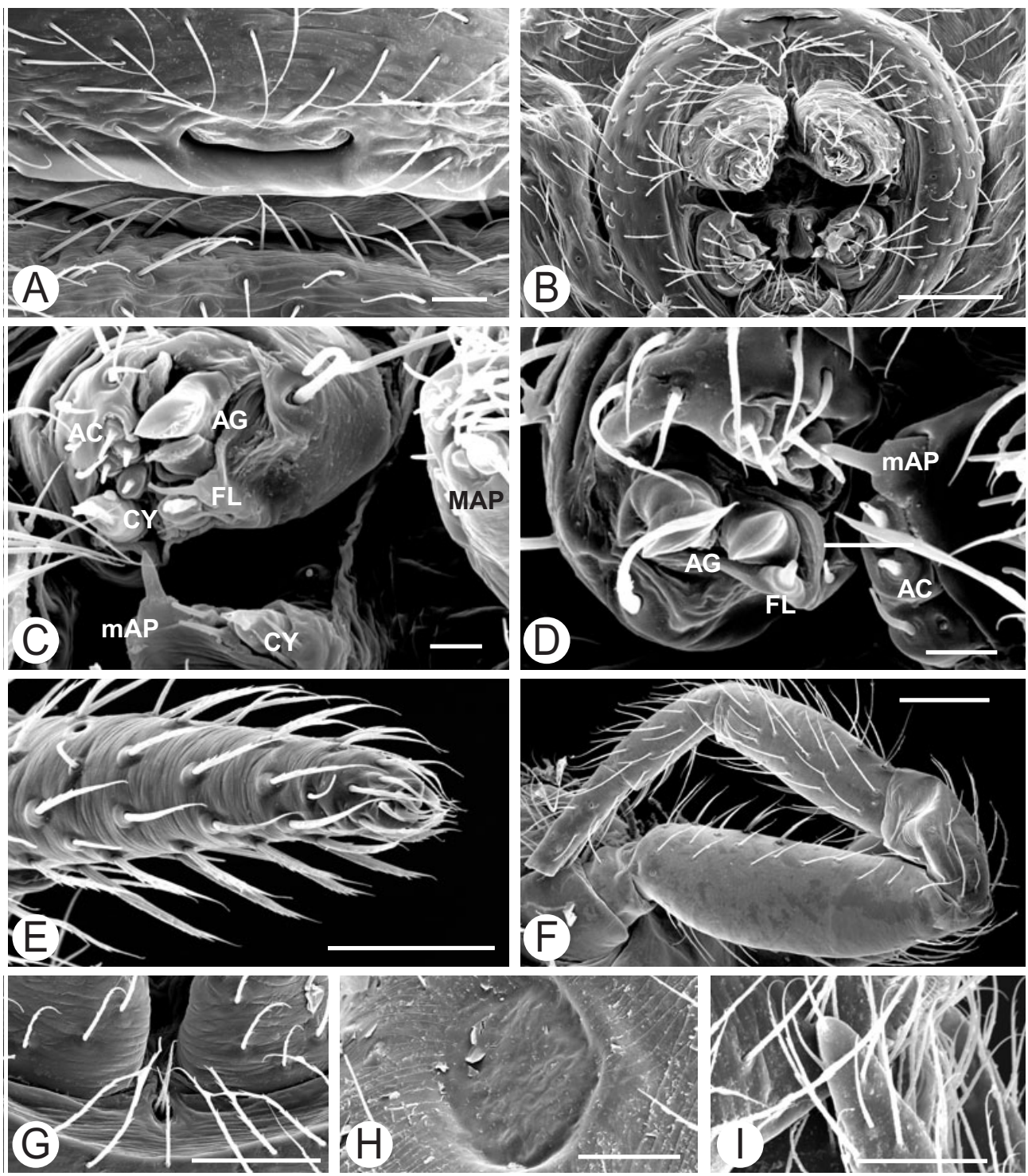

Figure 63. *Phoroncidia* sp. A–C, female. A, epigynum. B, spinnerets; note sclerotized ring around them (**202-1**). C, close-up of spinnerets. D–H, male. D, spinnerets. E, fourth tarsus. F, leg I; short and sturdy legs are typical for the genus. G, colular setae. H, abdominal apodeme. I, tip of female palpal tarsus, claw absent (**176-1**). Scale bars: A, 20 μm. B, F, 100 μm. C, D, 10 μm. E, G–I, 50 μm.

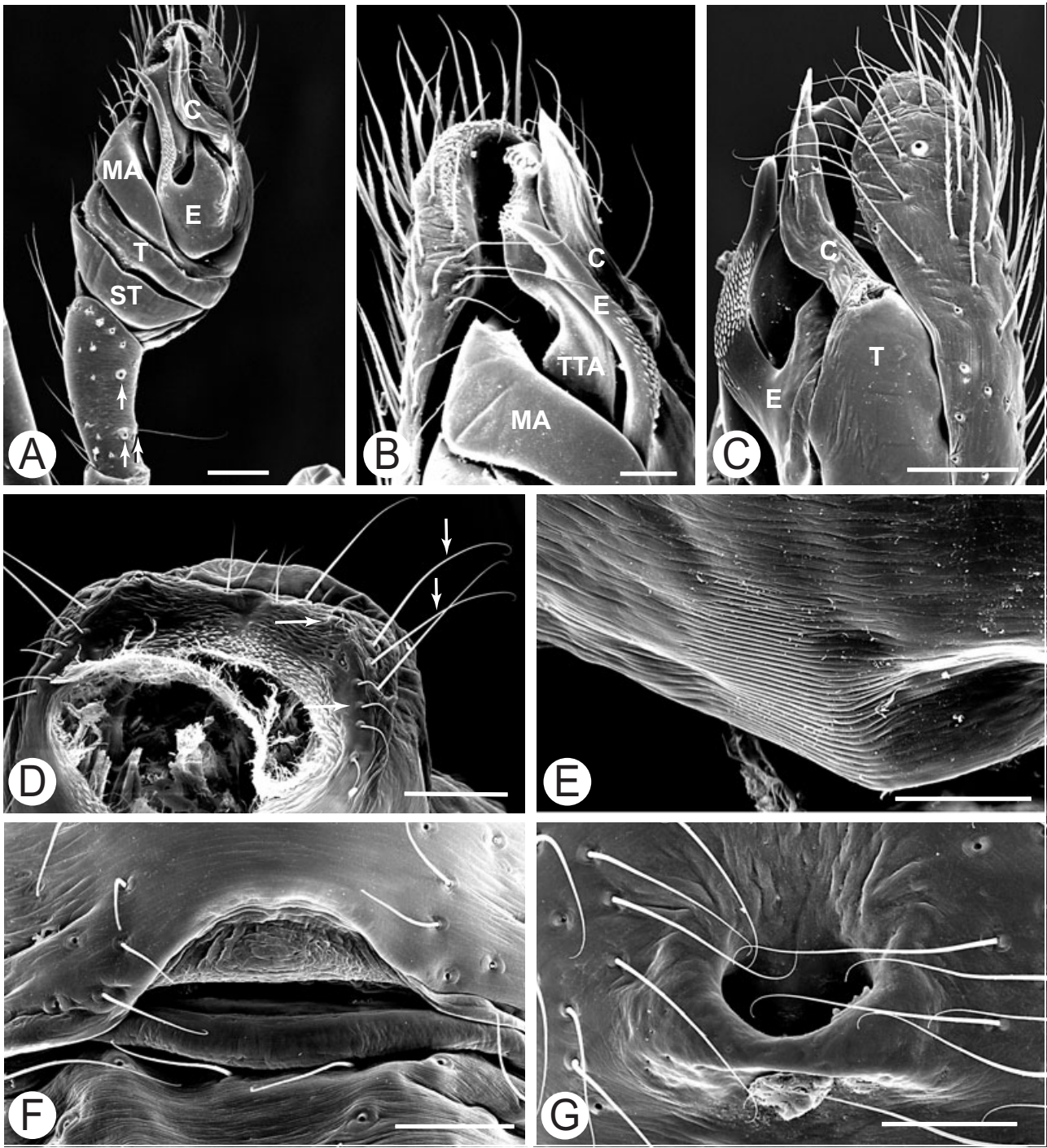

Figure 64. *Rhomphaea metaltissima*. A–C, male palp. A, ventral with tibia. B, submesial, apical part. C, ectal. D, abdominal SPR (horizontal arrows) and proprioreceptors (vertical arrows) around pedicel. E, stridulatory ridges on prosoma. F, genital furrow, epiandrous gland spigots absent (**168-1**). G, epigynum. Scale bars: A–D, 100 μm. E–G, 50 μm.

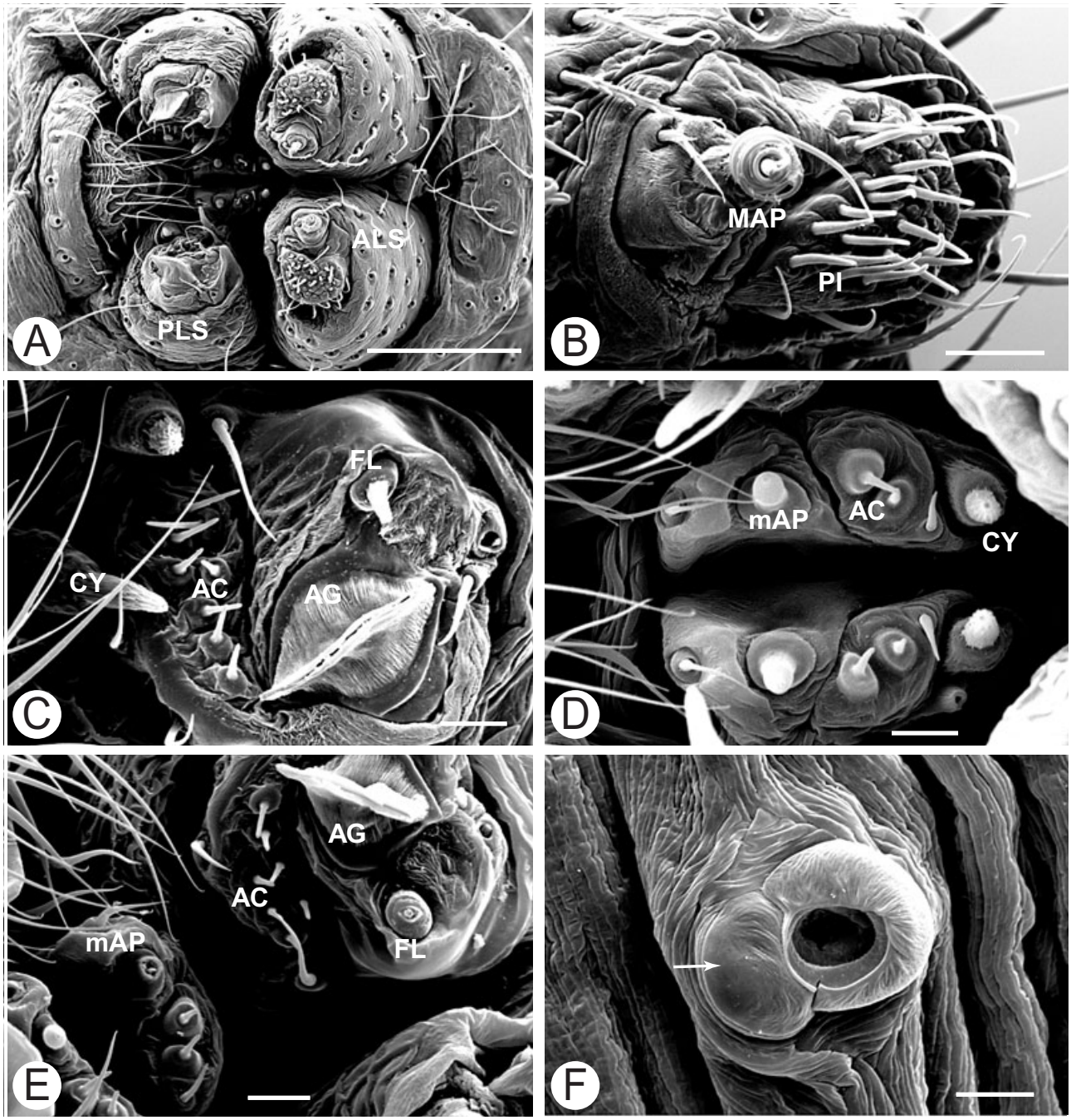

Figure 65. *Rhomphaea metaltissima*. A–E, spinnerets. A–D, female. A, all. B, ALS. C, PLS. D, PMS. E, male PMS and PLS. F, unusual setal base (arrow) posteriorly on female abdomen. Scale bars: A, 100 μm. B, 20 μm. C–F, 10 μm.

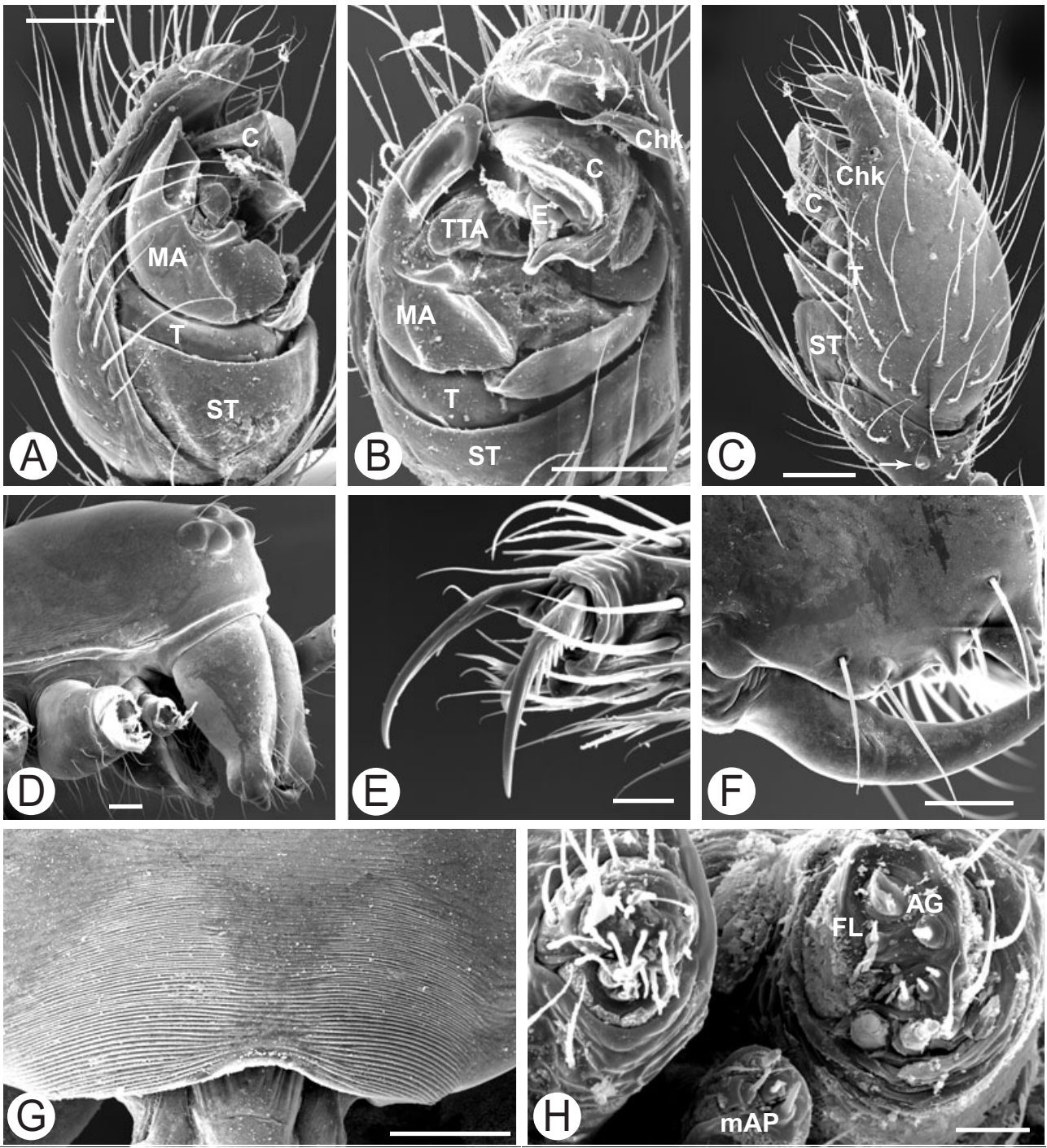

Figure 66. *Robertus lividus*. A–C, male palp; note that nomenclature of palpal sclerites is uncertain. A, mesial. B, ventral; note strongly tapered tip of the cymbial hook (Chk, **37-1**). C, ectal; note single trichobothrium on tibia (arrow, **18-2**, **19-2**). D, male prosoma. E, male fourth tarsal claws. F, male chelicera. G, prosomal stridulatory ridges. H, female spinnerets. Scale bars: A–D, G, 100 μm. E, F, H, 20 μm.

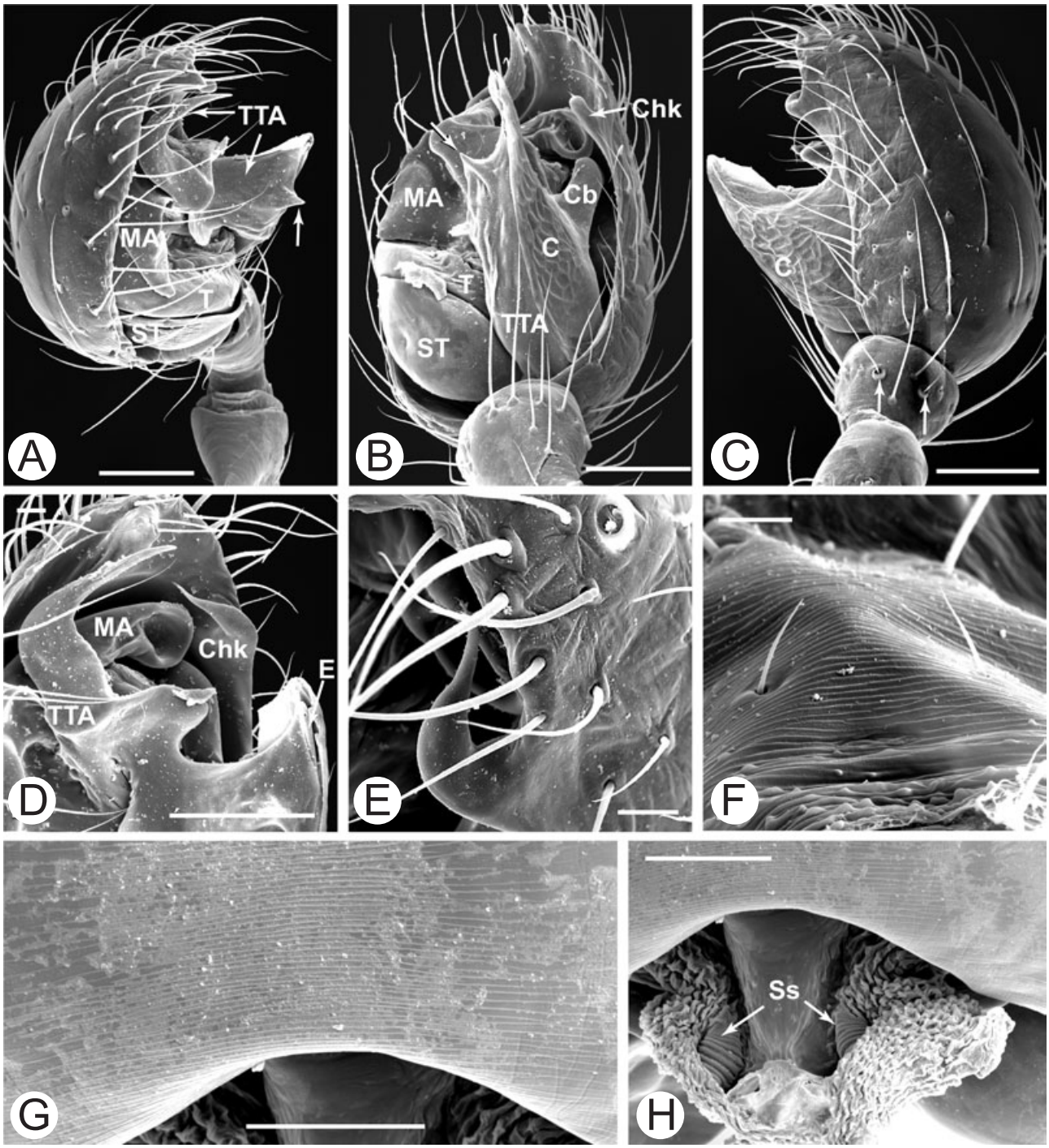

Figure 67. *Selkirkiella* sp. A–D, male palp. A, mesial; note knob on the TTA (lowest arrow, **82-1**). B, ventral, left arrow shows TTA knob. C, ectal; note two trichobothria on tibia (arrows, **18-2**, **19-1**). D, subapical; note hood on MA (**78-1**) and the complementary cymbial hook (Chk, **33-0**), on the cymbial margin (**35-1**). The highly tapered tip (**37-1**) is a synapomorphic condition for a group within Pholcommatinae (tapered cymbial hook clade). The E is visible tightly wrapped by the C, and the TTA (**87-1**). E, details of the upward pointed (**34-1**), tapered, cymbial hook. F, stridulatory area of abdomen; note a pair of SP, and numerous nubbins and ridges (**155-1**). G, H, *S. magallanes*. G, prosoma stridulatory ridges. H, pedicel; note slit sensilla (Ss) and nubbins. Scale bars: A–D 100 μm. E, F, 20 μm. G, H, 50 μm.

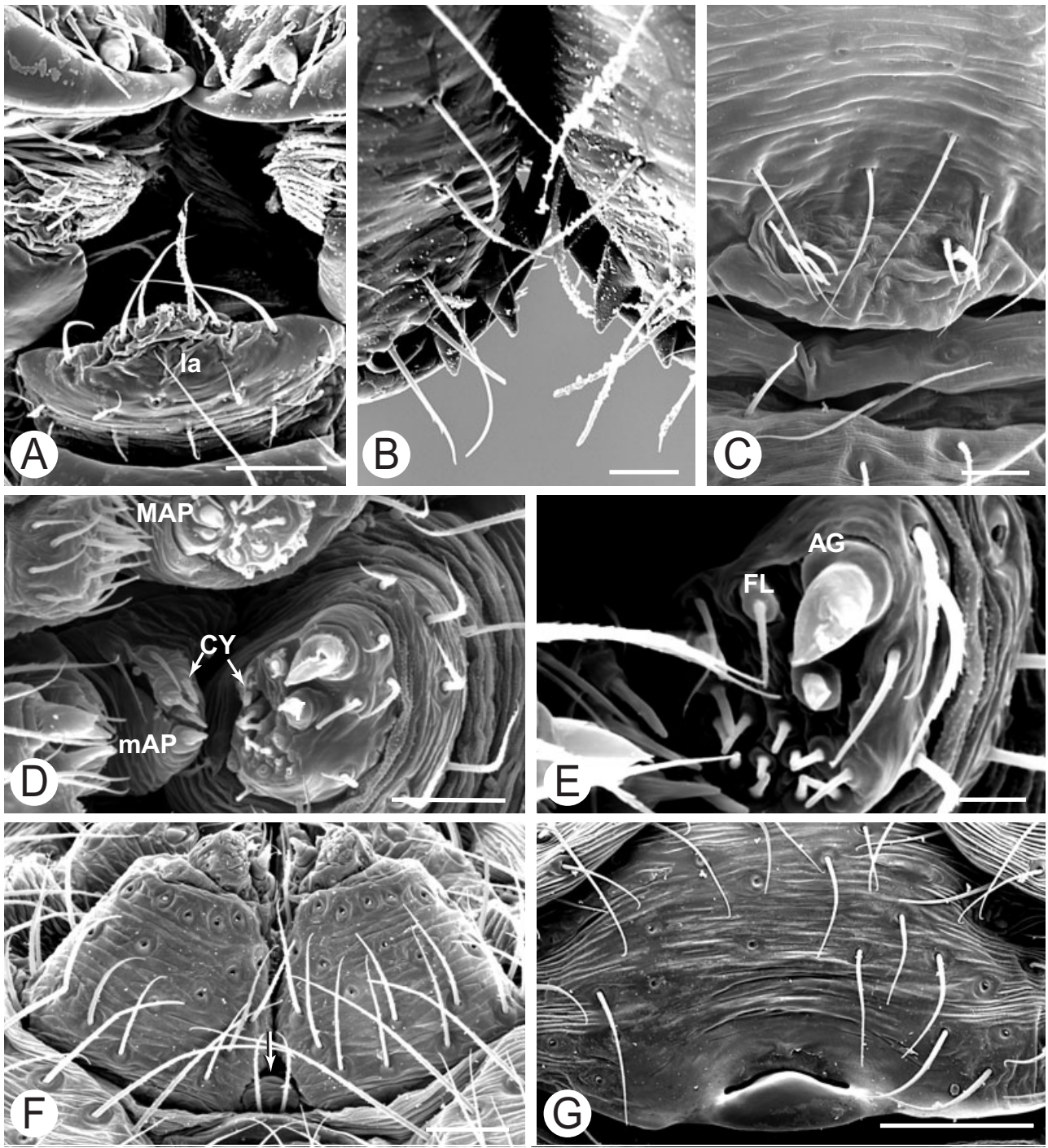

Figure 68. *Selkirkiella magallanes*. A, B, D–F, female. A, labium (la) and tips of chelicera. B, cheliceral promarginal teeth. C, epiandrous gland spigots. D, spinnerets. E, PLS. F colulus (arrow). G, epigynum. Scale bars: A, D–G, 100 μm. B, 20 μm. C, 50 μm.

