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A revision of the New World *eximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars

INGI AGNARSSON*

Systematic Biology – Entomology, E-530, Smithsonian Institution, NHB-105, PO Box 37012, Washington, DC 20013-7012, and Department of Biological Sciences, George Washington University, 2023 G Street NW, Washington, DC 20052, USA

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The overwhelming majority of spiders are solitary and territorial. Of the handful of web-sharing social species, most belong to the cobweb genus *Anelosimus* Simon, 1891 (Theridiidae). *Anelosimus* species, especially those from the Americas, have therefore become model organisms in the study of spider sociality. However, lack of a phylogeny and outdated taxonomy have hindered progress in understanding the evolution of social behaviour. The identity of many species studied behaviourally is in doubt, and choice among the competing hypotheses on the course of evolution of sociality in *Anelosimus* requires a robust phylogeny. This paper offers a revision of the New World '*eximius* lineage' containing the most intensely studied *Anelosimus* species, and a phylogenetic study including worldwide exemplars. Previous taxonomic work on the group was incomplete and oversimplified. Some species-level taxa, e.g. *A. jucundus* (O. P.-Cambridge, 1896) and *A. studiosus* (Hentz, 1850), as previously circumscribed represent a compendium of species and are here re-examined. Eight new species are here described: *A. arizona*, *A. baeza*, *A. octavius* and *A. puravida*, of the '*jucundus* group', and *A. gucamayos*, *A. oritoyacu*, *A. pantanal* and *A. tungurahua* of the '*studiosus* group'. Furthermore, *Enoplognatha dubia* Chamberlin, 1916 and *Theridion tosum* Chamberlin, 1916 previously synonymized with *A. jucundus*, and *Anelosimus fraternus* Bryant, 1948, previously synonymized with *A. studiosus*, are here again considered valid. *Enoplognatha dubia* becomes a junior secondary homonym of *Brattia dubia* Tullgren, 1910 (= *Anelosimus dubius*) and the replacement name *Anelosimus elegans* Nomen Novum is here provided. The parsimony analysis of the morphological matrix (43 taxa, 147 characters) resulted in two equally most parsimonious trees, with four trichotomies in the strict consensus. Three of these lack character evidence to resolve them; one is a result of character conflict. One of the two trees is optimal under successive weighting. The New World *Anelosimus* are not monophyletic, but rather form three clades, the *eximius* lineage (20 species), the '*rupununi* group' (two species) and the '*ethicus* group' (six species). The phylogenetic results corroborate previous transfer of species to *Kochiura* and *Selkirkiella*. The following additional species are removed from *Anelosimus*: *Styposis camoteensis* (Levi, 1967) (comb. nov.), *Styposis tepus* (Levi, 1967) (comb. nov.), *Chrosiothes episinoides* (Levi, 1963) (comb. nov.) and *Stemmops osorno* (Levi, 1963) (comb. nov.). Four species are here treated as nomina dubia, *Anelosimus nigrobaricus* Barrion & Litsinger, 1995 (type in very bad condition, original description lacks sufficient detail for identification), and *A. salaensis* Barrion & Litsinger, 1995, *Theridion fasciatum* Holmberg, 1876 and *T. sordidum* Holmberg, 1876 (types lost, original descriptions lacks sufficient detail for identification). The results corroborate previous findings of convergent evolution of permanent sociality in the genus. However, instead of sociality evolving twice as previously suspected, the current phylogeny suggests no less than six, independent origins. Each time, the evolution of sociality seems to be responsible for a dramatic shift in population structure from outbred panmictic to strongly inbred subdivided populations. Perhaps as a consequence, once they are permanently social, species seem to fail to diversify; all social clades are small (one or two species) and usually smaller than their sister clade. No losses of social behaviour are inferred. The maternal care route hypothesis is again supported. To explain sociality in *Anelosimus* it seems sufficient to hypothesize a temporal extension of the juvenile web-sharing, co-operation and conspecific tolerance, displayed in basic maternal care, coupled with depression of dispersal. Given the most parsimonious phy-

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*Current address: The University of British Columbia, Departments of Zoology and Botany, 3529-6270 University Blvd., Vancouver, BC V6T 1Z4, Canada. E-mail: ingi@zoology.ubc.ca, ingi@theridiidae.com

logeny, the basal-most *Anelosimus* species occur in the Old World, and three *Anelosimus* clades occur in the New World. Sufficient data are not available to estimate the age of the *Anelosimus* lineage accurately, but the sparse fossil record hints at a relatively recent origin (20–40 mya). If true, vicariance could not account for this distribution; rather, the pattern may suggest three independent colonization events of Old World *Anelosimus* in the Americas. Support for most branches within *Anelosimus* is relatively low, especially the support for the relationships within species groups. Thus, although the forgoing conclusions are clearly implied by the phylogeny, weak support limits their force.

ADDITIONAL KEYWORDS: evolution of sociality – inbreeding – maternal care – morphology – parallel gains – quasisociality – subsociality – taxonomy – theridiid phylogeny.

INTRODUCTION

> 'It is possible, however, that both *T. studiosum*, Hentz, and *T. jucundum*, O. P.-Cambr. (as Simon thinks probable), the varieties here figured, and also those from Bogota, are all one and the same species, the larger and more highly developed examples being *T. jucundum*, the smaller and more slender being *T. studiosum* . . . It is also possible, on the other hand, that there are several species of these social spiders, and that the varieties above noted may prove to be really good species. I cannot at present reconcile myself to either view, but must be content with giving drawings and descriptions of them.' (F. O. P.-Cambridge, 1902: 395).

The cosmopolitan spider genus *Anelosimus* Simon, 1891 (Theridiidae) prior to this revision contained 45 described species (Platnick, 2006), with most species living in tropical or subtropical areas. In contrast to the majority of spiders, which are aggressive and solitary (Coddington & Levi, 1991; Foelix, 1996), most *Anelosimus* species are social, including all studied New World species. *Anelosimus* species are placed in two social categories, both non-territorial (web-sharing): (1) subsociality, in which co-operative siblings and their providing mother temporarily share a nest, and (2) quasisociality (hereafter sociality), with multiple adult spiders in semi-permanent communal webs (Kullmann, 1972; Avilés, 1997; Agnarsson, 2004). Subsocial *Anelosimus* have nests usually containing between 20 and 100 individuals, whereas social nests can contain thousands of individuals. Avilés (1997) classified four New World *Anelosimus* species [*A. domingo* Levi, 1963, *A. eximius* (Keyserling, 1884), *A. lorenzo* Fowler & Levi, 1979, *A. rupununi* Levi, 1956] as social and six [*A. analyticus* (Chamberlin, 1924), *A. dubiosus* (Keyserling, 1891), *A. ethicus* (Keyserling, 1884), *A. jabaquara* Levi, 1956, *A. jucundus* (O. P.-Cambridge, 1896) and *A. studiosus* (Hentz, 1850)] as subsocial. *Anelosimus oritoyacu* sp. nov., *A. guacamayos* sp. nov. and apparently *A. puravida* sp. nov. are also social, while the remaining seven species treated here are either subsocial or their behaviour is not known.

The behaviour of species outside the New World is poorly known, but at least some are also social, including, for example, several recently discovered subsocial species from Madagascar (Agnarsson & Kuntner, 2005), and South East Asia (my pers. observ.). Positive evidence for solitary lifestyles is rarely reported; even the fairly common two European *Anelosimus* species cannot be presumed to be solitary (sociality seems likely given their phylogenetic position). The many solitary species placed in *Anelosimus* by Levi (1956, 1963, 1967) do not belong to this genus and have been transferred (see Agnarsson, 2004, and below).

The degree of co-operation varies across species, but is most extensive in social species and includes collaborating in web construction, prey capture, feeding, defences and, in some instances co-operative brood care. Co-operative brood care may deny some females of any reproductive output, and because of this, some authors have used the term eusociality for some of the most social species (Buskirk, 1981; Vollrath, 1986b; Rypstra, 1993). This, however, indicates a resemblance to eusocial insects that is simply misleading (Avilés, 1997; Avilés & Tufiño, 1998). Unlike eusocial insects, social spiders lack castes, every nest member is totipotent (although adult males contribute minimally towards the colony) and it remains to be shown if differential reproductive output is atypically high in social spiders; no doubt a proportion of females of solitary species also fail to reproduce.

Sociality seems to be responsible for a dramatic shift in population structure from outbred panmictic to strongly inbred subdivided populations. With this comes the possibility of selection acting on the colonies as units (Avilés, 1986, 1987, 1993, 1997). Among colony selection and inbreeding may have many consequences, including biased sex ratios (Riechert & Roeloffs, 1993; Avilés, 1997). Therefore it is not surprising to observe that the social *Anelosimus* have highly female-biased sex ratios (Avilés, 1986; Avilés & Maddison, 1991; Avilés et al., 2000).

Anelosimus are model organisms in the study of spider sociality. Numerous studies have examined the biology of social *Anelosimus* (e.g. Kullmann, 1972; Brach, 1975, 1977; Buskirk, 1981; Levi & Smith, 1983; Overal & Ferreira da Silva, 1982; Uetz, 1983; Vollrath & Rohde-Arndt, 1983; Nentwig, 1985; Nentwig &

Christenson, 1986; Yoshida, 1986; Pasquet & Krafft, 1989, 1992; Rypstra & Tirey, 1989; Cangialosi, 1990a, b; Krafft & Pasquet, 1991; Ito & Shinkai, 1993; Venticinque, Fowler & Silva, 1993; Smith & Hagen, 1996; Pasquet *et al.*, 1997; Avilés & Tufiño, 1998; Furey, 1998; Marques, Vasconcellos-Neto & Britto-De-Mello, 1998; Avilés & Salazar, 1999; Saffre, Mailleux & Deneubourg, 1999, 2000; Avilés, 2000; Avilés *et al.*, 2001; Gonzaga & Vasconcellos-Neto, 2001; Vakanas & Krafft, 2001), dispersal and the formation of colonies (e.g. Vollrath, 1982; Pasquet & Krafft, 1989; Leborgne, Krafft & Pasquet, 1994; Avilés & Gelsey, 1998; Avilés, 2000; Jones & Parker, 2000, 2002), and sex ratio bias and inbreeding (e.g. Avilés, 1986, 1987; Smith, 1986, 1987; Vollrath, 1986a, b; Elgar & Godfray, 1987; Avilés & Maddison, 1991; Avilés *et al.*, 2000; Bukowski & Avilés, 2002), to name but a few.

Many of these studies also discuss the implications of their results to the evolution of sociality in the genus. Two main hypotheses have been proposed to explain the origins of social behaviour in theridiids, as in spiders in general (e.g. Shear, 1970; Kullmann, 1972; Krafft, 1979; Avilés, 1986, 1993, 1997, 1999; Frank, 1987). Sociality may have evolved through development of aggregations around an abundant resource (Brach, 1975, 1977; Krafft, 1979; Nentwig, 1985; Nentwig & Christenson, 1986; Rypstra, 1986; Pasquet & Krafft, 1989). Others have pointed out that the early stages of both sub- and sociality, in which a mother cares for her newly hatched offspring (see Gillespie, 1990), are closely similar to solitary species showing maternal care. Sociality then may have arisen through temporal extension of juvenile web sharing during maternal care – the 'maternal care hypothesis' (Burgess, 1978; Vollrath, 1982; Uetz, 1983; Smith, 1986, 1987; Avilés, 1986, 1997, 1999, 2000; Avilés & Gelsey 1998; Agnarsson, 2002). However, although contributing valid and perceptive hypotheses, such considerations have hitherto lacked an essential basis: a phylogeny (e.g. Coddington, 1988). Agnarsson (2004, see also Agnarsson, 2002; Arnedo *et al.*, 2004) for the first time tested these hypotheses phylogenetically, and his results corroborated the maternal care hypothesis.

The phylogenetic pattern of sociality can also help answer the questions about why there are so many social theridiids. From the outset we might expect independent origins of sociality in each of the three genera in which it occurs. Within *Anelosimus*, however, it could range between two extremes: a single origin followed by diversification, in which case social species form a single clade, or multiple origins, in which case sociality is polyphyletic. The two extremes imply entirely different evolutionary consequences of sociality. The former suggests diversification of a successful lineage (sociality as a viable evolutionary strategy), and the latter short-term benefits, perhaps leading to an evolutionary dead end. Failure to diversify would be particularly intriguing given a population structure that seems atypically propitious for speciation.

Despite intense behavioural work, the most recent revisionary taxonomic work on *Anelosimus* dates back half a century (Levi, 1956, 1963), and although excellent, is now outdated. Consequently, some of the aforementioned studies have been made on undescribed, and sometimes misidentified species. As behavioural studies rarely designate vouchers, a portion of the available behavioural data cannot be linked to a specific taxon, limiting their utility. Many 'species' have striking ranges and show enormous geographical variation in both morphology and behaviour. Some report '*A. studiosus*', for example, to show only temporary sociality (subsociality) and have equal sex ratios (Fowler & Levi, 1979; Nentwig & Christenson, 1986), whereas others have documented social behaviour and distinctly female-biased sex ratios in the same species (Furey, 1998). Reports on *A. jucundus* are similarly diverse, and in one instance social structure differs distinctly between populations only a few hundred metres apart, although they appear morphologically identical (Avilés & Maddison, pers. comm. and pers. observ.). These '*A. studiosus*' and '*A. jucundus*' do not seem to represent coherent units, but are rather a compendium of species whose discovery and study has been hindered by the limited systematic knowledge and perplexing taxonomy of the genus.

Clearly, phylogenetic context and a revised taxonomy are essential to progress in understanding the phylogenetic distribution and evolution of social behaviour. In this work, the *eximius* lineage of *Anelosimus* is revised, continuing efforts to revise the genus worldwide (see Agnarsson, 2005, for a revision of the *rupununi* and *ethicus* groups, and Agnarsson & Kuntner, 2005, and Agnarsson & Zhang, 2006, for descriptions of Old World species).

PHYLOGENETICS

Two phylogenetic hypotheses of theridiid genera are available, based on morphology (Agnarsson, 2004, see also Agnarsson, 2003c, 2006) and molecular data (Arnedo *et al.*, 2004). Although differing in many details, both place *Anelosimus* relatively distally. Molecules place *Kochiura* sister to *Anelosimus*, and together these are sister to Theridiinae (Arnedo *et al.*, 2004). Morphology places *Anelosimus* sister to Theridiinae, together forming the 'lost colulus clade'; *Kochiura* is then sister to the lost colulus clade (Agnarsson, 2004). Among the most important synapomorphies of the lost colulus clade are: a cymbial hood, entire median apophysis and the secondary loss of a colulus.

This clade is especially important because it includes all known instances of theridiid sociality: *Anelosimus* (e.g. Avilés, 1997), the social *Achaearanea wau* Levi, Lubin & Robinson, 1982, *A. vervoorti* Chrysanthus, 1975 (see Levi, Lubin & Robinson, 1982; Lubin, 1982, 1986, 1991, 1995), and *A. disparata* Denis, 1965 (Darchen, 1968; Darchen & Ledoux, 1978) and *Theridion nigroannulatum* Keyserling, 1884 (Avilés *et al*., 2001, in press). This clade also includes most instances of maternal care documented in theridiids, including several *Achaearanea*, *Theridion* (e.g. Gillespie, 1990) and *Chrysso* (Miller & Agnarsson, 2005).

The study of Arnedo *et al*. (2004) included only a single *Anelosimus* species and is thus silent about interspecies relationships. Agnarsson (2004) included 12 *Anelosimus* species and found the monophyly of a revised *Anelosimus* (minus *Kochiura* and *Selkirkiella*) to rest on a single unambiguous synapomorphy: ridges on the surface of the epigynal plate. In his hypothesis species from the New World were not monophyletic. Two clades, the *eximius* lineage and the *rupununi* group were recovered but, perhaps surprisingly, two undescribed *Anelosimus* from Tanzania (the first to be discovered in sub-Saharan Africa) formed a clade between the two. The species from Europe then formed a clade sister to the remaining *Anelosimus*. Agnarsson (2004) found that sociality evolved at least twice within the genus, and the results were congruent with the maternal care route hypothesis of social evolution. His phylogeny, however, included only a portion of the social species, and lacked representatives from several areas, likely to impact the phylogenetic structure.

TAXONOMIC HISTORY

The taxonomic history of *Anelosimus* goes back two centuries. The European *Anelosimus pulchellus* (Walckenaer, 1802) was described earliest. The American *Anelosimus studiosus* (Hentz, 1850) was the first social species to be described and like *A. pulchellus* was originally placed in *Theridion* (then *Theridium*). Keyserling (1884, 1891) described three additional social species, before Simon (1891) erected the genus *Anelosimus* based on the South American species *Theridium eximius* Keyserling, 1884. Simon later transferred the species back to *Theridion*, but most authors rejected his synonymy. F. O. P.-Cambridge (1902) used *Anelosimus* exclusively for social species, and Archer (1946, 1950) and Kaston (1948) included the North American *A. studiosus*. Levi (1956) revised *Anelosimus* and transferred to it many New World species. He also broadened the genus, by synonymizing with it the European *Kochiura* Archer, 1950, and later (Levi, 1963) expanded its boundaries even further by including several rather dissimilar species from Chile, in part by subsuming *Selkirkiella* into *Anelosimus* (see also Levi, 1967). Levi (2005: 236) recently offered a reflection on his treatment of theridiids in general: 'In retrospect it appears that to avoid splitting, I lumped.' Levi's grand treatise of theridiid genera greatly improved the naturalness of their classification; most genera in his circumscription appear monophyletic. Hence, Levi's preference for large genus groups in Theridiidae was not generally problematic, but it did result in a couple of 'waste-basket genera', including *Theridion*, and *Anelosimus*.

Three characters seem to define Levi's broad view of *Anelosimus*: 'colulus replaced by two setae', retrolateral cheliceral denticles, and a regular longitudinal band-like folium dorsally on the abdomen. The first of these included taxa with either a small colulus, or colulus absent, but two setae present. However, Agnarsson (2004) found that loss of a colulus unites *Anelosimus* with Theridiinae, and that the presence of a pair of colular setae is plesiomorphic for theridioids. Retrolateral cheliceral teeth are probably primitive for araneoids as a whole (see e.g. Coddington, 1986b, c; Griswold *et al*., 1998) occurring sporadically in theridiids, including all genera closely related to *Anelosimus* (Agnarsson, 2004), and a dorsal abdominal band is widespread and clearly extremely homoplastic within spiders. This loose definition admitted many species to *Anelosimus* that lacked characters placing them elsewhere. In retrospect, it is unsurprising that a genus defined by plesiomorphic characters became paraphyletic, for symplesiomorphies define such groups.

New American species were described by Levi (1967, 1972), Fowler & Levi (1979), Levi & Smith (1983) and Agnarsson (2005). European species were described by Walckenaer (1802) and C. L. Koch (1836, 1838), Mediterranean species by Simon (1890), Wiehle (1931), Locket & Millidge (1951), species from the Seychelles and Madagascar by Blackwall (1877), Roberts (1983) and Agnarsson & Kuntner (2005), and Asian and African species by Bösenberg & Strand (1906), Yoshida (1986, 1993), Barrion & Litsinger (1995), Paik (1996), Zhu (1998) and Agnarsson & Zhang (2006). Although many *Anelosimus* species are correctly placed, others merely approximately fit the broad (symplesiomorphic) circumscription of *Anelosimus*, and have little in common with the type species *A. eximius*. The range of dissimilar genera to which *Anelosimus* species have been transferred to date is revealing (*Chrosiothes*, *Enoplognatha*, *Episinus*, *Nesticodes*, *Stemmops*, *Styposis*, *Theridion*).

OBJECTIVES

The primary goal of this paper is to relimit and recircumscribe *Anelosimus*, and to provide a revision of the American *eximius* lineage and a phylogenetic hypothesis including worldwide exemplars. A worldwide revision was an optimistic early goal, but research disclosed an order of magnitude more species than suspected at the outset. This work thus continues efforts to clarify the circumscription and taxonomy of *Anelosimus* worldwide (see Agnarsson, 2005; Agnarsson & Kuntner, 2005; Agnarsson & Zhang, 2006). Given that knowledge of the biology of *Anelosimus* is biased towards the New World (all species whose social structure has been studied in detail occur there), it seems appropriate to direct taxonomic effort to that region. Three *Anelosimus* clades occur there: the *eximius* group, including the type species and most of the classic social exemplars, the *rupununi* group represented by two social species, and the *ethicus* group, representing six poorly known species from South America (the latter two groups are revised by Agnarsson, 2005).

MATERIAL AND METHODS

Methodology is further detailed in Agnarsson (2004).

SPECIMEN PREPARATION AND IMAGES

Specimens were examined under a Wild M-5A dissecting microscope. Male palps were immersed in concentrated KOH (~1 g mL^{-1}) for 1 min and then transferred to distilled water where rapid expansion took place in less than 1 min (Coddington, 1990, as modified from Shear, 1967). Full expansion often required unhooking the median apophysis 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. Immersing palps in 70% ethanol containing maximally concentrated KOH (using the minimum amount of ethanol sufficient to solve a KOH pellet) and then transferring to ‘clean’ 70% ethanol gives similar results and is convenient for preparation of expanded palps for scanning electron microscopy (Agnarsson, 2003c). 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), and internal female genitalia were always drawn from the dorsal side. All genitalia were furthermore photographed using a LEICA digital camera attached to the microscopes. 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, 1986a; Agnarsson, 2004).

Habitus photographs were made with the LEICA digital camera. For scanning electron microscope examination dissected specimens were transferred to 100% ethanol overnight, and then cleaned ultrasonically for 1 min. The specimens were then submitted to critical-point drying, apart from male palps which were air-dried. For examination of silk spigots the spinnerets were forcefully spread as described in Coddington (1989), when suitable specimens were unavailable. Specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin, and then sputter coated.

When only one side of the animal, or a part of it, is illustrated, it is the left side unless otherwise indicated. All drawings were rendered in Adobe Photoshop, using either hand-drawn sketches or digital photographs as a base. In most palpal drawings tibial and cymbial macrosetae are omitted, and in some cases macrosetae forming a row at tibial tip are shown; these are characteristics for theridiids (see Agnarsson, 2004). Plates were composed and labelled in Adobe Illustrator.

TAXON CHOICE

Outgroups

The putative sister group is the subfamily Theridiinae, together forming the lost colulus clade (note that Arnedo *et al.*, 2004 found *Kochiura* to be sister to *Anelosimus* and together these were sister to Theridiinae). This subfamily is here exemplified by *Theridion varians* Hahn, 1833 and *Achaearanea tepidariorum* (C. L. Koch, 1841). The genera *Kochiura* and *Selkirkiella*, both previously synonymized with *Anelosimus* are represented by *K. aulica* (C. L. Koch, 1838) and *K. rosea* (Nicolet, 1849), and *S. magallanes* (Levi, 1963), respectively. Other outgroup taxa are *Argyrodes argyrodes* (Walckenaer, 1842) and *A. elevatus* Taczanowski, 1873 (Argyrodinae), and *Enoplognatha ovata* (Clerck, 1757) (Pholcommatinae); the results are then rooted on the relatively basal *Steatoda grossa* (C. L. Koch, 1838) (Latrodectinae).

Ingroup taxa

For the phylogenetic study, taxon choice was biased towards well representing the New World species of *Anelosimus* (all included here, apart from three new species of the *ethicus* group described by Agnarsson, 2005). Species from other areas were sampled in an effort to represent morphological diversity maximally within the genus. Representatives were chosen of all a priori suspected lineages, or major *Anelosimus* subclades. As a worldwide revision was outside the possible scope of this work, the most inclusive clade of American *Anelosimus* containing the type species *A. eximius* was chosen for revision. Although arbitrary, this delimitation of the work has the benefit of being explicit, focusing on a monophyletic group (rather than, for example, a strictly regional revision), and covering most of the intensely studied *Anelosimus* species.