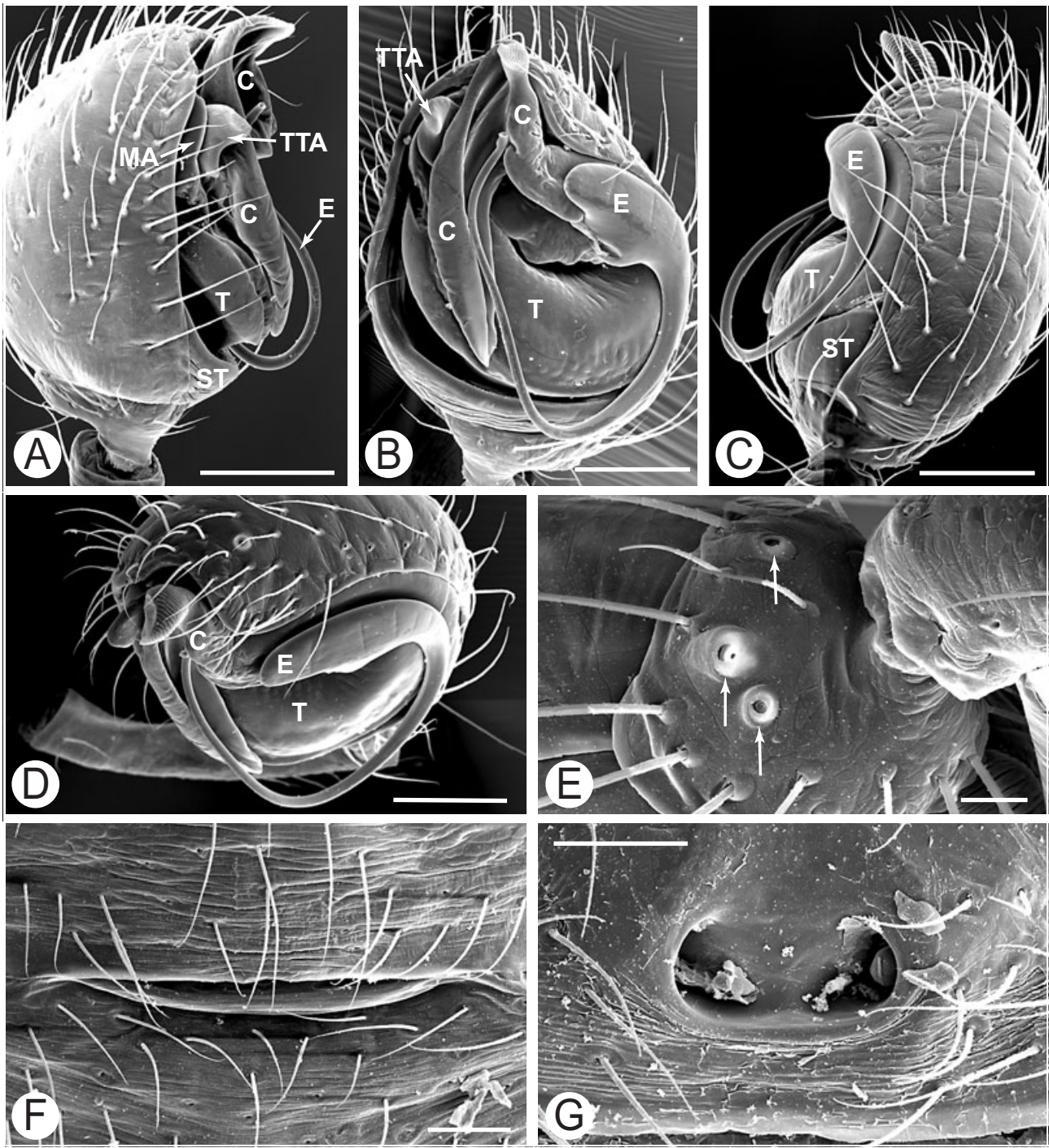

Figure 69. *Spintharus flavidus*. A–E, male palp. A, mesial. B, ventral; note huge conductor (**63-1**, **66-1**). C, ectal. D, apical. E, tibia; note three trichobothria (arrows). F, male genital furrow; note absence of epiandrous gland spigots (**168-1**). G, epigynum. Scale bars: A–D, 100 μm. E, F, 20 μm. G, 50 μm.

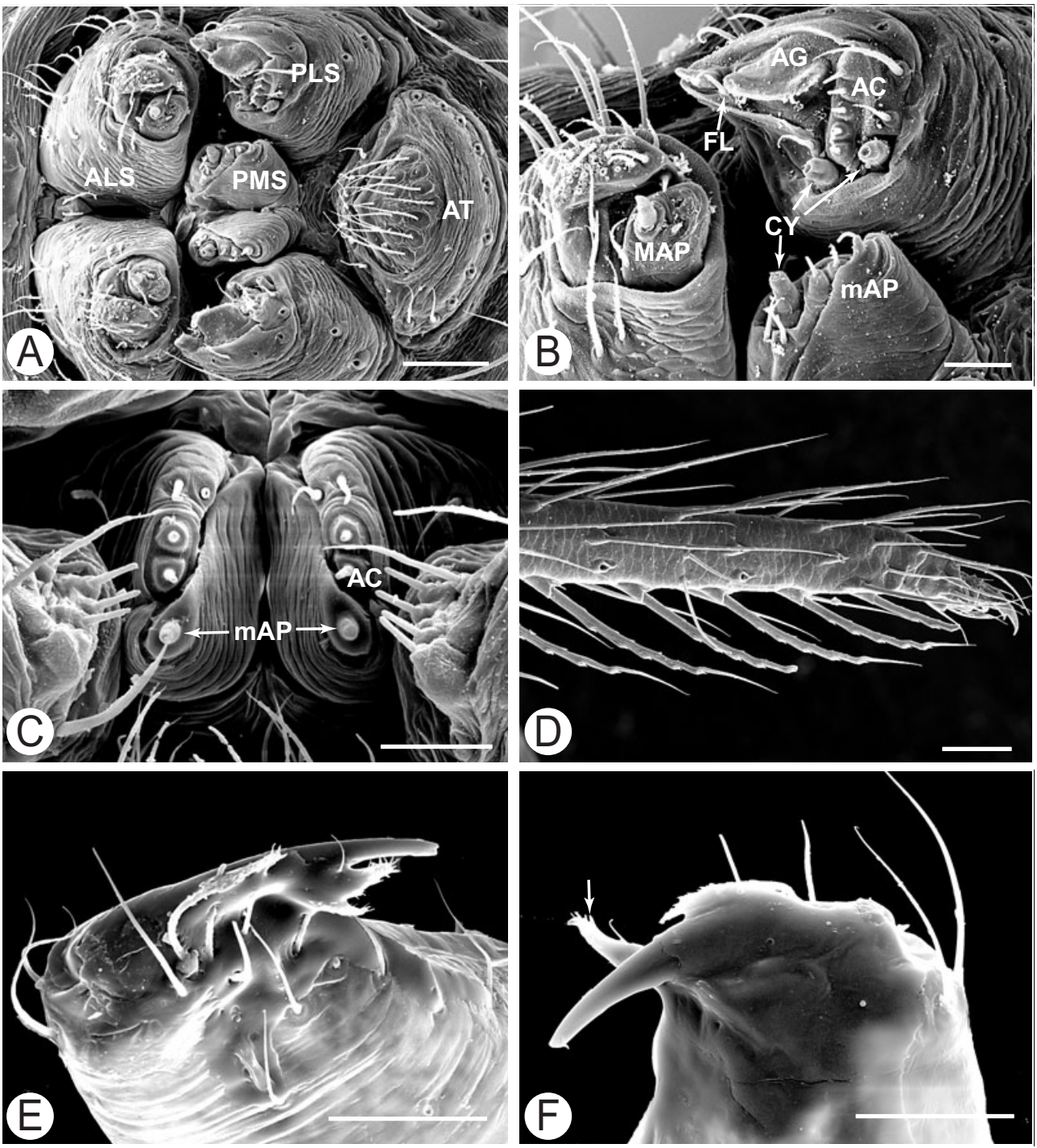

Figure 70. *Spintharus flavidus*. A–C, spinnerets. A, B, female. A, all. B, left field. C, male PLS and PMS. D, tarsal comb, the notched dorsal margin (**196-1**) is a spintharine synapomorphy. E, chelicera prolateral margin. F, ditto, retrolateral margin, the peculiar outgrowth (arrow) was only seen in this species. Scale bars: A, D–F, 50 μm. B, C, 20 μm.

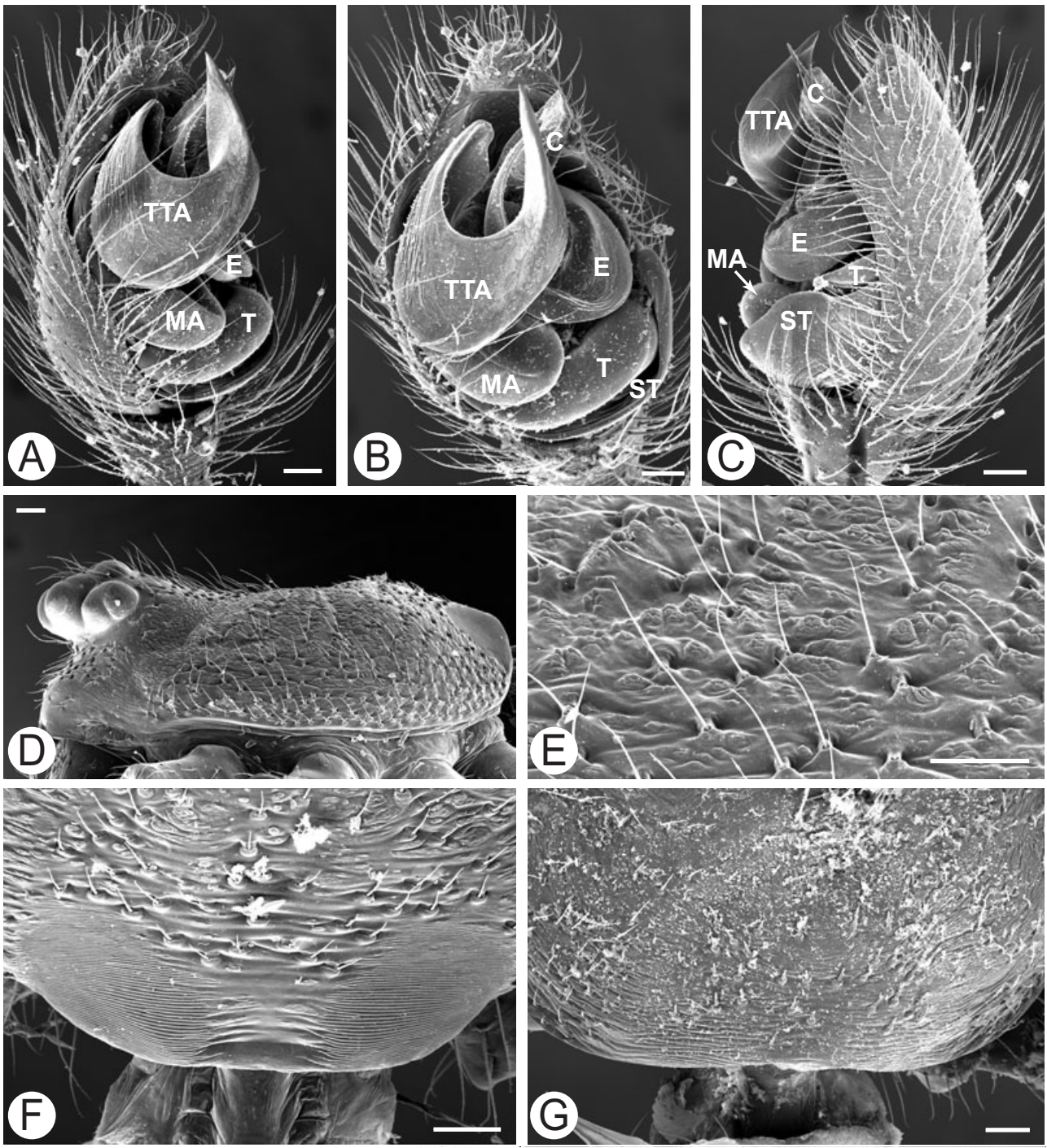

Figure 71. *Steatoda bipunctata*. A–F, male. A–C, palp. A, mesial. B, ventral. C, ectal. D–G, prosoma. D, profile. E, details of setae; note raised bases (**123-1**). F, posterior tip with stridulatory ridges (**128-1**) in two clearly separate patches (**129-0**). G, female with inconspicuous stridulatory ridges. Scale bars: 100 μm.

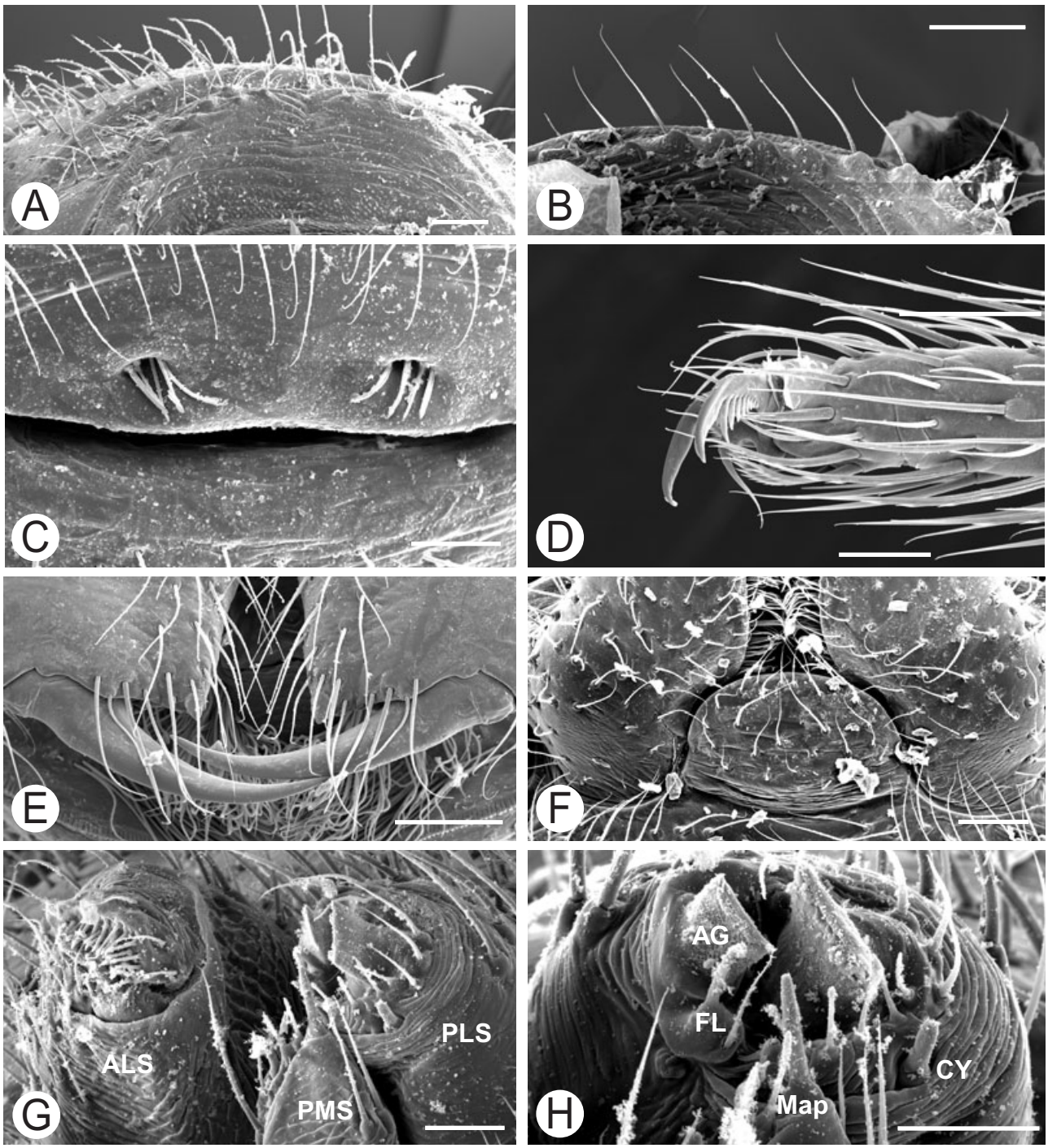

Figure 72. *Steatoda bipunctata*. A–F, male. A, stridulatory picks. B, details of picks and setae. C, epiandrous gland spigots. D, fourth tarsal claws. E, cheliceral fangs. F, labium. G, H, female spinnerets. G, left field. H, PLS. Scale bars: A, B, E, F, 100 μm. C, D, G, H, 50 μm.

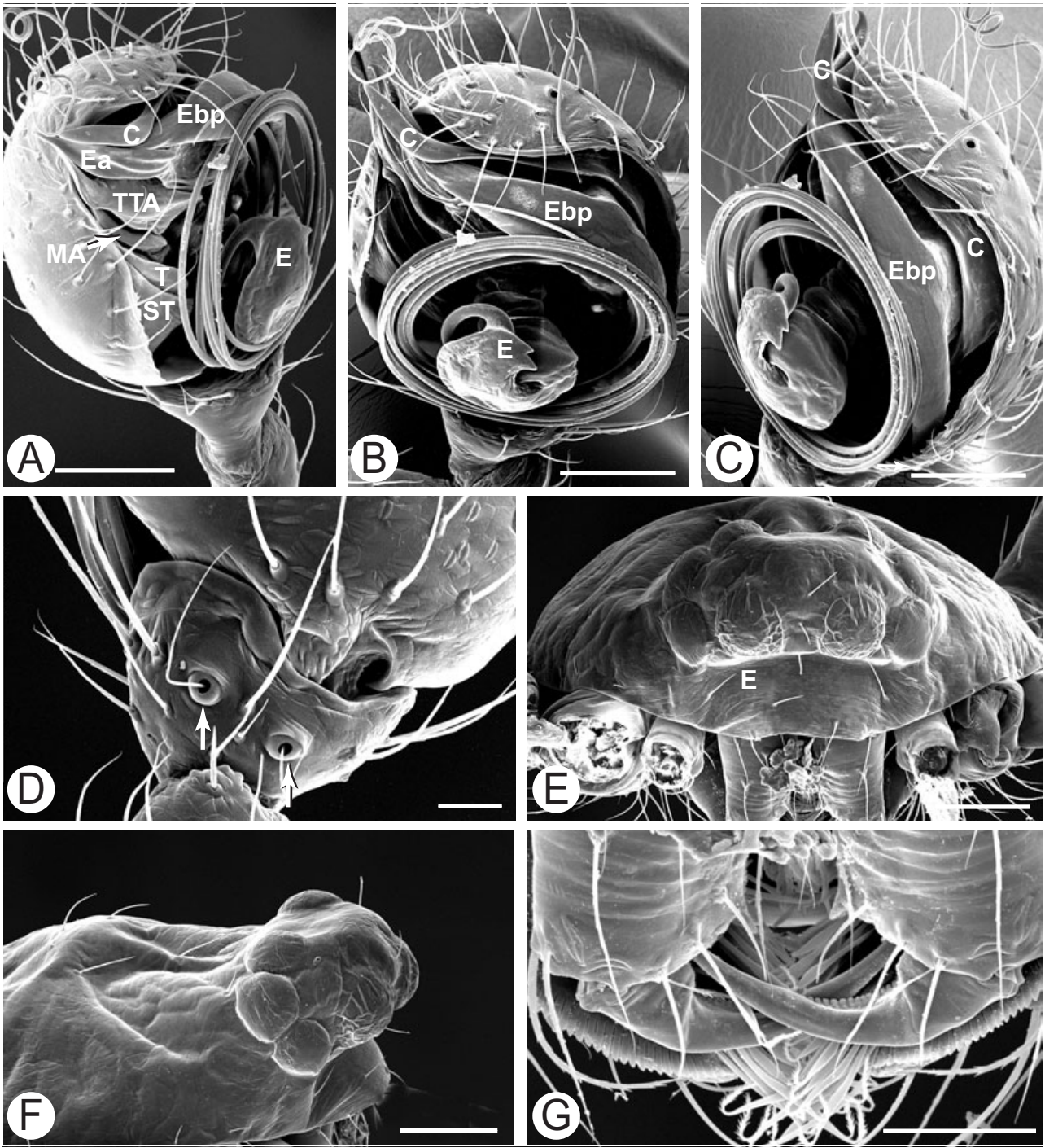

Figure 73. *Stemmops* nr. *servus*. A–D, male palp; this palp is unique in that the sperm duct exits not through the extremely long and thin spiral, but rather through a basal process of the embolus (Ebp). The Ebp is tightly associated with the C, and the TTA, as would normally be the E spiral. A, mesial. B, ventral. C, ectal. D, tibia, with one retrolateral and one prolateral trichobothria. E, front of male prosoma, the dome shape is unusual. F, male prosoma; note eyes on a tubercle similar to *Phoroncidia* (**102-3**). G, male cheliceral fangs. Scale bars: A–C, E, F, 100 μm. D, 20 μm. G, 50 μm.

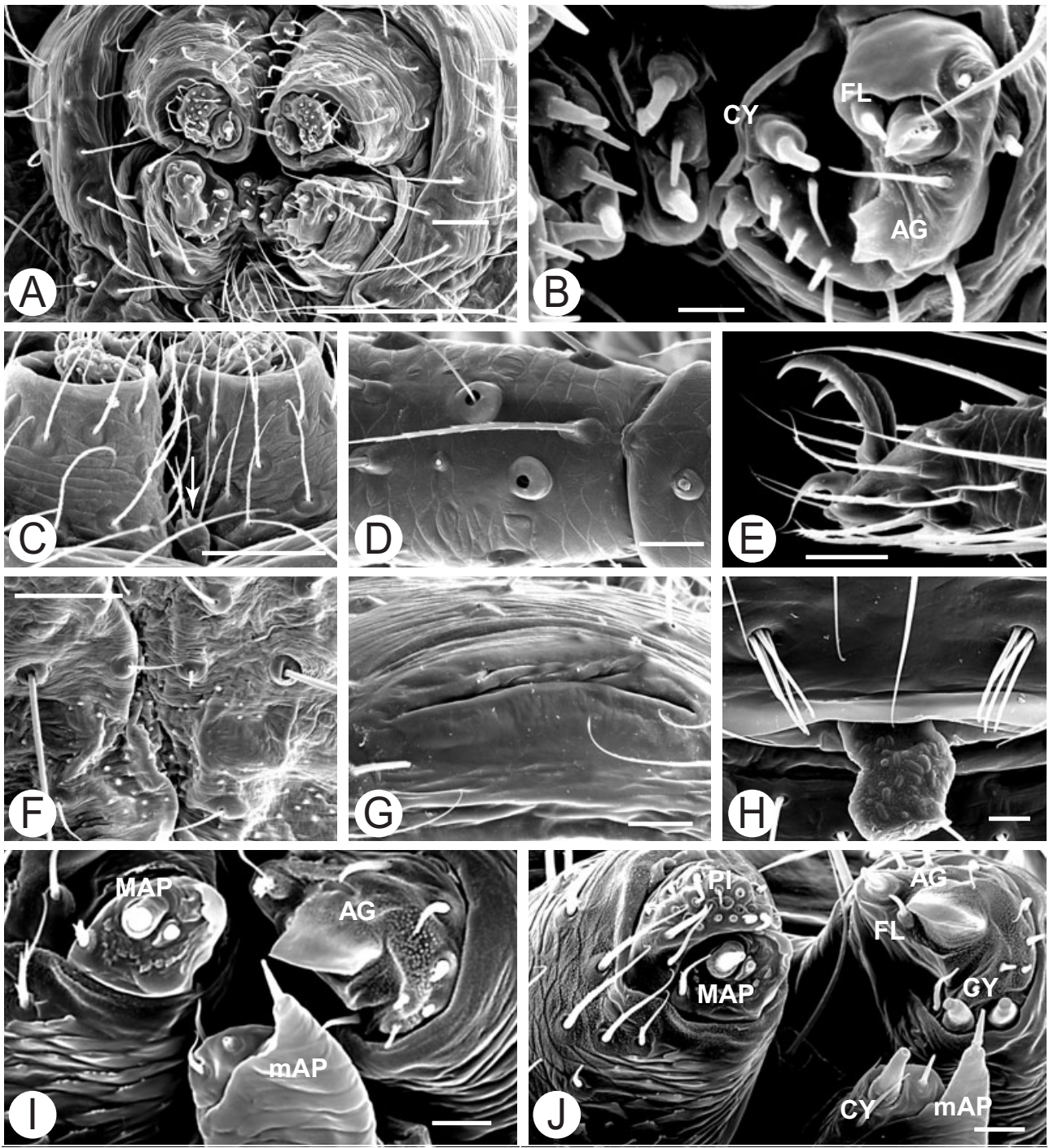

Figure 74. *Stemmops*. A–G, *Stemmops* nr. *servus*. A–C, female spinnerets. A, note sclerotized ring around spinnerets (**202-1**). B, PLS and PMS. C, colulus (arrow). D, female palpal tibia, dorsal view. E, male fourth tarsal claws. F, female pedicel area. G, epigynum. H–J, *S. bicolor*. H, epiandrous gland spigots. I, male spinnerets; note functional AG (**219-1**). J, female spinnerets. Scale bars: A, 100 μm. C, F, 50 μm. D, G, 20 μm. B, E, H–J, 10 μm.

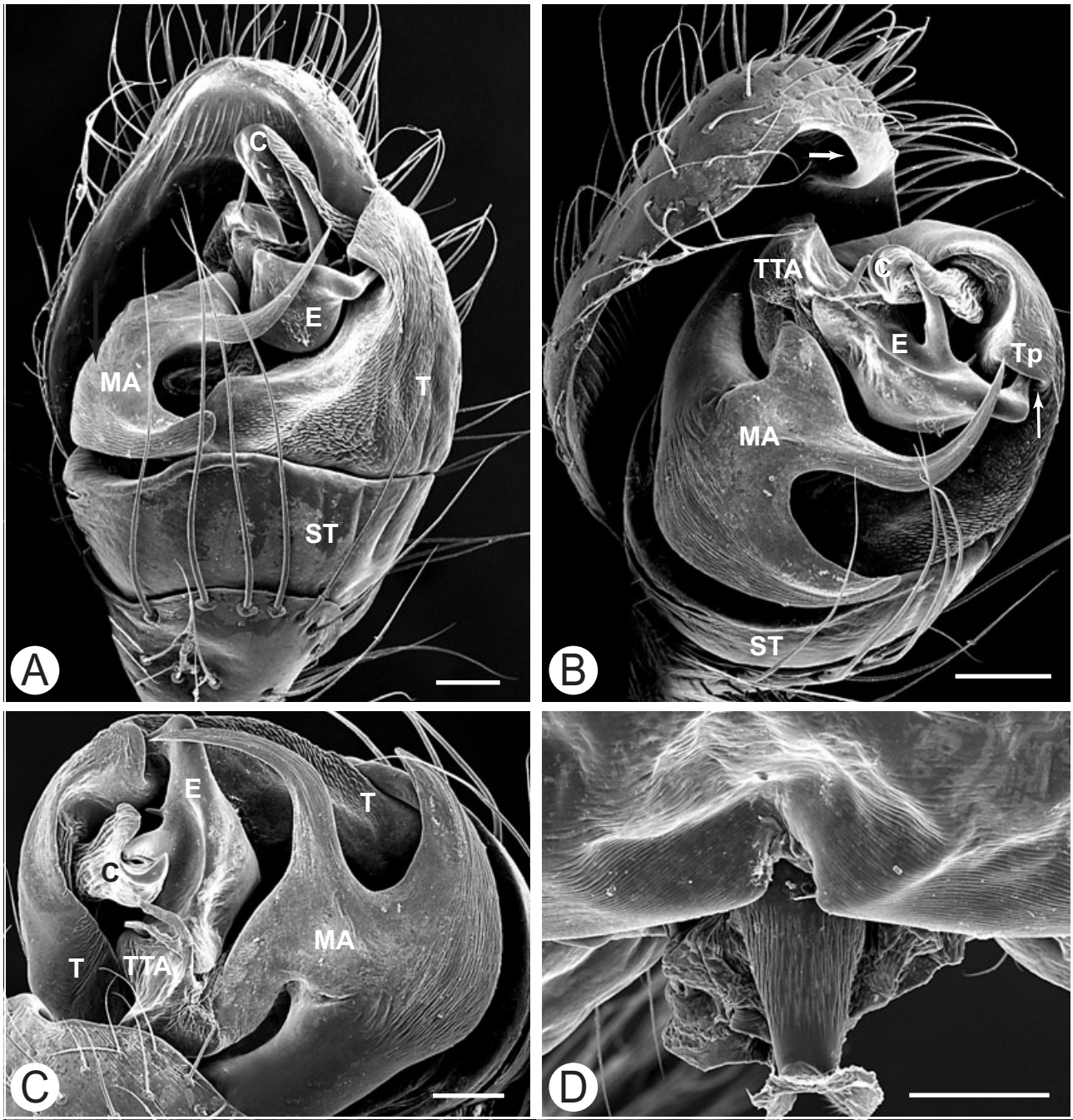

Figure 75. *Theridion frondeum* male. A–C, palp. A, ventral. B, mesial; note two lock mechanisms, embolus-tegulum lock mechanism, the apophysis on the E base (putatively homologous to the El in some other taxa, **98-1**) fitting (**50-1**) in the tegular pit (lower arrow, **49-1**), and the bulb-cymbium lock mechanism with a large cymbial hood (upper arrow, **33-1**) where the distal arm of the MA fits (**78-0**). C, apical. D, prosomal stridulatory ridges. Scale bars: 100 μm.

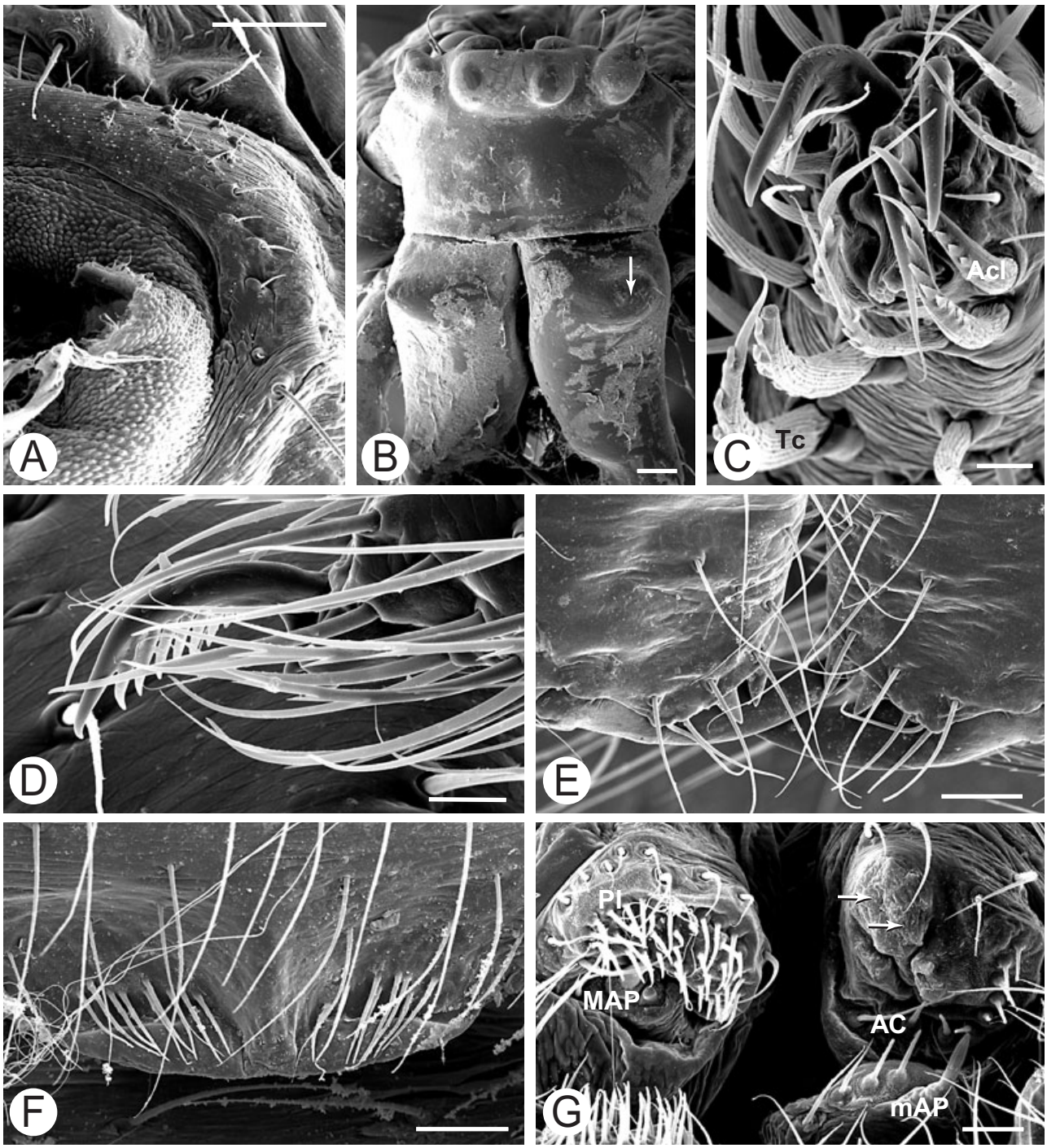

Figure 76. *Theridion frondeum*. A, male SPR. B, male prosoma front view; note humps on chelicera (arrow, **115-1**). C, female fourth tarsal claws; note elongated central claw (**200-1**) and the similarity of the serrated bristles of the tarsal comb (Tc, **195-1**) to the accessory claws (Acl). D, palpal claw. E, promarginal cheliceral teeth. F, epiandrous gland spigots. G, male spinnerets; note absence of a functional triplet (arrows, **219-0**). Scale bars: A, B, 100 μm. C, 10 μm. D, F, 20 μm. E, G, 50 μm.

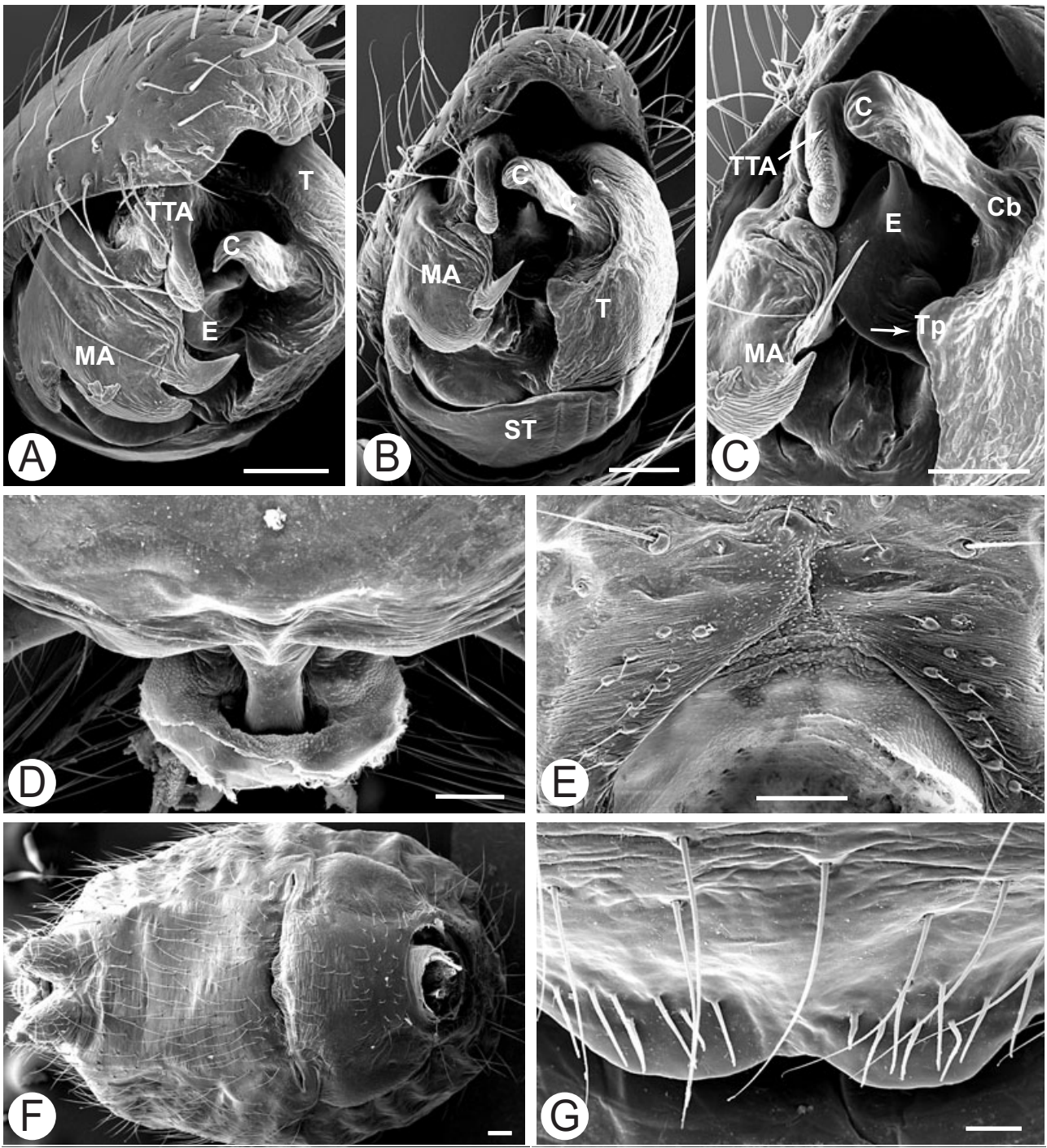

Figure 77. *Theridion longipedatum*, male. A–C, palp. A, mesial; note multifurcated MA (**76-1**, **77-1**). B, ventral; note placement of the C apically on T (**69-1**), as opposed to the more common placement on T margin (**69-0**). C, ventral close-up; note outgrowth of T, harbouring the tegular pit (Tp, **49-1**), the embolus has an apophysis fitting under it (arrow, **50-1**, **98-1**). D, prosomal stridulatory ridges. E, abdominal SPR. F, abdomen venter, with 'sclerotized ring around pedicel' (**147-1**, **148-1**) swollen area around pedicel reaching to the epigastric furrow. G, epiandrous gland spigots. Scale bars: A–F, 100 μm. G, 50 μm.

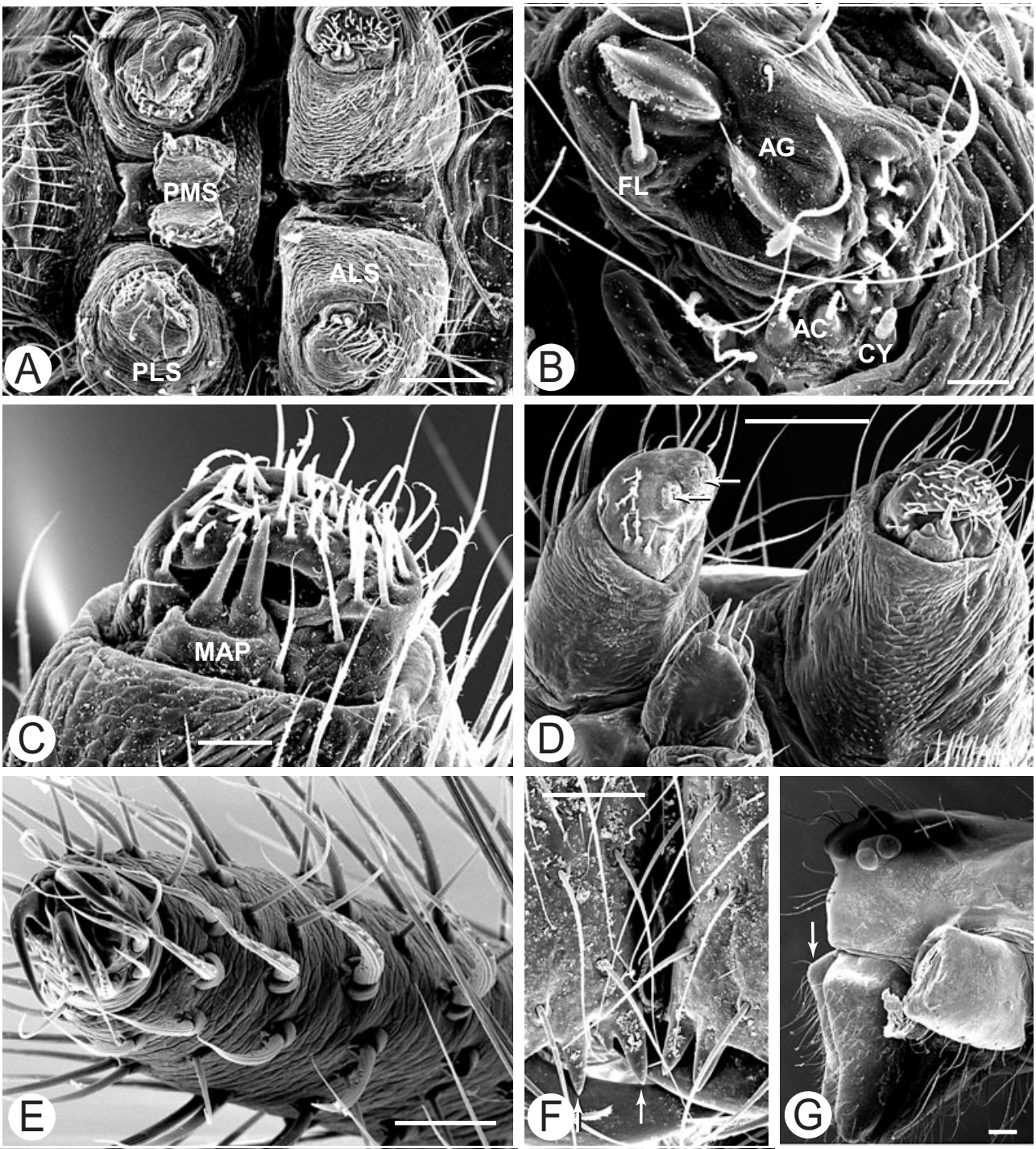

Figure 78. *Theridion longipedatum*. A–D, spinnerets. A, all. B, PMS. C, ALS; note unusual presence of two major ampullate spigots (MAP), no doubt teratological, as other specimens inspected had a single MAP, see e.g. D. D, male left field, arrows indicate AG scars (nonfunctional triplet, **219-0**). E, female fourth tarsal comb. F, cheliceral promarginal teeth (arrows, **106-1**). G, anterior part of male prosoma; note basal protrusions on chelicera (arrow, **115-1**), a feature of many *Theridion* spp. and also, e.g. *Coleosoma*. Scale bars: A, D, G, 100 μm. B, C, E, 20 μm. F, 50 μm.

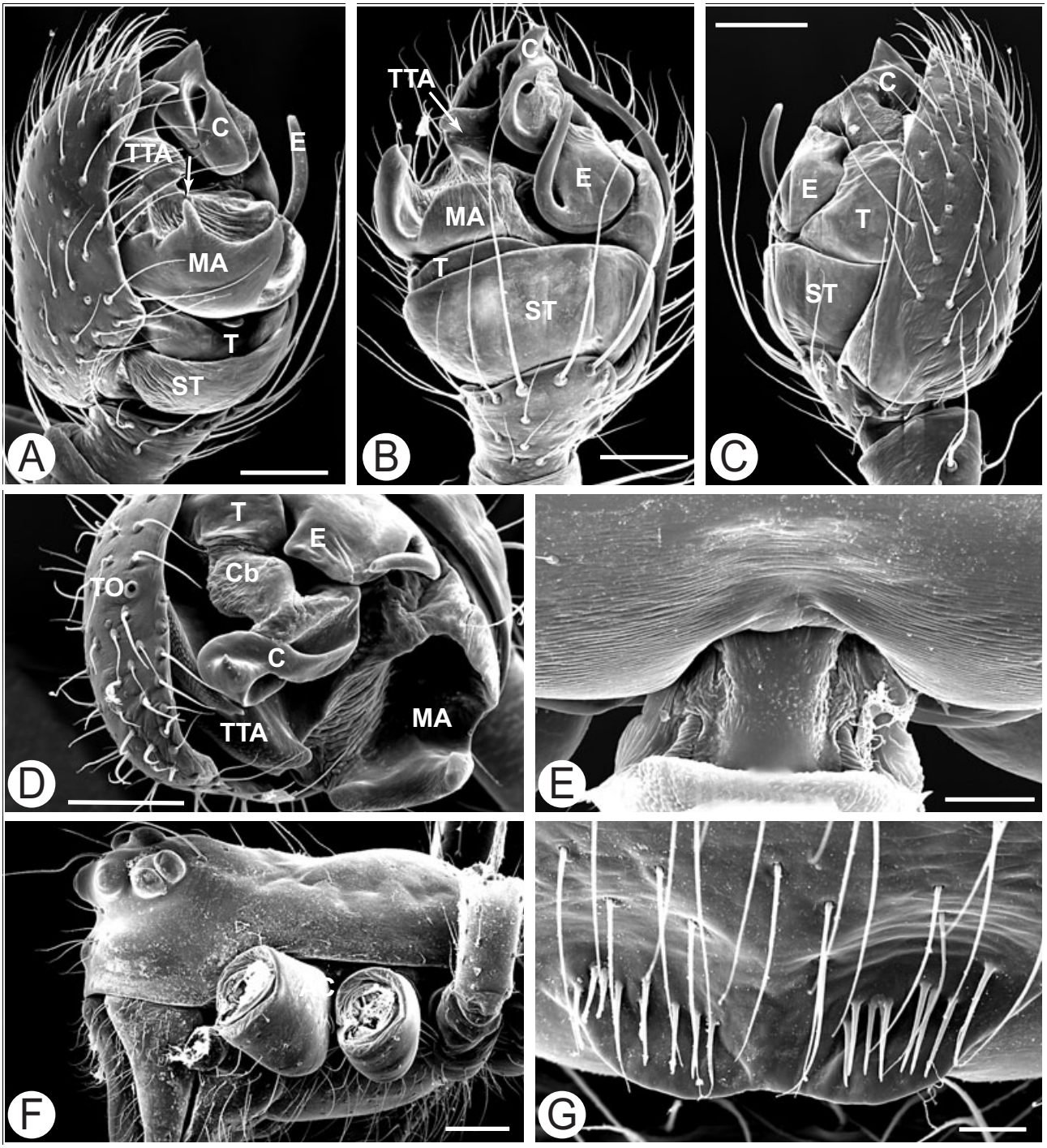

Figure 79. *Theridion varians*, male. A–D, palp. A, mesial; note apophysis on MA (arrow, **71-1**). B, ventral. C, ectal. D, apical; note membranous (**67-1**) conductor base (Cb). E, prosomal stridulatory ridges. F, epiandrous gland spigots. G, prosoma. Scale bars: A–D, G, 100 μm. E, 50 μm. F, 20 μm.

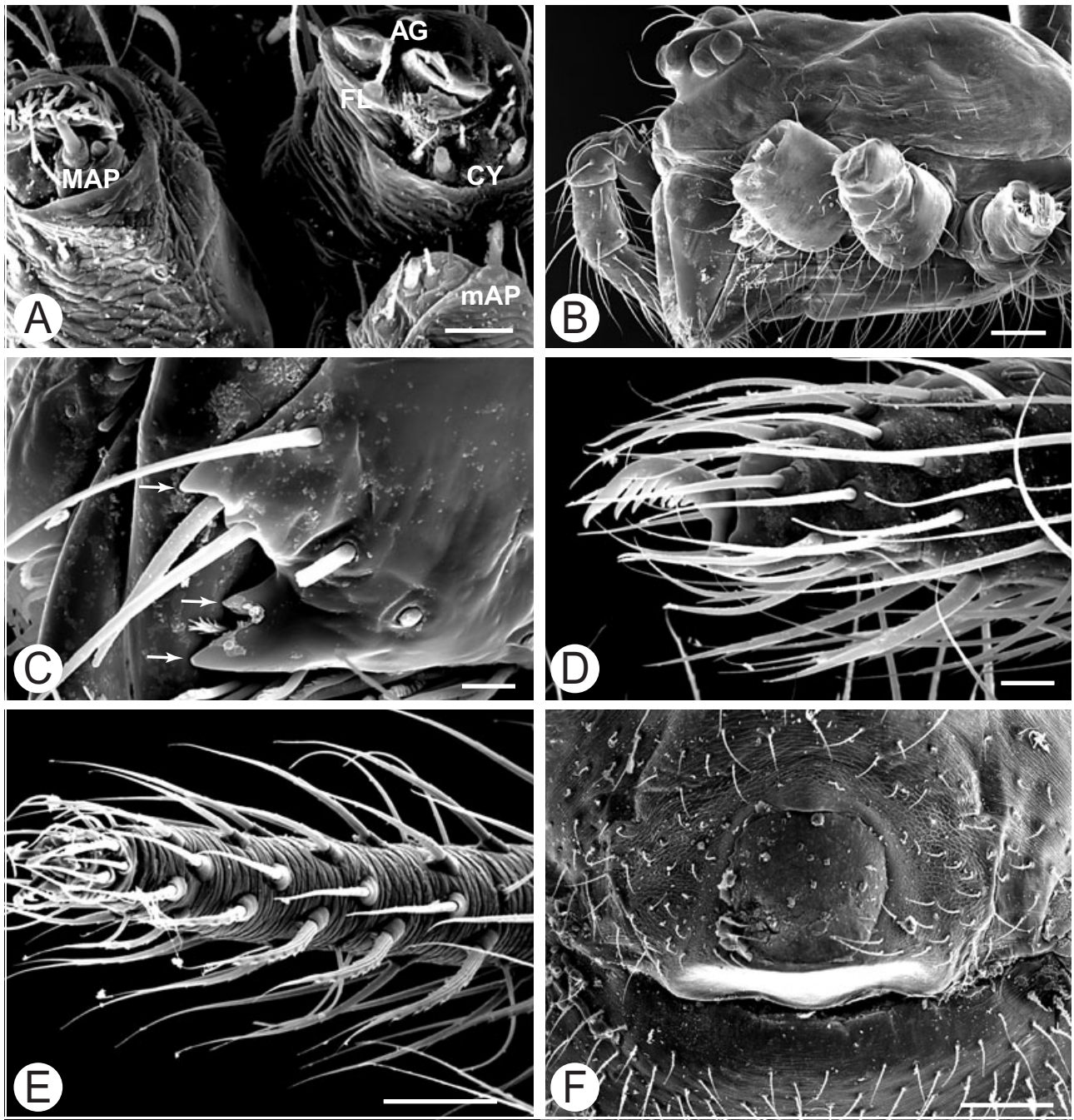

Figure 80. *Theridion varians*, female. A, spinnerets. B, prosoma. C, promarginal cheliceral teeth (arrows). D, palpal claw. E, tarsal comb, note position of serrated bristles relative to claws. F, epigynum. Scale bars: A, C, D, 20 μm. B, 100 μm. E, F, 50 μm.