CHARACTER CHOICE

Characters from Agnarsson (2004) relevant to the relationships among *Anelosimus* and the outgroups (111 characters, see Appendix 1) in this study were used. Furthermore, 36 new characters were added.

The data comprise 147 characters, including: female genitalic morphology (ten characters), male genitalic morphology (72 characters), somatic morphology (47 characters), spinneret morphology (nine characters), and behaviour and web building (nine characters). Eight characters (13, 23, 104, 116, 123, 125, 128, 135) are parsimony-uninformative in the present context, but are included because of their likely relevance (as putative species group synapomorphies) to future studies on *Anelosimus* and their relatives.

Character descriptions and definitions are given in Appendix 1. A list of specimens examined for phylogenetics [other than those in Agnarsson (2004) and of species here described] is given in Appendix 2.

MATCHING SEXES

One problem encountered was matching males and females, not an uncommon problem in spider taxonomy (e.g. Levi, 1985). The presence of both sexes in a single sample is a commonly used criterion along with somatic morphology, but sometimes two or more species are sympatric, and often found in the same samples. This may be due to the collecting method used (such as beating and canopy fogging) being non-selective, lumping together a large number of specimens from various layers of the canopy. Somatic morphology, furthermore, offers little aid in *Anelosimus*; most related species are strikingly similar. Males can be told apart (sometimes with difficulty) by the genitalia, but in most cases I have discovered no reliable somatic characters to do so. Females of many species are extremely difficult to tell apart, each species being variable and the variation in epigynal morphology seemingly overlapping between the species. One way of dealing with sex-matching problems is matching the male and female genitalia; Maddison (1996), for example, correlated robust emboli with strong epigynal flaps. In some *Anelosimus* (including undescribed species from Tanzania, my unpubl. data) males differ mainly in the length of the emboli, and these can be correlated with the length of the female copulatory ducts, aiding taxonomic decisions. However, for species within the *jucundus* and *studiosus* species groups, the female genitalia offer few clues. Thus, matching sexes can be pure guesswork, and identifying unaccompanied females of some species groups may not be possible based on morphology alone.

HOW MANY SPECIES ARE THERE?

Species boundaries in some groups of *Anelosimus* are unclear (see also F. O. P.-Cambridge, 1902; Levi, 1956, 1963). In numerous instances supposedly conspecific specimens from different localities differ, and geographical variation is profuse. Secondly, for some species, 'populations' from different localities are known to differ dramatically in behaviour, but are not morphologically diagnosable from one another. In some cases these seemingly identical animals do not seem to interbreed and thus fulfil most existing criteria in being, or becoming, separate species. I have used behavioural data (including mating experiments) to help with species delimitation, but describe species as new only if they clearly have a unique combination of morphological characters (at least in one sex). This probably underestimates actual diversity, but in the absence of genomic data, morphological diagnosability is essential to recognize different species. Given the observed variation in morphology and behaviour, and the apparent absence of breeding among some extremely similar populations, it seems likely that several morphologically 'cryptic' species remain to be discovered and described.

CHARACTER CODING

For details of character coding strategies see Agnarsson (2004). Most characters were coded using reductive (binary) coding with inapplicables treated as '–', combined with multistate characters (see Strong & Lipscomb, 1999). All the multistate characters are treated as unordered.

Morphological characters were coded according to direct observations on museum specimens. Behavioral data are largely based on literature (Kullmann, 1972; Brach, 1975, 1977; Buskirk, 1981; Levi & Smith, 1982; Avilés, 1986, 1987, 2000; Nentwig & Christenson, 1986; Cangialosi, 1990a, b; Avilés & Maddison, 1991; Ito & Shinkai, 1993; Avilés & Gelsey, 1998; Avilés & Tufiño, 1998; Furey, 1998; Marques *et al*., 1998; Avilés & Salazar, 1999; Saffre *et al*., 1999, 2000; Avilés *et al*., 2000, 2001; Gonzaga & Vasconcellos-Neto, 2001; Vakanas & Krafft, 2001; Jones & Parker, 2000, 2002; Bukowski & Avilés, 2002; Powers & Avilés, 2003; Knoflach, 2004), combined with personal observations.

Altogether 147 characters were scored and used for the phylogenetic analysis. One additional 'character' was scored, the level of social behaviour (solitary, subsocial, social). This character is used to map these social categories on the cladogram to understand the evolution of the classically defined sociality (akin to mapping 'characters' such as herbivory, habitat and distribution). This character was deactivated prior to the phylogenetic analysis, as discussed in this paper; these social classes are mosaics of various primitive and derived characteristics, rather than well-defined independent characters. Such arbitrary concepts are not useful for phylogenetic inference, although their phylogenetic distribution may crudely approximate that of the characters they encompass. Some of the component characters such as co-operative web building and sex ratios are, however, used.

In a few cases examination of very numerous exemplars led to the discovery of rare polymorphism in a character in the matrix (e.g. specimens of *A. analyticus* and *A. oritoyacu* that have four, instead of the much more common three, female tibial trichobothria). In such cases, the characters were scored after the condition in the type material (which always was the common condition).

Missing information is represented by a '?' in the matrices, inapplicable entries by a '–', although current software makes no distinction between the two. Character coding problems and source of information are discussed, where appropriate, under each character description.

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://theridiidae.com/cladogramsi.html.

CHARACTER DESCRIPTION

Character definitions include written description and figures, and if necessary discussion of how homology assessment in this study differs from that in the literature (see also Agnarsson, 2004).

ANALYSES

For a detailed discussion and justification of methodology see Agnarsson (2004).

The character data were analysed using parsimony, seeking hypotheses that maximally explain observed similarity as due to common ancestry (synapomorphy), or in other words, that minimize *ad hoc* hypotheses of homoplasy (Farris, 1983).

Cladistic analyses were done with NONA (Goloboff, 1993b) using mult*1000 command and the ratchet 'island hopper' (Nixon, 1999) with 1000 replications, holding 10 trees and selecting 25 characters for each, and PAUP* (Swofford, 2002) with 1000 random stepwise additions, and subtree-pruning and regrafting branch swapping algorithm (all searches done with both amb - and amb =).

Successive weighting (Farris, 1969) was performed to assess the sensitivity of the results to weighting against homoplasies (Wheeler, 1995; Prendini, 2001). The analysis was conducted in NONA using the swt.run file, command line: 'run swt.run hold10000 hold/1000 mult*1000;' and in PAUP* with equivalent settings. NONA reweights characters based on the consistency index, but in PAUP characters were reweighted using the rescaled consistency index. In both cases using default settings (weights are recalculated on a scale of 0–100).

Parsimony analyses under implied weights was performed using the computer program Pee-Wee (Goloboff, 1993a, c) (command line: hold10000; hold/1000; mult*1000;').

Sensitivity of the data to taxon sampling was assessed by excluding some clades or taxa based on *a posteriori* identification of 'major clades' (e.g. species groups) or other taxa deemed to be in key positions in the phylogeny. The pruned dataset was then reanalysed and the results compared with trees obtained from the entire matrix.

Node support was estimated with bootstrapping (Felsenstein, 1985), parsimony jackknifing (Farris *et al*., 1996) and Bremer support values (Bremer, 1988, 1994). Support analyses were done in the program T.N.T. (Goloboff, Farris & Nixon, 2003). The number of characters that support each node was determined by optimizing all characters onto the preferred tree.

Continuous Jackknife Function Analysis (Miller, 2003) was also performed on the data to evaluate the extent to which the data are converging on a phylogeny, and to measure the sensitivity of tree structure to character removal.

CHARACTER OPTIMIZATION

MacClade 4.01 (Maddison & Maddison, 2002) and Winclada 1.00.08 (Nixon, 2002) were used to optimize and trace character state changes onto the preferred tree.

Ambiguous optimization was generally resolved in favour of secondary losses over parallel gains of complex structures. The optimization of each character was examined in Winclada and ACCTRAN or the DELTRAN commands used as necessary (Swofford & Maddison, 1987), favouring the preservation of homology of complex structures, and resolving ambiguous optimizations (see Agnarsson, 2004).

SPECIES DESCRIPTIONS

Under 'Additional material examined', information on each record reflects information on the label and may thus be more or less detailed. Generally the material is organized hierarchically under country (upper-case letters), state/province, locality, etc. Information on country, province, locality, collector and museum, or date, is not repeated if it is the same as in the previous record. All records from the same state/province are connected with a semicolon, countries and states/provinces are separated with a full point, as well as records for which locality is unknown. In each case the number of individuals of each sex is given, except collections from some (usually large) nests where precise counts were not made, the presence of multiple specimens is indicated by ♀♀ (females) and ♂♂ (males).

Each collection is followed by a code in square brackets ('[IA0101]', '[IALA0103]', etc.). This refers to a unique ID number generated for all collections examined (except existing type material) and placed in each specimen vial. Each specimen examined here should therefore be easily located, facilitating future work. If the ID number is preceded by a 'cf.' the identification of the specimen is uncertain (single females are often hard to identify with certainty). GPS coordinates follow each record – when locality information is sufficiently detailed – and are placed in parentheses when the co-ordinates are accurate (e.g. taken directly from the collection label), but in square brackets when estimated based on locality name.

In descriptions a distinction is made between small teeth and denticles (even smaller, not necessarily pointy, projections). When a range of number of teeth is given, these represent intraspecific variation, often asymmetric within a specimen.

Under 'Variation' the size ranges and other variation is given based on all specimens examined, hence the number of animals measured is not given. I did not measure all specimens, or randomly select a number of specimens and measure them; rather, I measured especially large or small specimens as they became available during sorting.

Under 'Synonymies' first uses of names (introduction of a new name) are followed immediately by their author, whereas use of existing names is indicated by a ':' after the species names. For example:

Anelosimus chickeringi Levi, 1956 is original description of name, while:

Anelosimus chickeringi: Levi, 1963: 36; Platnick, 2006 indicates that the name was referred to by Levi (1963) and Platnick (2006).

Due to the complex taxonomy of species within the 'sclerotized CD clade', the two major clades within it (the *studiosus* and *jucundus* groups) are fully described and diagnosed.

ABBREVIATIONS

Bold numbers in the text refer to character numbers in each chapter; if followed by a '–' and a number, that indicates the character state (**124**-0 is character 124, state 0), Fig. refers to a figure in this paper, fig. to figures in others. Informal clade names are indicated by quotation marks the first time they are mentioned in the text.

A04	in character descriptions, refers to characters taken from Agnarsson (2004)
AC	aciniform gland spigot (s)
Acl	accessory claw (s)
AG	aggregate gland spigot (s)
ALS	anterior lateral spinneret
AME	anterior median eye (s)
ASP	abdominal stridulatory picks
AT	anal tubercle
BL	booklung covers
C	conductor
CD	copulatory duct (s)
CDm	copulatory duct membrane
Chd	theridiid cymbial hood
Chk	theridiid cymbial hook
CI	consistency index
CO	copulatory opening
Cy	cymbium
CY	cylindrical gland spigot (s)
dh	distal hematodocha
E	embolus
EA	embolic apophysis
Eb	embolic division b
Ebp	embolic basal process
El	embolus lobe
Ep	epigynum
etm	embolus-tegulum membrane
ETP	ectal tegular process
FD	fertilization duct (s)
FL	flagelliform gland spigot (s)
Fu	fundus
k	constant of concavity
MA	median apophysis
mAP	minor ampullate gland spigot (s)
MAP	major ampullate gland spigot (s)
MH	middle hematodocha
mpt (s)	most parsimonious tree (s)
PI	piriform gland spigot (s)
PLS	posterior lateral spinneret
PMS	posterior median spinneret
RI	retention index
S	spermathecae
SB	switchback

SC	subconductor
SDT	sperm duct trajectory
SN	stridulatory nubbins
SP	stridulatory pick (s)
SPR	stridulatory pick row
ST	subtegulum
T	tegulum
Tb	trichobothria
Tc	tarsal comb
THD	Theridiidae
Ti	tibia
Tr	tegular ridge
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
HDO	Hope Department of Entomology, Oxford University, UK
IB	Instituto Butantan, São Paulo, Brasil.
ICN	Instituto de Ciencias Naturales, University of Colombia, Colombia.
INBio	Instituto Nacional de Biodiversidad, Costa Rica.
IZUI	Institut für Zoologie der Universität, Insbruck, Austria
KBIN	Koninklijk Belgisch Instituut vor Natuurwetenschappen, Brussels, Belgium
MCP	Museu de Ciéncias da PUCRS, Porto Alegro, Brazil
MNHG	Museum of Natural History, Geneva, Switzerland
MHN	Museé National d'Histoire Naturelle, Paris, France
MHNSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
MP	Museu Paraense Emilio Goeldi, Belem, Brazil
MNR	Museu Nacional, Rio de Janeiro, Brazil
WAM	Western Australian Museum, Perth, Australia
ZMUC	Zoological Museum, University of Copenhangen, Denmark

RESULTS

The parsimony analysis resulted in two equally most parsimonious trees (L = 289, CI = 58, RI = 84). The strict consensus has four trichotomies within the *ethicus*, *jucundus* and *studiosus* groups (see Fig. 58). Three of these are unresolved in both most parsimonious trees when unsupported nodes are 'hard collapsed', in other words, there is no character evidence to resolve them. The only difference between the two most parsimonious trees is in the position of *A. puravida*, as sister to *A. baeza* (tree 1) or sister to the remaining species of the *jucundus* group (tree 2). Successive weighting using Nona stabilizes on the second iteration and finds a single tree of 16 762 weighted steps, identical to tree 1. This tree is therefore preferred here (Fig. 59). Results from parsimony analyses under implied weights using the default concavity function ($k = 3$) found 11 optimal trees, one of which is identical to tree 1. The strict consensus differs from the equal weights analysis only in that most resolution is lost within the *studiosus* group; only the clade *A. pantanal* plus *A. fraternus* is resolved. Results using concavity functions 2–5 were identical. When $k = 6$, a single tree is preferred, identical to tree 1. When $k = 1$ (weighing most strongly against homoplasies) 22 trees are found and the strict consensus is identical to $k = 3$ except a new tetrachotomy is formed with *A. kohi* Yoshida, 1993, *A. nelsoni* Agnarsson, 2006, the Madagascar group and the *eximius* group, together sister to the epigynal scape clade.

About half of the clades within *Anelosimus* have Bremer support values of 1, thus alternative hypotheses challenging their monophyly would require postulating only a single additional instance of homoplasy (Fig. 58). Important exceptions are support for *Anelosimus*, clade 19, the 'Eb clade', clade 14, the 'bulky E clade', and the *jucundus* group all with support of 2; the *ethicus* group, and the sclerotized CD clade (*studiosus* plus *jucundus* groups) with support of 3, and the *eximius* lineage and the *domingo* group with support of 5. Other well-supported clades include the *rupununi* group, the Tanzania group, the Madagascar group and the epigynal scape clade, with support ranging from 4 to 6.

Results from bootstrapping and parsimony Jackknifing were similar, and thus only the bootstrapping scores are shown (Fig. 58). The majority of nodes are relatively weakly supported. *Anelosimus* monophyly and the monophyly of the *eximius* lineage are marginally supported, and support for most internal nodes is weak. A few groups are moderately to well supported: the *rupununi* group, the Tanzania group, the *ethicus* group (exclusive of the South African species), the Madagascar group, the *domingo* group and the *jucundus* group.

Taxon removal had the following effect (here the strict consensus is compared with the strict consensus of the equally weighted analysis of all data). Removing either *A. kohi*, the *rupununi* group, the *ethicus* group or the *studiosus* group had no effect. Removing *A.* sp. 1 (Australia) obscured outgroup relationships, resulting in six most parsimonious trees and a tetrachotomy in the strict consensus containing *Argyrodes*, *Kochiura*, *Theridiinae* and *Anelosimus*. Removing the Tanzania group resulted in eight most parsimonious trees, a basal tetrachotomy in the consensus containing *A.* sp. 1, *A. kohi*, the *rupununi* group and the Eb clade, and a second tetrachotomy containing *A. nelsoni*, the Madagascar group, the *ethicus* group and the *eximius* group. Removing *A. nelsoni* found four most parsimonious trees; the consensus differs only in *A. kohi* moving to a basal trichotomy. When clade 23 is removed, resolution is lost within the *domingo* group. Removing the Madagascar group found four most parsimonious trees; the consensus has a pentachotomy at the base of the *eximius* group containing *A. pacificus* Levi, 1956, *A. eximius* (*A. analyticus*, *A. chickering*i Levi, 1956), unresolved *domingo* group, the *studiosus* group and the *jucundus* group. Removing the *analyticus* group (three most parsimonious trees) renders the *studiosus* group paraphyletic as in one of the three trees the *jucundus* group rests within it. Removing the *domingo* group results in six trees, with a trichotomy within the *eximius* group containing *A. pacificus* (*A. analyticus*, *A. chickeringi*), and the robust embolus clade. Removing *A. eximius* results in two most parsimonious trees with the same trichotomy as above. Removing the *jucundus* group results in two most parsimonious trees, a slight loss of resolution within the *studiosus* group.

Results of the CJF analysis (Fig. 65) indicate that more data are needed to reach a stable phylogeny; the phylogenetic structure is likely to change with the addition of data.

Character support for all nodes (synapomorphies and autapomorphies) is mapped in Fig. 60, and character coding is shown in Table 1.

In summary, the preferred phylogeny is one of two most parsimonious trees, and is optimal under successive weights, and among the optimal solutions using implied weights under all conditions but $k = 1$. Although most major nodes are supported by at least one character with a perfect fit to the cladogram (homoplasy free), the phylogeny in general is relatively weakly supported (based on Bremer support and bootstrap values), and is sensitive to data perturbations. Results from sensitivity analyses, and CJF indicate the phylogeny is likely to change with addition of data. Sensitivity analyses generally mirrored support measures in indicating weakly supported clades, and further work is most urgently needed to test these weakly supported hypotheses (e.g. see Grant & Kluge, 2003) [note, however, that they discount most sensitivity analyses as unscientific, a view I do not share; see, for example, Ramírez (2005)].

It is important to note that some clades were present in all sensitivity analyses including *Anelosimus*, and the *eximius* lineage, although support (BS = 2–3, bootstrap = 50–60) was marginal. This low support is probably due to sparse data rather than character conflict.

When categories of sociality (solitary, subsocial, social) are included as characters the same results are obtained. The results are congruent with previous phylogenetic analyses (Agnarsson, 2002, 2003c, 2004) in corroborating the maternal care route hypothesis to sociality. On the preferred cladogram maternal care precedes subsociality phylogenetically, which in turn precedes sociality (Fig. 61). Previous work has suggested at least two origins of sociality in *Anelosimus* (Agnarsson, 2004), but the current phylogeny implies at least 5–6 origins (Fig. 61, note that *A. studiosus* may be polymorphic for this trait).

DISCUSSION

The discussion of synapomorphies of major clades focuses on those characters that are deemed more reliable in the recognition and diagnosis of those clades, in general characters showing relatively little homoplasy. The optimization of all characters is shown in Figure 60.

LOST COLULUS CLADE – CLADE 32

Synapomorphies of the lost colulus clade (*Anelosimus* plus Theridiinae) found by Agnarsson (2004) are corroborated here: the hooded lock system (**20**-1, Figs 18A, 30B), median apophysis entire (**48**-0, Fig. 30C), median apophysis broadly and medially attached to tegulum (**46**-0, Fig. 30A), and colulus absent (**113**-1, Fig. 51E). Although bootstrapping and Bremer indicate low support for the clade, these four synapomorphies have perfect fit to the cladogram. The hypothesis may thus be more robust than indicated by these measures. This clade is pivotal in the discussion of sociality because it contains all known social theridiids.

ANELOSIMUS – CLADE 30

The results corroborate the monophyly of *Anelosimus s.s.* (excluding *Kochiura* and *Selkirkiella*, see Agnarsson, 2004), Figures 58 and 59. Agnarsson (2004) found marginal support for *Anelosimus*, based on a single synapomorphy: ridges on the surface of the epigynal plate (**4**-1, Figs 48A, B, 53B). With more species in the analysis this synapomorphy supports the subsidiary Eb clade within *Anelosimus* (see Fig. 58 and below). Here *Anelosimus* synapomorphies are: an entire conductor (**37**-1, Fig. 8C), lack of pars stridens on prosoma

Table 1. Character state matrix

Characters	Ste	Eno	Sel	Ara	Are	Koa	Kor	Ach	The	koh	sp1	lor	rup	big	dud	vit	pul	nel	rab	nig	eth	may	sal	ana	chi	pac	dom	jab	dub	exi	oct	juc	ari	bae	pur	stu	gua	ele	tos	pan	ori	fra	tun
FEMALE GENITALIA																																											
001. Epigynal ventral margin: entire; with scape;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	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
002. Epigynal ext.: cop. openings not visible; visible;	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	0	0	0
003. Epigynal depression: narrow; wide;	0	–	–	–	–	–	1	0	0	0	0	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
004. Epigynal plate surface: smooth; ridged;	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	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
005. Epigynal septum: 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
006. Copul. bursa ant. margin: entire; medially acute;	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
007. Cop. duct to spermath: posterior; lat./anterior;	1	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
008. Copul. duct rel. to spermath.: apart; encircling;	0	0	0	0	0	1	1	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
009. CD term. sclerot.: as other; distinctly sclerotized;	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	1	1	1	1	1	1	1	1	1	1	1	?	1
010. Sclerot.CD: ectal to the spermathecae; caudal;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	–	–	–	–	0	0	0	0	0	1	1	1	1	1	1	?	1
MALE GENITALIA																																											
011. Tibial rim: slightly asymmetric; scoop-shaped;	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
012. Tibial prol.trichob.: = > two; one; none;	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
013. Cymbial ectal setae: unmod.; curved towards bulb;	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
014. Cymbial dist. prom.: entire; w/apoph.;	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
015. Cymbial mesal margin: entire; incised; notched;	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	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
016. Cymbial tip sclerotization: normal; light;	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	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
017. Cymbial tip setae: normal; thick and curved;	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
018. Cymbial sheath: absent; present;	0	0	0	0	0	1	1	0	0	0	0	1	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
019. Lock placement: basal; distal; central;	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

Table 1. *Continued*

Characters	Ste	Eno	Sel	Ara	Are	Koa	Kor	Ach	The	koh	sp1	lor	rup	big	dud	vit	pul	nel	rab	nig	eth	may	sal	ana	chi	pac	dom	jab	dub	exi	oct	juc	ari	bae	pur	stu	gua	ele	tos	pan	ori	fra	tun
020. Lock mechanism: hook; hood; Theridula;	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
021. Cymbial hook orient.: downwards; upwards;	0	1	1	0	0	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
022. Cymbial hook: inside cymbium; ectal margin;	0	1	1	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
023. Cymbial hook tip: blunt; strongly tapering;	0	0	1	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
024. Cymbial hood size: narrow; broad;	–	–	–	–	–	–	–	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
025. Cymbial hood region: translucent; opaque;	–	–	–	–	–	–	–	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
026. Alveolus shape: suboval; mesal extension;	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
027. 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	1	1	0	0	0	0	0	0	0	0
028. Tegular groove: absent; present;	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
029. SDT SB I: separate; touching;	0	–	0	0	0	0	0	0	0	?	–	0	0	0	0	1	1	0	?	1	1	?	?	0	0	?	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
030. SDT post-SB II turn: absent; present;	0	–	0	0	0	0	0	0	0	?	–	0	0	0	0	0	0	1	0	0	0	0	0	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
031. SDT SB I & II segm. alignment: diverg.; parallel;	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
032. SDT SB I & II orient.: in plane; out of plane;	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
033. SDT RSB I & II: absent; present;	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
034. SDT SB III: absent; present;	0	1	1	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
035. SDT SB IV: absent; present;	–	0	0	1	1	–	–	–	0	?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	?	–
036. C: simple; fan; Eno.; Arg.; Ach.; The; rup.; tan.; cup;	0	2	1	3	3	1	1	4	5	0	–	6	6	7	7	0	0	0	0	0	0	0	0	8	8	8	0	0	0	0	8	8	8	8	8	8	8	8	8	8	8	8	8
037. C: with a groove for embolus; entire;	–	0	0	0	0	0	0	0	0	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
038. C surface: smooth; heavily ridged;	0	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	0	0	0	0	0	0
039. C tip sclerotization: like base; more than base;	0	1	1	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
040. Subconductor (SC): absent; present;	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	1	1
041. SC pit upper wall: entire; forms a regular oval lip	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0