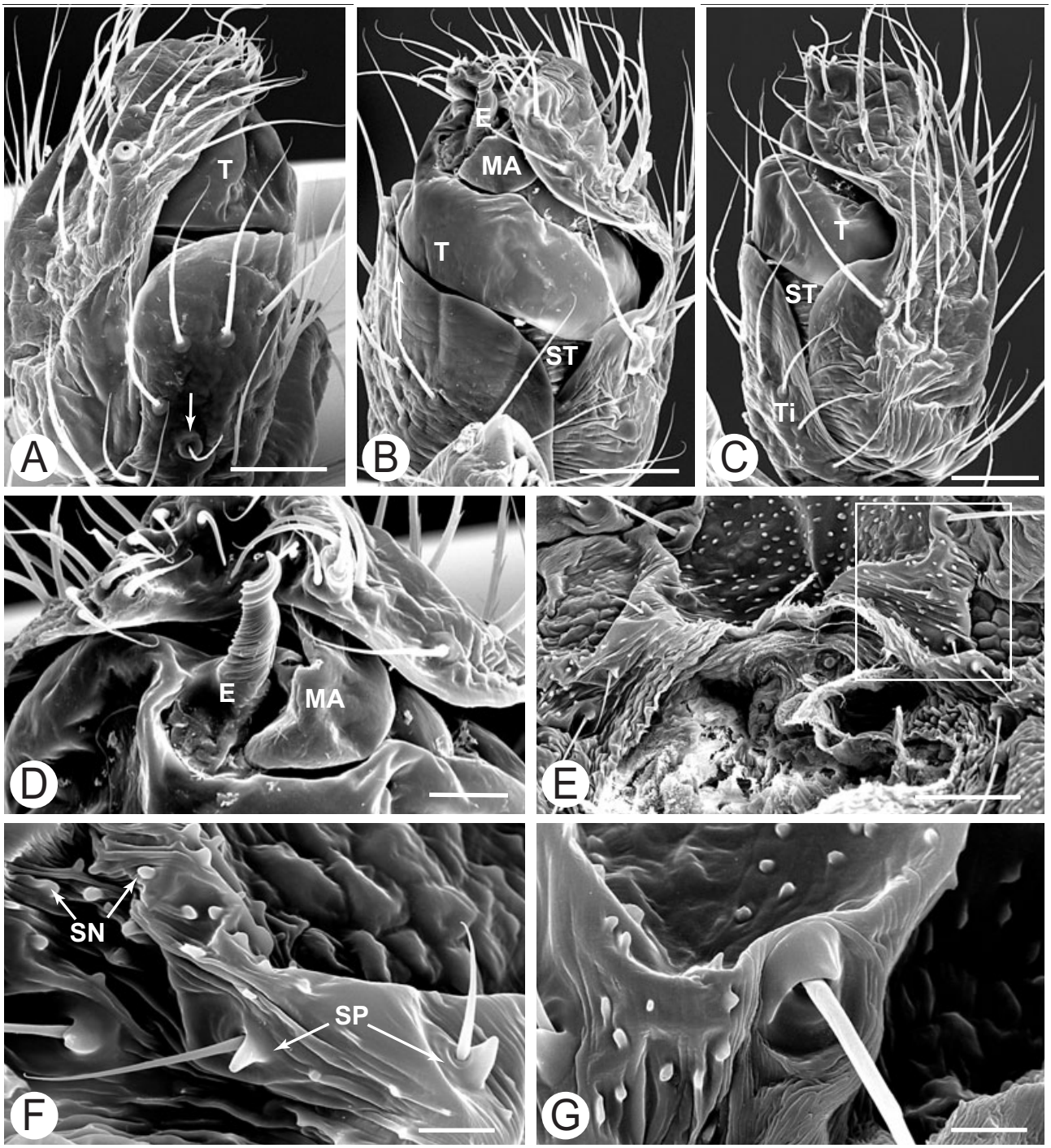

Figure 81. *Theridula opulenta*, male. A–D, palp. A, mesial; note single trichobothrium on tibia (arrow, **18-2**, **19-2**). B, ventral; note presence of a membranous sclerite, possibly MA, which attaches both to the tegulum and the cymbium. C, ectal. D, embolus and MA. E, area above pedicel on abdomen, white square indicates area enlarged in F and G. F, stridulatory nubbins and picks; note extremely high keel on the picks (**158-1**), a condition also found in *Ameridion*. G, base of setal proprioreceptor. Scale bars: A–C, E, 50 μm. D, 20 μm. F, G, 10 μm.

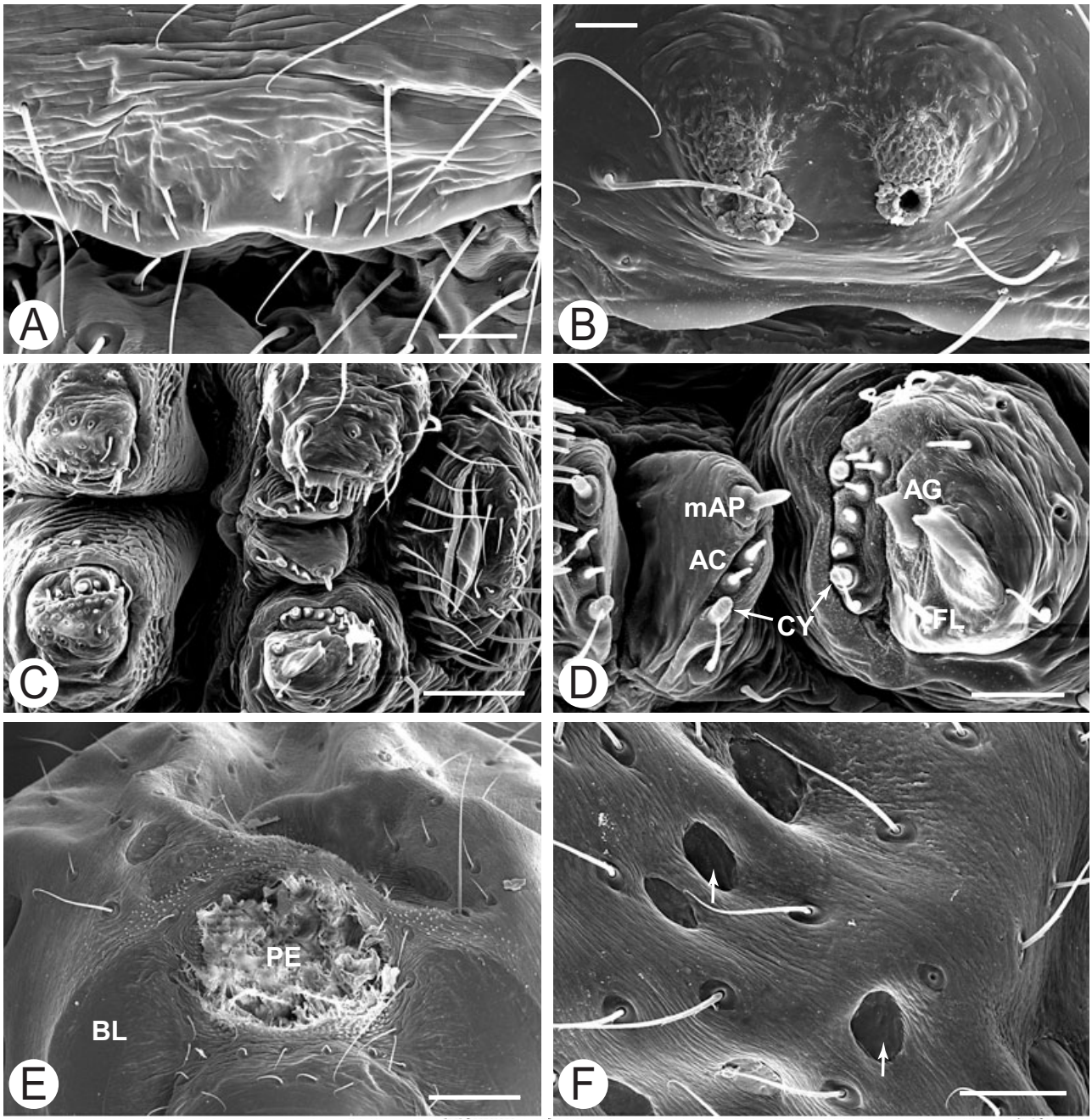

Figure 82. *Theridula opulenta*. A, epiandrous gland spigots. B–F, female. B, epigynum. C, spinnerets. D, PLS and PMS. E, area around pedicel on abdomen. F, abdomen surface; note abundance of sclerotized depressions, possibly apodemes (arrows). Scale bars: A, B, D, 20 μm. C, F, 50 μm. E, 100 μm.

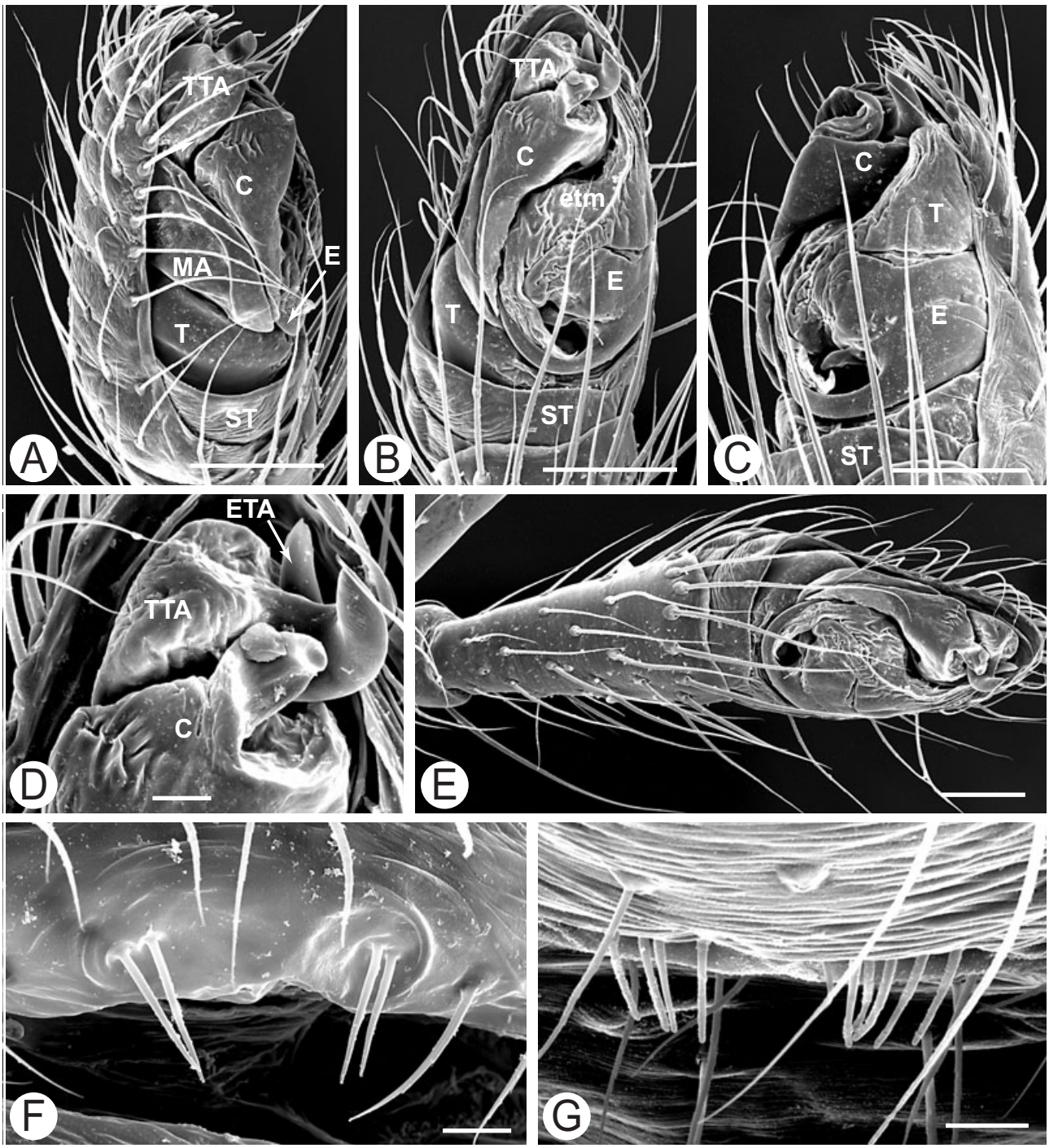

Figure 83. *Thwaitesia* male. A–F, *Thwaitesia* sp. A–E, palp. A, mesial. B, ventral. C, ectal. D, ventral close-up; note extra tegular apophysis (ETA, **101-1**). E, the extremely elongated tibia is a putative synapomorphy of *Thwaitesia*. F, epiandrous gland spigots. G, *T. margaritifera*, epiandrous gland spigots. Scale bars: A–C, E, 100 μm. D, F, G, 20 μm.

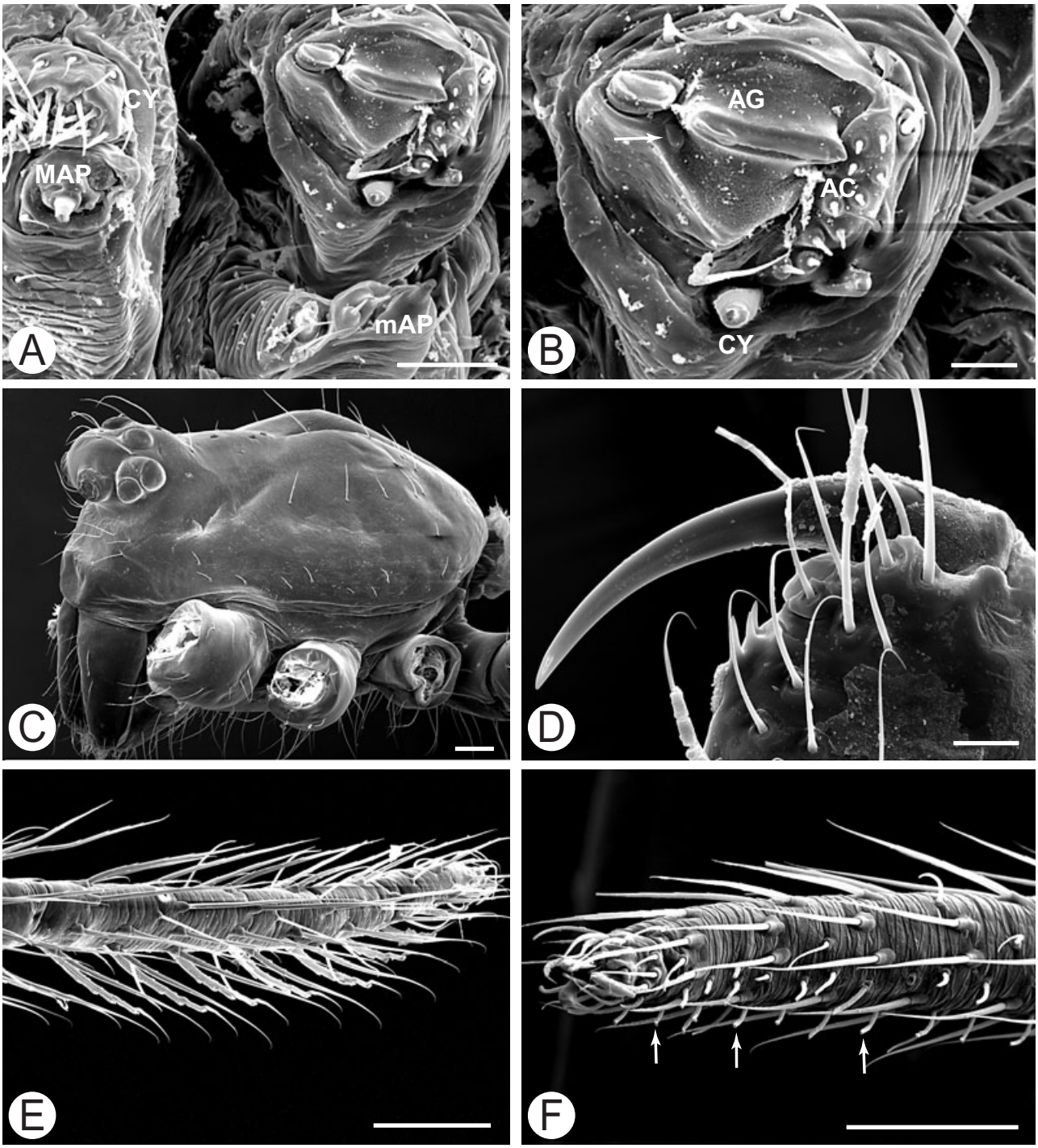

Figure 84. *Thwaitesia*. A–C, *Thwaitesia* sp. A, female left spinning field. B, female PLS; note absence of FL (arrow, **212-1**). C, male prosoma. D–F, *T. margaritifera* female. D, cheliceral fang and the characteristically sharp (**107-1**) teeth. E, tarsal comb. F, tarsus I, the modified ventral setae (arrows) are similar to those present in hadrotarsines, but unlike in hadrotarsines, are not tightly grouped (**197-0**). Scale bars: A, 50 μm; B, D, 20 μm; C, E, F, 100 μm.

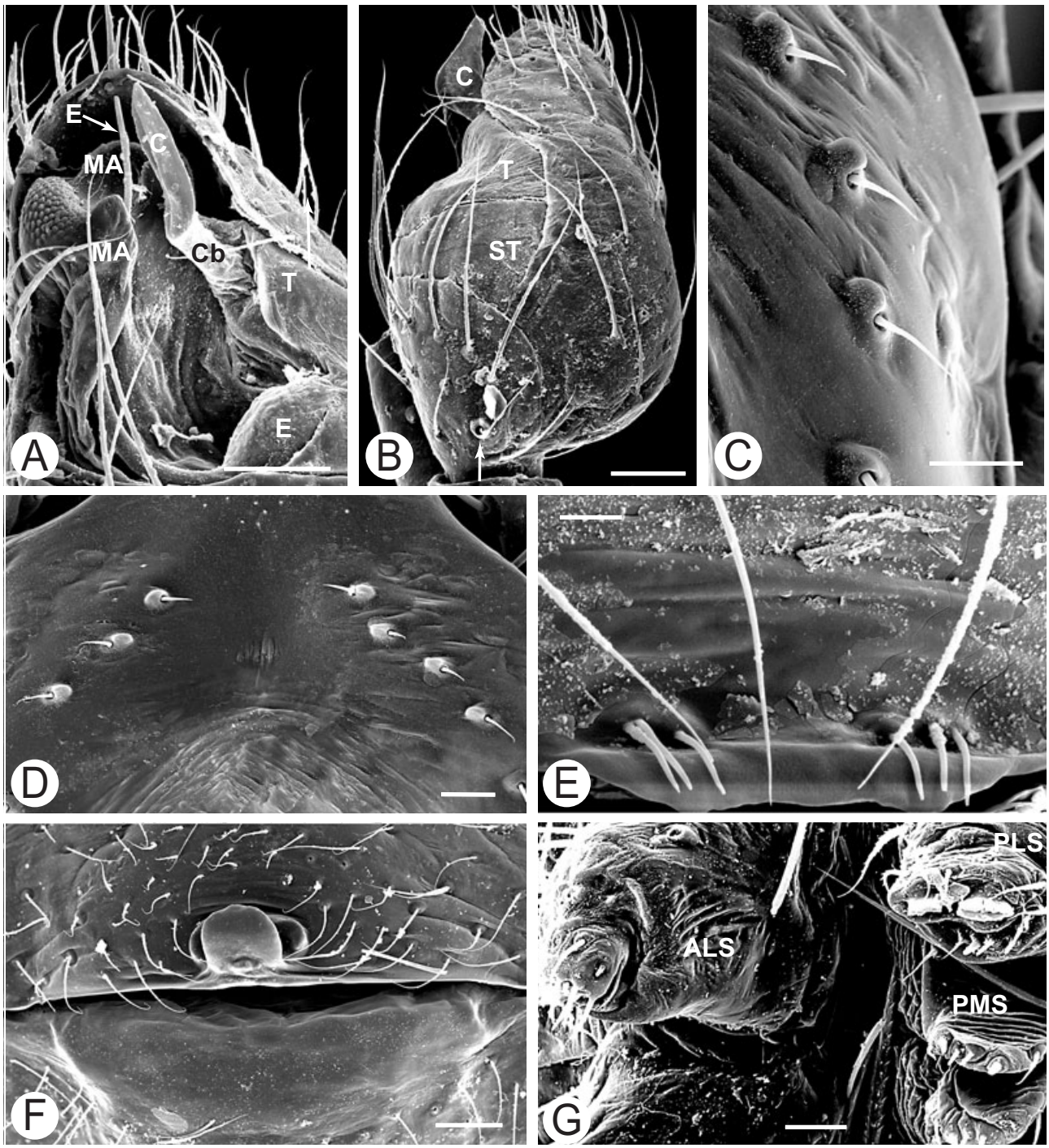

Figure 85. *Thymoites unimaculatum*. A, B, male palp. A, ventral; note membranous Cb (**67-1**), rising from the apical part of the T. B, ectal; note single trichobothrium on tibia (arrow, **18-2**, **19-2**). C, male SPR left side. D, ditto, both sides; note asymmetry in numbers. E, epiandrous gland spigots. F, epigynum. G, spinnerets. Scale bars: G, 100 μm; A, B, F, 50 μm; C, D, 20 μm; E, 10 μm.

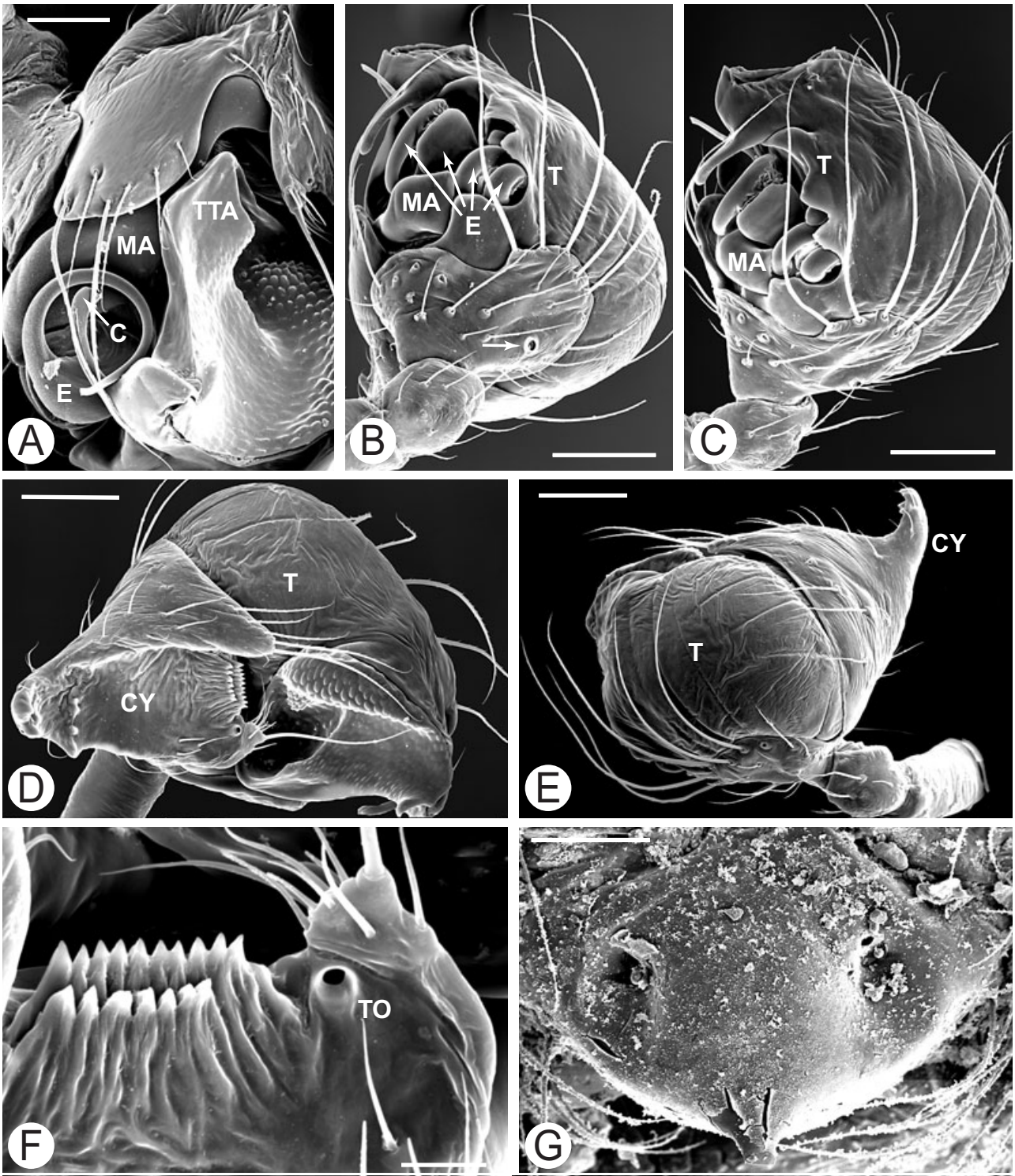

Figure 86. *Tidarren sisyphoides*. A–F, highly modified male palp. A, ventral, close-up. B, ectal from below; note single trichobothrium (arrow). C, ectal. D, apical; note extremely modified cymbium. E, dorsal. F, details of cymbial ridges (**23-2**), and the tarsal organ. G, epigynum. Scale bars: A, 50 μm; B–E, G, 100 μm; F, 20 μm.

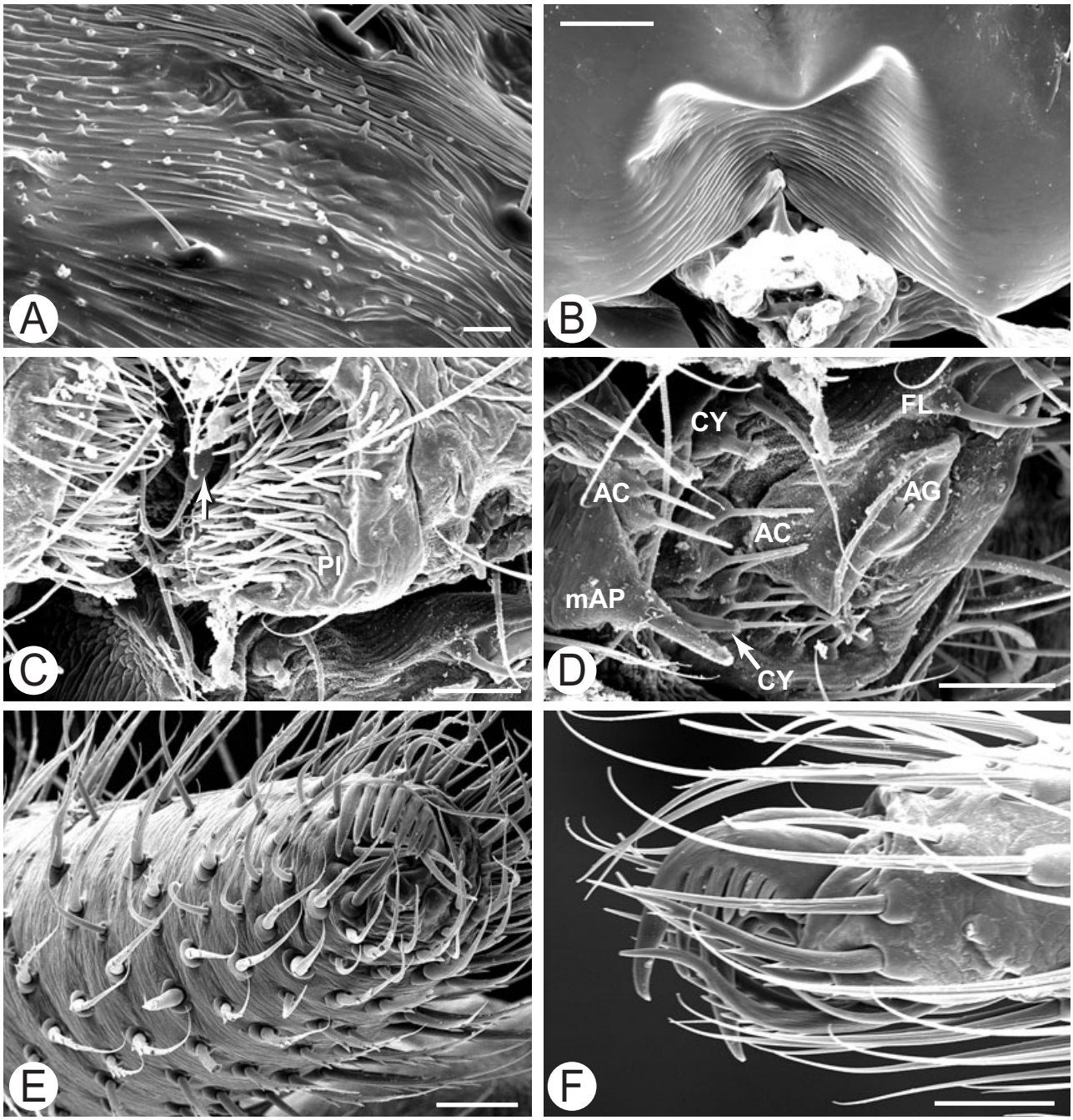

Figure 87. *Tidarren sisyphoides*. A, B, male stridulatory system. A, pick and nubbins on abdomen. B, ridges on prosoma. C, female ALS; arrow indicates the MAP. D, PLS and PMS. E, tip of female tarsus; note semipalmate claw (**177-2**). F, female first tarsus. Scale bars: A, 10 μm; B–F, 50 μm.

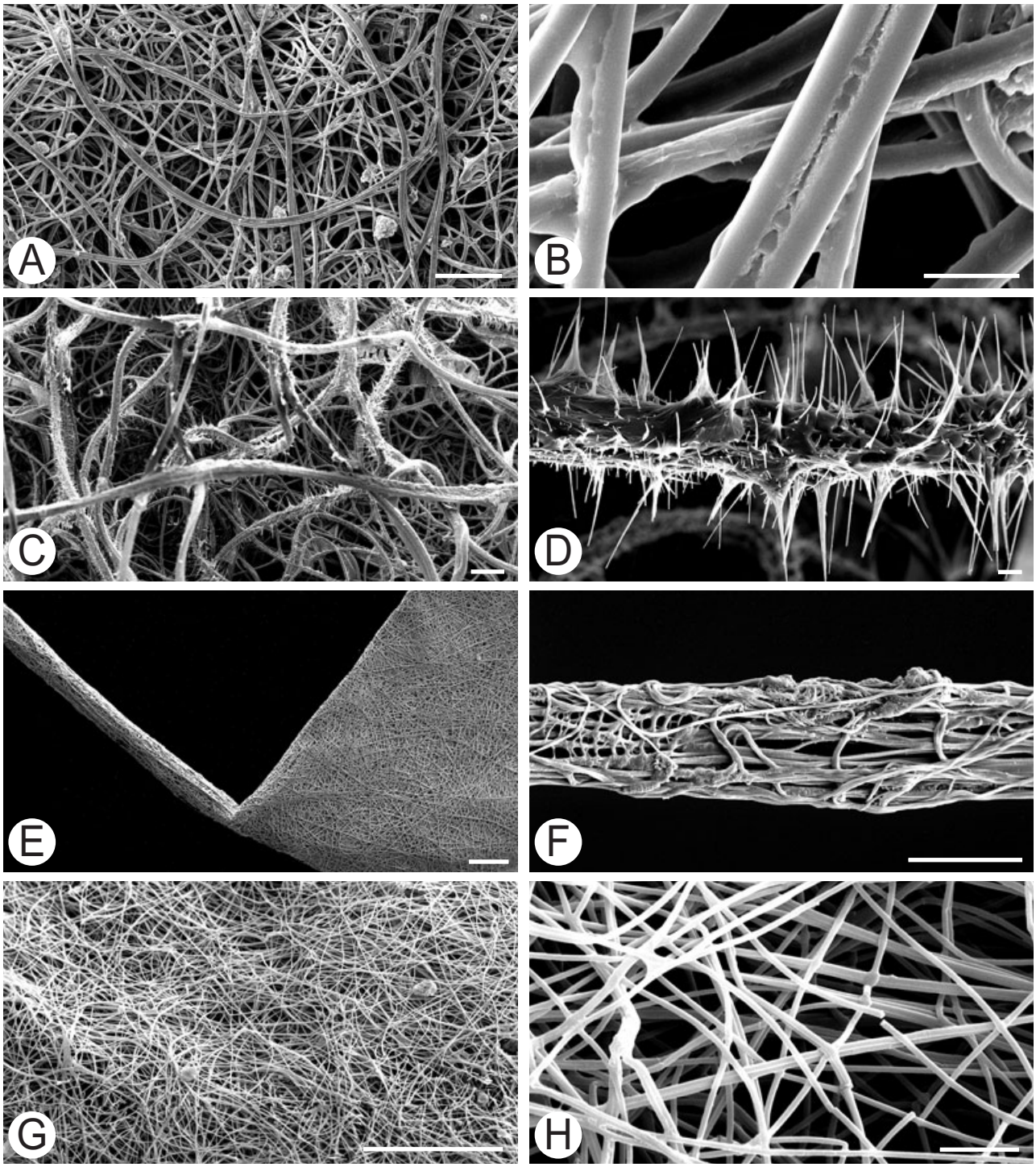

Figure 88. SEM images of theridiid egg sacs. A, B, *Latrodectus geometricus*. A, sac with fairly densely woven fibres (**232-0**). B, details of individual fibres (**233-0**). C, D, *Thwaitesia* sp. C, loosely woven sac, the outermost fibres extremely loose (**232-1**). D, details of an extremely spiny fibre (**233-1**), perhaps a protection against predators/parasites. The phylogenetic distribution of spiny eggsac fibres is unknown. E, F, *Argyrodes* sp. E, densely woven sac with smooth fibres (**233-0**) and a distinct stalk (**230-1**). F, details of stalk, a synapomorphy of Argyrodinae. G, H, *Theridion* sp. G, dense egg sac. H, details of fibres. Scale bars: A, C, E, G, 100 μm; F, 50 μm; B, D, H, 10 μm.

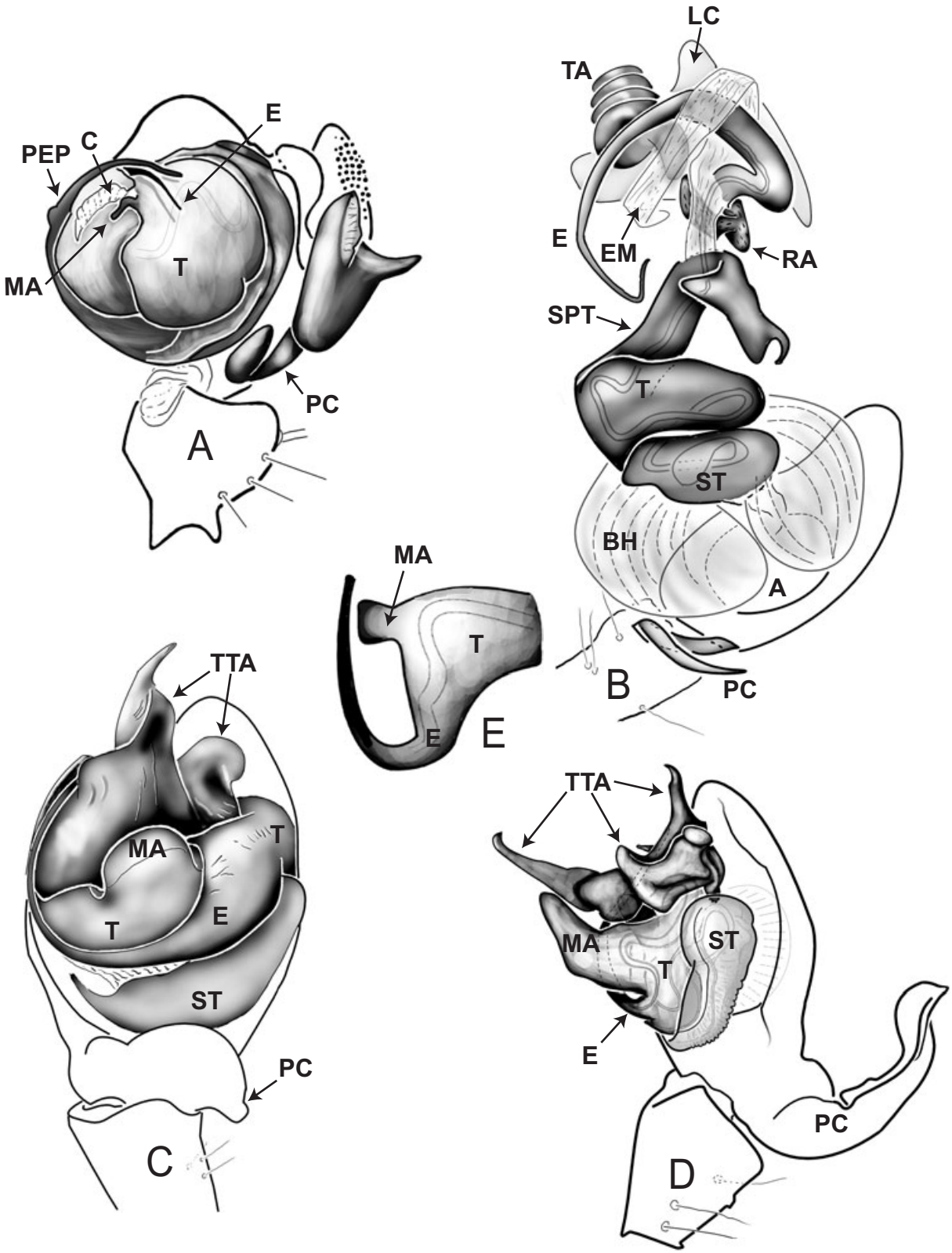

Figure 89. Male palps of outgroups. A, *Pimoa rupicola* (redrawn from Hormiga, 1994a). B, *Linyphia triangularis* (redrawn from Hormiga, 1994b). C, *Synotaxus monoceros*. D, *Nesticus cellulanus* (Clerck) (redrawn from Huber, 1993). E, *Eidmanella pallida*.

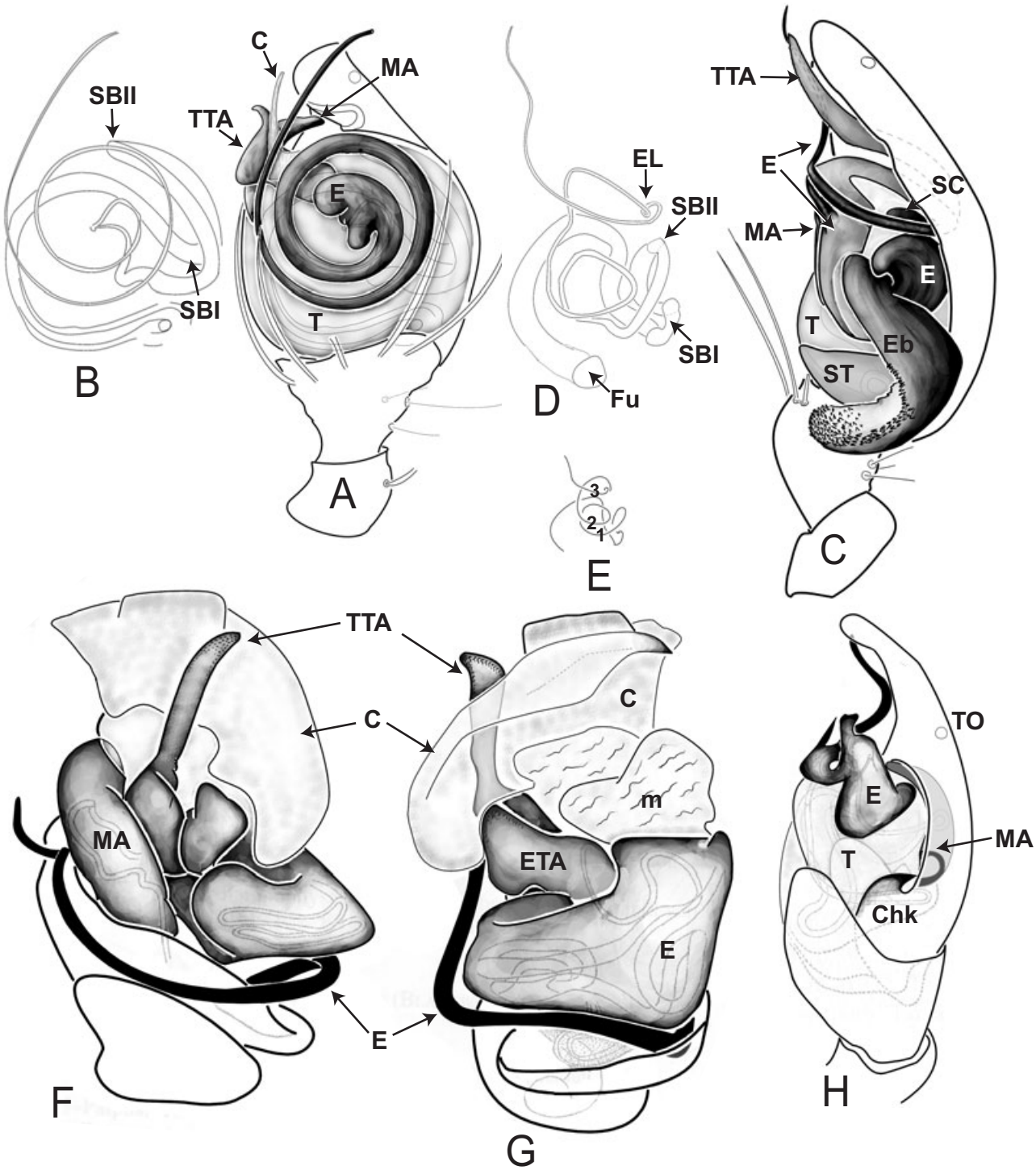

Figure 90. Theridiid palps. A, ***Anelosimus* sp. nov.** (Tanzania). B, ditto, sperm duct trajectory. C, *Anelosimus vittatus*. D, ditto, sperm duct trajectory. E, indicating loops of *A. vittatus* sperm duct trajectory. F, G, *Episinus angulatus* (Blackwall) (redrawn from Knoflach, 1993). H, *Carniella schwendingeri* Knoflach (redrawn from Knoflach, 1996). Trichobothria omitted in F–H.

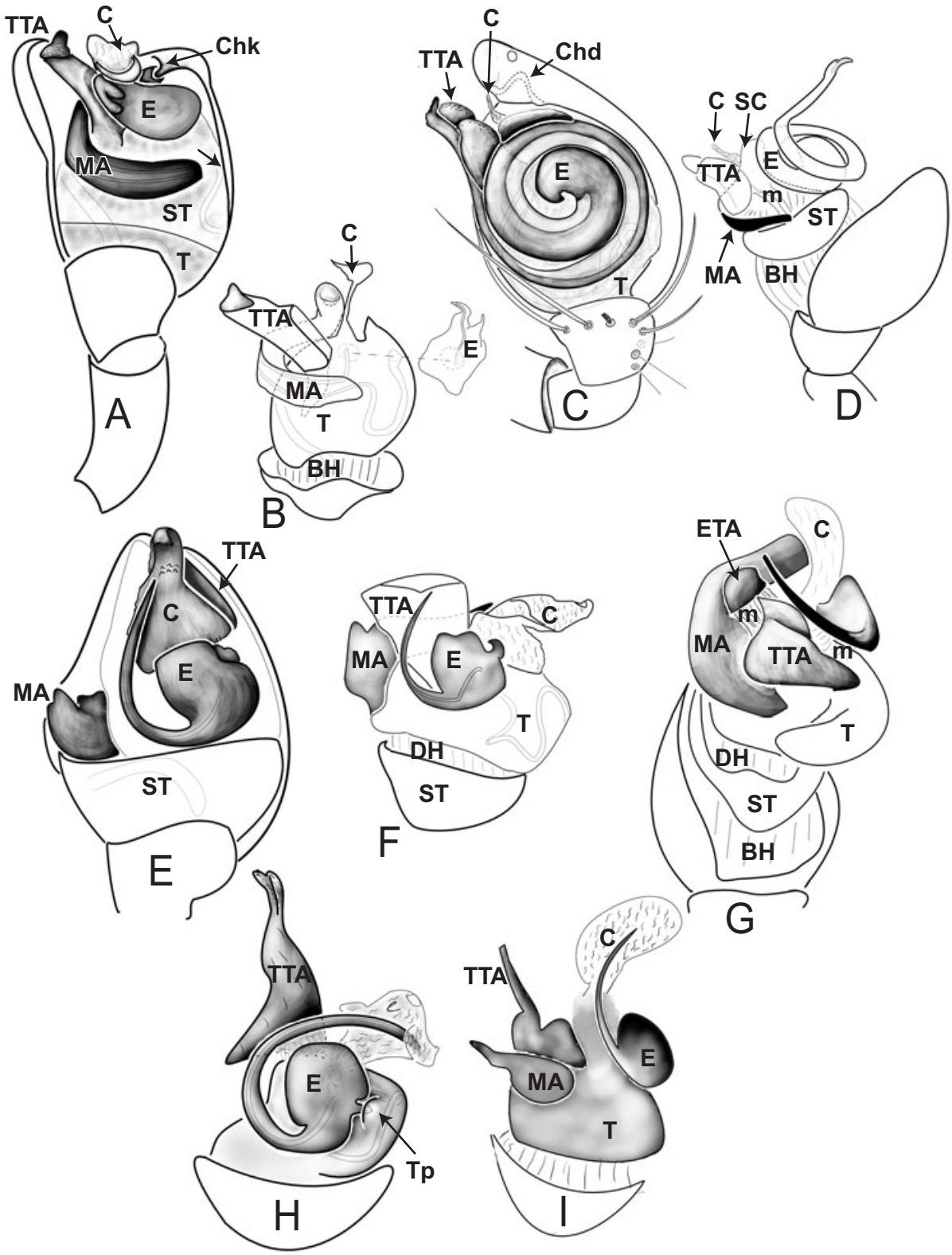

Figure 91. Schematic illustrations of theridiid palps. A, *Argyrodes argyrodes* (redrawn from Saaristo, 1978). B, ditto. C, *Anelosimus eximius*. D, *A. eximius* expanded palp. E, *Theridion pictum* (redrawn from Levi & Levi, 1962). F, *T. pictum*, expanded palp. G, *Enoplognatha gemina* Bosmans & Van Keer [redrawn from Levy, 1998, sub *E. mandibularis* (Lucas)]. H, *Coleosoma floridanum*, expanded palp, ventral. I, ditto, dorsal. Trichobothria omitted in A, D and E.

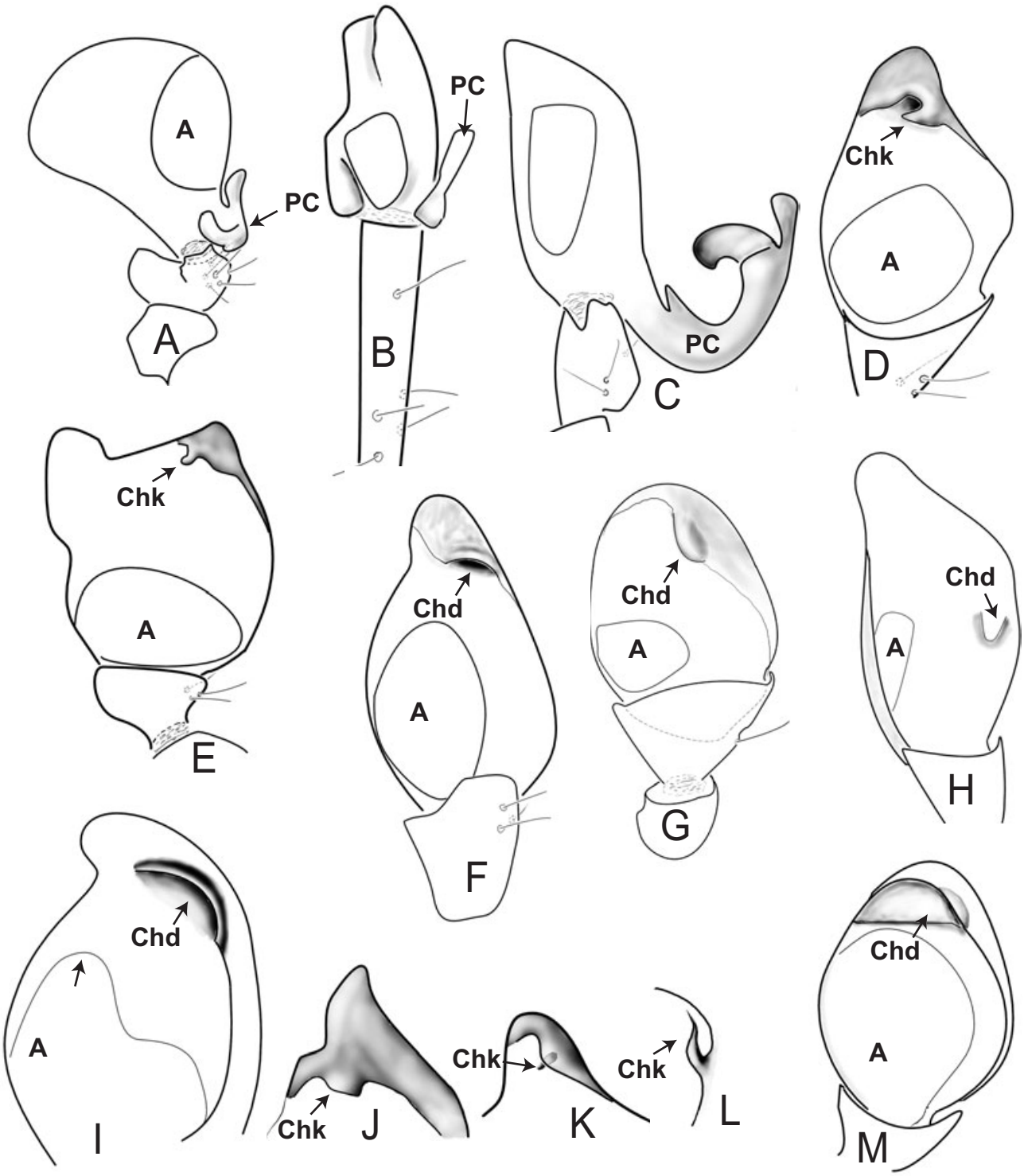

Figure 92. Schematic illustrations of palpal cymbia. A, *Argiope argentata*. B, *Tetragnatha extensa*. C, *Nesticus reclusus*. D, *Steatoda americana*. E, *Argyrodes argyrodes*. F, *Anelosimus studiosus*. G, *Thymoites* sp. H, *Anelosimus vittatus*. I, *Ameridion* nr. *petrum*. J, *Euryopis* sp. K, *Thwaitesia* sp. L, *Selkirkiella alboguttata*. M, *Spintharus flavidus*. Note that trichobothria are omitted in G, H and M.