042. SC narrowing at C base: abrupt; gradual; broad	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	2	2	2	0	0	0	0	0	1	1	1	2	1	1	1	1	1	0	0	0	0	0	0	0	0
043. E base-SC relation: E hooked in; E surpasses SC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	0	2	2	2	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
044. T ectally: < 1/2 cymbial cavity; > 1/2 cymbial cavity;	0	0	0	0	0	0	0	0	0	0	1	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
045. MA and sperm duct: not in MA; inside MA;	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
046. MA-tegular connection: broad; narrow;	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
047. MA form: unbranched; two branches;	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
048. MA distal tip: entire; hooded;	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
049. MA hood form: narrow, pit-like; scoop-shaped;	0	0	1	0	0	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
050. TTA form: entire; grooved; excavate;	0	1	1	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
051. TTA: bulky ; prong shaped	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
052. TTA distal tip: entire; *Argyrodes*; hooked;	0	0	0	1	1	0	0	–	2	0	–	0	0	2	2	0	0	0	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
053. TTA hook distal branch: short; extending beyond;	–	–	–	–	–	–	–	–	0	–	–	–	–	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
054. TTA hook distal branch: thick; thin, finger-like	–	–	–	–	–	–	–	–	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
055. TTA hook proximal branch: broad; bladelike	–	–	–	–	–	–	–	–	0	–	–	–	–	0	0	–	–	–	1	1	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
056. TTA surface subterminally: smooth; ridged;	0	0	0	0	0	0	0	–	1	0	–	0	0	0	0	0	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
057. TTA tip surface: smooth; ridged;	0	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
058. E and TTA: loosely assoc.; E enclosed in TTA;	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
059. E tip surface: smooth; denticulate;	0	0	0	0	0	0	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
060. E spiral curviture: gentle; whip like; corkscrew;	0	0	0	0	0	0	0	0	0	0	2	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
061. 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	1	1	1	1	1	1	1	1	1	0	1	0	1
062. E origin: ectoventral on tegulum; retrolateral;	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
063. E surface: smooth; ridged;	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1
064. E shape: short to moderate; extremely long;	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
065. 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	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 1. *Continued*

Characters	Ste	Eno	Sel	Ara	Are	Koa	Kor	Ach	The	koh	sp1	lor	rup	big	dud	vit	pul	nel	rab	nig	eth	may	sal	ana	chi	pac	dom	jab	dub	exi	oct	juc	ari	bae	pur	stu	gua	ele	tos	pan	ori	fra	tun
066. E distal rim: entire; deeply grooved;	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
067. E terminus: abrupt; with a distal apophysis;	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
068. E base: entire; lobed;	0	0	0	0	0	1	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
069. Embolus-dh connection grooves: 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	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
070. Embolus-dh grooves: deep; short;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
071. E spiral subterminally: thin or filiform; thick; rup.;	0	0	0	0	0	0	0	0	0	1	1	2	2	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
072. E spiral: entire; biparted; 'pars pendula';	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	1	1	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
073. Eb orientation: towards E tip; towards tibia;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	?	0	?	0	0	0	0	0	–	1	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0
074. Eb: separates early from E; E and Eb tight;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
075. Eb terminally: broad; narrow;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
076. Eb distal portion, ectal margin: level; ridged;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
077. Eb form, basally: flat, in ectal view; globose;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
078. Eb form: separate apophysis; barely separate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
079. E spiral tip: separated; Eb and E tips juxtaposed	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	?	0	0	0	0	0	–	0	2	2	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1
080. Eb snout: short, snug with E; long, separate;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	1	0	0	1	0	0
081. Eb distal portion: entire; with apophysis; ridged;	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	?	0	0	0	0	0	–	0	1	1	1	–	2	2	2	0	0	0	0	0	0	0	0	0	0
082. E tail: lobe simple; lobe bifurcate, snug with Eb	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	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
083. Extra tegular sclerite: absent; present;	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
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084. AME (M): normal; on tubercle; eye region raised	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
085. AME size vs. ALE (M): subequal; smaller;	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
086. Chel. posterior margin: toothed; smooth;	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
087. Chel. post. tooth no.: four+ three; two; one;	–	2	0	2	2	0	0	–	–	?	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

088. Chel. furrow: smooth; denticulate;	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
089. Carapace hairiness: sparse or patchy; uniform;	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
090. Carap. pars stridens: irregular; regular ridges;	1	1	1	1	1	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
091. Interocular area: flush with clypeus; projecting;	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
092. Clypeus: concave or flat; projected;	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
093. Ocular area setae (M): sparse; in a dense field;	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
094. Labium-sternum connection: seam; fused;	0	1	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	0	0	0	0	0	0
095. Sternocoxal tubercles: present; absent;	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
096. Pedicel location: anterior; medial;	0	0	1	0	0	0	0	1	0	?	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
097. Abd. folium: spots or blotches; central band;	0	1	1	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
098. Abdomen folium: irregular; distinctly notched	0	0	0	0	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	1	1	1	1	1
099. Dorsal band: edge light; edge dark; Ameridion;	–	1	1	–	–	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
100. Abd. dot pigment: silver; non-reflective, dull;	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
101. SPR form: weakly keeled; strongly keeled;	1	0	0	1	1	1	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	1	1	1	1	1	1	1	1	1
102. SPR pick number: three or less; four or more;	1	0	0	1	1	1	1	1	0	1	1	0	0	1	1	2	2	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
103. SPR insertion: flush with abd. surface; on ridge;	1	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
104. SPR mesal pointing picks: absent; 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	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
105. SPR mp-picks angle: dorsal; perp. or ventral;	0	0	–	0	0	0	0	0	0	1	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
106. SPR: straight; distinctly curved; argyrodine;	0	0	–	2	2	0	0	0	0	1	0	0	0	0	0	0	0	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	1
107. SPR dorsal pick spacing:normal; compressed;	0	0	–	0	0	0	0	0	0	1	0	0	0	0	0	0	0	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	1
108. SPR relative to pedicel: lateral; dorsal;	1	0	1	0	0	1	1	1	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
109. SPR setae: separate; tight;	0	0	0	0	0	0	0	0	0	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	1	1	1	1	1	1	1	1	1
110. Suprapedicillate ventrolat. proprio.: abs.; pres.;	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

Table 1. *Continued*

Characters	Ste	Eno	Sel	Ara	Are	Koa	Kor	Ach	The	koh	sp1	lor	rup	big	dud	vit	pul	nel	rab	nig	eth	may	sal	ana	chi	pac	dom	jab	dub	exi	oct	juc	ari	bae	pur	stu	gua	ele	tos	pan	ori	fra	tun
111. Epiandrous fusule: in pair of sockets; in a row;	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
112. Epiandrous fusule pair number: > ten; ≤eight;	2	0	2	3	3	1	0	1	1	?	0	1	1	1	1	0	0	1	?	0	0	1	1	1	1	?	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	?	1
113. Colulus: present; absent; invaginated;	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
114. Colulus size: large; small;	0	0	0	0	0	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
115. Colular setae: present; absent;	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
116. Colular setae number (F): three or more; two;	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
117. Palpal claw dentition (female): dense; sparse;	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
118. Palpal tibial dorsal trichobothria (female): 4; 3; 2; 5;	?	0	2	1	1	2	2	3	2	1	1	1	1	1	1	1	1	?	1	1	1	3	3	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	?	0
119. Femur I relative to II: subequal; robust, larger;	0	0	0	0	0	0	0	0	0	?	1	0	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	0	?	0
120. Leg IV rel. length (M): third; second; longest;	1	1	1	0	0	0	0	?	1	?	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
121. Leg IV rel. length (F): third; second; longest;	1	1	1	0	0	1	1	1	1	?	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
122. Femur vs. metat.: metat. longer; metat. shorter;	1	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	1	1	1	1	1	1	1	1	1	1	1	?	1
123. Metat. vs. tibia: metat. longer; metat. shorter;	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
124. Metatarsal ventral macrosetae: normal; thick;	0	0	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
125. Metatarsus vs. tibia length (male): longer; shorter;	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
126. Metatarsal ventral macrosetae: normal; thick;	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	0	1	0	1	1	0	0	0	1	1	?	1
127. Tarsus IV comb: simple, straight; curved hooks;	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128. Tarsal organ size: small (normal); enlarged;	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
129. Tarsus IV central claw vs. lat. (M): short; longer;	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
130. Tarsus IV central claw (F): normal; long; minute;	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
SPINNERETS																																											
131. Spinneret insert.: normal; abd. extend. beyond;	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

132. PLS FL spigot: = PLS CY; longer than PLS CY;	0	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	0	0	0	?	0
133. CY spigot bases: =< ampullates; huge;	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
134. CY shaft surface: smooth; grooved;	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
135. PLS AC spigot number: 5+ four or less;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
136. PLS FL spigot: present; absent;	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
137. PLS posterior AG spigot shape: normal; flat;	1	1	0	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
138. PLS theridiid AG position: parallel; end to end;	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
139. PMS mAP spigot shaft: short; > CY shafts;	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	1	1	1	1	1	1	1	1	1	1	1	?	1
BEHAVIOUR																																											
140. Web form: sheet; cobweb; mesh web; dry line-web;	1	1	1	3	3	1	1	1	1	?	?	2	2	?	?	1	?	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
141. Knock-down lines: absent; present;	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	?	?
142. Sticky silk in web: present; absent;	0	0	1	?	?	?	?	0	0	?	?	1	1	?	?	?	?	?	?	?	?	1	1	?	?	?	?	0	0	1	?	1	1	1	?	1	1	1	?	?	1	?	?
143. Egg sac: spherical to lenticular; stalked;	?	0	0	1	1	?	?	0	0	?	?	0	0	?	?	0	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	?	?	0	?	0	?	?
144. Egg case: round; knob.; rhomb.; elong.; spiky;	?	0	0	1	1	?	?	0	0	?	?	0	0	?	?	0	?	?	?	?	?	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	?	?	0	?	0	?	?
145. Web construction: solitary; communal;	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
146. Mating thread: present; absent;	0	0	?	?	?	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
147. Adult females per nest: one; multiple;	0	0	0	0	0	0	0	0	0	?	0	1	1	?	?	0	0	?	?	0	0	0	0	0	?	?	1	1	1	1	?	?	0	?	1	?	1	0	0	?	1	?	?
[148. Behavior: solitary; subsocial; quasisocial;]	0	0	0	0	0	0	0	0	0	?	1	2	2	?	?	0	0	?	?	1	1	1	1	1	?	?	2	1	1	2	?	?	1	1	2	?	2	1	1	?	2	?	1

Rows represent characters and columns taxa. The first state is '0', second '1' etc. '?' represent missing data, '–' inapplicable states. Refer to 'Character descriptions and comments' for further information on characters. Taxon abbreviations: Ste, *Steatoda*; Eno, *Enoplognatha*; Sel, *Selkirkiella*; Ara, *Argyrodes argyrodes*; Are, *Argyrodes elevatus*; Koa, *Kochiura aulica*; Kor, *Kochiura rosea*; Ach, *Achaearanea*; The, *Theridion*; koh, *A. kohi*; lor, *A. lorenzo*; rup, *A. rupununi*; big, *A. biglebowski*; dud, *A. dude*; vit, *A. vittatus*; pul, *A. pulchellus*; nel, *A. nelsoni*; rab, *A. rabus*; nig, *A. nigrescens*; eth, *A. ethicus*; may, *A. may*; sal, *A. sallee*; ana, *A. analyticus*; chi, *A. chickeringi*; pac, *A. pacificus*; dom, *A. domingo*; jab, *A. jabaquara*; dub, *A. dubiosus*; exi, *A. eximius*; oct, *A. octavius*; juc, *A. jucundus*; ari, *A. arizona*; bae, *A. baeza*; pur, *A. puravida*; stu, *A. studiosus*; gua, *A. guacamayos*; ele, *A. elevatus*; tos, *A. tosum*; pan, *A. pantanal*; ori, *A. oritoyacum*; fra, *A. fraternus*; tun, *A. tungurahua*. Abbreviations sp. 1–7 refer to undescribed *Anelosimus* spp. numbered as in the text and figures.

(**90**-0, Figs 14G, 15A), three palpal tibial trichobothria (**118**-1, Fig. 15G), robust femur I (**119**-1, Fig. 55G) and communal (subsocial) behaviour (**145**-1). The clade excluding *Anelosimus* sp. 1 (this undescribed species differs so much in genitalia from other species that it substantially changes the diagnosis of the *Anelosimus* and may, for the sake of clarity, later be placed in a new genus) is supported by: elongate (wide) epigynal plate (**3**-1, Figs 19C, D, 44C, D, I, K), incised cymbial mesal margin (**15**-1, see e.g. Agnarsson, 2004, fig. 22A), terminally ridged theridiid tegular apophysis (**57**-1, Fig. 55D), lobed embolus tail (**68**-1, Fig. 28B), abdomen pattern (**98**-1, Figs 27H–M, 49E), and absence of sticky silk in web (**142**-1, but see Discussion on character 142).

THE *RUPUNUNI* GROUP – CLADE 28

The *rupununi* group contains only two species, the very similar *A. rupununi* and *A. lorenzo*, both social. The species have unusual genitalia in comparison with other *Anelosimus* (see e.g. Fig. 56F). Synapomorphies supporting the group include: loss of epigynal ridges (**4**-1), medially acute copulatory bursa margin (**6**-1), copulatory ducts attaching posteriorly to spermathecae (**7**-0), broad cymbial hood (**24**-1), branched MA (**47**-1) and folded embolus rim (**66**-1, Fig. 56F). The *rupununi* group is one of the three isolated clades containing American *Anelosimus*; it was revised by Agnarsson (2005).

THE TANZANIA GROUP – CLADE 26

The two undescribed species from Tanzania form a clade sister to the curved stridulatory pick row clade. It seems likely that most of the Asian species (e.g. see Yoshida, 1986, 1993), with a characteristically large tegulum and thin spiraling embolus, belong to the same clade. Here, synapomorphies of this group include: cymbial tip lightly sclerotized (**16**-1), a groove on the tegulum (**28**-1, see Agnarsson, 2004: fig. 28B), conductor shape (**36**-7, **37**-0, Fig. 56G) and tegulum large (**44**-1, see Agnarsson, 2004: fig. 28C).

THE EPIGYNAL SCAPE CLADE (CLADE 22) AND *ETHICUS* GROUP – CLADE 21

To my knowledge an araneid-like epigynal scape (**1**-1, Fig. 55A) is present in only eight theridiid species, and these are all closely related, together forming the epigynal scape clade (Fig. 59, clade 23). In addition to the scape the monophyly of this clade is also supported by the sperm duct trajectory switchback I touching (**29**-1), and modification of the stridulatory system, with a straight row of tightly spaced, numerous, stridulatory picks on the abdomen (**102**-2, **106**-0, see Agnarsson, 2004: fig. 26D,E). This lineage contains the *ethicus* group, the third American clade, containing *A. ethicus*, *A. nigriscens* (previously subsumed within *A. ethicus*), *A. rabus* Levi, 1963, and four new species (revised by Agnarsson, 2005). The *ethicus* group is united by: copulatory ducts encircling spermathecae (**8**-1), a bulky theridiid tegular apophysis (**51**-0, Fig. 57C), with a distal hook (**52**-2, Fig. 57B) and a simple short Eb (**78**-1, Fig. 57C).

THE CURVED STRIDULATORY PICK ROW CLADE – CLADE 25

The abdomen–prosoma stridulatory system is a characteristic feature of theridiid spiders. *Anelosimus* species are unusual in lacking regular ridges on the prosoma, but have a well-developed and conspicuous row of stridulatory picks on the male abdomen (**90**-0, Figs 3C, 12A, 14G, 22D, 24C). Most characteristic is a curved row of several tightly arranged picks that are distally distinctly compressed (**105**-1, **106**-1, **107**-1, Figs 4F, 5A, 24C, 38C, 54D). These features optimize to clade 25, here termed the curved stridulatory pick row clade.

THE EB (EMBOLIC DIVISION B) CLADE – CLADE 24

Ridges on the epigynal plate (**4**-1, Figs 48A, B, 53B) were the only synapomorphy of *Anelosimus* in the study of Agnarsson (2004). However, such ridges are lacking in some basal *Anelosimus* species here included, and are here a synapomorphy of the subsidiary Eb clade, and convergently of the *rupununi* group. Other synapomorphies of the Eb clade include bipartite embolus (the presence of Eb, **72**-1, Figs 1B, 7B, F, L, 19A, B, F, G, J–L), and a subconductor (**40**-1, Figs 2C, 17E, 30D, 56H).

THE MADAGASCAR GROUP – CLADE 18

The sister group of the *eximius* lineage is formed by a pair of species from Madagascar, *A. may* Agnarsson, 2005 (in Agnarsson & Kuntner, 2005), and *A. sallee* Agnarsson & Kuntner, 2005. A number of subsocial *Anelosimus* species were recently discovered in Madagascar (Agnarsson & Kuntner, 2005). The two included here as exemplars share characteristic features with other species from Madagascar, including an epigynal septum (**5**-1, Fig. 55B), and five trichobothria on female palp (**118**-3), and it seems likely that the group as a whole is monophyletic. Further features from the male palpal organ may support their monophyly, but males are thus far known only for two species.

THE *EXIMIUS* LINEAGE

The *eximius* lineage occurs only in the New World (Fig. 63A) and contains the majority of American species. It includes all the most intensively studied *Anelosimus* species and is revised below. Eight unambiguous synapomorphies support its monophyly, including: deeply notched cymbial margin (**15**-2, Figs 23A, B, 29A, 33A), translucent cymbial hood (**25**-0), an abrupt post-switchback II turn of the sperm duct (**30**-1, Fig. 57D–G), subterminally ridged theridiid tegular apophysis (**56**-1, Figs 2B, 42C), and embolus-distal hematodocha grooves (**69**-1, Figs 35B, H, L, 36C, 39B, C). Five of the seven known social *Anelosimus* species belong in five subgroups of the *eximius* group.

THE *ANALYTICUS* GROUP – CLADE 16

The *analyticus* group contains three species (*A. analyticus*, *A. chickeringi* and *A. pacificus*). The group is weakly supported by two convergent characters, sclerotized CD (**9**-1, Fig. 1D), and a cup-shaped conductor (**36**-8, Fig. 2C), both also present in the *studiosus* and *jucundus* groups. This clade is particularly sensitive to perturbations of data and often collapses, for example when related taxa are removed from the analysis. The position of *A. pacificus* is particularly weakly supported; preliminary molecular data suggest a very different placement of *A. pacificus*, as sister to the *ethicus* group (I. Agnarsson, L. Avilés & W.P. Maddison, unpubl. data).

THE *DOMINGO* GROUP – CLADE 13

Three species, *A. jabaquara*, *A. domingo* and *A. dubiosus* (Keyserling, 1891), belong to this well-defined group. The females are nearly indistinguishable from other *Anelosimus* externally, but internal female genitalia, and male genitalia, offer easy diagnosis. The clade is supported by four unreversed palpal synapomorphies: finger-like apophysis on the theridiid tegular apophysis (**54**-1, Fig. 7A, K), whip-like embolus spiral (**60**-1, Figs 7A, B, E, F, K, L, 9B, C, E), cup-shaped Eb apophysis (**81**-1, Figs 7B, E, L, 9E, 11D, 13E), and embolus supported by Eb apophysis (**79**-2, Fig. 7B, E, F, L). Having sticky silk in the web (**142**-0) may be an additional synapomorphy, but absence of sticky silk in most *Anelosimus* webs remains doubtful (see below). All three species are social and adult females at least sometimes share webs. *Anelosimus domingo* is a typical social species with permanent colonies and strongly biased sex ratio.

THE SCLEROTIZED COPULATORY DUCT CLADE – CLADE 10

As suspected already by F. O. P.-Cambridge (1902) the *studiosus* and *jucundus* groups are closely related, and here together form the sclerotized copulatory duct clade (Fig. 59, clade 10). The group is supported by: sclerotized copulatory ducts (**9**-1, Figs 1D, 27D, F, G), cup-shaped conductor (**36**-8, Fig. 25C), denticulate (**59**-1, Fig. 28E) and bifid (**61**-1, Figs 23F, 25F, 28E, 39E) embolus tip, and Eb and embolus tightly associated along their entire trajectory (**74**-1, **79**-1, Fig. 19B, F, G, J). Interestingly, the first two of these synapomorphies are shared with the similar *analyticus* group, but this similarity is convergent given the current cladogram.

THE *STUDIOSUS* GROUP – CLADE 5

F. O. P.-Cambridge (1902) described a variable and widespread *A. studiosus*, but commented that the variation could indicate several similar species (see quote at beginning of this chapter). Levi (1956) agreed with F. O. P.-Cambridge's (1902) previously suggested synonymies, and added *Enoplognatha dubia* and *A. fraternus*. The species thus became even more variable and widespread, from Argentina to northeastern United States (e.g. Washington, DC), and from a wide range of altitudes (0–4000 m) and habitats (e.g. tropical forest, temperate scrub). In a section called 'subspecies' Levi (1956: 419) commented on, and illustrated, the considerable geographical variation in size and genitalic, especially palpal, morphology of his *A. studiosus*. Given the complexity of *Anelosimus* taxonomy, and virtual absence of behavioural data, Levi understandably preferred to treat all these taxa as one species. However, in addition to differences in morphology, recent studies indicate differences in behaviour (including different levels of sociality) and barriers to breeding (failed breeding experiments) between several geographically separated populations (Brach, 1977; Furey, 1998; Jones & Parker, 2002; L. Avilés, pers. comm.). With access to much more material, and armed with new behavioural observations, it seems now that Levi's (1956) *A. studiosus* is rather a species complex, including at least eight species. The *studiosus* group (see Fig. 59, clade 5) is here supported by two unambiguous synapomorphies: closely arranged sclerotized copulatory ducts (**10**-1, Fig. 44D), and a snout-like Eb (**75**-1, Figs 44A, F, 49B, H, K, L).

THE *JUCUNDUS* GROUP – CLADE 9

As with *A. studiosus*, F. O. P.-Cambridge's (1902) and Levi's (1956) concept of *A. jucundus* included several synonymies and bountiful geographical variation. Likewise, recent work discloses behavioural differences and breeding barriers (under laboratory conditions) between some geographically separate populations (Nentwig & Christenson, 1986; Avilés & Gelsey, 1998; Bukowski & Avilés, 2002). I recognize five species of the *jucundus* species complex. Two unambiguous synapomorphies with perfect fit to the cladogram support *jucundus* group monophyly: elongated theridiid tegular apophysis distal branch (**53**-1, Fig.19A), and shallow embolus-distal hematodocha grooves (**70**-1, Fig. 20C).