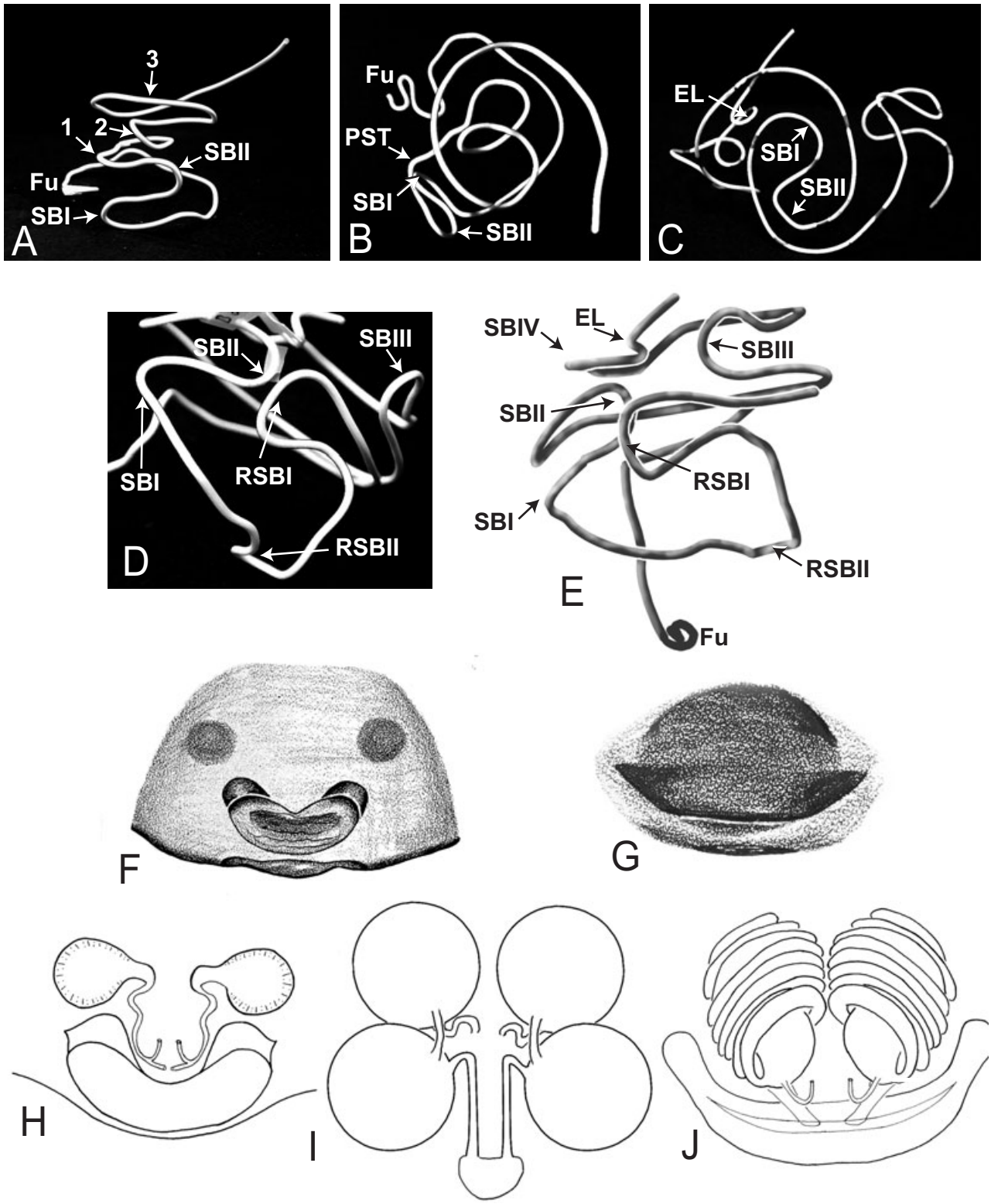

Figure 93. A–D, models of male sperm duct trajectory. A, *Anelosimus eximiu*: ectal view, numbers indicate where the duct completes loops 1–3. B, *A. eximius*, dorsal view. C. *Theridion*. D, *Faiditus*. E–J, schematic illustrations. E, *Faiditus chickeringi*, ducts. F, *Anelosimus rupununi*, epigynum. G, *Kochiura aulica*, epigynum. H, *A. rupununi*, internal female genitalia. I, *Dipoena nigra*, internal female genitalia. J, *Kochiura aulica*, internal female genitalia. (F–H & J, drawn by Sarah Crews.)

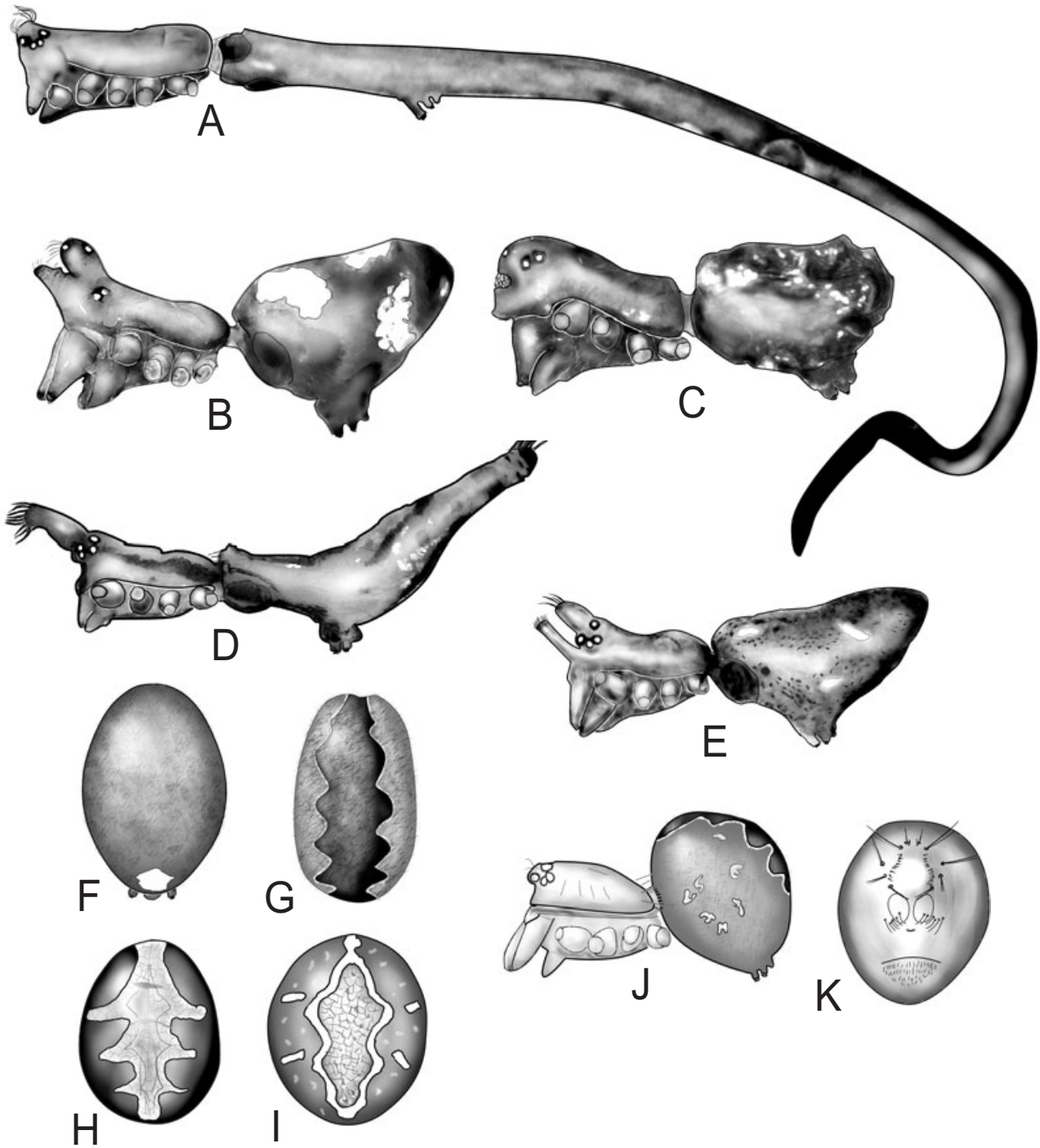

Figure 94. A, *Ariamnes*, male habitus. B, *Argyrodes*, male habitus. C, *Faiditus*, male habitus. D, *Rhomphaea*, male habitus. E, *Neospintharus*, male habitus. F, *Stemmops* sp., female abdomen. G, *Anelosimus eximius*, female abdomen. H, *Theridion pictum*, female abdomen. I, *Ameridion petrum*, female abdomen. J, *Anelosimus* sp. 1, habitus. K, *Anelosimus* sp. 1, abdomen ventral.

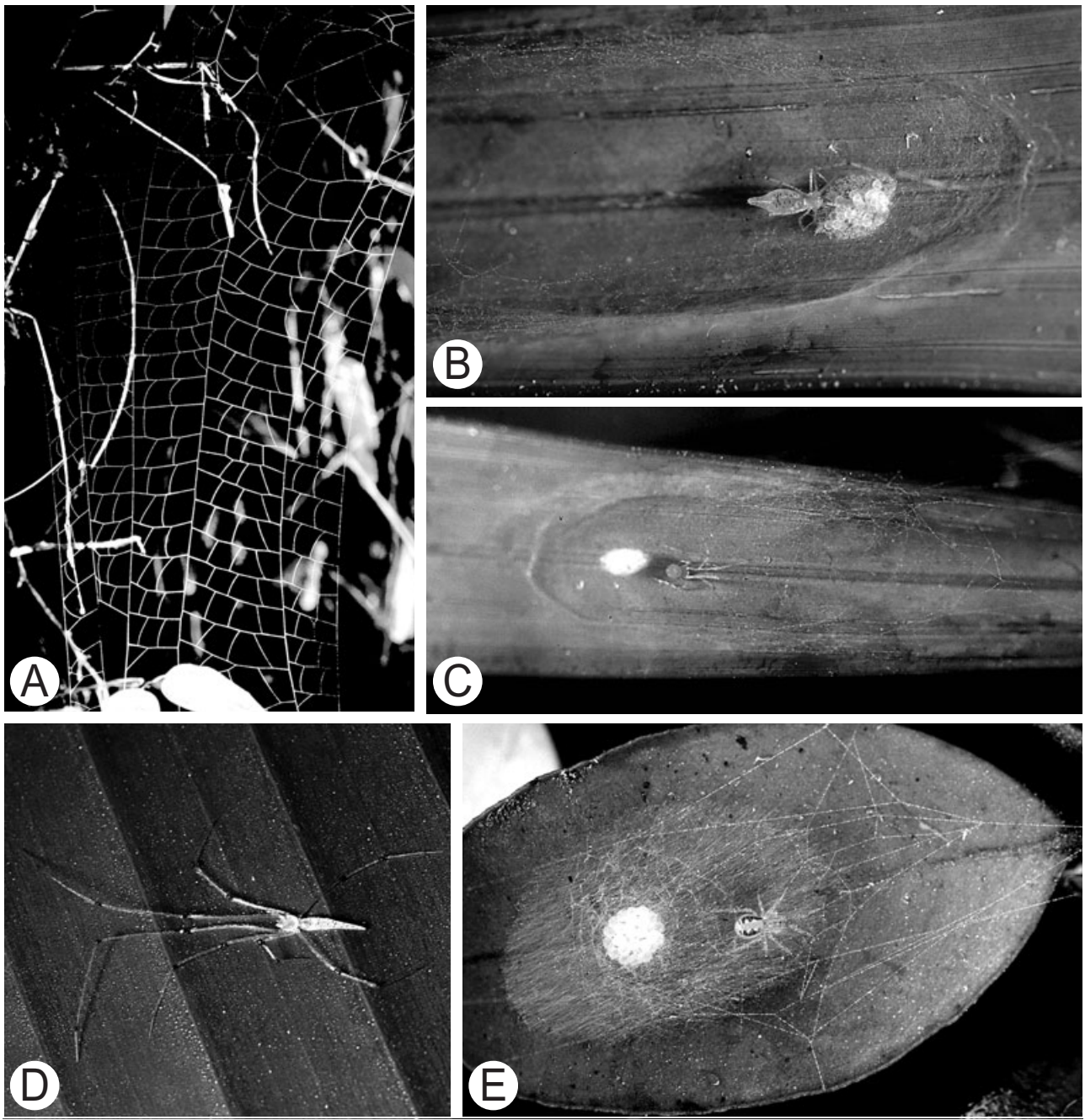

Figure 95. A, typical 'chicken-wire' web (**225-2**) of *Synotaxus monoceros*, characteristic of this genus (Bartika, Guyana). B, *S. waiwai*, female guarding egg sac in a simple 'egg sac web'. (Gunn's landing, Guyana) C, *S. monoceros*, female guarding egg sac in an identical web (Bartika, Guyana). D, male of *S. monoceros* (Bartika, Guyana). E, *Selkirkiella luisi* (Puyehue, Chile) in an egg-guarding web typical of the genus, superficially similar to *Synotaxus*. Note that the dense silk mat in *Selkirkiella* covers the loosely woven egg sac entirely. *Enoplognatha ovata* is similar (e.g. Nielsen, 1932: 41)

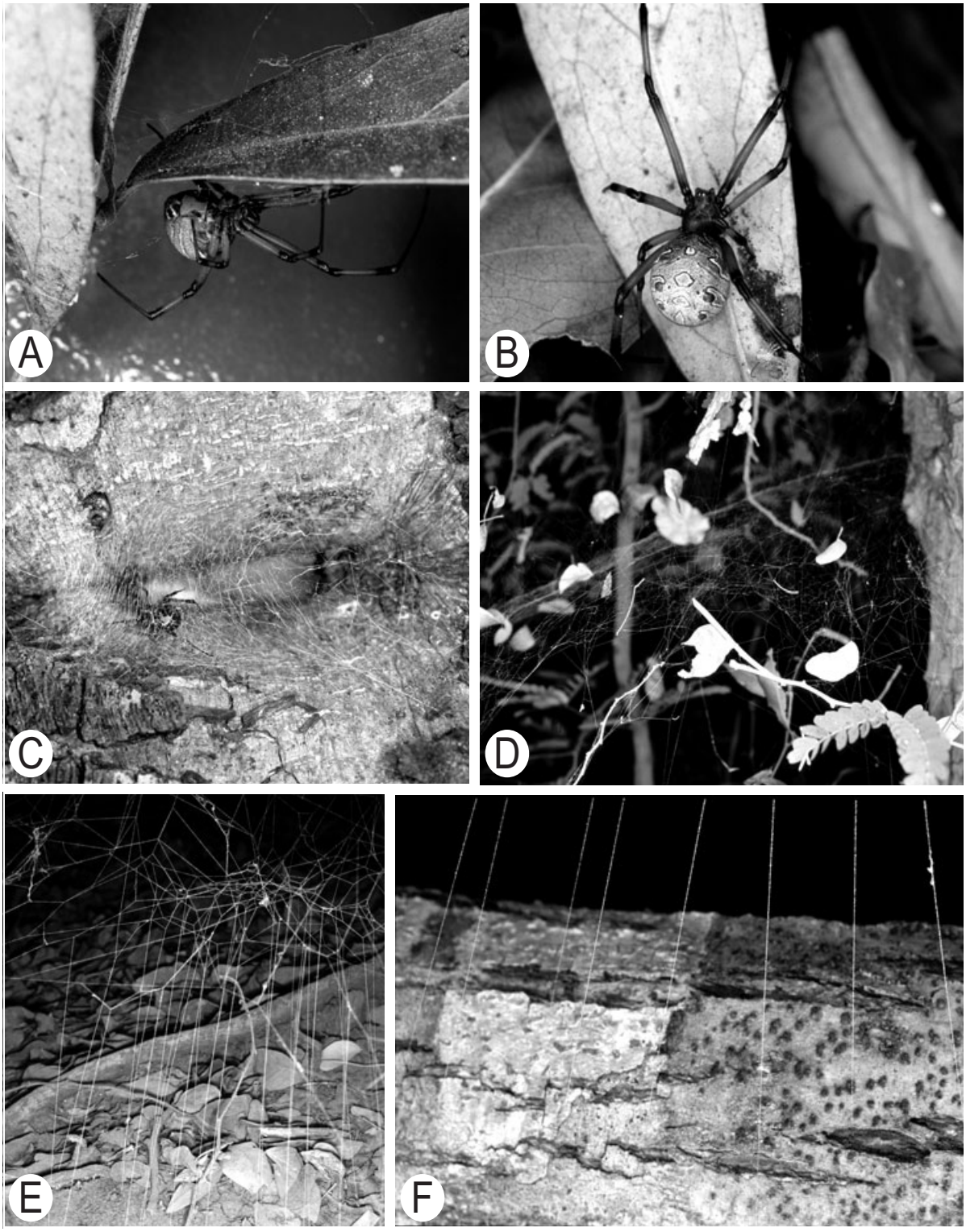

Figure 96. *Latrodectus* female and web. A, *Latrodectus* sp., ventral view (Phinda, S-Africa). B, ditto, dorsal view. C–F, *L. geometricus* web (Berenty reserve, Madagascar). C, female in retreat of web, located in a crevice on a tree trunk about 1.5 m above the ground. D, the retreat opens to a domed sheet, that leads down nearer to the ground. E, 20–30 cm above the ground the sheet turns into a typical cobweb mesh, from which gumfoot lines lead to the ground. F, tips of gumfoot lines (**227-1**); this trapping area of the web is nearly 2 m away from the female's retreat.

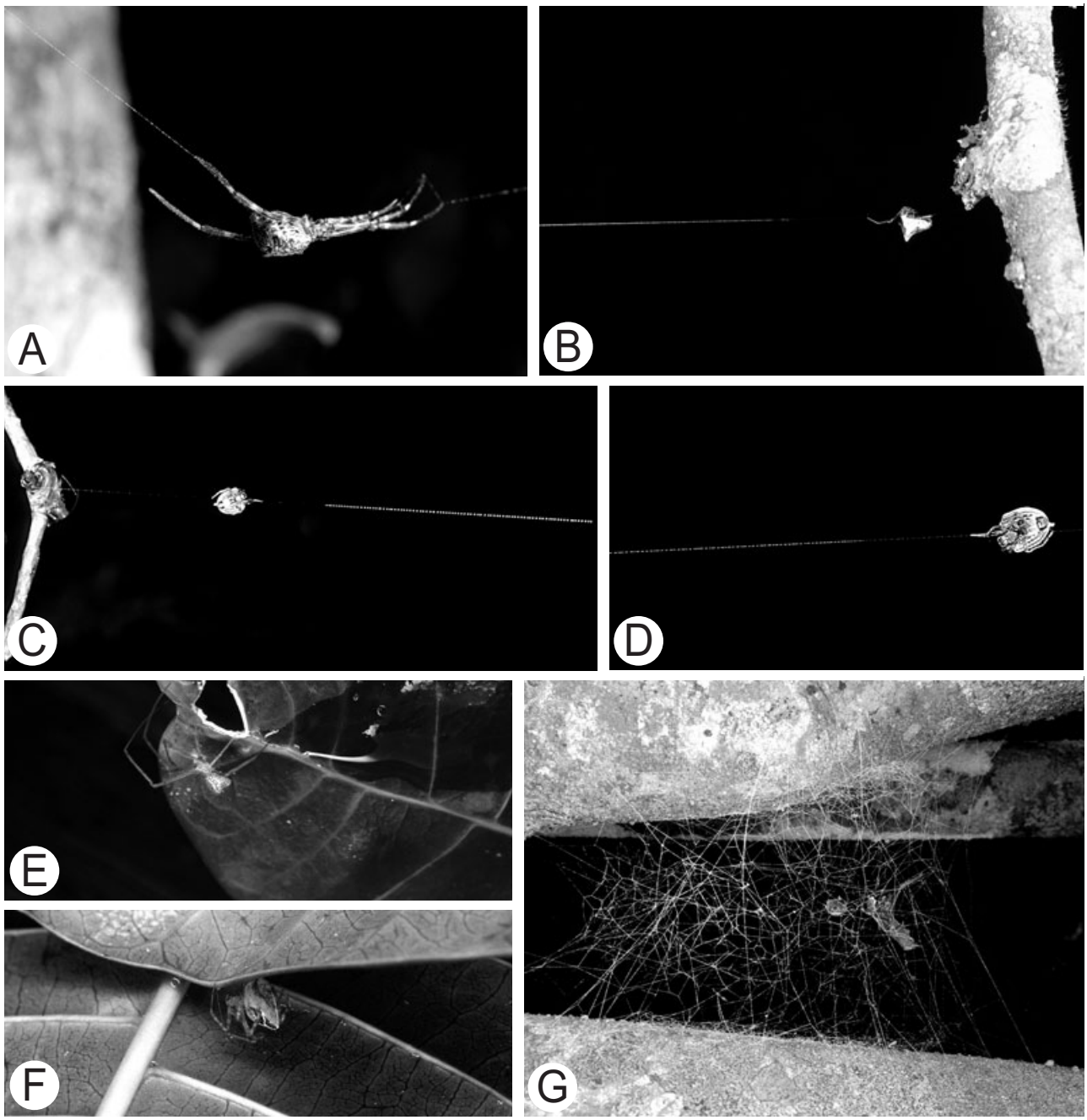

Figure 97. A, *Episinus* sp. in web (**225-4**), posterior line held with one leg IV; leg pairs I, II both holding on to the line in front of the animal (Perinét, Madagascar). B–D, *Phoroncidia* spp., simple line webs (**225-6**). B, typical posture of a single line web, the spider holding on to dry silk near substrate; note transition to sticky silk (Ranamofana, Madagascar). C, similar position to *Episinus*, but uses only single leg I to hold line in front of the animal (Puyehue, Chile). D, closer. E, *Thwaitesia* sp. habitus (Sodwana Bay, S. Africa). F, *Tidarren* sp. (Fanies Island, S. Africa); note characteristic thin white band on abdomen. G, ditto, web.

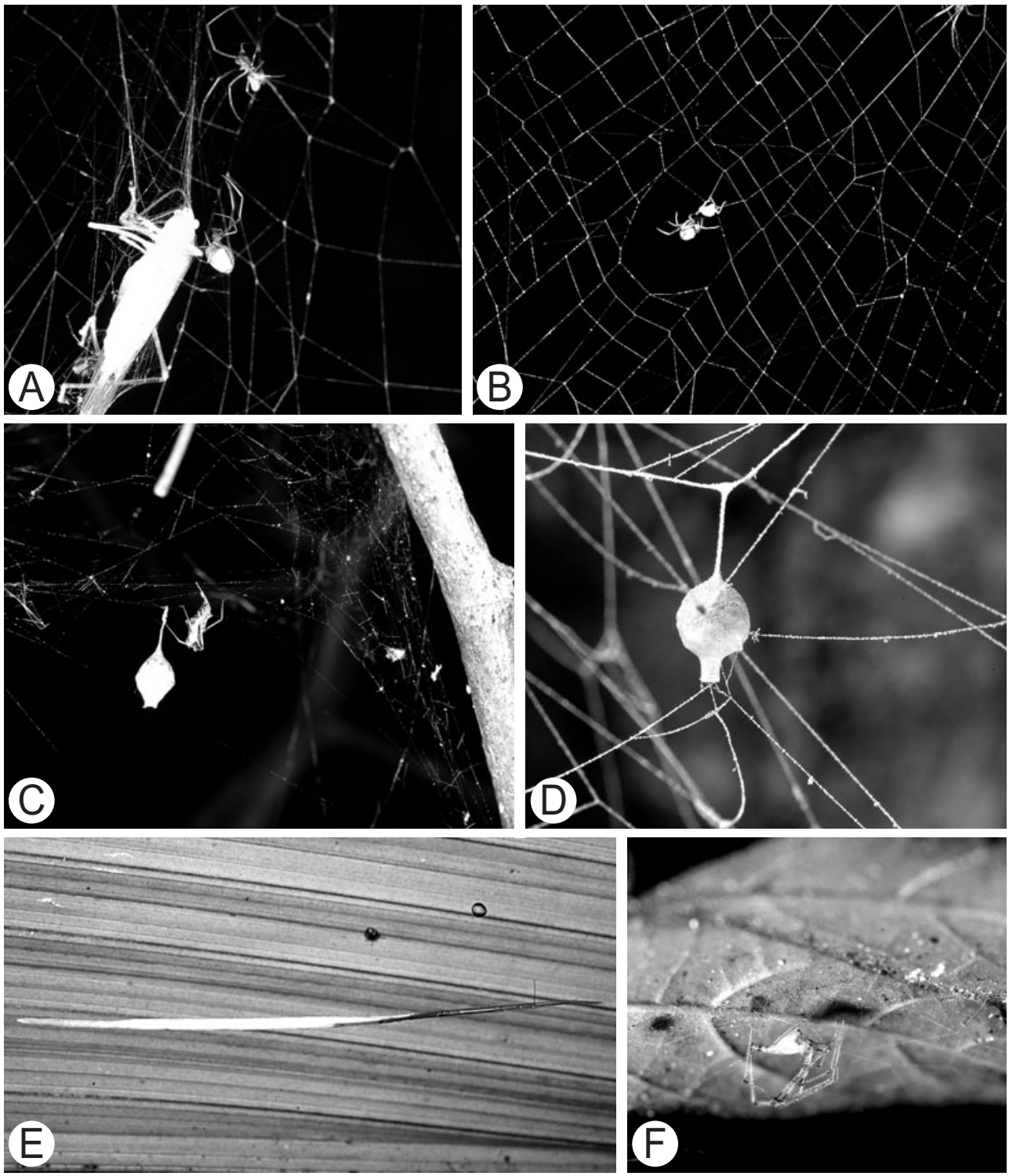

Figure 98. Argyrodinae. A, *Argyrodes* sp. and *Faiditus* sp. stealing food caught by its *Nephila* host (Cabo Blanco, Costa Rica). B, *Argyrodes* sp. pilfering tiny prey, ignored by the *Nephila* host (Cabo Blanco, Costa Rica). C, *Faiditus* female in a nonsnare web at edge of host web, attaching egg sac. D, *Faiditus* sp. egg sac; note distinct stalk (**230-1**), a synapomorphy of Argyrodinae (Cabo Blanco, Costa Rica). E, *Ariamnes* female with egg sac (**231-3**), both extremely elongated (Gunn's Landing, Guyana). F, *Rhomphaea draca* (Chamberlin & Ivie) female in a very simple, nonsticky web (Gunn's Landing, Guyana).

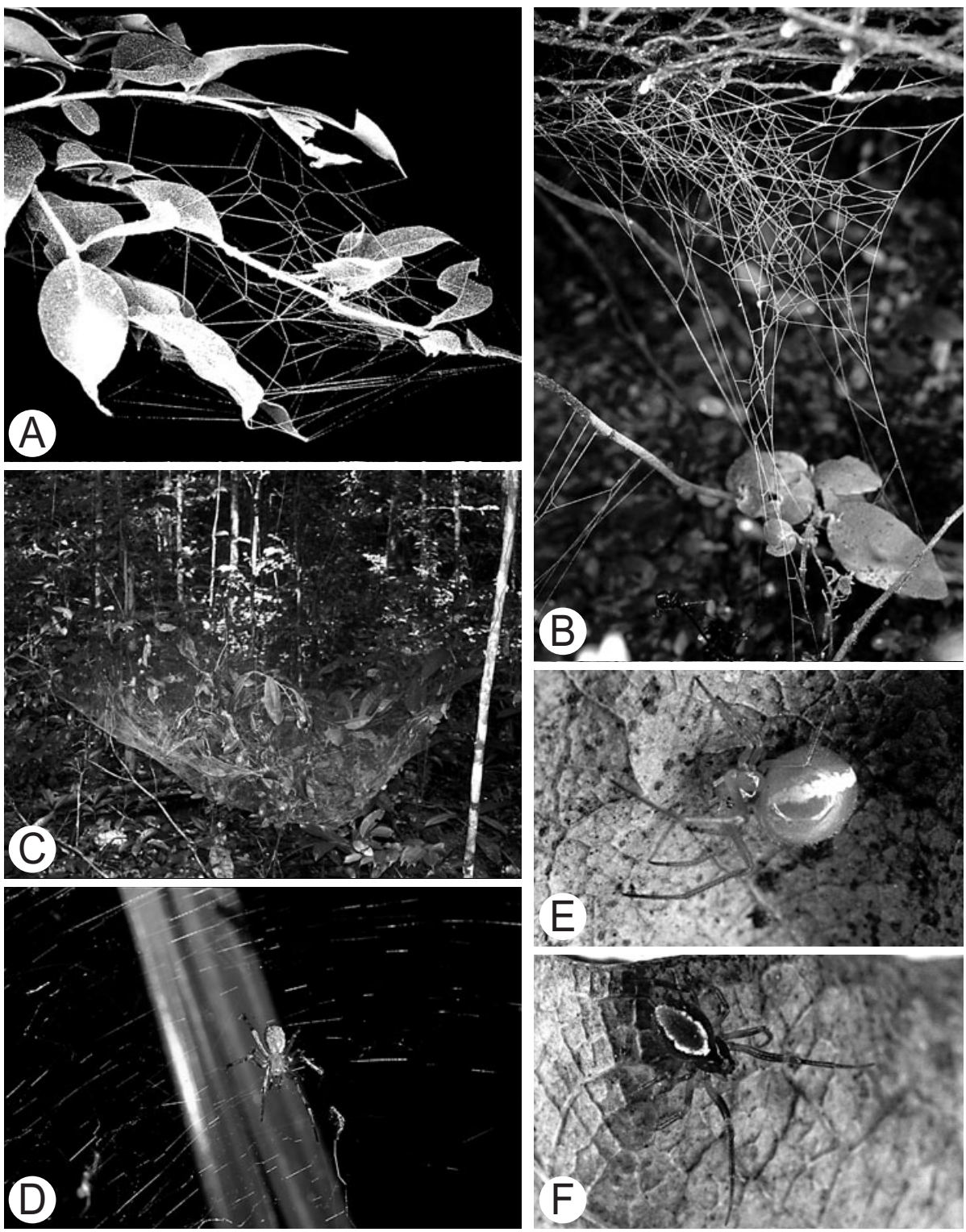

Figure 99. Webs and habitus of species all previously in *Anelosimus*. A, *Kochiura attrita* web (Puyehue, Chile, **225-3**). B. *Selkirkiella luisi* web (Puyehue, Chile, **225-3**, **226-1**). C. *Anelosimus eximius* web (Kaieteur falls, Guyana, **225-1**). D, *A. eximius* female, standing on the dense mat of silk which forms the dome of the web (Bartika, Guyana). E, *Selkirkiella luisi*, female habitus (Puyehue, Chile). F, *Kochiura* sp., female habitus (Puyehue, Chile).

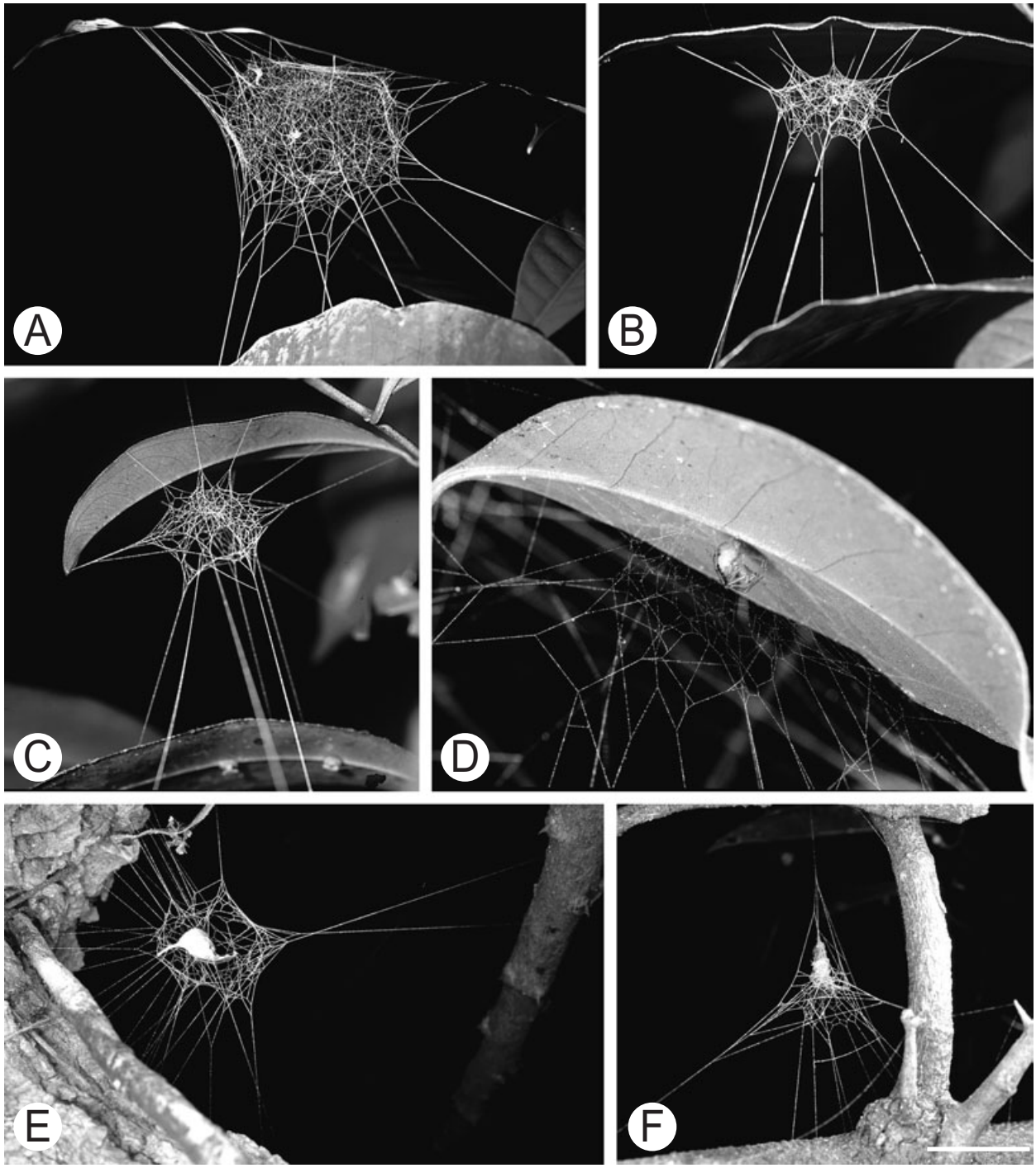

Figure 100. *Achaearanea* spp. webs. The 'star-shaped' web (**225-3**, **226-0**, **227-1**) of all species displayed here is typical of many *Achaearanea* and has also been reported in some *Theridion* and *Chrysso*. A–C from Gunn's Landing, Guyana. D from Ranamofana, Madagascar. E, F from Fanies Island, S. Africa. This web structure will no doubt be of use in further phylogenetic studies on Theridiinae. Some species consistently have a leaf retreat in the web's centre (E, F).

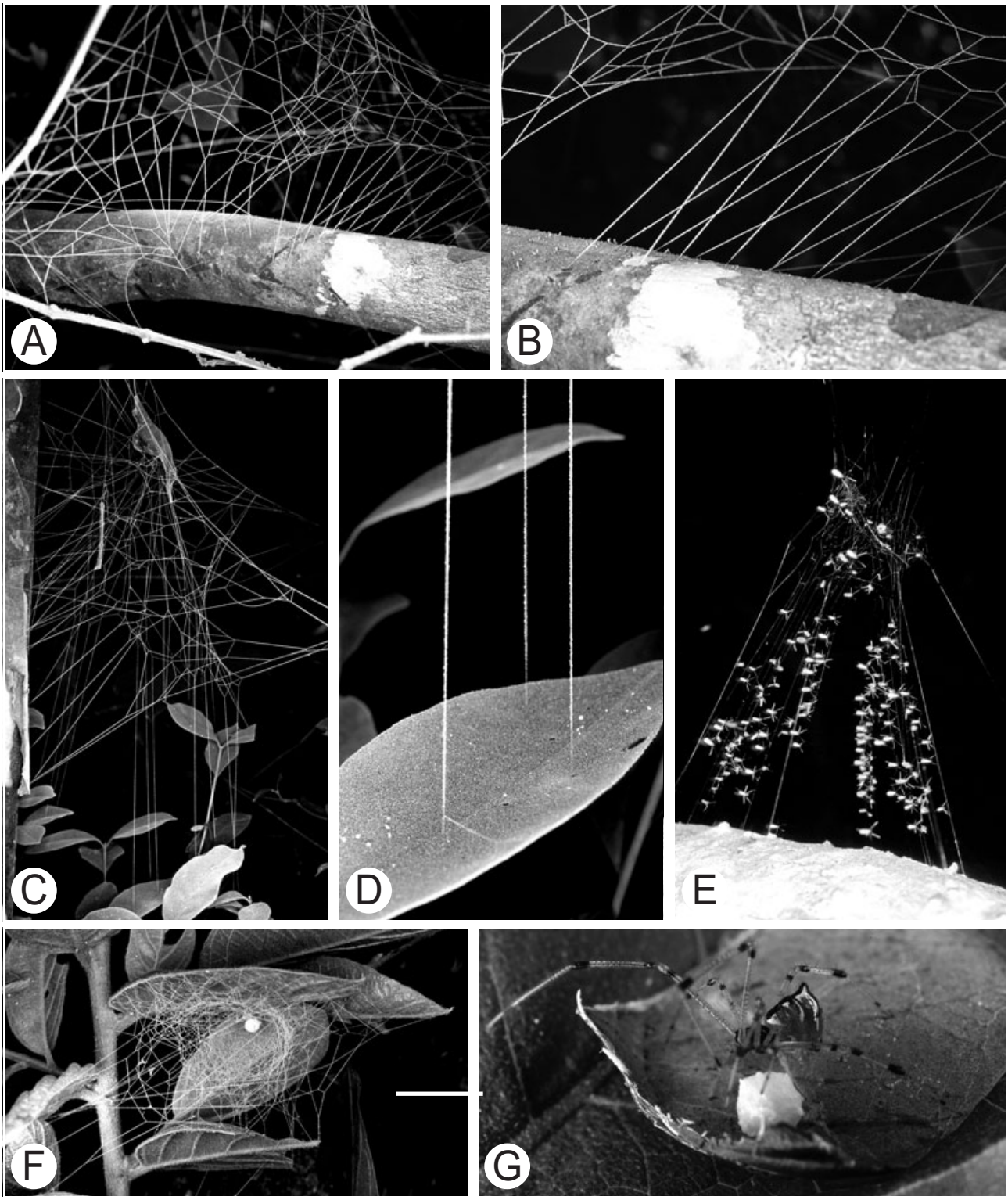

Figure 101. A–D, 'nonstar' *Achaearanea* spp. webs (**225-3**, **226-0**, **227-1**). A, platform and gumfoot lines, surrounding a tree trunk (Ranamofana, Madagascar). B, ditto, gumfoot lines. C, gumfoot lines radiating in several directions, attached to a tree trunk and surrounding leaves (Ranamofana, Madagascar). D, ditto, gumfoot lines. E, *Achaearanea* sp. web covered with flies that use silk lines for resting (Fanies Island, S. Africa), the extremely simple, nonsticky, web of the argyrodine *Ariamnes* helps to lure nematocerous flies into proximity with the spider. F, *Theridion* sp., egg sac is protected in a special (non-snare) web (Fanies Island, S. Africa). G, *Chrysso* sp. female and egg sac (Fanies Island, S. Africa).

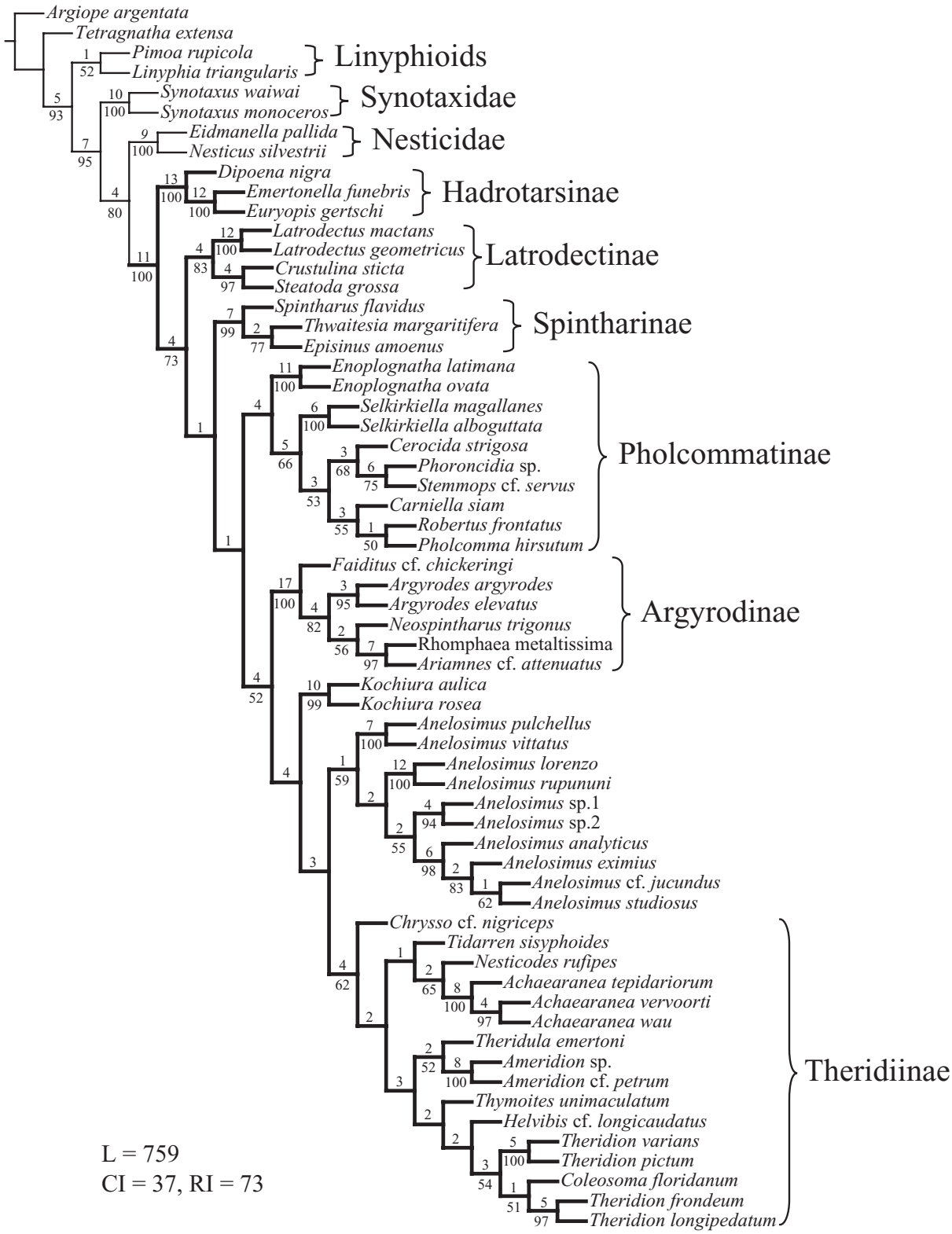

Figure 102. Single most parsimonious cladogram (L = 759, CI = 37, RI = 73) and preferred phylogenetic hypothesis of theridiid spiders with major groups identified and the family Theridiidae shown with thick lines. Numbers above branches indicate Bremer support; below branches are bootstrap values (above 50%). Parsimony jackknife scores were nearly identical and are not shown.

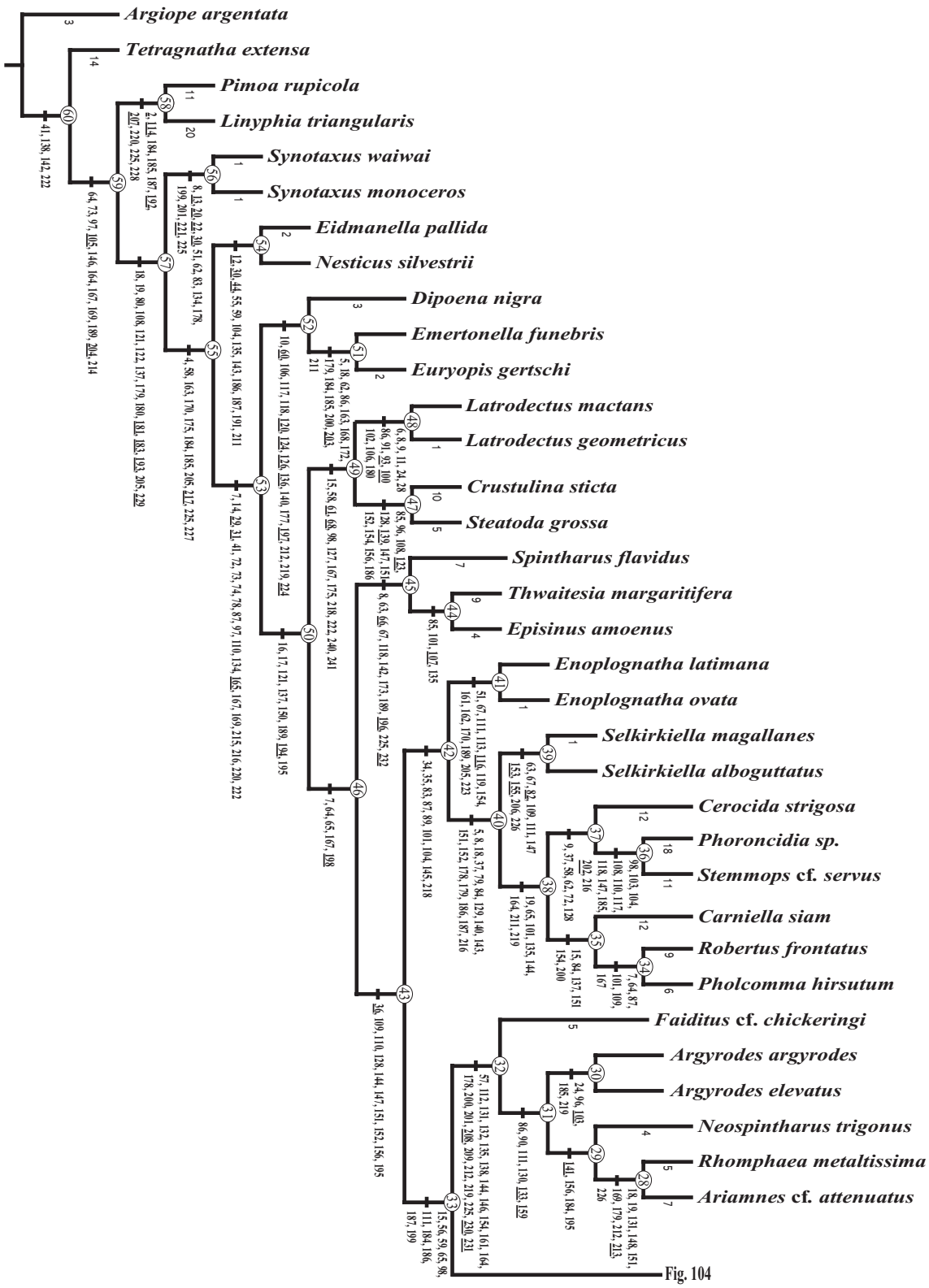

Figure 103. Cladogram of outgroups and basal theridiids. Clade numbers in circles at nodes; other numbers indicate characters changing on those nodes; underlined characters have perfect fit to the cladogram. Numbers on terminal branches are branch lengths (steps) when different from zero. All changes are shown (changes in terminal branches are reported in Table 2), ambiguous character optimization was generally resolved in favour of parallel losses, over parallel gains of structures (see Methods).

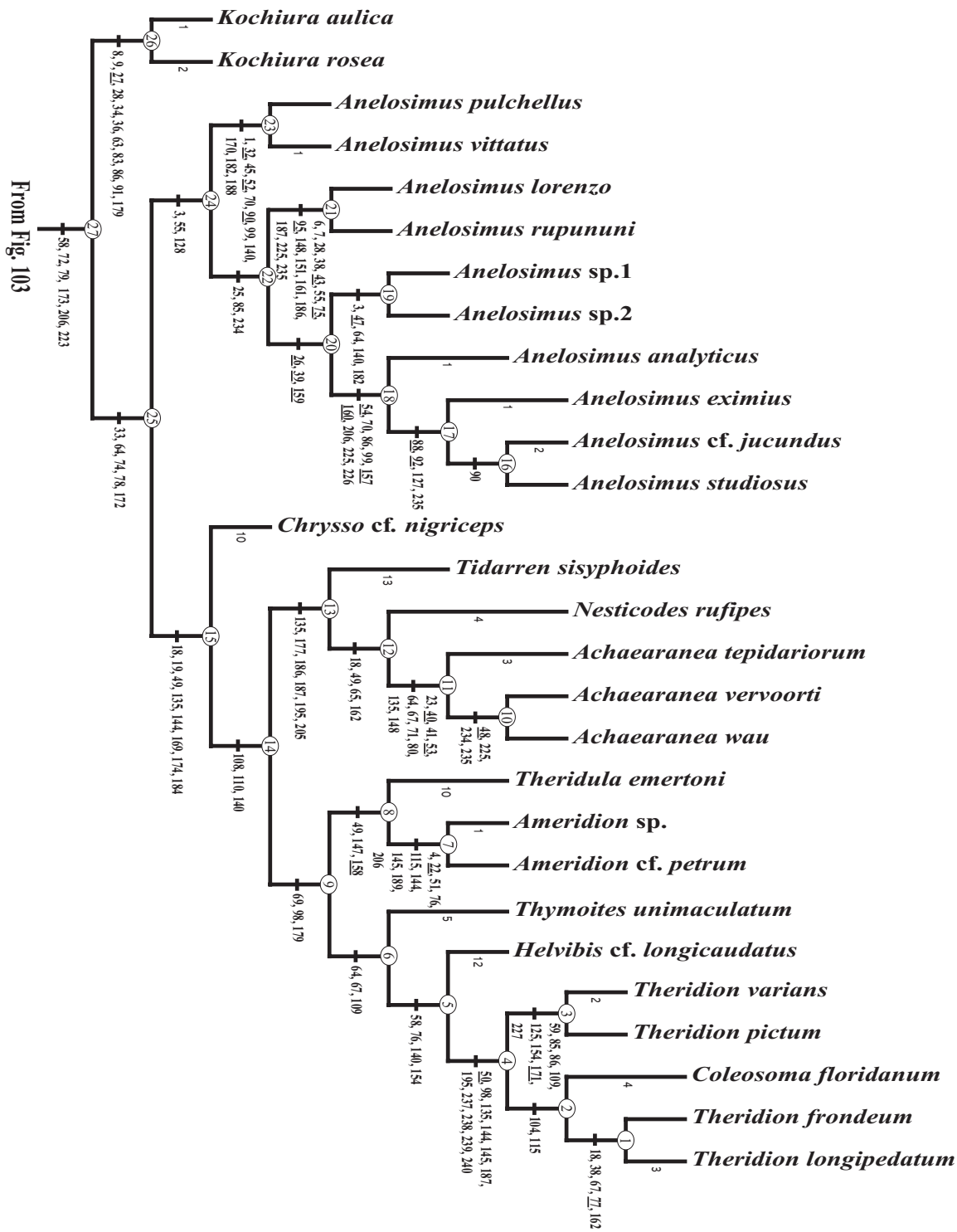

Figure 104. Cladogram of distal theridiids. Clade numbers in circles at nodes; other numbers indicate characters changing on those nodes; underlined characters have perfect fit to the cladogram. Numbers on terminal branches are branch lengths (steps) when different from zero. All changes are shown (changes in terminal branches are reported in Table 2), ambiguous character optimization was generally resolved in favour of parallel losses, over parallel gains of structures (see methods).