EVOLUTION AND CATEGORIZATION OF SOCIALITY IN *ANELOSIMUS*

Strikingly, the preferred phylogeny implies that sociality evolved independently within five *Anelosimus* species groups, and apparently twice within the *studiosus* group for a total of six origins within the genus (Fig. 61). Permanent sociality therefore originates at least 7–8 times in the lost colulus clade (see Agnarsson, 2004). This relatively small clade (~1200 species, about 3% of spider diversity, calculated from Platnick, 2006) thus accounts for about half of the origins of spider sociality. The clustering of 7+ origins of sociality in the lost colulus clade suggests a common cause, perhaps preadaptations to sociality that are unique to this group of spiders (see Agnarsson, 2002, 2004). One such modification might be the prolongation of cohabitation by juveniles due to maternal care (e.g. Shear, 1970; Kullmann, 1972; Brach, 1975, 1977; Burgess, 1978; Krafft, 1979; Cangialosi & Uetz, 1987; Avilés, 1997; Jones & Parker, 2002; Schneider, 2002; Agnarsson, 2002). The origin of sociality from maternal care and intermediate subsociality seems strongly corroborated (Fig. 61, see also Agnarsson, 2004). A three-dimensional web has also been frequently considered as a preadaptation for sociality (e.g. Shear, 1970; Krafft, 1979, 1982; Buskirk, 1981; D'Andrea, 1987; Cangialosi & Uetz, 1987; Avilés, 1997). On the preferred phylogeny sociality is indeed concentrated where maternal care and a three-dimensional web overlap (see Agnarsson, 2004). Interestingly, corroborating data come from the other group of spiders with multiple origins of sociality (the distantly related, non-orbicularian *Stegodyphus*, see Kraus & Kraus, 1988, 1990) where maternal care and three-dimensional webs also overlap. However, no doubt additional, as yet undiscovered, features have facilitated the evolution of sociality in both *Stegodyphus* and the lost colulus clade.

Although sociality evolves repeatedly from subsociality, thereafter social lineages apparently fail to diversify: all social clades are small (one or two species, see Fig. 61). The pattern repeats: social species succeed in the short term (ecological time) but fail to diversify in the long term (over evolutionary time). Sociality seems to be responsible for a dramatic shift in population structure from outbred panmictic to strongly inbred, subdivided populations. Social individuals are thus comparatively homozygous and intrapopulational variation is slight compared with subsocial or solitary individuals or populations (Smith, 1986, 1987). Group living and co-operation benefit social species in diverse environments (see Avilés, 1997, for review). On the other hand, low genetic variance can be maladaptive during rapid environmental change. These fleetingly well-adapted populations may be quite vulnerable in environments where change is episodic or fast, or where unexpected challenges arise (disease, parasites, specialized predators, etc.). Subsocial populations may not be able to compete with the more fecund social species, but their survival rate over the long run may be higher. Testing such ideas and investigating the potential disconnection between ecological and evolutionary time scales will require research in several areas. Phylogenies can corroborate or falsify patterns by addition of morphological and molecular data. Population genetics can compare gene trees within and among species to indicate whether slow divergence or frequent turnover of lineages best explains the phylogenetic patterns, and computer modelling can clarify how inbred social genotypes can out-compete outbred subsocial genotypes in the short run, but are unable to track environmental change over evolutionary time.

It should be noted that 'maternal care', 'subsociality' and 'sociality' are not three well-defined categories linked in a simple two-step road to permanent sociality. The categories themselves (derived from Wilson, 1971), although useful as summaries for discussion, are faulty and should be used with care. First, if sociality requires co-operation, only non-territorial web-sharing spiders are truly social in my view (Agnarsson, 2002, 2004). Second, defining classes of sociality by the duration of cohabitation is ambiguous at best. Third, the categories contain a mosaic of primitive and derived characters and overlap considerably. Sociality requires multiple behavioural mechanisms and the real world presents a continuum rather than discrete classes of sociality; which behaviours precede others phylogenetically thus needs more detailed scrutiny. Nevertheless, social species are generally quite similar. The entire range of social behaviour displayed by all species that leave their natal nest prior to or just after mating is then described as 'subsocial.' Agnarsson (2004) remarked that '[s]ubsociality is maternal care that spans several, rather than few, juvenile instars. Sociality is another point on the continuum in which maternal care never ceases.' In such a continuum the transition from 'maternal care' to 'subsociality' to 'sociality' is unclear; two subsocial species may differ more than some subsocial and maternal care species. Other components of social behaviour such as co-operation in web building, attacking prey, regurgitation feeding, intra- and interspecific tolerance mechanisms, sex ratio, communication, brood care, inbreeding, generational overlap and per female reproductive output will enrich the comparison of social behaviour among species. Table 2 attempts to compare the levels of sociality shown by a selection of relatively well-studied species. All the species differ and, interestingly, increasing sociality generally occurs by 'terminal addition'. In other words derived behaviour B requires A, and C only occurs in the presence of A and B. Egg sac guarding precedes post-hatching maternal care, which precedes co-operation in web building and prey capture, and so on. In addition, more social species exhibit greater sex ratio bias (see also Avilés, 1986; Avilés & Maddison, 1991; Rowell & Main, 1992; Avilés *et al*., 2000) and larger colonies. Such detailed categorizations can therefore not only facilitate the comparison of species, but also suggest testable hypotheses about the evolution of sociality. It should be noted that this is intended as a first attempt to atomize social behaviour into discrete characters. Owing to the preliminary nature of these categories and limited data, the inclusion of these characteristics in the phylogenetic data matrix seems premature; rather, this table may serve as a guideline on possible ways of identifying potentially homologous behavioural units among social theridiids.

The behaviour of species outside the New World is poorly known, but some are also social, including several recently discovered subsocial species from Madagascar (Agnarsson & Kuntner, 2005), and Malaysia (Agnarsson & Zhang, 2006). Positive evidence for solitary lifestyles is rarely reported, and even the two European *Anelosimus* species (no reports exist of social behaviour of these) cannot be presumed to be solitary [maternal care or subsociality seems likely given their phylogenetic position, see Agnarsson (2004), and Fig. 61]. The many solitary species placed in *Anelosimus* by Levi (1956, 1963, 1967) do not belong to this genus and have been transferred (see Agnarsson, 2004, and below).

BIOGEOGRAPHY

Given the above phylogeny, the monophyly of New World *Anelosimus* is unambiguously refuted. *Anelosimus* appears to be primitively an Old World lineage, while three different *Anelosimus* clades occur in the New World (Fig. 62). This distribution could be congruent with a Gondwanan origin, but the sparse available fossil evidence suggests a much more recent origin of the *Anelosimus* lineage. All reliably identifiable theridiids preserved in Baltic amber seem to belong to basal subfamilies (most notably Hadrotarsinae and Spintharinae; see Agnarsson, 2004, for information on theridiid subfamilies) or extinct lineages (Marusik & Penney, 2005). 'Higher' theridiids, including the subfamilies Theridiinae (e.g. *Achaearanea* and *Theridion*), Argyrodinae (e.g. *Argyrodes*) and Pholcommatinae (e.g. *Stemmops*) are known from Dominican Republic amber (Penney & Perez-Gelabert, 2002). Therefore, if one is willing to interpret the absence of Theridiinae and *Anelosimus* fossils from Baltic amber as positive evidence (rather than just absence of evidence), the origin of the lost colulus clade (including Theridiinae and its sister group *Anelosimus*) could be estimated between the mid-Eocene and early Miocene, some 20–40 mya [note that *Anelosimus clypeatus* described from Dominican Republic amber by Wunderlich (1988) is not *Anelosimus*; see Penney (2001)].

If this lineage is of recent origin, one would reject a vicariance explanation of *Anelosimus* biogeography in the New World. Rather, three independent colonization events would be postulated. Long-distance dispersal by ballooning (flying by means of silk threads) is commonly found in small spiders and seems the simplest way to explain the observed pattern.

TAXONOMY

THERIDIIDAE SUNDEVALL, 1833

Theridiides Sundevall, 1833, Conspectus Arachnidum, p. 15 (an invalid original spelling for Theridiidae). Type species *Theridium pictum* Walckenaer 1802 (= *Theridion pictum*).
Hadrotarsidae Thorell, 1881, Ann. Mus. Civico Storia Nat. Genova 17: 190. Type species *Hadrotarsus babirussa* Thorell, 1881.

For detailed description, diagnosis and synapomorphies of Theridiidae see Agnarsson (2003a, 2004), Arnedo *et al*. (2004) and Knoflach (2004).

ANELOSIMUS SIMON, 1891

Anelosimus Simon, 1891, 60: 11. Type species: *Anelosimus socialis* Simon, 1891 (= *Theridium eximium* Keyserling, 1884).

Diagnosis: *Anelosimus* can be readily diagnosed by the abdomen colour pattern: a dark (in alcohol, often red in life specimens) notched longitudinal central band edged by a narrow, notched, white band, and bilateral white blotches distributed outside the dorsal band (Figs 1J, 7G, H, 19E). *Anelosimus* differs from most theridiids (except some hadrotarsines, and perhaps *Chrosiothes*) in lacking a colulus, but a pair of colular setae are present (Fig. 31E). Most *Anelosimus* differ from other theridiids in genitalia: having conspicuous ridges on the epigynal plate (Fig. 31A), a subconductor present in the male palp (Fig. 33C, D), and an incised mesal cymbial distal margin (Fig. 33A). The organization of abdominal stridulatory picks, although variable, is also diagnostic, usually a conspicuous curved

Table 2. Categorization of sociality in 14 relatively well-studied taxa

Species	Sex ratio (f/m)	Max. colony size	Dispersal at instar	Egg-sac guarding	Maternal care	Sibling co-operation	Regurgitation	Multiple females
Enoplognatha ovata	1	n/a	I	X				
A. crassipes	1	n/a	II	X	X			
Theridion pictum	1	30–40?	III–IV?	X	X	?		
A. analyticus	?	?	?	X	X	X		
A. arizona	1	~60	IV–VII (most at V)	X	X	X	?	
A. baeza B	1	~90	V	X	X	X	X	
A. studiosus B	1(?)	~100	VII (adult)	X	X	X	X	some
A. baeza C	1	~200?	?	X	X	X	?	X
A. jabaquara	1.8	97	VII (adult)	X	X	X	X	X
A. studiosus F	4	100	VII (adult)	X	X	X	X	X
A. dubiosus	3.2	176	VII (adult)	X	X	X	X	X
A. domingo	9.3	3–4000	VII (adult)	X	X	X	?	X
A. rupununi	12.5	10 000	VII (adult)	X	X	X	X	X
A. eximius	12.5	10 000	VII (adult)	X	X	X	?	X

	Adult tolerance	Adult co-operation	Tolerance to introd. adults	Natal nest mating	Co-operative brood care	Overlapping gener
Enoplognatha ovata						
A. crassipes						
Theridion pictum						
A. analyticus						
A. arizona						
A. baeza B	x		?			
A. studiosus B	x	some	juvs only			
A. baeza C	X	X	?	?		
A. jabaquara	x	?	X	x		
A. studiosus F	X	X	?	x	X	
A. dubiosus	X	X	X	X	X	
A. domingo	X	X	X	X	X	X
A. rupununi	X	X	X	X	X	X
A. eximius	X	X	X	X	X	X

A. studiosus B refers to populations studied by Brach (1977), F to populations studied by Furey (1998). Sex ratio is indicated at females per male (f/m). Maximum colony size is estimated from the literature, not applicable (n/a) for solitary species. Stage of development at dispersal is estimated from the literature, number indicates instar, not counting moults inside the egg sac. Maternal care (beyond care of egg sac) is defined as provisioning by mother after the spiderlings emerge from the egg sac. Sibling co-operation (and adult co-operation) is defined as shared effort towards a common task. Regurgitation indicates mother donating predigested food. Multiple females refers to nests containing more than one adult female. Adult tolerance implies absence of aggression between (unrelated) females sharing a web. Tolerance to introduced aldults indicates lack of aggression to unrelated (introduced) adult females. Female non-brood care indicates females indiscriminately caring for young (own or those of other females) in the nest. Overlapping generations indicates co-occurrence and co-operation of mother and her adult offspring, even though brief. Non-reproductive females indicates the presence of adult females partaking in the tasks of the colony, but failing to reproduce themselves. Question marks indicate unknowns, ‘x’ a rare behaviour, ‘X’ a common behaviour, and ‘some’ indicates presence of behaviour in some populations.

row of picks with the distalmost distinctly compressed (Figs 5A, 14E, 24C, 34D), sometimes a straight row of very numerous picks (see Agnarsson, 2004: fig. 26D,E). As in most theridiids, females have much weaker picks (e.g. Figs 5A versus 5B, 54D versus 54E). Finally, most *Anelosimus* differ from other theridiids in building communal webs, usually sheet like with knockdown-threads, sometimes irregular meshes.

Description: Small- to medium-sized theridiids (1.8–7.5 mm total length). Prosoma longer than wide, pear shaped (Figs 19E, 43D, 46C), clypeus flat, its height usually about three times AME diameter (Fig. 43E). Eyes subequal in size, lateral eyes touching (Figs 19E, 37C), anterior row usually slightly procurved, posterior row slightly recurved (Figs 32F, 41F, 48F). Sternum extending between fourth coxae, tapered (Figs 15B, 24D). Chelicerae with three (usually) to four teeth on anterior margin (Figs 14D, 38F, 51F), the mesal-most one largest, others subequal, 3–6 equal-sized denticles on posterior margin (Figs 3D, 5F, 12G). Abdomen ovoid, longer than wide (Fig. 7G, H), hirsute (Fig. 31C, D, 32G, 41D), with a diagnostic dorsal band-like, hatched, folium, dark centrally (red in live specimens), bordered by a narrow white rim (Figs 7G, H, 19E). Abdominal apodemes (muscle attachments), fairly indistinct, smooth, or slightly rugose (Fig. 54B, C). Pedicel inserted anteriorly or medially (abdomen then appearing 'higher than long') on the abdomen (Figs 1E, 31C, 34B). Stridulatory apparatus on abdomen conspicuous in males (Figs 34D, 38C), with stridulatory picks consisting of raised setal basis (Fig. 47F), in distinctly curved, paired, rows dorsal to the pedicel (Fig. 24C, 41C, 43C, 46D, 50F) often asymmetric, and stridulatory nubbins interspersed in between (Fig. 32D). Stridulatory picks less pronounced in females (Figs 34C, 37D). Prosomal ridges, interacting with stridulatory picks, inconspicuous, irregular and shallow (Fig. 15A). Colulus absent, two colular setae present (Figs 31E, 51E). Spinnerets with typical theridiid spigots (Figs 26G, 51A–D, 53D–F): anterior lateral spinnerets with a major ampullate and 30–45 piriform spigots (Figs 12C, 32A, 38D, 54F), posterior median spinnerets with a minor ampullate spigot, a cylindrical spigot (female) and two aciniform spigots (Fig. 31F, 38E), posterior lateral spinnerets with two enlarged and flattened aggregates, a flagelliform, two cylindrical (female), and 3–15 aciniform spigots (Figs 14C, 31F). Cylindricals absent, and aggregate and flagelliform spigots reduced to nubbins in males (Figs 12D, 43F, 54G, H). Anal tubercle as in Figure 34G. Epiandrous gland spigots in two groups, sometimes placed in distinct sockets (Figs 3A, 5D, 10E, 11F, 14B, 18E, 22C, 24A, 48C, 54A). Usually 5–15 spigots in each group, number variable between and within species, often asymmetric within a specimen (Figs 31B, 37B, 41B, 43B, 50G). Female leg length formula usually 1423, male usually 1243. Femur I of male often more robust than other femora (Fig. 26F), typically somewhat curvy (Fig. 41G); in some species femur I is not robust (Fig. 46E). Several (usually 4–8) small trichobothria dorsally on all tibia (Fig. 53G, H), usually three on palpal tibia (rarely four or more, e.g. Figs 2F, 43G) of both male (Figs 29F, 47D) and female (Figs 31C, E, 32E). Central tarsal claw elongate on tarsus IV, especially so in males (Figs 15E, 32B, 38B), relatively short on other legs (Figs 18F, 22H, 34E, 43H, 46F). Accessory claws distinct, especially on tarsus IV (Fig. 48E). Female palpal claw straight, densely dentate, tarsal ventral setae serrate (Fig. 38A). Typical theridiid tarsal comb on female tarsus IV (Fig. 41E). Venter of tarsus I (Fig. 22E, 38G), and tip of metatarsus I (Fig. 22F) with series of small, bent tipped, setae, absent on other tarsi (similar setae are widespread in theridiids, and particularly densely grouped in some hadrotarsines, see Agnarsson, 2004). These setae are presumably sensory; recognition (e.g. kin vs. prey) often involves touch with the first pair of legs.

Males of some permanently social species about half the size of females or less, but only very slightly smaller than females in other species.

Epigyna lightly sclerotized, epigynal plate distinctly depressed, usually bearing conspicuous ridges (Fig. 53B). One pair of seminal receptacles, usually showing clearly through the cuticle (Fig. 16C). Copulatory ducts usually simple, often distinctly sclerotized proximally (Fig. 27F,G), fertilization ducts short and simple, curving towards each other. Palpus (Fig. 28A–F) with a median apophysis without a hood, a hooked theridiid tegular apophysis, large spiralling embolus and usually a small to tiny conductor, resting on a subconductor (e.g. Figs 28A–F, 29A–F, 30A–E). Subconductor forms a pit (Fig. 30B) into which the lobed tail of the embolus, or a part of the embolus spiral, fits. Cymbium constricted mesally (Fig. 29A), usually with a distal lightly sclerotized tip. Cymbial process hooded, distally on ectal margin (Figs 18A, 30B).

Webs usually basket shaped, a more or less domed sheet, reinforced with dead (or sometimes living) leaves, with aerial strands leading upwards that intercept prey in flight (Fig. 66B, E). Webs may be somewhat amorphous, following the contour of the vegetation (e.g. Fig. 66A, D). Sticky silk usually not visible in webs.

Egg sacs dull grey, spun densely with fine silk strands (Fig. 37E, F), appearing papery. Egg sacs are deposited and guarded in the web, but when moved, females carry egg sacs in the chelicerae.

Phylogenetics: (see above)

Composition: *Anelosimus* currently contains 53 described species: *A. agnar* Agnarsson, 2006, *A. analyticus*, *A. andasibe* Agnarsson & Kuntner, 2005, *A. arizona*, *A. baeza*, *A. biglebowski* Agnarsson, 2006, *A. chickeringi*, *A. chonganicus* Zhu, 1998, *A. crassipes* Bösenberg & Strand, 1906, *A. decaryi* (Fage, 1930), *A. dialeucon* (Simon, 1890), *A. domingo*, *A. dubiosus*, *A. dubius*, *A. dude* Agnarsson, 2006, *A. elegans*, *A. ethicus*, *A. exiguus* Yoshida, 1986, *A. eximius*, *A. fraternus*, *A. guacamayos*, *A. inhandava* Agnarsson, 2005, *A. iwawakiensis* Yoshida, 1986, *A. jabaquara*, *A. jucundus*, *A. kohi* Yoshida, 1993, *A. linda* Agnarsson, 2006, *A. lorenzo*, *A. may*, *A. misiones* Agnarsson, 2005, *A. monskenyensis* Agnarsson, 2006, *A. nazariani*, *A. nelsoni A. nigrescens* (Keyserling 1884), *A. octavius*, *A. oritoyacu*, *A. pacificus*, *A. pantanal*, *A. placens* (Blackwall, 1877), *A. pulchellus*, *A. puravida*, *A. rabus*, *A. rupununi*, *A. sallee*, *A. salut* Agnarsson & Kuntner, 2005, *A. studiosus*, *A. sulawesi* Agnarsson, 2006, *A. sumisolena* Agnarsson, 2005, *A. taiwanicus* Yoshida, 1986, *A. tosum*, *A. tungurahua*, *A. vittatus* (C. L. Koch 1836) and *A. vondrona* Agnarsson & Kuntner, 2005.

Distribution: Worldwide, found on all continents except Antarctica. Most speciose in tropical areas, many species occur at altitudes of 1000–2800 m, a number of species are coastal.

Natural history: *Anelosimus* species range from showing extended maternal care (subsocial, e.g. *A. arizona*) to permanent, co-operative adult web-sharing (social, e.g. *A. eximius*) (see Avilés, 1997, for a review). Some species (including *A. pacificus* and *A. ethicus*) may be solitary. Co-operation is most extensive in social species and includes collaborating in web construction, prey capture, feeding, defence and in some instances co-operative brood care (including care of offspring of other females). The primary benefit of group living appears to be an increase in the probability of offspring survival (Avilés & Tufiño, 1998), coupled with avoiding the cost of dispersal (Uetz & Hieber, 1997). Social species are also able to handle larger prey than solitary species of a similar size (Christenson, 1984; Nentwig, 1985; Nentwig & Christenson, 1986).

Levels of sociality and inter- and intraspecific variation. As discussed elsewhere social categories (subsocial, social) are approximations, broad terms used to generalize about the range of characteristics that make a species 'social'. A closer look indicates variation, both inter- and intraspecific, in individual components of sociality forming more of a continuum than discrete categories of sociality.

Brach (1977) after studying *A. studiosus* in Florida came to the conclusion that '*A. studiosus* social behavior consists almost entirely of subsocial elements' (p. 160) its colonies lasting only a season and almost exclusively composed of a mother and her brood, most of which disperse prior to or just after mating. However, Furey (1998) showed that some populations of *A. studiosus* in Tennessee form longer lasting nests with multiple egg-laying females and moderately biased sex ratio (about 3.2 females per male). Nentwig and Christenson (1986) studied '*A. jucundus*' (most likely *A. baeza*, see below), and considered it to be 'more social' than *A. studiosus* (as described by Brach, 1977), showing greater adult–adult tolerance and some generation overlap. L. Avilés & W. P. Maddison (pers. comm.), however, found that allopatric populations of *A. baeza* differ and the range of social behaviour in *A. baeza* includes both extremes described for *A. studiosus* by Brach (1977) and Furey (1998).

Marques *et al*. (1998) compared the level of sociality in *A. dubiosus* and *A. jabaquara* in Brazil. They found that although most *A. jabaquara* formed single-mother/offspring colonies, some colonies had two to several adult egg-laying females. In the latter case the females showed aggression towards one another while guarding egg sacs, but at around the time the mothers started dying (brood instar IV) the broods of different mothers started mixing. Most *A. jabaquara* dispersed away from their natal nest as subadults, or adults, before mating. The sex ratio in *A. jabaquara* was slightly female biased (1.8 females per male). *A. dubiosus* formed multi-female colonies more commonly than *A. jabaquara*. The females guarded their own egg sacs, but showed less aggression than *A. jabaquara* towards other adults in the web (both in natural conditions and when adult females were introduced into established webs). Brood-mixing took place by the second instar, after which they were fed indiscriminately by regurgitation by any adult female (or even an older juvenile) in the nest. Co-operation in web building started earlier and was more extensive in *A. dubiosus* than in *A. jabaquara* and only a portion of individuals dispersed away from the natal nest prior to mating. The sex ratio of *A. dubiosus* was slightly more female biased with 3.2 females per male. Recently, Gonzaga and Vasconcellos-Neto (2001) described *A. jabaquara* populations in which juveniles commonly remained in the natal nest to mate and rear brood. The probability of emigration correlated positively with size. In this species seasonal rupture of social structure thus seems not to be obligatory.

The 'level' of sociality displayed by members of the genus *Anelosimus* therefore varies continuously between and even within species. One extreme is populations/species exclusively consisting of a mother and her progeny who co-operate until dispersal at or near maturity, and the other, species such as *A. eximius* with multiple egg-laying females in huge communal webs that last several generations and contain hundreds to thousands of spiders.

Colonies. Webs of most *Anelosimus* species, whether subsocial or social, are similar. Typically the webs contain a tough basket-shaped sheet, enforced with dead leaves and debris, and with aerial threads extending upwards that intercept insects in flight (Fig. 66A–E). Sometimes the sheet may be divided into several tiers or silk platforms, perforated by silk reinforced holes (Brach, 1975). Smaller nests of subsocial species usually occur in open areas (hillsides, along paths and rivers, etc.) at the ends of branches, often in clusters. Social nests of most species occur along rivers, in clearings and in forest edges, while *A. domingo* nests primarily occur in the forest understory. Social webs often beset the vegetation and cover bushes or even entire tree canopies. Very large webs may lose the 'basket-shape' and rather follow the contour of the vegetation. Webs of some species (e.g. *A. rupununi* and *A. lorenzo*) are irregular meshes that lack aerial threads; these species forage below the sheet.

New subsocial colonies are established by dispersing individuals (subadults or young adults). In social species new colonies can also be formed by swarms of individuals, or by colony 'budding', i.e. a large colony splitting into two or more smaller colonies. Social colonies may last several generations, whereas in subsocial species colonies typically last one generation. Subsocial nests, however, may last more than one generation as the first female to mature may remain in the natal nest, but drive her female siblings out of the nest (Brach, 1977).

Colonies contain anywhere from about 20 (small subsocial nests) to several tens of thousands of individuals (large social nests) (Avilés, 1997; Avilés & Tufiño, 1998; Venticinque *et al*., 1993). Colony size and survival depend on many factors. In *A. eximius*, offspring survival increased with colony size, while individual female reproductive output was highest at intermediate colony size, and risk of parasitism was higher the larger the colony (Avilés & Tufiño, 1998). Therefore, individual fitness seems to be highest at intermediate colony size.

Daily 'routine'. The spiders spend most of the day 'resting' under the dead leaves incorporated into the sheet of the web, or 'patrolling' the sheet (Brach, 1975, 1977). Activity is lowest around noon, but high at dusk.

When a prey item hits the sheet and tries to struggle free, the vibrations alert nearby nest members (in large nests most prey items only draw the attention of a small portion of the nest members), who attack the prey. Usually larger individuals (adult females, subadults) attack first, typically first swathing larger prey with sticky silk (so called 'wrap attack'), before delivering bites on the extremeties. Smaller individuals then join, and also bite the prey, often at the tip of the legs. The prey is then consumed communally, and nest members not involved in the killing may also feed on the prey. In *A. eximius* the prey is approached in a synchronized and rhythmical fashion, bursts of activity alternated with periods of immobility (Krafft & Pasquet, 1991). The synchronized 'silence' periods help to isolate the vibrations coming from the struggling prey and thus facilitate prey catching.

Another task that draws the spiders out of their retreats is web construction. The sheet is fixed by patching; sheet repair may be done individually or communally and seemingly can take place at any time during (at least) the night. Aerial thread building is more synchronized. In some species the spiders ritually swarm up the aerial threads on a daily basis, typically in the late afternoon or early nighttime. Presumably the spiders are laying new aerial threads or reinforcing pre-existing ones.

During rain, patrolling, web-building or feeding individuals quickly return to their retreats.

Tolerance and co-operation. Mothers show extensive maternal care in *Anelosimus* colonies. Maternal care includes guarding the egg sac (individual egg sacs, or groups of egg sacs of different mothers as in *A. rupununi*), regurgitative feeding of young in many species and provisioning offspring with killed, predigested, prey items (Avilés, 1997). Juveniles start contributing to the colony early, and typically all colony members (excluding adult males) co-operate. Co-operation includes collective prey catching, web building, defence, communal feeding, egg sac guarding, and in the most social species, co-operative care of the brood. In social species intraspecific tolerance seems to be universal, with apparent absence of nest-specific recognition mechanisms (Tapia & de Vries, 1980; Avilés & Tufiño, 1998). Recognition of conspecifics is primarily tactile (with apparent secondary loss of conspecific recognition via vibration); nest members frequently exchange touches with the pair of first legs, but show no aggression (Brach, 1975). Heterospecific spiders do generally not induce aggression by the vibrations they cause walking on the web (unlike struggling prey), but are recognized by touch and are then attacked. In subsocial species tactile cues are apparently less important than in social species. Rather, conspecific recognition is via vibrations, and heterospecific spiders may be detected from distance and attacked (Brach, 1977). Tolerance is also less stereotypic. Subsocial siblings collaborate in the natal nest until dispersal, but tolerance and co-operation break down with age (adults are aggressive towards one another) and when food is scarce. In a laboratory experiment under conditions of crowding or low food supply, co-operation broke down among subsocial juveniles and the spiders readily cannibalized each other (Avilés & Gelsey, 1998). Tolerance can also be artificially prolonged in subsocial species, by supplementing colonies with food (Krafft, Horel & Julita, 1986; Ruttan, 1990; Gundermann, Horel & Krafft, 1993).

Sex ratios. At odds with Fisher's (1930) general rule of equal sex ratios, sex ratios are female biased in many of the *eximius* lineage species. Brach (1975) attributed this bias to differential cannibalism on males. Avilés (1986, 1987, 1993), Avilés & Maddison (1991) and Avilés *et al*. (2000), however, showed that the primary sex ratio itself is biased and that males are not disproportionately cannibalized. In *A. eximius*, for example, the sex ratio is strongly biased with about 10% of subadults and 9% of embryos being males (Tapia & de Vries, 1980; Avilés, 1986; Avilés & Maddison, 1991). The sex ratio bias in *Anelosimus* seems to be correlated with the level of sociality – the 'more social' the greater the bias (see Table 2).

According to the 'local mate competition' idea (Hamilton, 1967) sex ratio bias can be expected when populations are subdivided into reproductive units, and especially when mating occurs among siblings. As long as a male is available to fertilize his sisters, mothers gain by producing mostly females; additional males would only compete for mates but not increase the number of second-generation progeny. However, others have argued that female-biased sex ratios are selected for by the differential contribution of genetically different groups to the population's gene pool (Colwell, 1981; Wilson & Colwell, 1981). The importance of interdemic selection in explaining biased sex ratios is much debated (e.g. Borgia, 1982; Charlesworth & Toro, 1982; Nunney, 1985; Wilson, Pollock & Dugatkin, 1992), especially in systems where single-mother offspring interact briefly (e.g. fig wasps). Avilés (1986, 1993, 1997), however, argued that in the social spiders, interdemic selection is powerful enough to override individual selection, mainly because only colonies above some threshold size proliferate (benefiting faster growing colonies), and rate of colony extinction is very high (hence many selection events at the colony level). Using computer simulations, Avilés (1993) showed that in multi-female nests lasting many generations, individual selection acted towards equal sex ratios, and sex ratio bias could only be maintained by selection at the colony level: Colonies producing more females grew faster and left more daughter colonies in the next generation.

The mechanisms used to bias the sex ratio in *Anelosimus* are not understood, but in at least one species, sex ratios appear precisely biased, implying a sperm sorting mechanism (Avilés *et al*., 2000). In *A. domingo*, the primary sex ratio is biased with approximately 9.3 females per male. Egg sacs contain between nine and 22 embryos and by chance many egg sacs should lack male embryos. Yet every egg sac examined by Avilés *et al*. (2000) contained at least one male embryo; in this species males are thus allocated to clutches with significantly greater precision than expected by chance.

Parasitism. Various organisms parasitize *Anelosimus* individuals, their eggs and their colonies. Parasites include both endoparasites (e.g. nematodes), ectoparasites (hymenopterans) and kleptoparasites (true bugs, spiders).

I am unaware of any research on *Anelosimus* endoparasites, but occasional museum specimens contain a nematode, typically in the abdomen. Hymenopteran ectoparasites appear to be common. Females lay their egg on the abdomen of the spider and the whitish-yellow larva feeds on the spider as it grows. In some *Anelosimus* colonies, most or all of the colony members are parasitized in this manner (my pers. obs.). In orb-weavers at least one such parasite induces behavioural changes where the host abandons normal web-building and instead makes a cocoon web for the host's larvae (Eberhard, 2000, 2002).

In *A. eximius*, one-quarter of the egg sacs are parasitized on average, the risk increasing with colony size (Avilés & Tufiño, 1998). Generally very small colonies have no parasites, whereas larger ones usually do and the parasite load can reach an amazing 100%.

Most *Anelosimus* species have communal or kleptoparasitic organisms occupying their nests (e.g. Cangialosi, 1990a, b). The plant bug genus *Ranzovius* (Heteroptera, Miridae) is common in *Anelosimus* nests, and different *Ranzovius* species seem to specialize on particular *Anelosimus* species (Henry, 1984, 1999; Wheeler & McCaffrey, 1984; Nentwig, 1985). Argyrodine spiders of the genera *Argyrodes* and *Faiditus* also commonly occur in *Anelosimus* webs, their numbers generally increasing with colony size and longevity (Avilés & Tufiño, 1998; see also Agnarsson, 2003b). Some are species specific; *F. ululans* for example specializes on *A. eximius* nests (Cangialosi, 1990a,b). As many as 10% of the adult spiders of an *Anelosimus* colony may be kleptoparasites.

Commercial damage? Stejskal (1976) suggested that some *Anelosimus* pierce the epidermis of mango, citrus and coffee leaves and drink from them. Some *Anelosimus* species reach very high densities in orchards, and may eventually kill the vegetation by shading (Stejskal, 1976).

THE *EXIMIUS* LINEAGE

Diagnosis: Males of the *eximius* lineage differ from other *Anelosimus* in having deeply notched cymbial margins (Figs 23A, B, 29A, 33A), a subterminally ridged theridiid tegular apophysis (Figs 2B, 42C), embolus-distal hematodocha grooves (Figs 35B, H, L, 36C, 39B, C) and from most species by a translucent cymbial hood. Females may be difficult to diagnose from other *Anelosimus*, most species (excluding the *domingo* group and *A. eximius*) differ in having strongly sclerotized copulatory ducts. They differ from the closely related Madagascar group by lacking an epigynal septum, and the epigynal scape clade (including three other American species) by lacking a scape. Females differ from the *rupununi* group (including the remaining American species) by entire anterior epigynal bursa.

Description: Prosoma light orange or yellow, eye region pale orange with rest of cephalic area greyish. Narrow rim around the edge of prosoma slightly darker bearing a regular row of small thickened setae. Sternum extending between coxae IV (Fig. 24D). Sternum base colour (in alcohol) brownish-yellow, mostly covered by dusky gray dots, with a darker rim around edge and an indistinct brownish-yellow central streak. Labium separated by a seam (Fig. 24D). Abdomen light grey to bright red (dark in alcohol), with a dark grey dorsal longitudinal notched folium (Fig. 7G). Abdomen-prosoma stridulatory apparatus present. Colulus absent, but two colular setae present (Fig. 31E). Leg base colour pale yellow, femur, patella and distal tip of tibia and metatarsus covered with dusky grey dots. Two parallel pale yellow streaks distally on ventral side of femur I, may be only one streak or no streak on other femora. Pedipalp with a small outgrowth of tegulum – the subconductor – at base of a lamelliform conductor; theridiid tegular apophysis large, pointed, supporting embolus, attached to the tegulum via the distal hematodocha; median apophysis medially attached to the tegulum via the distal hematodocha, interacting with hood on cymbial margin, embolus large, usually bipartite (embolus plus the embolic division b) (Fig. 19A, B, F, G, J–L). Cymbium with a large tarsal organ, tip of cymbium weakly sclerotized, whitish in preserved specimens. Pedipalpal tibia cup shaped (Fig. 2F) with ventral side forming a lip with the characteristic theridiid row of very long setae (Fig. 27B, C).

Phylogenetics: The *eximius* lineage is the largest clade containing only New World species. The monophyly of the *eximius* lineage is supported by at least the following putative synapomorphies: deeply notched cymbial margin (**15**-2, Figs 23A, B, 29A, 33A), translucent cymbial hood (**25**-0), an abrupt post-SBII turn of the sperm duct (**30**-1, Fig. 57D–F), subterminally ridged theridiid tegular apophysis (**56**-1, Figs 2B, 42C), and embolus-dh grooves (**69**-1, Figs 35B, H, L, 36C, 39B, C). The Madagascar group is sister to the *eximius* lineage.

Composition: The *eximius* lineage contains 20 species: *A. analyticus*, *A. arizona*, *A. baeza*, *A. chickeringi*, *A. domingo*, *A. dubiosus*, *A. elegans*, *A. eximius*, *A. fraternus*, *A. guacamayos*, *A. jabaquara*, *A. jucundus*, *A. octavius*, *A. oritoyacu*, *A. pacificus*, *A. pantanal*, *A. puravida*, *A. studiosus*, *A. tosum* and *A. tungurahua*.

Distribution: New World, from north-eastern USA to Argentina (Fig. 63A). Most speciose in Ecuador and Mexico, particularly at altitudes of 1000 m or above.

Natural history: All studied *eximius* lineage species are social; for an overview of the natural history of social species see under *Anelosimus* above.

SPECIES DESCRIPTIONS

ANELOSIMUS ANALYTICUS (CHAMBERLIN, 1924)
(FIGS 1A–E, 2, 3, 64A)

Types: Male holotype and 18 female paratypes from Mexico, San Esteban Island, [28°58′0″N, 112°22′0″W], 20 April 1921, E. P. van Duzee, in CAS no.1221 and 1422, examined [IA40672]. Paratypes from same collection series in NMNH, examined.

Etymology: Chamberlin (1924) did not explain the species epithet.

Synonymies:
Linyphia dorsalis Banks, 1898: 244, pl. 14, fig. 9, ♂, types destroyed in the California earthquake of 1906, name preoccupied by *L. dorsalis* Wider, 1834. Levi (1972) proposed this synonymy, but based on Banks (1898) description and illustrations I am not able to confirm, or disconfirm it. It is not clear if Levi had access to additional data, or specimens.
Theridion analyticum Chamberlin, 1924: 637, figs 76–77, ♂♀.
Linyphia dorsatula Roewer, 1942: 588 (replacement name for *L. dorsalis*).
Anelosimus analyticus: Levi, 1956: 421, figs 19, 40–4, ♂♀ Levi, 1972: 536; Stejskal, 1976: 344, fig. 4.5, ? (probably *A. analyticus*, although photographs are not recognizable); Platnick, 2006; Agnarsson, 2004; Figs 15A–G, 16A–G ♂♀.

Diagnosis: Male *A. analyticus* are separated from most other *Anelosimus* by the simple embolus and cylindrical E spiral (Fig. 1A, B). The related *A. chickeringi* lacks an embolic division b (Fig. 1G), and *A. pacificus* has a much more complex palp (Fig. 1K). Females differ from most *Anelosimus* in lacking ridges on the epigynal plate, and from the related *A. chickeringi* by a less rounded epigynal plate (Fig. 1C, D, compare with 1H).

Male (paratype): Total length 3.06. Prosoma 1.50 long, 1.22 wide, 0.99 high, light orange-brown with cephalic region darker brown. Sternum 0.92 long, 0.83 wide, extending between coxae IV, colour as carapace, but darker brown centrally. Abdomen 1.76 long, 1.32 wide, 1.39 high. Pattern as in Figure 1E. PME smallest, about 0.07 in diameter, AME and laterals about 0.09 in diameter. Clypeus height about 3.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.41, patella 0.65, tibia 2.18, metatarsus 1.82, tarsus 0.85. Femur about 6 times longer than wide, metatarsus I about 18 times longer than wide, with distinctly thickened ventral spines. Leg formula 1243. Leg base colour as carapace, distal tip of femora and tibia slightly darker, metatarsus–tarsus joint dark. Tarsal organs slightly distal (around 0.5–0.6) on tarsi I–III, central (0.50) on IV. Five to six small trichobothria dorsally on all tibia, 5–6 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.45), absent on metatarsus IV. Two prolateral and one, or two, retrolateral palpal tibial trichobothria. Palp as in Figures 1A, B, 2A–F.

Female (paratype): Total length 3.84, coloration pattern as in male, but lighter. Prosoma 1.63 long, 1.35 wide, 1.16 high, brown. Sternum 1.12 long, 0.97 wide, extending between coxae IV. Abdomen 2.28 long, 1.73 wide, 1.77 high. Pattern as in male. Eyes subequal, about 0.09 in diameter, PME slightly smaller. Clypeus height about 2.6 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.31, patella 0.72, tibia 1.95, metatarsus 1.69, tarsus 0.75. Femur about 6 times longer than wide, metatarsus I about 21 times longer than wide. Leg formula 1243. Leg base colour as carapace, almost unicolorous in the paratypes. Tarsal organs distal on all tarsi, around 6.5–0.7 on tarsi I and II, 0.55–0.60 on III and IV. Four to five small trichobothria dorsally on all tibia, 4–5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.45), absent on metatarsus IV. Three trichobothria dorsally on palpal tibia. Epigynum as in Figures 1C, D, 3B.

Variation: Male total length 2.47–3.06, prosoma 1.20–1.50, first femur 2.00–2.41, female total length 3.20–4.40, prosoma length 1.45–1.63, first femur 1.85–2.35 mm. Colour of central abdominal band varies from light grey to almost black, leg coloration from unicolorous to distinctly darkened distal tips of femora, patella, tibia and metatarsus.

Additional material examined: MEXICO. Baja California, La Paz [24°8′0″N, 110°18′0″W], 4.xi.1921 (R. V. Chamberlin, MCZ), 1♀ [IA070701]; 1♀ [IA070801]. Baja California Sur, Desierto del Vizcaíno, Rancho San José de Castro [27°38′0″N, 113°23′0″W], 2.xi.1987 (F. Cota, NMNH), 1♀ [IA40651]. Sonora, Tiburon [28°59′0″N, 112°22′0″W], 7.v.1921 (R. V. Chamberlin, MCZ), 1♀ [IA071201]; Guyamas [27°55′0″N, 110°54′0″W], 16.vi.1939 (L. I. Davis, MCZ), 2♂, 2♀ [IA072301]; Kino Bay (28°49′0″N, 111°56′0″W), 4.vi.1997, hand collected (L. Avilés, MCP), 2♂, 1♀ [IALA10]; 1♀ [IALA11]; San Esteban [probably Isla Tiburon], [28°58′0″N, 112°22′0″W], 20.iv.1921 (E. P. van Duzee, MCZ), 3♂, 3♀ [IA070901]. San Pedro, 17.iv.1921 (E. P. van Duzee, MCZ), 2♀ [IA071301]. [Locality unknown], 10.v.1921 (R. V. Chamberlin, MCZ), 1♀ [IA072101]. USA, California, La Jolla, [33°51′26″N, 117°52′32″W], 20.i.2004 (W. Maddison, NMNH), 1♂ [IAV03].

Distribution: Recorded from south-west USA to Venezuela, most records from Mexico (Fig. 64A). Apparently only found at low altitudes (*c.* 0–200 m).

Natural history: Subsocial (Stejskal, 1976), with two generations per year in Arizona (L. Avilés, pers. comm.).

ANELOSIMUS CHICKERINGI LEVI, 1956
(FIGS 1F–J, 4–5, 64A)

Types: Male holotype, female paratype and male and female paratypes from Panama, Barro Colorado Island, Panama Canal Zone, 16.vi.–15.vii.1934, A. M. Chickering, in MCZ, examined.

Synonymies:
*Anelosimus chickeringi*Levi, 1956: 421, fig. 20, 43–45, ♂♀.
Anelosimus chickeringi: Levi, 1963: 36; Platnick, 2006.

Etymology: The species epithet honours A. M. Chickering, who collected the type material.

Diagnosis: The relatively short, entire (not split) embolus separates males from all other *Anelosimus* (Fig. 1F, G). Females are very similar to *A. analyticus*, but differ in having a narrower, more rounded, epigynal plate (Fig. 1H), and simpler pathway of the copulatory duct (Fig. 1I).

Male (paratype): Total length 1.69. Prosoma 0.78 long, 0.66 wide, 0.53 high, brown. Sternum 0.46 long, 0.41 wide, extending between coxae IV, brown. Abdomen semi-cylindrical 0.91 long, 0.64 wide, 0.66 high. Pattern as in other *Anelosimus* (Fig. 1J). Eyes subequal, about 0.07 in diameter. Clypeus height about 2.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.14, patella 0.23, tibia 0.85, metatarsus 0.68, tarsus 0.49. Femur about 9 times longer than wide, metatarsus I about 11 times longer than wide. Leg formula 1423. Leg base colour yellowish, femur I usually darker than other femora, distal tips of segments not noticeably darkened in available specimens. Tarsal organs central (around 0.50) on tarsi I, proximal (0.35–0.40) on II–IV; positions vary slightly between specimens. Three to five small trichobothria dorsally on all tibia, 3–5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 1F–G, 4A–E.

Female (paratype): Total length 2.60. Prosoma 1.17 long, 0.76 wide, 0.63 high, brown. Sternum 0.61 long, 0.58 wide, extending between coxae IV, brown. Abdomen 1.43 long, 0.99 wide, 1.04 high. Pattern as in Figure 1I. Eyes subequal, about 0.08 in diameter. Clypeus height about 1.9 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.33, patella 0.39, tibia 1.11, metatarsus 0.98, tarsus 0.59. Femur about 7 times longer than wide, metatarsus I about 12 times longer than wide. Leg formula 1423. Leg base colour yellowish, distal tip of tibia, and sometimes femora darker in most specimens. Tarsal organs central (0.50) on tarsus I, slightly proximal (0.40–0.45) on tarsi II–IV, distal (0.85) on palp. Numerous (probably 3–6, very hard to see on available specimens) small trichobothria dorsally on all tibia, 3–5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III proximal (0.40–45) absent on metatarsus IV. Three dorsal trichobothria on female palpal tibia. Epigynum as in Figures 1H, I, 5C.

Variation: Male total length 1.50–2.10, prosoma length 0.75–0.98, first femur 1.05–1.27. Female total length 2.47–2.60, prosoma 1.03–1.17, femur I 1.33–1.46. Specimens from different countries often differ in subtle details of the genitalia, but as so few individuals are available outside Panama there is little evidence if this is more than intraspecific variation.

Additional material examined: BRAZIL. Roraima, Ilha de Maracá, Alto Alegre [2°56′0″N, 61°28′0″W], 31.i.–14.ii.1992 (M. A. de Marques, MCP), 1♀ [IA40610]. HONDURAS. Atlantida, Progrisso & La Frahua [15°32′0″N, 87°49′0″W], vii.1929 (A. M. Chickering, MCZ), 1♂, 1♀ [IA0114]. MEXICO. Veracruz, Martinez de la Torre [20°3′0″N, 97°2′0″W], 4.vii.1946, *c.* 77 m (H. Wagner, AMNH), 1♂ [IA40577]. NICARAGUA. Granada [11°55′0″N, 85°57′0″W], *c.* 50 m (C. F. Baker, MCZ), 1♂ [IA0117]. PANAMA. Panamá, Canal Zone, BZ Forest reserve, Barro Colorado Island [9°9′17″N, 79°50′53″W], 10–12.viii.1939 (A. M. Chickering, MCZ), 1♂ [IA010301]; 1.vi.–15.vii.1934, 1♂, 2♀ [IA010901]; 18–25.viii.1939, 1♀ [IA011201]; 14.viii.1954, 1♀ [IA0115]; viii.1939, 1♂ [IA0116], 28–31.vii.1939, 1♀ [IA0118]; 14.vii.1950, 1♀ [IA0119]; 30.vii.1954, 1♀ [IA0120]; 18.vii.1954, 1♂ [IA0123]; Panama City (8°57′0″N, 79°32′0″W), 15–30.vii.1979, canopy fogging (E. Broadhead *et al.*, NMNH), 3♂ [IA1111]; 1♀ [IA40405].

Distribution: Occurs from north-eastern Mexico to Peru (Fig. 64A). Apparently restricted to low altitudes (*c.* 0–200 m).