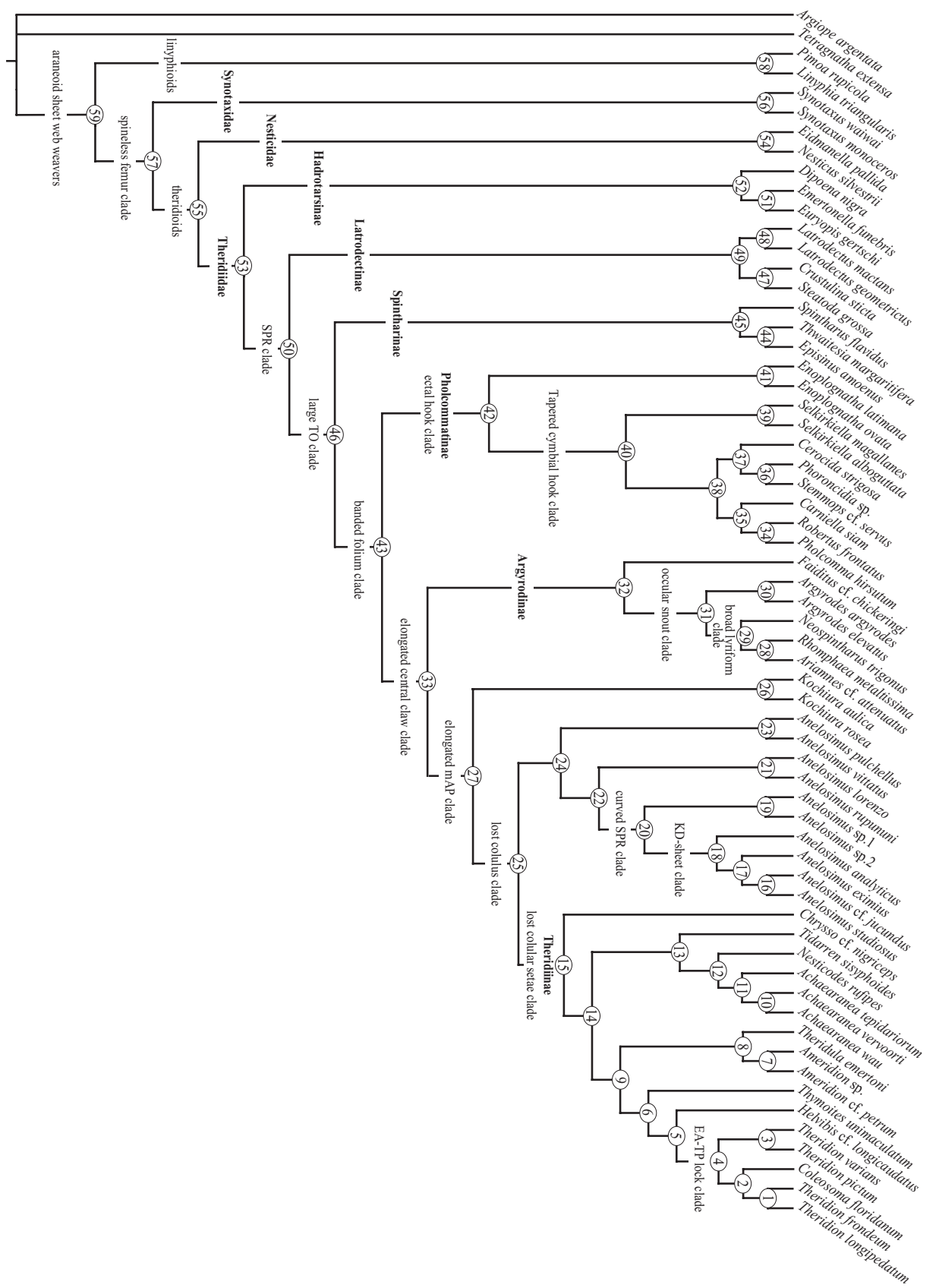

Figure 105. Cladogram of theridiids and relatives with clade names and numbers. Family and subfamily names shown in bold.

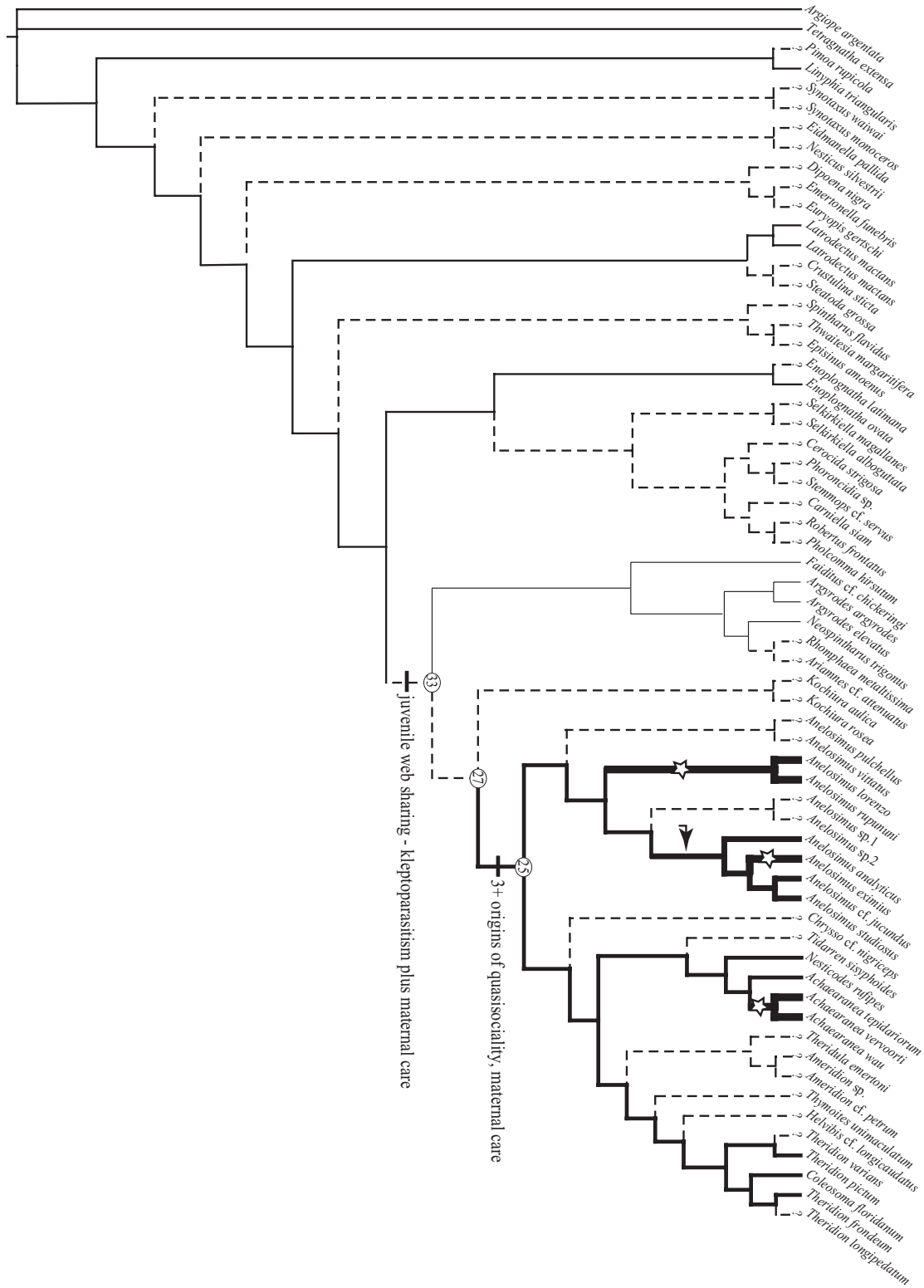

Figure 106. Maternal care and sociality. Question marks indicate unknown behaviour, Thin lines indicate no maternal care beyond care of egg sac, broken lines ambiguous optimization, bolder lines indicate maternal care, subsociality (periodic sociality) and quasisociality (permanent sociality), respectively, with increasing width of lines. Stars indicate the three origins of quasisociality, arrow the single origin of subsociality. Maternal care can be unambiguously optimized to the lost colulus clade (clade 25), but deeper optimization is ambiguous due to missing information. Small juveniles dependent on a large host (whether mother or not), or 'juvenile web sharing' optimizes to clade 33, containing nearly all instances of maternal care, sociality and kleptoparasitism (very thin lines).

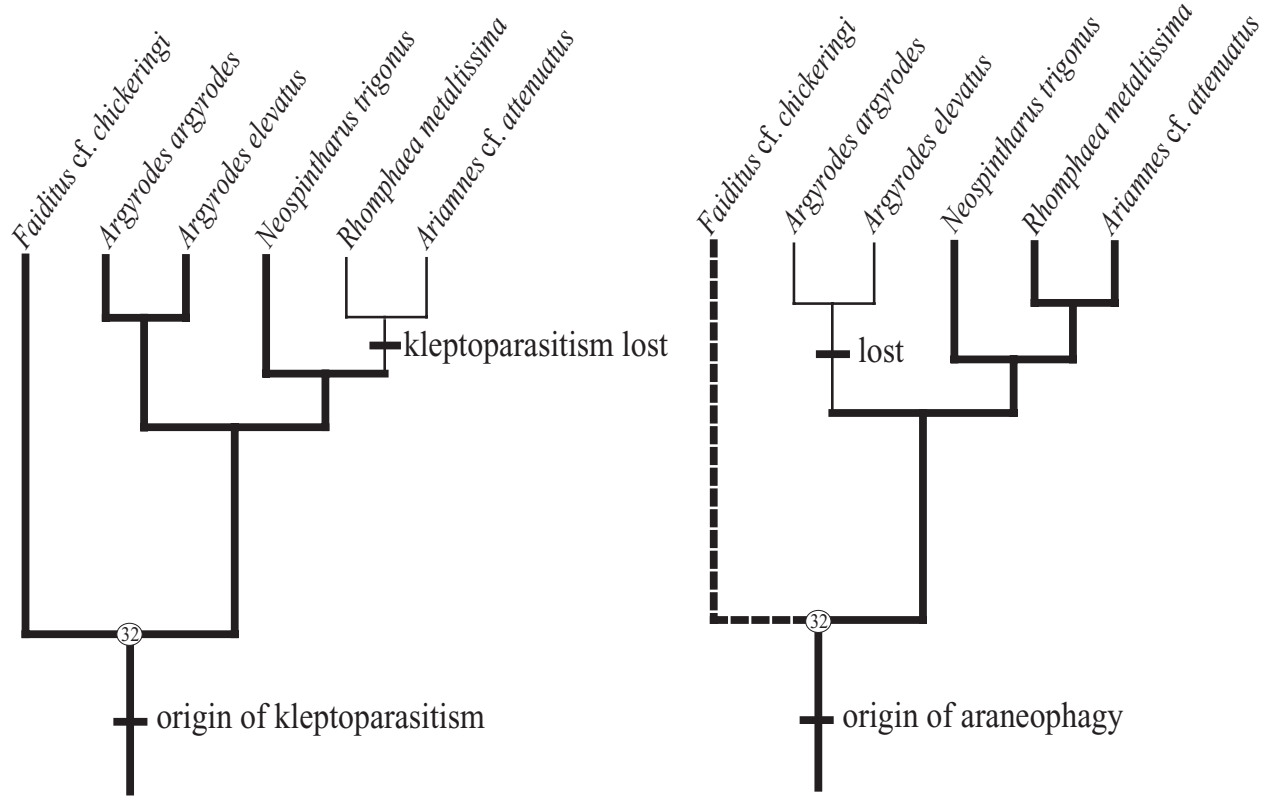

Figure 107. Optimization of kleptoparasitism and araneophagy within Argyrodinae. Kleptoparasitic behaviour unambiguously optimizes at the base of Argyrodinae (clade 32); specialized araneophages have secondarily lost kleptoparasitism. Araneophagy is present in some but probably not all *Faiditus* species; the behaviour of the species included in this phylogeny is not known. Given the cladogram, the optimization of this character will either be ambiguous (gain and loss, or two gains), or if *Faiditus* is primitively nonaraneophagous, multiple gains will be inferred. However, given the data at hand, and logical preference for retaining homology of complex features, I prefer the hypothesis that araneophagy arose once and was lost in the strictly kleptoparasitic *Argyrodes*.

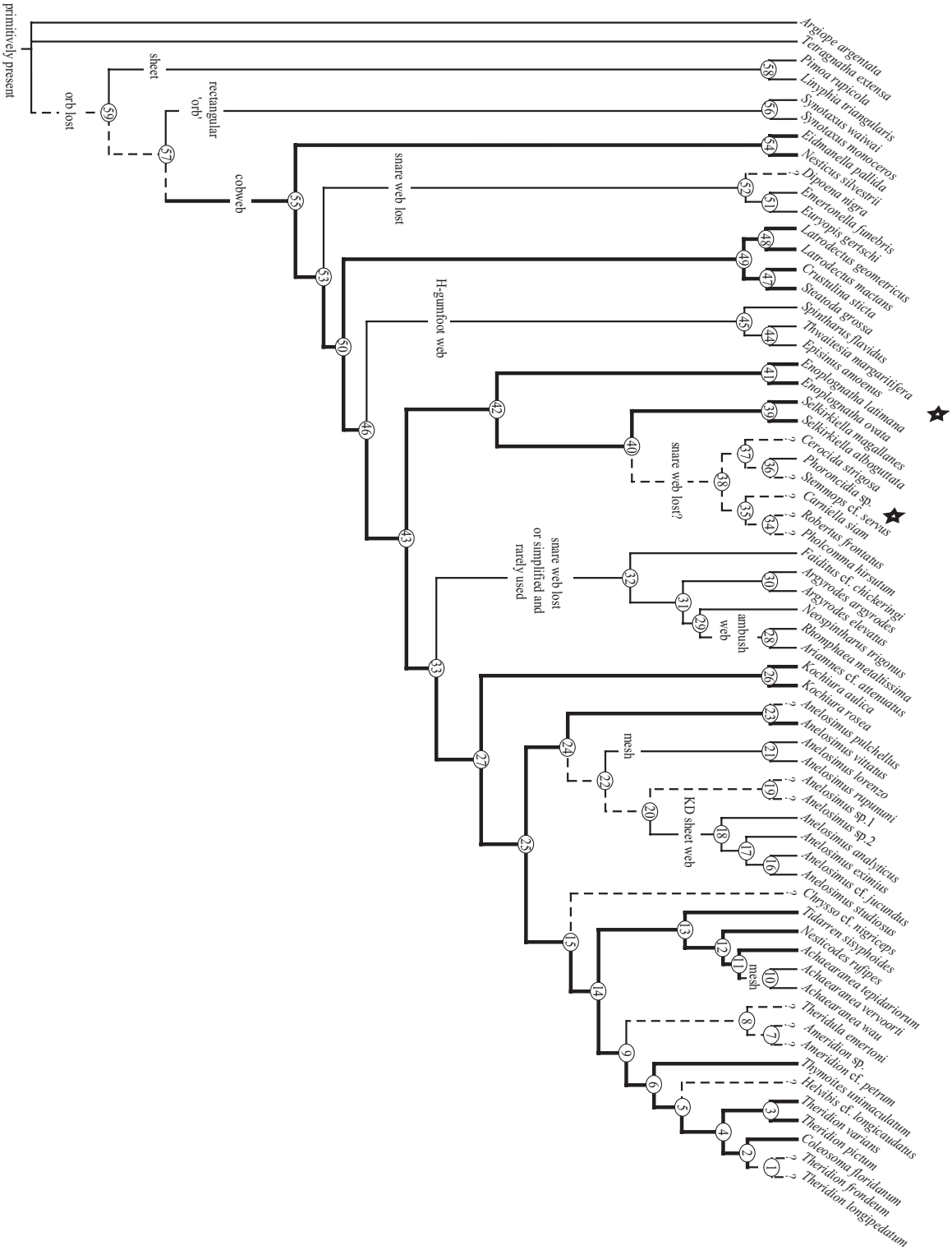

Figure 108. Evolution of the theridiid web. A three-dimensional cobweb (thick lines) is an unambiguous synapomorphy of the theridioids, but has been lost, or modified, multiple times. Ambiguous optimization is indicated with broken lines, unknown web types with question marks. Taxa marked with a star are autapomorphic. *Thwaitesia* does not make the typical H-shaped web of other spintharines, but still depends on only a few lines. *Phoroncidia* builds a unique single line web (sometimes a few lines) with sticky silk on one end (see Fig. 97B–D); related taxa are probably all litter dwellers and some may well be web-less.

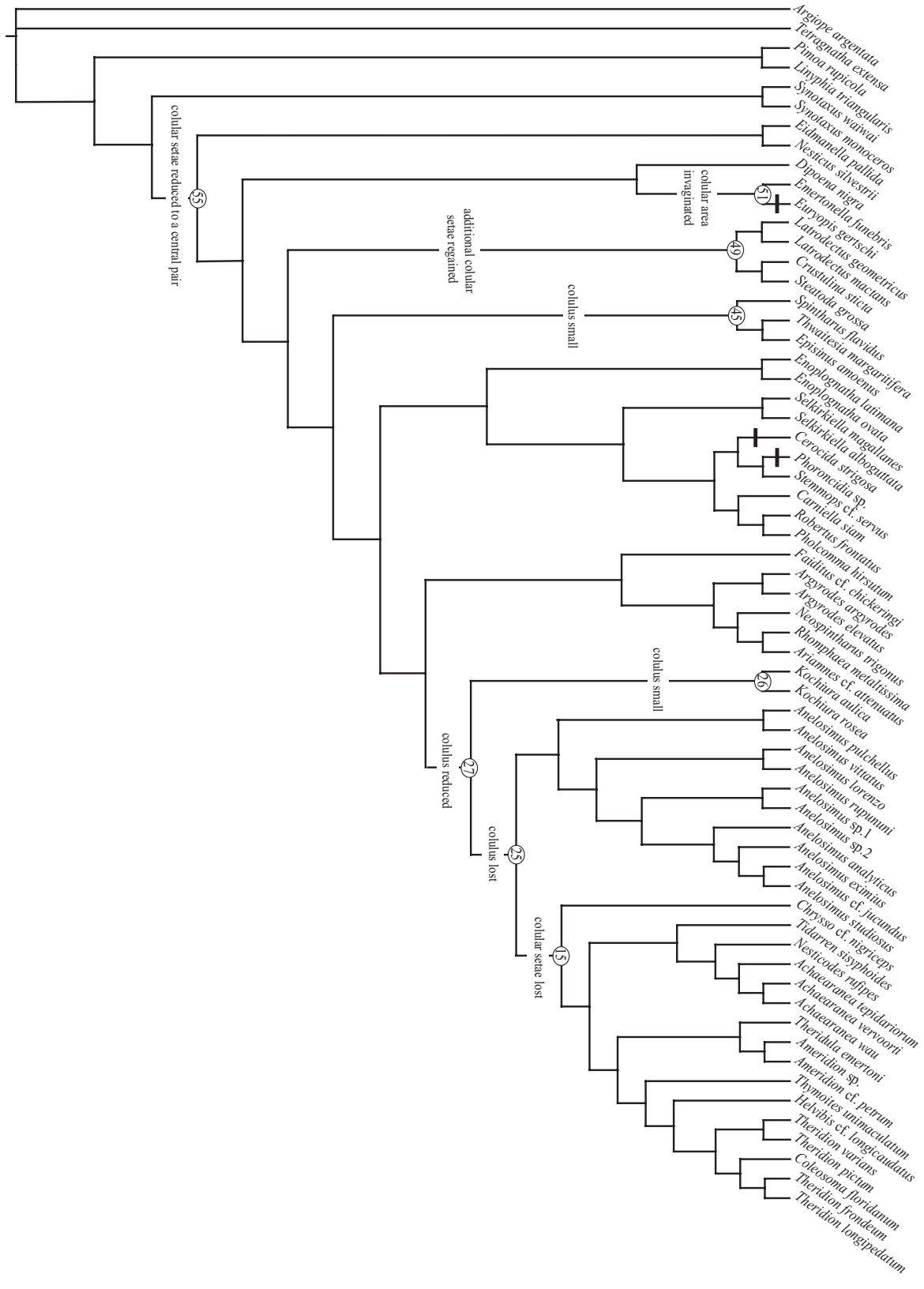

Figure 109. Evolution of the colulus. Reduction in number of colular setae, reduced colular size, loss of the colulus, and loss of the paired central colular setae are nested synapomorphies of less and less inclusive clades (relevant clade numbers shown as in Fig. 105). Bars indicate autapomorphic homoplasy. *Euryopis gertschi* has independently lost the paired central colular setae; *Cerocida strigosa* has a tiny colulus, and in *Phoroncidia* sp. the colular area is invaginated.

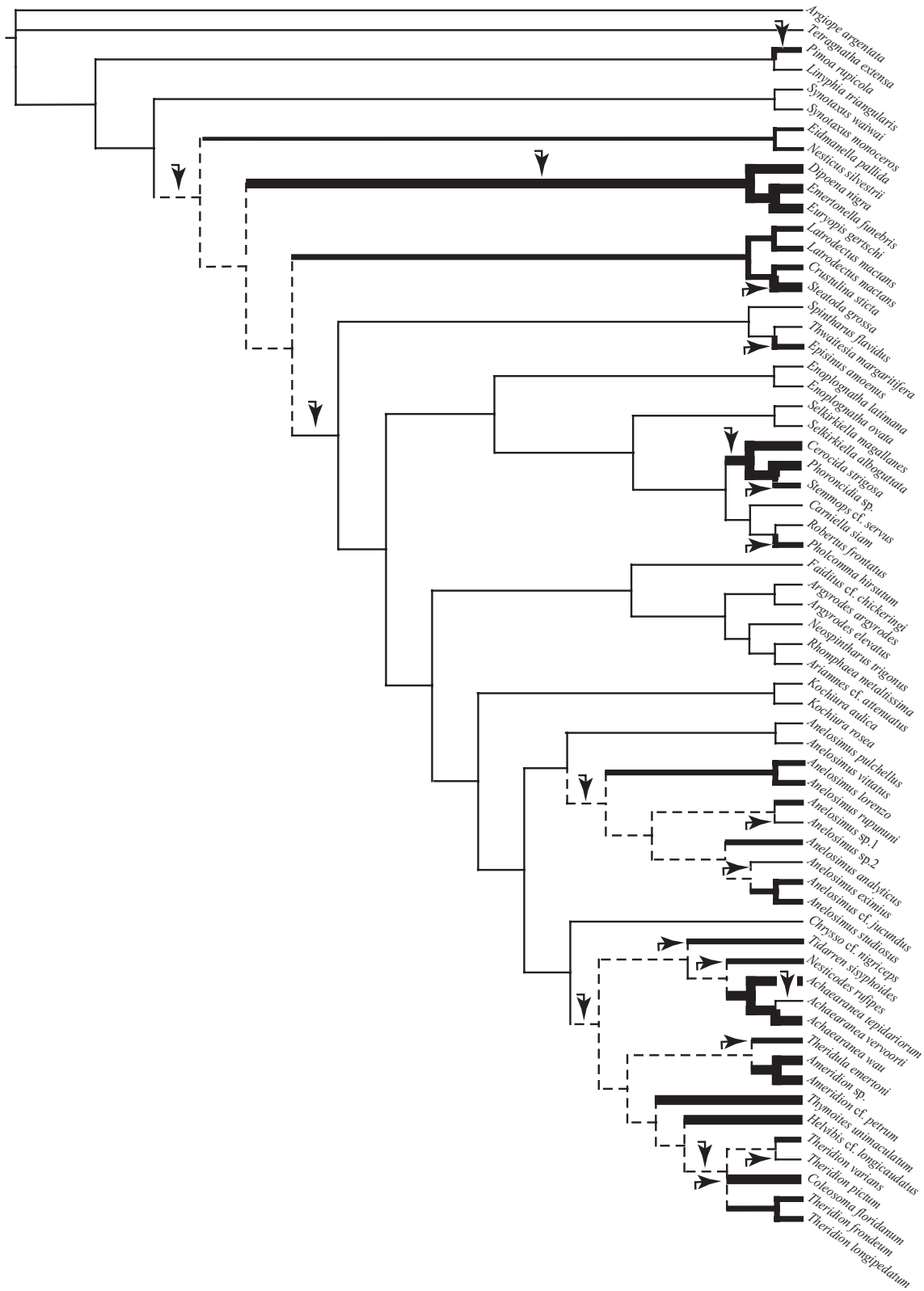

Figure 110. Eye arrangements played a key role in early classification of Theridiidae, but were criticized by Levi & Levi (1962) as an unreliable character system. Here the separation of PME has been coded as a three-state character – separation less than (very thick lines), equal to (thick lines) or greater than (thin lines) width of eyes – and the data reanalysed. Treated in this way the character needs no less than 20 changes on the cladogram (arrows), lending support to Levi & Levi's claim.

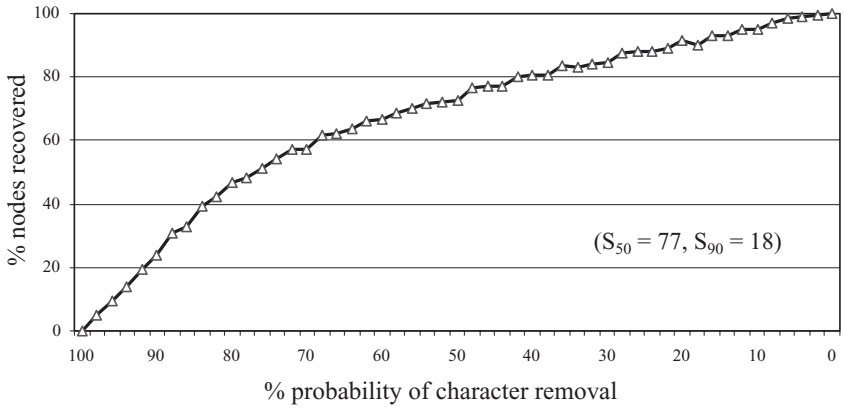

Figure 111. Results of the Continuous Jackknife Function Analysis (Miller, 2003). The current analysis is converging on the preferred hypothesis. The stability of the data is greater than in any morphological, and most molecular (or total evidence), datasets explored by Miller. In other words, comparatively few data are necessary to recover e.g. 50% and 90% of the nodes, supported by the entire matrix (S_{50} = 77, S_{90} = 18). Interestingly, at 50% probability of character removal, 73% of the nodes are retained.