Natural history: Unknown. Some specimens have been collected with canopy fogging.

ANELOSIMUS PACIFICUS LEVI, 1956
(FIGS 1K–O, 6, 64A)

Types: Female holotype, two female and one juvenile male paratype from Mexico, Guerrero, Pie de la Cuesta, 8 miles west of Acapulco, 29.vi.1941, L. I. Davis, in AMNH, examined, one of the paratypes lacks the epigynum.

Synonymies:
*Anelosimus pacificus*Levi, 1956: 417, figs. 48–49, ♀.
Anelosimus pacificus: Levi, 1963: 35, fig. 62, ♀ Platnick, 2006.

Etymology: Not explained in Levi (1956).

Diagnosis: Males can be diagnosed from all other *Anelosimus* by the folded and membranous embolus base, and the long thin and sclerotized embolus tip (Fig. 1K, L). The females can be identified by the shape of the epigynum, whose anterior bursal wall characteristically bears a small invagination (Fig. 1M–O).

Male (IA031201): Total length 1.95. Prosoma 1.04 long, 0.73 wide, 0.63 high, yellowish. Sternum 0.63 long, 0.54 wide, extending between coxae IV, yellowish. Abdomen 1.30 long, 0.91 wide, 1.04 high. pale yellow without pattern in the single available specimen. Eyes subequal, about 0.07 in diameter. Clypeus height about 2.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.33, patella 0.39, tibia 1.24, metatarsus 0.98, tarsus 0.55. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1243. Legs unicolorous yellowish-brown, but spines conspicuous and dark, with dark bases. Tarsal organs distal (0.55–0.60) on tarsus I, proximal (0.40–0.50) on II–IV, closest to centre on II. Three to five small trichobothria dorsally on all tibia, 4 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III slightly proximal, or central (about 0.45–0.50), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia (Fig. 6F). Palp as in Figures 1K, L, 6A–F.

Female (IA032401): Total length 2.67. Prosoma 1.30 long, 0.91 wide, 0.79 high, yellowish. Sternum 0.86 long, 0.68 wide, extending between coxae IV, yellowish. Abdomen 1.69 long, 1.35 wide, 1.37 high, pale yellowish, very faint pattern can be detected, reminiscent of other *Anelosimus*. Eyes subequal, about 0.10 in diameter. Clypeus height about 1.8 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.63, patella 0.39, tibia 1.37, metatarsus 1.30, tarsus 0.62. Femur about 5 times longer than wide, metatarsus I about 13 times longer than wide. Leg formula 1423 with legs 4 and 2 subequal. Legs unicolorous yellowish-brown, but spines conspicuous and dark, with dark bases. Tarsal organs distinctly distal (0.65–0.70) on tarsus I, slightly distal (0.55) on II, central (0.50) on III and proximal (0.4) on IV. Four to five small trichobothria dorsally on all tibia, 4 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III slightly proximal, or central (about 0.45–0.50), absent on metatarsus IV. Three dorsal trichobothria on palpal tibia. Epigynum as in Figure 1M–O.

Variation: Most of the available specimens are all very pale and have presumably lost their colour and pattern in alcohol. A faint outline of a dorsal band may be detected. The female holotype, however, and the specimens from Costa Rica have a typical *Anelosimus* folium. Female total length 2.55–3.51, the holotype was the largest specimen examined, prosoma length 1.26–1.32, first femur 1.60–1.79.

Additional material examined: COSTA RICA. Puntarenas, Parrita [9°31′0″N, 84°19′0″W], ii.2005, *c.* 5 m (W. Eberhard, NMNH), 3♂, 2♀ [IAEB01]. JAMAICA. St. Catherine, Port Henderson [17°56′0″N, 76°52′0″W], 20.vi.1954, *c.* 15 m (A. M. Chickering, MCZ), 1♀ [IA031101]. MEXICO. Guerrero, Pie de la Cuesta, 8 mi. W. of Acapulco, *c.* 0–1 m, [19°54′0″N, 99°57′0″W], 29.vi.1941, 0–10 m (L. I. Davis, AMNH, paratypes), 2♀ [IA40580]. Sinaloa, Mazatlán [23°12′0″N, 106°25′0″W], 6.ix.1956, *c.* 0–1 m (A. F. Archer, MCZ), 1♂ [IA031201]; 23.vii.1954, *c.* 0–1 m (W. J. Gertsch, MCZ), 1♀ [IA032401]; 21.vi.1943, 0–10 m (F. H. Pough, AMNH), 1♀ [IA40579].

Distribution: Known from four females and one male from type locality in Mexico, a single female from Jamaica, and recently collected specimens from Costa Rica (Fig. 64A). Also reported from Nicaragua (Maes, Palacios Vargas & Jimenez, 1989). All records from low altitudes (less than 100 m).

Natural history: In Costa Rica solitary females and males were encountered; females make irregular, three-dimensional webs around live leaves, with sticky silk dispersed throughout the nest (W. Eberhard, pers. comm.). These data indicate the species is either subsocial or solitary.

Phylogenetic note: Preliminary molecular data suggest *A. pacificus* may belong to the American *ethicus* group, rather than the *eximius* lineage (I. Agnarsson, L. Avilés & W. P. Maddison, unpubl. data).

ANELOSIMUS DOMINGO LEVI, 1963
(FIGS 7A–D, 8–10, 63B, 66E)

Types: Male holotype and female paratype from Ecuador, Pichincha, 10 km W of Santo Domingo de los Colorados, 23.ii.1955, E. I. Schlinger & E. S. Ross, in CAS, examined.

Synonymies:
Anelosimus domingo Levi, 1963: 36, figs 63–65, ♂♀.
Anelosimus domingo: Levi, in Rypstra & Tirey, 1989: 368 (proposed synonymy of *A. saramacca*); Platnick, 2006.
Anelosimus saramacca Levi & Smith, 1983: 275, figs 1–3, ♂♀. Male holotype and female paratype from Surinam, Voltzberg-Raleighvallen Nature Reserve, Saramacca Province, 04°32′N. 56°32′W, ii.1982, Smith-Trail, in MCZ, examined. Two additional female paratypes (same collection data) in BMNH, examined.

Etymology: The specific name is a noun in apposition for the type locality.

Diagnosis: Both sexes can be separated from most other *Anelosimus* by the cylindrical shape of the abdomen, with a small knob overhanging the spinnerets, as in *A. eximius* (Fig. 16A). Male separated from *A. eximius* by narrow embolus spiral and voluminous embolus base (Fig. 7A, B). It differs from all *Anelosimus* except *A. dubiosus* and *A. jabaquara* by its whip-shapeD E tip (Fig. 7A). It differs from the latter two by a shorter and less curved (less whip-like) embolus (Fig. 7A). Females separated from other *Anelosimus* by the shape of the epigynal plate, with the posterior margin extending (Fig. 7C).

Male (IA070101): Total length 2.28. Prosoma 0.91 long, 0.76 wide, 0.73 high, yellowish. Sternum 0.61 long, 0.53 wide, extending between coxae IV, yellow with a narrow dark band around the edges. Abdomen 1.24 long, 0.83 wide, 0.76 high, cylindrical with a small hump overhanging spinnerets, as in *A. eximius*. Pattern as in *A. eximius*, sometimes lost in preserved specimens, abdomen appearing uniformly greyish. Eyes subequal, about 0.07 in diameter. Clypeus height about 2.3 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.33, patella 0.33, tibia 1.04, metatarsus 0.88, tarsus 0.59. Femur about 10 times longer than wide, metatarsus I about 13 times longer than wide. Leg formula 1423, legs four and two subequal. Leg base colour yellowish, unicolorous, sometimes femora slightly darker than other segments. Tarsal organs central (around 0.50) on tarsi I, proximal (0.35–0.45) on II–IV. Four to six small trichobothria dorsally on all tibia, 5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia.

Palp as in Figures 7A, B, 8A–F, 9A–F. The palp is similar to that of *A. dubiosus* and *A. jabaquara*, with an Eb-process distally on the E. The palp is unusual in the theridiid tegular apophysis being inconspicuous and lacking ridges, and – uniquely among *Anelosimus* – the sperm duct trajectory lacks SBI–II.

Female (IA070101): Total length 3.51. Prosoma 1.56 long, 0.99 wide, 0.91 high, yellow to orange. Sternum 0.87 long, 0.74 wide, extending between coxae IV, yellowish with dusky brown markings scattered on it. Abdomen 2.02 long, 1.24 wide, 1.07 high, cylindrical with a small hump overhanging spinnerets, as in *A. eximius*. Pattern as *A. eximius*. Eyes subequal, about 0.10 in diameter. Clypeus height about 2.3 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.82, patella 0.85, tibia 1.63, metatarsus 1.40, tarsus 0.75 . Femur about 8 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1423, legs II and IV subequal. Leg base colour yellowish, with distal tip of some or all segments slightly darkened. Tarsal organs slightly distal (0.50–0.55) on tarsi I and II, proximal (0.35–0.45) on III and IV. Four to seven small trichobothria dorsally on all tibia, 4–5 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 7C, D, 10A.

Variation: Male total length 2.20–2.60, prosoma length 0.91–1.07, first femur 1.33–1.63. Female total length 3.10–4.0, prosoma 1.50–1.62, first femur 1.82–1.95. Coloration of abdomen varies in preserved specimens, especially males, from like that of female to unicolorous grey, sternum varies from yellow or orange to almost black, depending on the extent of dusky markings.

Additional material examined: BRAZIL. Amazonas, *c.* 80 km from Manaus, Cabo Frio Reserve [2°24′S, 59°52′W], 11.v.1989 (H. G. Fowler *et al.*, MCZ), 1♀ [IA40757]; 16.v.1990, 1♀ [IA081001]. COLOMBIA. Valle, Río Digna, 28 km from Buenoventura [3°51′0″N, 76°50′0″W] (MCZ), 1♀ [IA030201]. ECUADOR. Napo, Estación Biológica Jatun Sacha (1°4′1.20″S, 77°37′1.20″W), 21–24.vii.2004, 400 m, forest understory (I. Agnarsson *et al.*, NMNH), ♂♂♀♀ [IAV04]. Pichincha, km 113 via Pto. Quito Reserva [0°2′0″N, 79°15′0″W], 27.xii.1984 (F. Ponce, MCZ), 1♂, 2♀ [IA070101]; 10 km W. of Santo Domingo de Los Colorados [0°15′0″S, 79°15′0″W], 23.ii.1955, *c.* 600 m (E. I. Schlinger & E. S. Ross, MCZ), 1♂, 1♀ [IA071701]. FRENCH GUIANA. Arrondissement de Cayenne, Cayenne, Montagnas Kaw, nr. Camp Caiman, *c.* 27 km SE. of Roura (4°33′0″N, 52°9′0″W), 5.viii.1988, 100–300 m (S. Marshall, NMNH), 4♀ [IA40650]. GUYANA. Potaro-Siparuni, Tumatumari [5°11′0″N, 59°3′0″W], 11.vii.1911 (F. E. Lutz, AMNH), 1♀ [IA40709]. PERU. Amazonas, Alto Río Comainas, puesto de vigilancia 22 – Falso Paquisha [3°58′0″S, 78°25′0″W], 28.x.1987, 850 m (D. Silva, MHNSM), 1♀ [IA40599]. Madre de Dios, Zona Reservada Tambopata, Caticocha Lagoon, edge [12°50′0″S, 69°17′0″W], 1.vii.1987 (*A. L.* Rypstra, NMNH), 2♂, 2♀ [IA40538]; 14.vi.1988 (J. Coddington, NMNH), 1♂, 12♀ [IA40539]; Katiecocha [12°43′0″S, 69°11′0″W], 14.vii.1987, 290 m (D. Silva, MHNSM), 3♂, 1♀ [IA40585]; 11.v.1988 (D. Silva, MHNSM), 2♂, 5♀ [IA40589]. Reserva Cuzco Amazonico (12°33′0″S, 69°3′0″W), 21.vi.1989, 200 m (D. Silva, MHNSM), 4♂, 8♀ [IA40542]; 14.vi.1989, 200 m (D. Silva, MHNSM), 1♂, 1juv [IA40546]; 15 km E. of Puerto Maldonado (12°33′0″S, 69°3′0″W), 14.vi.1989, 200 m (D. Silva, MHNSM), 1♀ [IA40603]. SURINAM. Saramacca, Voltzberg-Raleig Vallen Nature Reserve (4°32′0″N, 56°32′0″W), ii.1982 (D. Smith, MCZ), 1♂, 4♀, 8juv [IA033201].

Distribution: From Surinam to Peru. Mostly found at altitudes of 100–600 m (Fig. 63B).

Natural history: *Anelosimus domingo* has social structure and nest very similar to *A. eximius* (Levi, 1963; Levi & Smith, 1983; Rypstra & Tirey, 1989; Avilés, 1997; Avilés *et al.*, 2001). The nests are typical *eximius* group basket webs with aerial interception threads (Fig. 66E). The nests of *A. domingo* tend to have fewer dry leaves and be lighter in appearance than the nests of *A. eximius*, and the nests are smaller than the biggest *A. eximius* nests. Nevertheless, a few hundred to nearly 2000 individuals (including all life stages, and at least 140 females with egg sacs) have been recorded occupying a single web (Levi & Smith, 1983; Rypstra & Tirey, 1989; Avilés *et al.*, 2001). The species occurs in subtropical to tropical Amazonian moist to wet forest (Avilés *et al.*, 2001), including an upper floodplain forest community dominated by palms (Rypstra & Tirey, 1989). Unlike most other *Anelosimus*, *A. domingo* is mostly limited to primary forests. The webs seem confined to the forest understory and are made in the undergrowth where they are exposed to minimum amounts of direct sunlight (0–3 h/day). Rypstra & Tirey (1989) found the webs of *A. domingo* to be isolated and uncommon (smallest nearest neighbour distance was 2.5 km) and thus the species appears not to form clusters. Females guard egg sacs and young in retreats and prey capture appears identical to *A. eximius*. The young may be fed by regurgitation, but this has yet to be confirmed. *Anelosimus domingo* easily tolerate introduced juvenile or adult conspecifics, but do not tolerate introduced *A. eximius*, or vice versa (Rypstra and Tirey, 1989). Primary sex ratio is strongly female biased; only about 8% of embryos are males (Avilés & Maddison 1991). This ratio is precisely controlled; every egg sac contains at least one male even though numbers of embryos per egg sac can be as low as nine (Avilés *et al.*, 2000). When mating occurs among progeny in subdivided populations (as in all social *Anelosimus*), groups with more females grow and proliferate faster, favouring female-biased sex-ratios (acting *contra* individual selection within the colonies). However, extreme sex ratio bias, if not precisely controlled, would lead to a considerable portion of male-less clutches, with disasterous consequences in nests founded by a single females. Hence, when clutch size is small, as in *A. domingo*, precision in sex allocation is key.

ANELOSIMUS JABAQUARA LEVI, 1956
(FIGS 7E–J, 11, 12, 63B)

Types: Male holotype from Brazil, Jabaquara, Cidade São Paulo, 21.xii.1945, 7–800 m, Sick, in AMNH, examined.

Synonymies:
Anelosimus jabaquara Levi, 1956: 414, fig. 18, ♂.
Anelosimus dubiosus: Levi, 1963: 34, not *A. dubiosus* (Keyserling, 1891), synonymy rejected by Levi & Smith (1983) (= *A. jabaquara*).
Anelosimus jabaquara: Levi & Smith, 1983: 277 (removed from synonymy of *A. dubiosus* (Keyserling, 1891); Gonzaga & Santos, 1999: 434, figs 4–5, ♀ Platnick, 2006.

Etymology: The species epithet is presumably a noun in apposition, after the type locality.

Diagnosis: The male is readily distinguished from most other *Anelosimus* by the shape of the cymbium extending beyond the alveolus and a half-moon-shaped tegular process (Fig. 7E, F). It differs from *A. dubiosus* by a simple embolus base and shorter embolus (Fig. 7F), and from *A. domingo* by a larger Ebp (Fig. 7E, F). Females closely resemble those of *A. dubiosus*, *A. domingo* and the *jucundus* and *studiosus* groups. Females can only be reliably separated by examination of the internal genitalia where *A. jabaquara* differs from others by the thick copulatory ducts, ectally inserted on the spermathecae and nearly entirely hiding the fertilization ducts (Fig. 7J).

Live specimens: In live or freshly caught specimens the carapace, sternum and labium are bright red, clypeus, chelicerae and endites are orange (or rarely red). Abdomen dorsal band ends with four transverse red strips (Gonzaga & Santos, 1999).

Male (IA40536): Total length 2.93. Prosoma 1.50 long, 1.19 wide, 0.87 high, brown. Sternum 0.92 long, 0.79 wide, extending between coxae IV, brown. Abdomen 1.76 long, 1.12 wide, 0.99 high. Pattern as in Figure 7G, H. Eyes subequal, about 0.10 in diameter. Clypeus height about 2.7 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.11, patella 0.55, tibia 1.79, metatarsus 1.63, tarsus 0.72. Femur about 8 times longer than wide, metatarsus I about 17 times longer than wide. Leg formula 1423, legs 4 and 2 subequal. Leg base colour yellowish to dark brown, with distal tip of all segments darkened, and sometimes darker central bands. Tarsal organs central (0.50) on tarsi I, proximal (0.35–0.45) on II–IV, most proximal on tarsus III. Four to five small trichobothria dorsally on all tibia, 4–5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.30–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 7E, F, 11A–E.

Female (IA40536): Total length 4.23. Prosoma 1.90 long, 1.29 wide, 0.99 high, brown. Sternum 0.99 long, 0.91 wide, extending between coxae IV, brown. Abdomen 2.60 long, 1.65 wide, 1.65 high. Pattern as in Figure 7G–H. Eyes subequal, about 0.11 in diameter. Clypeus height about 2.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.95, patella 0.65, tibia 1.69, metatarsus 1.63, tarsus 0.81. Femur about 5 times longer than wide, metatarsus I about 13 times longer than wide. Leg formula 1423, with legs 4 and 2 subequal and leg 3 only slightly shorter. Leg base colour yellowish with distal tip of all segments darkened, and a central band on tibia. Tarsal proximal (0.40–0.45) on tarsi 1, III and IV, central on II. Five to six small trichobothria dorsally on all tibia, 5–6 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (0.40–0.45), absent on metatarsus IV, distal (0.85) on palpal tarsus. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 7I, J, 11G; see also Gonzaga & Santos (1999: figs 4–5).

Variation: Male total length variable, 2.93–3.30, prosoma 1.40–1.55, first femur 2.00–2.11. Female total length 3.90–4.33, prosoma 1.50–1.90, first femur 2.60–2.90. Male coloration (in alcohol) very variable, one specimen with dark base colours, dark brown legs slightly lighter at base. Another male very pale, whitish-yellow, pale legs with distal tip and central part of segments darker. Abdomen of male from completely black to light grey with a central band, male holotype with a typical *Anelosimus* folium. Gonzaga & Santos (1999: 434) further report: ‘Dorsal median band and sternum are sometimes totally black, mainly in males. Spermathecae occasionally visible externally.’ Males with dark abdomens appear to have slightly broader palps; it is possible that *A. jabaquara* as here circumscribed represents two closely similar species (L. Avilés, pers. comm.).

Additional material examined: BRAZIL. São Paulo, São Paulo botanical garden [23°34′0″S, 46°37′0″W], 10.iv.1965, *c.* 600m (H. Levi & P. de Biasi, MCZ), 2♀

[IA051801]; 33 km S. of Sao Paulo, camino de mar [23°54′0″S, 46°38′0″W], 2.iv.1965 (H. Levi & P. de Biasi, MCZ), 1♀ [IA052001]; Serra do Japi, Jundiaí [23°15′0″S, 47°0′0″W], 8.xii.1989, *c.* 1000–1100 m (Marques, MCZ), 1♂ [IA070501]; 4.xii.1989, *c.* 1000–1100 m, 1♂ [IA072601]; Parque Estadual da Serra do Japi [23°11′0″S, 46°52′0″W], 13–16.xi.1997, *c.* 1000–1100 m (M. O. Gonzaga, IB), 4♂, 3♀ [IA40536]; 19.ii.1997 (NMNH), 2♂, 1♀ [IA40570].

Distribution: Only known from Brazil at altitudes of 600–1100 m (Fig. 63B).

Natural history: *Anelosimus jabaquara* build typical *Anelosimus* nests using leaves as retreats and featuring knock-down threads to intercept prey (Marques *et al*., 1998). They are sympatric with the very similar *A. dubiosus*, but were 1 month ahead in phenology in the study site of Marques *et al*. (1998).

Anelosimus jabaquara shows a level of sociality somewhat intermediate between 'typical' subsociality and sociality and has a very slightly female-biased sex ratio (1.8 : 1). Marques *et al*. (1998) found that most *A. jabaquara* formed univoltine, single-mother colonies, where offspring left the natal colony prior to mating. Gonzaga & Vasconcellos-Neto (2001), however, found that in some *A. jabaquara* colonies, a portion of the siblings remained to mate within their natal nest and formed multiple-female colonies. Gonzaga & Vasconcellos-Neto (2001) concluded that rupture of social structure is not obligatory in this species.

In the study of Marques *et al*. (1998) females laid 5–47 eggs (mean 23). They were able to produce a second egg sac but appeared to do so rarely if the first egg sac develops normally or if they are caring for brood. The colonies contain 1–60 individuals (an exceptional colony had 97 individuals, presumably from more than one egg sac), which develop synchronously, and maturity is reached in seven instars (not counting an additional one inside the egg sac). Spiderlings are fed by regurgitation until the second instar when they can catch small prey on their own. Fourth instar or older members of the nest participate in all activities, and at the same time broods began to mix in multiple-female nests. Mothers usually die when their brood is reaching the fourth instar. The offspring then leave the natal colonies at, or near, adulthood to found new ones, dispersing by wafting silk lines and climbing them after they become entangled in the vegetation.

Anelosimus jabaquara is aggressive towards conspecific adult females (even those sharing the web) when guarding egg sacs, and even more so towards heterospecific *Anelosimus* females (Marques *et al*., 1998; Gonzaga & Vasconcellos-Neto, 2001). Curiously, despite being aggressive in its own nest, some *A. jabaquara* when dropped into *A. dubiosus* nests lack aggression and even start hunting with the other species. *Anelosimus dubiosus* females were, however, immediately attacked when introduced into *A. jabaquara* nests.

*A*NELOSIMUS DUBIOSUS (KEYSERLING, 1891)
(FIGS 7K–P, 13–15, 63B)

Types: Male holotype from Brazil, Nova Friburgo, Rio de Janeiro, *c.* 900 m, Göldi, presumably in BMNH (see Levi, 1963: 34), not examined. The type material could not be located at BMNH (J. Beccaloni, pers. comm.).

Synonymies:
Theridion dubiosum Keyserling, 1891: 187, pl. 6, fig. 133, ♂.
Anelosimus dubiosus: Levi, 1963: 34; Levi & Smith, 1983: 277, fig. 4, ♂ Gonzaga & Santos, 1999: 432, figs 1–3, ♀ Platnick, 2006.

Etymology: Keyserling (1891) did not explain the species epithet, but it seems clear it reflects his uncertainty about its generic placement.

Diagnosis: The male is readily distinguished from most other *Anelosimus* by the shape of the cymbium extending beyond the alveolus and a half-moon-shaped Eb-process (Fig. 7K, L) (not a tegular process as suggested by Gonzaga & Santos, 1999: 432). It differs from *A. jabaquara* by the complex embolus with a very thin distal spiral (Fig. 7K, L). Females closely resemble those of *A. jabaquara*, and species of the *jucundus* and *studiosus* groups. The epigynal plate of *A. dubiosus* is larger than in most other *Anelosimus* (Fig. 7M), similar to *A. domingo.* Females can only be reliably separated by examination of the internal genitalia where *A. dubiosus* differs from others by the complex trajectory of the elongated copulatory ducts (Fig. 7N; see also Gonzaga & Santos, 1999: fig. 3).

Male (IAIB01): Total length 3.19. Prosoma 1.63 long, 1.34 wide, 0.83 high, yellowish-brown. Sternum elongate, 0.99 long, 0.66 wide, extending between coxae IV, dusky brown. Abdomen 1.82 long, 1.22 wide, 0.99 high. Pattern as in other *Anelosimus*. Eyes subequal, about 0.12 in diameter. Clypeus height about 2.3 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.02, patella 0.65, tibia 1.89, metatarsus 1.69, tarsus 0.75. Femur long and thick about 6 times longer than wide, metatarsus I about 15 times longer than wide. Leg formula 1243, leg 1 by far the longest. Leg base colour yellowish-brown, distal tip of all segments darkened, femora darkened except from base, femur I darkest. Tarsal organs central (around 0.50) on tarsi I, proximal (0.35–0.40) on II–IV. Four to seven small trichobothria dorsally on all tibia, 4–6 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia.

Palp as in Figures 7K, L, 13A–F. It is evident in the expanded palp that the moon-shaped, grooved, distal sclerite is a process of the embolus, being connected to the Eb, via a membranous plate. It is not a process of the tegulum as suggested by Gonzaga & Santos (1999: 432). The term embolic division b-process (Ebp) is here suggested for this sclerite; it differs from the Eb-ridge in being membranously connected to the Eb.

Female (IA40537): Total length 3.77. Prosoma 1.63 long, 1.24 wide, 1.01 high, light brown to yellow. Sternum 1.01 long, 0.84 wide, extending between coxae IV, dusky brown. Abdomen 2.34 long, 1.82 wide, 1.82 high. Pattern as in other *Anelosimus*. Eyes subequal, about 0.11 in diameter. Clypeus height about 2.5 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.89, patella 0.55, tibia 1.63, metatarsus 1.40, tarsus 0.72. Femur about 6 times longer than wide, metatarsus I about 12 times longer than wide. Leg formula 1423 with legs 2 and 4 subequal. Leg base colour yellowish, distal tip of some or all segments (minus tarsi) slightly darkened, also median ring like bands on femora. Tarsal organs slightly distal (0.50–0.55) on tarsus I, proximal (0.35–0.45) on II–IV, most proximal on III. Four to six small trichobothria dorsally on all tibia, 4 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.45), absent on metatarsus IV. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 7M–O, 14A; see also Gonzaga & Santos (1999: figs 2–3).

Variation: Male total length 3.02–3.40, prosoma length 1.50–1.69, first femur 1.92–2.15. Female total length 3.80–4.70, prosoma 1.23–1.51, first femur 1.81–2.11. Coloration of legs varies in preserved specimens depending on the extent of darker markings on segment tips. The trajectory of the female copulatory duct varies slightly between specimens. In one male specimen the palps were distinctly asymmetRICA. The right palp was 'normal' with a clearly grooved Eb-process (see Figs 7L, 13E). The left palp, however, lacked the groove, the Eb-process instead was a simple thin plate. The left palp otherwise appeared normal, apart from the tip of the E, which was broken off.

Additional material examined: BRAZIL. São Paulo, Serra do Japi, Jundiaí [23°15′0″S, 47°0′0″W], 29.i.1990, *c.* 1000–1100 m (E. S. A. Marques, MCZ), 1♂ [IA070201]; 1♂ [IA070301]; 24.i.1990 (IB), [IAIB01]; Parque Estadual da Serra do Japi [23°11′0″S, 46°52′0″W], 13–16.xi.1997, *c.* 1000–1100 m (M. O. Gonzaga, IB), 1♂, 12♀ (in very poor condition) [IA40537].

Distribution: Only known from Brazil from altitudes of 900–1100 m (Fig. 63B).

Natural history: *Anelosimus dubiosus* make typical *Anelosimus* sheet-nests with leaves as retreats and with knock-down threads to intercept prey (Marques *et al*., 1998). Both the sheet and the retreats are spun with non-sticky silk, but according to Marques *et al*. (1998) the knock-down threads of *A. dubiosus* and *A. jabaquara* are adhesive. This contrasts with reports on other species with similar web structure but presumed to have no sticky silk in the web. Whether *A. dubiosus* and *A. jabaquara* are unique in this respect is unclear; perhaps further and more detailed web studies of other species will likewise find adhesive KD-threads.

Anelosimus dubiosus has been characterized as 'subsocial', but its social structure is clearly intermediate between 'typical' subsociality and sociality (Table 2). Colonies are made with one to several adult females, containing up to around 200 individuals. Unlike most subsocial species, the majority of *A. dubiosus* individuals stay in their natal colony after maturing, but unlike typical social species a few individuals always disperse. Sex ratio bias is also intermediate with about 3.2 females per male.

Anelosimus dubiosus, similar to the sympatric *A. jabaquara*, is univoltine with seven instars (plus one inside egg sac) and a synchronous colony development. Females lay egg sacs with 5–47 eggs and individually guard their own egg sacs in multi-female webs. However, unlike *A. jabaquara*, females show relatively little aggression towards conspecific females, and for example did not show any aggression to introduced (unrelated) females in a study by Marques *et al*. (1998). *Anelosimus dubiosus* juvenile broods mix at the second instar and are then fed by regurgitation, indiscriminately by any female (or even older juveniles) in the nest. All nest members (excluding adult males) from second instar on participate in the activities of the nest. The second instar juveniles help with web construction, and join prey catching after larger females have attacked the prey first. Female start dying as juveniles reach the third instar.

Anelosimus dubiosus females showed less aggression to introduced *A. jabaquara* females than vice versa (Marques *et al*., 1998). *Anelosimus jabaquara* dropped into *A. dubiosus* nest even started hunting with them, while *A. dubiosus* females were immediately attacked when introduced into *A. jabaquara* nests.

ANELOSIMUS EXIMIUS (KEYSERLING, 1884)
(FIGS 16–18, 64C, 66C)

Types: One male, 20 females, and one juvenile syntypes from the Amazon River, in HDO, in the Rev. Cambridge collection, examined. Additional syntypes from Northern Grenada, West Indies, and from Pará, Brazil, in MHN, in the Simon Collection, not examined. As syntypes are located in more than one collection, and include specimens that are not recognizable (juveniles and some females in bad condition) I here designate the male from the Amazon river syntype-series as a LECTOTYPE (in HDO), the remaining specimens of the series are designated as PARALECTOTYPES.

Synonymies:
Theridium eximium Keyserling, 1884, 1: 45, pl. 2, fig. 25, ♂♀
Theridium eximium: Simon, 1894a, 1: 548; 1903, 2: 989; Petrunkevitch, 1911, 29: 195; Comstock, 1912: 352; 1940: 366; Mello-Leitão, 1940a, 2: 176, 1940b, 2: 34; 1941, 13: 250; 1943, 37: 169; 1948, 20: 157; Roewer, 1942, 1: 492.
Anelosimus socialis Simon, 1891, 11, pl. 2 web, ♂♀ McCook, 1894, 3: 39, fig. 35. Type from Venezuela, probably lost (see Levi, 1956).
Anelosimus eximius: F. O. P.-Cambridge, 1902, 2: 394, pl. 37, figs 12, 13, ♂♀ Mello-Leitão, 1943, 3: 313; Gertsch, 1949, 167; Archer, 1950, 30: 22; Levi, 1956, 75: 413, figs 11–17, ♂♀ 1963, 82: 34; Stejskal, 1976, 26: 344, figs 4.3, 5.1–5.3 ♂♀ (not recognizable from figures); Coddington, 1990, 496: 18, fig. 94, ♂ Platnick, 2006; Agnarsson, 2004, figs 17–19, 91C-D, 93A, 94G, ♂♀.

Diagnosis: In life the abdomen and prosoma of both sexes are conspicuously orange or reddish, more so than in most other *Anelosimus*. Males can be easily distinguished by the large bulky embolus (Figs 16A, B, 17A–F). Females may be separated from others by the small spermathecae and the narrow epigynal plate (Fig. 16C, D).

Etymology: Keyserling (1884) did not explain the species epithet, but *eximius* is Latin for superb, or extraordinary.

Life specimens: As in most *Anelosimus*, both sexes have an orange to red prosoma, abdomen pinkish to orange/red with a red folium and dark brown legs. This coloration is largely lost in preserved specimens.

Male (IA111401): Total length 3.05. Prosoma 1.30 long, 1.00 wide, 0.80 high, light orange or yellow, eye region pale orange with rest of cephalic area greyish, with a narrow rim slightly darker. Sternum 0.80 long, 0.70 wide, extending between coxae IV, brownish-yellow, mostly covered by dusky grey dots, darker around the rim centrally. Abdomen 1.85 long, 1.05 wide, 1.10 high, light grey with a dark grey dorsal longitudinal notched folium (Fig. 16E). Eyes subequal, about 0.09 diameter. Clypeus height about 2.6 times AME diameter. Chelicerae with one large and two small prolateral teeth, three or four denticles retrolaterally, sometimes two denticles and a larger base, bearing three denticles. Leg I femur 2.15, patella 0.55, tibia 1.95, metatarsus 1.85, tarsus 0.85. Femur I about 11 times longer than wide, tibia I about 18 times longer than wide, thickening towards distal end. Leg formula 1243. Leg base colour pale yellow, femur, patella and distal tip of tibia and metatarsus covered with dusky grey dots. Two parallel pale yellow streaks distally on ventral side of femur I, may be only one streak or no streak on other femora. Tarsal organ central (0.50) on I, proximal on II (0.45), III (0.40), and IV (0.35). Five to six small trichobothria dorsally on all tibia, 5 on tibia I and III. Trichobothria on metatarsus I (0.45), II (0.40) and III (0.40) proximal, absent on IV. Two retrolateral and one prolateral trichobothria on palpal tibia. Palp as in Figures 16A, B, 17A–F.

Male lectotype, total length 2.93, prosoma 1.37, first femur 2.02.

Female (IA111401): Total length 4.60. Prosoma 2.00 long, 1.35 wide, 1.15 high, light orange or yellow, posterior part of cephalic area greyish, a narrow rim slightly darker. Sternum 1.10 long, 0.95 wide, extending between coxae IV, base-colour brownish-yellow, mostly covered by dusky grey dots, a bit lighter than in male, with a darker rim around edge. Abdomen 2.75 long, 1.65 wide, 2.00 high, light grey with a dark grey dorsal longitudinal notched folium. Eyes subequal about 0.13 in diameter. Clypeus height about 2.6 times AME diameter. Chelicerae with one large and two small prolateral teeth and a prolateral denticle, three or four denticles retrolaterally. Leg I femur 2.75, patella 0.80, tibia 2.50, metatarsus 2.45, tarsus 1.00. Femur I about 8 times longer than wide, tibia I about 13 times longer than wide, thickening towards distal end. Leg base colour pale yellow, femur and patella covered with dusky, light grey, dots, much lighter than male. Distal tip of tibia, metatarsus and sometimes patella dark grey. Indistinct parallel pale yellow streaks distally on ventral side of femur I, may be only one streak or no streak on other femora. Tarsal organ distal (0.55) on I–II, proximal (0.45) on III–IV, distal (0.85) on palpal tarsus. Five to six small trichobothria dorsally on all tibia, 5 on I and III. Trichobothria proximal (0.40) on metatarsi I–III, absent on IV. Epigynum as in Figures 16C, D, 18D. Seminal receptacles clearly showing through cuticle (Fig. 16C), fertilization duct lead to a very complex folded membrane, this structure is still poorly understood (Fig. 16D; see also Levi, 1956: fig. 12).

Variation: Male total length 2.80–3.20, prosoma 1.20–1.40, first femur 1.95–2.30. Female total length 3.50–5.20, prosoma 1.30–2.20 in length, first femur 1.82–2.90. Denticles on retrolaterally on chelicera 3–5, sometimes 2–3 of the denticles sharing a large base. Variation in denticle number can be within a single specimen (left and right side differ). Females in a colony from Madre de Dios, Peru, ranged from 3.50 to 5.10 in total length.

Additional material examined: BOLIVIA. El Beni, 18 mi. N. of Yucumo [14°55′0″N, 67°5′0″W], 22.xi.1989 (C. Griswold & J. Coddington, NMNH), 18♂, 50♀ [IA40555]; Estacion Biologica Beni, along Río Mattos, approx. 3 km SSW of Est. el Porvenir (14°47′0″N, 66°15′0″W), 15–16.ix.1987 (J. Coddington & S. Larcher, NMNH), 2♂, 2♀ [IA40645]. La Paz, Río Heath [12°29′0″S, 68°38′0″W], 19.vi.1987 (I. Bohorquez, MHNSM), 4♀ [IA40593]. BRAZIL. Acre, Rio Purus W of Sena Madueira, Boca de Chandless [9°4′2″S, 68°40′1″W], 5.ix.1973 (B. Patterson, MCZ), 2♀ [IA080201]. Amazonas, Tabatinga [4°14′0″S, 69°55′0″W], 12.vii.1991, *c.* 80 m, hand collected (J. Vidal, MCP), 5♀ [MCP04]; [4°14′0″S, 69°56′0″W], 12.vii.1991, *c.* 80 m (J. Vidal, MCP), 5♀ [IA40608]; Reserva da Campina, Manaus [1°40′0″S, 60°50′0″W], 1.iii.1992, *c.* 30 m, hand collected (A. A. Lise, NMNH), 1♂, 12♀ [MCP0801]; Manaus [3°7′0″S, 60°0′0″W], 28.xi.1985 (T. J. Henry, NMNH), 20♀ [IA40647]; *c.* 80 km N. of Manaus, Colosso Reserve [2°24′0″S, 60°9′0″W], 1989–1992 (H. G. Fowler, MCZ), 1♀ [IA40665]; 1♀ [IA40670]; *c.* 80 km N. of Manaus, Dimona Reserve [2°24′0″S, 60°3′0″W], 1989–1992 (H. G. Fowler, AMNH), 1♀ [IA40758]; *c.* 80 km from Manaus, Cabo Frio Reserve, 11.v.1989 (H. G. Fowler *et al*., MCZ), 1♀ [IA40759]. Mato Grosso, 260 km N. of Xavantina (12°49′0″S, 51°46′0″W), ii–iv.1969, 400 m (MCZ), 4♀ [IA080101]; Chapada dos Guimaraes (15°26′0″S, 55°45′0″W), 17.xi.1982 (W. *L.* Overal, NMNH), 1♀ [IA1107]; 12.vi.1991, *c.* 700 m, hand collected (J. Vidal, NMNH), 1♂, 2♀ [MCP12]. Mato Grosso do Sul, Fazenda San Carlos and Fazenda San Sebastian da Vagaria, 31 km NW. of Marilandia [14°10′0″S, 57°12′0″W], 7.x.1990 (C. Sobrevilla, NMNH), 1♂, 10♀ [IA40648]. Pará, Reserva Biologica do Rio Trombetas (91°3′0″S, 56°45′0″W), 20.viii.1979, hand collected (J. Grazia, NMNH), 6♀ [MCP11]; Ilha de Cotijuba [1°12′0″S, 48°32′0″W], 26.vii.1977 (R. F. da Silva, MP), 50♀ [IA40567]. COLOMBIA. Meta, Pto. Lieras, Lomalinda (3°18′0″N, 73°22′0″W), 300 m (B. T. Carrol, MCZ), 1♂, 2♀ [IA40762]; 19.i.1985, 300 m (B. T. Carrol, MCZ), 2♀ [IA40770]. Putumayo, Río Putumayo nr. Pto. Asis (0°31′0″N, 76°31′0″W) (W. Eberhard, MCZ), 1♀ [IA0218]; Puerto Asís, Río Putumayo [0°31′0″N, 76°29′0″W] (W. Eberhard, MCZ), 2♀ [IA022801]; 1♀ [IA031901]. Valle, Bajo Calima, Buenoventura [3°52′0″N, 77°2′0″W], 16–17.iii.1967, *c.* 0–1 m (R.B. Root & W.*L.* Brown, MCZ), 1♀ [IA052201]; Anchicaya [3°37′7″N, 76°54′48″W], xii.1976, 400 m (W. Eberhard, MCZ), 1♀ [IA080301]; Anchicayá [3°44′0″N, 77°0′0″W] (MCZ), 1♀ [IA40664]. Vaupés, Mitú [1°15′0″N, 70°13′0″W], ii.1975, 200 m (P. A. Schneble, MCZ), 2♀ [IA40663]. ECUADOR. Morona-Santiago, Taisha [2°20′0″S, 77°27′0″W], 16–21.vii.1975, 530 m (N. Engler, MCZ), 1♀ [IA080501]; Codrillera de Cutucú, road from Patuca to Santiago (2°48′20″S, 78°14′46″W), 13.vii.2004, 1000 m (I. Agnarsson *et al*., NMNH), ♂♂♀♀ [IAV06]. Napo, Estación Biológica Jatun Sacha (1°4′1.20′S, 77°37′1.20″W), 29.v.200, 400 m, forest understory (K. Powers, NMNH), 1♂ [IAV05]. Sucumbíos, Putumayo, Río Cuyabello, near Tipishca (0°15′0″S, 76°9′0″W), 29.ix.1994 (L. Avilés, NMNH), 1♂ [IALA01]; 1♂, 1juv [IA40566]. FRENCH GUIANA. Cayenne, Cayenne, pistes ONF km 17 [4°56′0″N, 52°19′0″W], 11.vi.1986 (NMNH), 8♂, 10♀ [IA40642]; Montagnas Kaw, nr. Camp Caiman, *c.* 27 km SE. of Roura (4°33′0″N, 52°9′0″W), 8.viii.1988, 100–300 m (S. Marshall, NMNH), 1♂, 2♀, 1juv [IA40649]. GUYANA. Upper Takutu-Upper Essequibo, bank of Essequibo river 4.42 km S of Gunns landing (1°36′46″S, 58°38′15″W), 5–14.vii.1999, hand collected, 240 m (J. Coddington *et al*., NMNH), 20♀ [IA1001]; 3♂, 50♀ [IA1002]; 5♂, 50♀ [IA111401]. Potaro-Siparuni, Kaieteur falls (5°9′0″N, 59°27′0″W), 25.vii.1999, hand collected (I. Agnarsson, NMNH), 5♂, 5♀ [IA110201]. Cuyuni-Mazaruni, Bartica [6°24′0″N, 58°37′0″W], 16.vii.1999, *c.* 0–10 m (I. Agnarsson, NMNH), 15♀, 48♀ [IA40565]. PANAMA. Bahía, 7.v.1973 (F. Vollrath, NMNH), 1♀ [IA0217]. PERU. Amazonas, Alto Río Comainas, puesto de vigilancia 22 – Falso Paquisha [3°58′0″S, 78°25′0″W], 1.xi.1987, 850 m (D. Silva, MHNSM), 2♂, 43♀, 15juv [IA40584]; 2♂, 12♀, 20juv [IA40586]; 25.x.1987, 850 m (D. Silva, MHNSM), 10♀, 10juv [IA40587]. Huánuco, km 35.5 de la ‘cantino’ Surgono-Pahazu [9°26′0″S, 74°57′0″W], 3.vii.1986 (D. Silva, MHNSM), 4♂, 10♀, 5juv [IA40595]; Dantas, La Molina, SW. of Puerto Inca (9°38′0″S, 75°0′0″W), 18.v.1987, 270 m (D. Silva, NMNH), 1♂, 2♀ [IA40643]; 24.v.1987, 270 m (D. Silva, MHNSM), 15♀, 5juv [IA40588]; 4♀ [IA40591]; 21.v.1987, 3♂, 10♀ [IA40597]. Loreto, Jenaro Herrera (4°55′0″S, 73°45′0″W), 27.viii.1989, 80 m (D. Silva, MHNSM), 1♂, 1♀ [IA40543]; 28.viii.1989, 80 m, 2♀ [IA40544]; 24.viii.1989, 3♀ [IA40549]. Tambopata, Madre de Dios, Zona Reservada Tambopata (12°50′0″S, 69°17′0″W), 5.vi.1988, hand collected, 290 m (J. Coddington, NMNH), 20♀ [IA1101]; 10♂, 10♀ [IA110101]; 5♂, 5♀ [IA110501]; 10.vi.1988, 290 m (J. Coddington, NMNH), 1♂ [IA40407]; 1♂ [IA40410]; 8.vi.1988, 2♀ [IA40411]; lagoon cocococha (12°50′0″S, 69°17′0″W), 14.vi.1988, 290 m (J. Coddington, NMNH), 5♂ [IA40644]; Pasco, Qbda. Castilla, NW. of Iscozacia (10°10′0″S, 75°15′0″W), 7.xi.1987 (D. Silva, MHNSM), 1♀ [IA40553]; Zona Reservada de Manu, Río La Torre and Río Tambopata [12°50′0″S, 69°17′0″W], vii-xii.1979 (*A.* Rypstra, NMNH), 3♀ [IA40413]; Reserva Cuzco Amazonico (12°33′0″S, 69°3′0″W), 18.vii.1989, 200 m (D. Silva, MHNSM), 9♂, 9♀, 2juv [IA40547]; Lago Sandoval (12°33′0″S, 69°3′0″W), 26.vi.1989 (D. Silva, MHNSM), 1♂, 3♀ [IA40550]. SURINAM. Brokopondo, Browns Berg [5°0′0″N, 55°27′0″W] (MCZ), 1♀ [IA080401]; 20.ii.1982 (D. Smith, MCZ), 1♀ [IA080801]; 1♀ [IA40669]; 1♀ [IA40671]. VENEZUELA. Monagas, Caripe [10°10′0″N, 63°30′0″W], 15.xii.1976 (H. Stejskal, MCZ), 2♀ [IA033101]; 20.xi.1977, 3♀ [IA080901]; outside Cueva del Guacharo [10°10′0″N, 63°30′0″W], 11.ii.1984, 1065 m (J. Coddington, NMNH), 50♀ [IA40564]; 1♂, 2♀ [IA40646]; Guacharo Cave [10°9′0″N, 63°32′0″W], 11.ii.1984, 1000 m (J. Coddington, NMNH), 3♀ [IA40554]. San Agustin (NMNH), 10♀ [IA40527].

Distribution: From Panama and the Caribbean to Peru and Brazil (Fig. 64C). Ranges in altitude from 0 to 1100 m, but most records from 0 to 400 m.

Natural history: *Anelosimus eximius* is the most extensively studied *Anelosimus* species, and copious literature is available on the natural history and various aspects of the biology of this species [e.g. Simon, 1891; Brach, 1975; Stejskal, 1976; Tapia & De Vries, 1980 (misidentified as *A. jucundus*, see Vollrath & Windsor, 1983); Buskirk, 1981; Overal & Ferreira da Silva, 1982; Vollrath, 1982, 1986a, b; Vollrath & Rohde-Arndt, 1983; Vollrath & Windsor, 1983; Christenson, 1984; Nentwig, 1985; Smith, 1986; Avilés, 1986, 1987, 1993, 1997, 1999; Pasquet & Krafft, 1989, 1992; Cangialosi, 1990a, b; Avilés & Maddison, 1991; Krafft & Pasquet, 1991; Rypstra, 1993; Venticinque *et al.*, 1993; Leborgne *et al.*, 1994; Fowler & Venticinque, 1996; Smith & Hagen, 1996; Pasquet *et al.*, 1997; Avilés & Gelsey, 1998; Avilés & Tufiño, 1998; Saffre *et al.*, 1999, 2000; Avilés *et al.*, 2001].

Anelosimus eximius is most common in lowland tropical rain forests and ranges from Panama to southern Peru and Brazil (Levi 1963). Nests are typically with a basket-shaped sheet enforced with dead leaves and debris, with aerial threads (flight interceptors) that can reach several metres up to the canopy (Fig. 66C). Very large nests may lose the typical shape and appear more irregular. Although single-female nests occur commonly, this is a predominantly social species. Webs can contain up to several tens of thousands of individuals with extensive co-operation (Avilés, 1992; Venticinque *et al.*, 1993; Avilés & Tufiño, 1998), and high intraspecific tolerance with apparently absence of nest-specific recognition mechanisms (Tapia & de Vries, 1980; Avilés & Tufiño, 1998).

When the web is disturbed, e.g. shaken vigorously, or attacked by a mammal seeking food, *A. eximius* responds in an unusual way, not recorded for other species. Swarms of spiders appear from their retreats, run towards the edge of the colony, and jump off (Vollrath & Windsor, 1983; my pers. observ.). Apart from being a fleeing mechanism, this probably represents nest defence, as they generally jump in the direction of the disturbance, and bite aggressively if they land on the intruder.

Sex ratio is strongly biased with about 10% of subadults and 9% of embryos being males (Tapia & de Vries, 1980; Avilés, 1986; Avilés & Maddison, 1991).

Colonies in the forest understorey can contain a few thousand individuals, while in the canopy nests can cover crowns of entire trees and contain tens of thousands of spiders (Christenson, 1984; Avilés, 1992; Venticinque *et al.*, 1993). Each generation cycle is about 8 months (Avilés, 1986). Average colony life is approximately five generations [but very variable as extinction is stochastic (Avilés, 1992)], each generation occupying and enlarging the native nest until the colonies either proliferate or become extinct. Parent and offspring generations overlap by approximately 3 months, but parents usually die before their offspring reach reproductive maturity.

Colony size and survival depend on many factors. While offspring survival increases with colony size, individual female reproductive output is highest at intermediate colony size, and risk of parasitism is higher the larger the colony (Avilés & Tufiño, 1998). Colonies typically proliferate at a large colony size (over 1000 individuals) and may form sister colonies (usually close to the parent colony) via budding or by propagules of one to several gravid females (Vollrath, 1982; Avilés, 1992). The success rate of the propagules is as low as 10% or less for single females, but increases with the size of the propagule (Vollrath, 1982; Avilés, 1992; Venticinque *et al.*, 1993). Colony extinction is frequent and has been estimated at 21% per generation in the forest understorey (Avilés, 1992), and even higher in the forest edge (Venticinque *et al.*, 1993). Allozyme electrophoresis has corroborated field observations suggesting that each colony constitutes an isolated endogametic lineage (Vollrath, 1982; Smith, 1986; Avilés, 1992; Smith & Hagen, 1996).

Brach (1975) offered evidence that sociality in *A. eximius* improves efficiency of catching large prey. Rypstra (1993) fed *A. eximius* in the lab prey of different size (fruit flies vs. house flies). Groups fed smaller flies (fruit flies) had a higher number of individuals reaching maturity, but those fed house flies that reached maturity were larger and produced more egg sacs. Small prey was attacked by individuals, larger prey by groups. Large prey items (or concentrated food resources) thus result in a less even distribution of food, allowing some members to dominate. Based on this, Rypstra (1993) suggested that this puts the species 'on the verge of eusociality'.

About 25% of egg sacs are parasitized on average and the risk increases with colony size (Avilés &

Tufiño, 1998). The variance is great in the percentage of egg sacs parasitized, and can reach an amazing 100%, but generally very small colonies have no parasites, whereas larger ones usually do.

Anelosimus eximius nests typically contain various kleptoparasitic organisms. Among the most notable are the mirid true bugs *Ranzovius* (Henry, 1984, 1999). *Ranzovius fennahi* Carvalho appears to be closely associated with *A. eximius*, but *R. moerenas* (Reuter) has also been found in their webs (pers. obs., identified by T. Henry). Several species of the argyrodine spider genus *Faiditus* (e.g. Cangialosi, 1990a, b) kleptoparasitize *A. eximius* webs. *Faiditus ululans* seems to specialize on *A. eximius* nests (Cangialosi 1990a, b). Other argyrodines known to occur in nests of *A. eximius* include *F. caudatus* and *F. alticeps* (Keyserling). The latter has not previously been associated with *Anelosimus*. In a nest close to Kaieteur Falls, Guyana, measuring about 1 m in diameter *F. alticeps* kleptoparasites were abundant (10 collected in a superficial search). A single male of *F. amplifrons* was found in a nest from Peru (my pers. obs.); *F. amplifrons* apparently specializes on *Theridion nigroannulatum*, another social theridiid sympatric with *A. eximius* in Peru and Ecuador.

Other commensal organisms in *A. eximius* nests include lepidopteran larvae, ants and anyphaenid and salticid spiders (Robinson, 1977; Tapia & de Vries, 1980). Several orbweaving spiders, including uloborids and araneids, also build their webs attached to *Anelosimus* nests.

THE *JUCUNDUS* GROUP

Diagnosis: Males of the *jucundus* group can be separated from the related *studiosus* group by a large, globose embolic division b (e.g. Fig. 19A, G, J) that is distally much broader than in species of the *studiosus* group. The basal lobe of the embolus always surpasses the hood of the subconductor, whereas it is hooked in it, or orientated towards it in the *studiosus* group. Epigyna are very similar among species, and to those of the *studiosus* group, but differ from the latter in the strongly sclerotized part of the copulatory ducts extending clearly beyond (ectal to) the ectalmost margin of the spermathecae (Fig. 27F, G). The external epigyna in the *jucundus* group are always strongly ridged (e.g. Fig. 19C, H, M), whereas they range from weakly to strongly ridged in the *studiosus* group. Species of the *jucundus* group are generally larger than those of the *studiosus* group, although the overlap is considerable. Palpal organs and epigyna are similarly larger in the *jucundus* group than in the *studiosus* group.

Description: Males with a large embolus and embolic division b, together covering the entire ventral portion of the palp (e.g. Fig. 19A, G, K). The basal lobe of the embolus surpasses the hood of the subconductor. Females with strongly ridged epigynal plates, and internally the sclerotized portion of the copulatory duct extends beyond (ectal to) the ectalmost margin of the spermathecae (Fig. 27F, G).

Phylogenetics: The *jucundus* group (*A. jucundus sensu* Levi, 1956, 1963) monophyly is supported by two unambiguous synapomorphies with perfect fit to the cladogram: elongated theridiid tegular apophysis distal branch (**53**-1, Fig.19A), and shallow embolus-distal hematodocha grooves (**70**-1, Fig. 20C).

Composition: As with *A. studiosus*, F. O. P.-Cambridge's (1902) and Levi's (1956) concept of *A. jucundus* included several synonymies and bountiful geographical variation. Likewise, recent work discloses behavioural differences and breeding barriers (under laboratory conditions) between some geographically separate populations (Tapia & De Vries, 1980; Nentwig & Christenson, 1986; Avilés & Gelsey, 1998; Bukowski & Avilés, 2002; L. Avilés, pers. comm.). I recognize five species of the *jucundus* species complex here: *A. arizona*, *A. baeza*, *A. jucundus*, *A. octavius* and *A. puravida*.

Distribution: From south-western USA bordering Mexico, to Brazil (Figs 63C, 64B, D). Most speciose in Ecuador and Mexico particularly at altitudes of 1000 m or above.

Natural history: Most species of the *jucundus* group are predominantly subsocial (*A. arizona*, *A. baeza*, and probably *A. octavius* and *A. jucundus*) while *A. puravida* appears to be social. Level of sociality varies within species in *A. baeza*, with some populations forming multiple female nests while others form single female nests.

***ANELOSIMUS ARIZONA* SP. NOV.**

(FIGS 19A–E, 20–22, 64B)

Types: Male holotype from Huachuca mountains, Arizona, USA, iv.1989, Avilés & Maddison, deposited in NMNH [IA40621]. Female and male paratypes from Garden Canyon, Huachuca mountains, Arizona, *c.* 31°33′N, 110°17′W, *c.* 1600 m, 28.vi.2003, T. Bukowski, deposited in NMNH [IA40622].

Synonymies:

Anelosimus jucundus: (Avilés & Gelsey, 1998: 2138). The authors discuss biology, but specimens are not illustrated, not *A. jucundus* O. P.-Cambridge (vouchers examined).

Anelosimus cf. *jucundus*: (Bukowski & Avilés, 2002: 193; Powers & Avilés, 2003: 727). The authors discuss biology, but specimens are not illustrated, not *A. jucundus* O. P.-Cambridge (vouchers examined).

Etymology: The species epithet is a noun in apposition referring to the type localitie's state.

Diagnosis: Males of *A. arizona* differ from other *Anelosimus* in the *jucundus* group by having an enlarged distal Eb-ridge, being more prominent than in any other *Anelosimus* species (Fig. 19A). Geography apart, I have not found a reliable way of separating females from others of the '*jucundus* group'.

Male (holotype): Total length 4.42. Prosoma 1.95 long, 1.65 wide, 1.42 high, pale yellow to brown, centre and rim darker. Sternum 1.16 long, 1.07 wide, extending between coxae IV, pale yellow, centre darker. Abdomen 2.80 long, 1.90 wide, 2.06 high. Pattern as in Figure 19E. Eyes subequal, about 0.11 in diameter. Clypeus height about 4 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 3.41, patella 0.91, tibia 3.41, metatarsus 3.15, tarsus 1.04, tibia and metatarsus unusually long. Femur about 8 times longer than wide, metatarsus I about 19 times longer than wide, with a ventral row of thick setae. Leg formula 1243. Leg base colour as carapace, femur 1 slightly darker than other leg segments, distal tip of tibia slightly darkened. Tarsal organs slightly distal (0.50–0.55) on tarsus I, central (0.50) on II, proximal (0.40–45) on III–IV. Five to six trichobothria dorsally on all tibia, 5–6 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 19A, B, 20A–F, 21A–G.

Female (paratype): Total length 4.62. Prosoma 2.08 long, 1.57 wide, 1.40 high, yellowish, with cephalic region and rim darker (Fig. 19E). Sternum 1.16 long, 1.04 wide, extending between coxae IV, yellowish, covered with darker spots, rim dark brown. Abdomen 2.73 long, 2.23 wide, 2.31 high. Pattern as in Fig. 19E. AME slightly the smallest, other eyes subequal, about 0.10 in diameter. Clypeus height about 3.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.60, patella 0.81, tibia 1.95, metatarsus 2.18, tarsus 0.91. Femur about 6 times longer than wide, metatarsus I about 12 times longer than wide. Leg formula 1423 with legs 4 and 2 subequal. Leg base colour as carapace, femora slightly darkened, especially at tip. Tips of patella, tibia and metatarsi darkened, tibia also with a darker central ring. Tarsal organs slightly distal on tarsi I–II (around 0.50–0.55), proximal (0.40–0.45) on III–IV. Five to seven small trichobothria dorsally on all tibia, 5–6 on tibia I, 6 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Three trichobothria dorsally on palpal tibia. Epigynum as in Figures 19C, D, 22A, B.

Variation: Carapace and sternum (in preserved specimens) range from unicolorous yellowish or light brown, to having centre and rim darker than rest. Male holotype pale coloured, some males much darker, with distinctly darkened femur I. Male total length from 3.25–5.00, carapace 1.69–2.60, femur I 2.67–4.10. Males from Mexico smaller than any from USA The palps of this species vary in subtle details (compare Figs 20A–F and 21A–G), males from Mexico have a more strongly developed E fork. The size of the male palp also varies, and some specimens have up to about 20% larger palps than that of the holotype. Female total length 4.50–6.18, carapace 2.00–2.47, femur I 2.60–2.99. Size of Mexican females overlaps with those from USA. Apparently populations from the Huachuca mountains and Patagonia mountains (about 40 km apart) differ in behaviour (T. Bukowski, pers. comm.). However, despite much variation, I did not find any consistent differences in their morphology and thus treat them as conspecific here.

Additional material examined: MEXICO. Districto Federal, Pedregal [19°18′0″N, 99°8′0″W], 8.viii.1947, *c.* 2200 m (H. Wagner, AMNH), 2♂ [IA40525]; xi-xii.1943, 2400m (AMNH), 3♀ [cf. IA40518]. Oaxaca [17°3′0″N, 96°43′0″W] (AMNH), 1♂, [IA40520]. Chihuahua, Santa Bárbara [28°26′0″N, 107°23′0″W], 18.vii.1947 (W. J. Gertsch, AMNH), 5♀ [cf. IA40514]. Veracruz, Jalapa City in residential park (19°31′1″N, 96°54′2″W), 17.xi.2003, on *Ficus* sp., 1400 m (T. J. Henry & E. Barrera, NMNH) 1♀, 15juv [cf. IA40528]. USA. Arizona, Patagonia, Sonoita Creek Preserve (31°30′0″N, 110°50′0″W), 27.vi.2003, 1500 m (K. Powers, NMNH), 1♂, 1♀ [IA40557].

Distribution: Only known from Arizona, USA, and Mexico (Fig. 64B). All collections from 1500–2500 m altitude.

Natural history: *Anelosimus arizona* is a univoltine subsocial species, forming mother-offspring associations that persist for several months but break up prior to mating (Avilés & Gelsey, 1998 [identified as *A. jucundus*]; Bukowski & Avilés, 2002; Powers & Avilés, 2003 [identified as *A.* cf. *jucundus*]). The nests are typical basket-shaped sheet webs with intercepting aerial threads extending upwards. Nests occur at the ends of branches, either singly or in clusters. New nests are established by individual subadults, or young adult males and females during the dispersal season (May–August in Arizona). Most individuals disperse at the fifth instar, but between fourth and seventh (adult) and males appear to disperse further. Mating takes place (during July–August in Arizona), typically in the female web, and she shortly thereafter lays a single egg sac containing 21–53 eggs (Avilés & Gelsey, 1998). Maternal care continues until the mother dies (sometimes eaten by her offspring), usually when the offspring are only a couple of moults away from adulthood. Siblings continue to collaborate in the natal nest until dispersal, including co-operative prey capture and prey sharing. However, tolerance and co-operation breaks down with age, and also broke down among juveniles in a laboratory experiment under conditions of crowding or low food supply, when the spiders readily cannibalized each other (Avilés & Gelsey, 1998).

Nest reoccupation occurs by older instar females (subadult or adult) and sometimes two females may reoccupy an old nest (Avilés & Gelsey, 1998). Remaining in natal nest seems to lower the probability of extinction, while dispersal may be a result of resource competition, mate competition and inbreeding avoidance (Bukowski & Avilés, 2002; Powers & Avilés, 2003). Bukowski & Avilés (2002) found that maturation of same-generation female and male kin is asynchronous, resulting in limited inbreeding. They therefore concluded that inbreeding avoidance is not key in *Anelosimus* (see also Powers & Avilés, 2003), but rather that resource competition seems most important.

Avilés & Gelsey (1998) reported equal sex ratios prior to dispersal, but distinctly female-biased post-dispersal sex ratios. They attributed this to male dispersal beyond the local area, resulting in greater cost of dispersal for males.

In Mexico, the mirid *Ranzovius crinitus* Distant (see Henry, 1984) has recently been collected (by T. J. Henry, pers. comm.) in the nests of *A. arizona*. Henry (1999) also reported *R. crinitus* in webs of *Anelosimus* sp., quite likely also *A. arizona*.

ANELOSIMUS JUCUNDUS (O. P.-CAMBRIDGE, 1896)
(FIGS 19F–H, 23–24, 64B)

Types: Male types, Mexico, Omilteme, col. Godman & Salvin BM1905.4.28.1811-30 (part), in BMNH, examined. O. P.-Cambridge (1896: 166–167) did not designate types, but later F. O. P.-Cambridge (1902: 394) indicated a male type. F. O. P.-Cambridge (1902: fig. 14a–d) illustrated two different specimens and the type vial contains two heterospecific males. One of them matches the original drawing of O. P.-Cambridge (1896, pl. 21, fig. 13) and is here designated as a LECTOTYPE (Fig. 19F, G). The other specimen belongs to *A. octavius* sp. nov., which is here described (see taxonomic history below).

Synonymies:
Theridion jucundum O. P.-Cambridge, 1896: 166, pl. 21, fig. 13, ♀.
Theridion jucundum: Petrunkevitch, 1911, 29: 198; 1925, 27: 67.
Anelosimus jucundus: F. O. P.-Cambridge, 1902: 394 (in part), pl. 37, figs 14a, 15, ♂♀ Levi, 1956: 417 (most of Levi's text and figures do not refer to *A. jucundus* O. P. Cambridge, see *A. octavius* and *A. baeza*); Levi, 1963: 43; Stejskal, 1976: 344, figs 4.4, 5.4, 6.3, ♂♀ (synonymy uncertain, from the figures it is not possible to tell what species Stejskal worked with, but based on the locality (Venezuela) it was most likely *A. baeza*. [Note, however, that some specimens labelled *A. jucundus* by Stejskal are in fact *A. eximius* (pers. obs.).] Platnick, 2006.
Anelosimus studiosus: Bryant, 1940, 86: 311, not *A. studiosus* (Hentz) according to Levi (1956); however, I have not been able to locate the Cuban specimens discussed by Bryant (1940) and thus cannot confirm their identity.

Etymology: O. P.-Cambridge did not explain the etymology, but *jucundus* is Latin for agreeable or merry, possibly referring to the social behaviour of this species.

Diagnosis: Males of *A. jucundus* differ from other *Anelosimus*, except *A. octavius*, by having a distinct ridge ectally on the Eb distal portion facing the embolus base (Fig. 19G). Males differ from *A. octavius* in a more robust embolus fork. I have not found a reliable way of separating females from others of the '*jucundus* group'.

Male (IA40623): Total length 3.25. Prosoma 1.50 long, 1.19 wide, 0.92 high, yellowish-brown, with centre and rim darker. Sternum 0.92 long, 0.76 wide, extending between coxae IV, yellowish-brown with a darker rim. Abdomen 1.89 long, 1.47 wide, 1.58 high. Pattern as in *A. arizona*. Eyes subequal, about 0.11 in diameter. Clypeus height about 2.9 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.28, patella 0.65, tibia 2.11, metatarsus 2.02, tarsus 0.78. Femur about 8 times longer than wide, metatarsus I about 20 times longer than wide. Leg formula 1423. Leg base colour yellowish, with distal tip of all segments darkened, a darker central bands on tibia, and femur I darker than other segments. Tarsal organs distal on tarsi I (0.55–60) and II (0.50–55), proximal III (0.45–50) and IV (0.40). Five to six small trichobothria dorsally on all tibia, 6 on tibia I and III. Trichobothria on metatarsi I–III proximal (about 0.35–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 19F, G, 23A–F.

Female (IA40623): Total length 4.36. Prosoma 1.76 long, 1.45 wide, 1.22 high, yellowish-brown, with centre and rim darker. Sternum 1.17 long, 0.97 wide, extending between coxae IV, brown with a darker rim. Abdomen 2.86 long, 2.15 wide, 2.15 high. Pattern as in male. Eyes subequal, about 0.09 in diameter. Clypeus height about 4.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.28, patella 0.81, tibia 1.95, metatarsus 1.79, tarsus 0.85. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1423. Leg base colour yellowish, with distal tip of all segments darkened, a darker central bands on tibia, and femur I darker than other segments. Tarsal organs distal on tarsi I (0.60–65) and II (0.55–60), proximal on III and IV (0.4–45). Five to six small trichobothria dorsally on all tibia, 5–6 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Epigynum as in Figures 19H, I, 24B.

Variation: Male total length 3.15–3.35, prosoma 1.45–1.55, femur I 2.20–2.28, female total length 4.20–4.55, prosoma 1.70–1.80, femur I 2.20–2.30. A female specimen in very poor condition had a prosoma reaching 2.6 mm, but the identity of the specimen, collected with a male *A. studiosus*, is doubtful.

Additional material examined: COLOMBIA. Antioquia, San Vicente [6°17′0″N, 75°20′0″W], 30.xii.1986, *c.* 2000 m (M.A. Serna, MCZ), 1♀ [IA030301]. COSTA RICA. Puntarenas, Monteverde Cloud Forest Reserve [10°2′0″N, 83°27′0″W], 28.vii.1979, 1500 m (J. Coddington, NMNH), 1♀ [cf. IA40408]. HONDURAS. [approx. country centre 14°50′0″N, 86°43′0″W] (Dyer, AMNH), 1♂ [cf. IA40212]. MEXICO. Chiapas, 5 km W of San Cristobal de Las Casas on HWY 190 (16°44′0″N, 92°41′0″W), 27–28.vii.1983, 2134 m (W. Maddison et. al, MCZ), 1♂ [IA0220]; Lagos de Montebello [16°6′0″N, 91°43′0″W] (CAS), 1♂ [IA40782]. Morelos, Cuernavaca [18°55′0″N, 99°13′0″W], *c.* 1500 m (N. Banks, MCZ), 1♂ [IA010401]. Oaxaca, S of Oaxaca at Monte Alban [17°2′0″N, 96°47′0″W], 22.ix.1989 (T. J. Henry, NMNH), 1♂, 5♀ [IA40623]. Veracruz, Fortín de las Flores [18°54′0″N, 96°59′0″W], vii–viii.1986, *c.* 1000 m (NMNH), 1♀ [cf. IA40636]. PANAMA. Chiriqui, Road between Volcan-Concepcion [8°38′0″N, 82°38′0″W], 28.x.1983, 1021 m (MCZ), 1♀ [IA031001].

Distribution: Mexico – Colombia (Fig. 64B), at altitudes of *c.* 900–2500 m.

Natural history: *Anelosimus jucundus* is reportedly a subsocial species, building single-mother/offspring nests. However, it is not certain that any behavioural studies have actually dealt with ‘true’ *A. jucundus*. The vial label of description series states: ‘Webs abundant on large *Ficus* sp., heavily infested with laurel thrips; two species of the mirid genus *Ranzovius* present.’ The webs were approximately 20 × 20 cm, numerous individual webs tightly grouped (T. J. Henry, pers. comm.). This is consistent with the species being predominantly subsocial.

Nentwig & Christenson (1986) studied ‘*A. jucundus*’ in Panama (likely either *A. jucundus* or *A. baeza*). Occasional nests had more than one adult female, but these appeared not to be co-operating. The spiders seemed to feed mostly on flying ants, cicadina and coleoptera. As in other *Anelosimus* species nests, kleptoparasites were common: *Faiditus caudatus*, *Argyrodes elevatus* and *A. spinosus* have been documented in the webs of ‘*jucundus*-like’ species. Nentwig & Christenson (1986) suggest that their study species is more social than *A. studiosus* which, in Brach’s (1977) study, did not tolerate the presence of other females. Also their species sometimes had more than one generation of spiders in the nest. However, the populations of *A. studiosus* studied by Furey (1998) showed much higher degree of social behaviour.

The species studied by Avilés & Gelsey (1998), Bukowski & Avilés (2002) and Powers & Avilés (2003), in their papers identified as *A. jucundus*, and *A.* cf. *jucundus*, respectively, is *Anelosimus arizona*. Tapia & de Vries (1980) studied ‘*A. jucundus*’ in Ecuador, but given their findings (they discuss a predominantly social species, from a lowland rainforest) the species was almost certainly *A. eximius* (see also Vollrath & Windsor, 1983).

Two kleptoparasitic mirid species live in the webs of *A. jucundus*, *Ranzovius crinitus* and *R. bicolor* Henry. The latter has only been found in nests of *A. jucundus* (T. J. Henry, pers. comm.).

Taxonomic history: Reverend Octavius Pickard-Cambridge (1896: 166–167) described this species presumably based on two males from Mexico. O. P.-Cambridge (1896) did not designate types, but later his nephew Frederick O. P.-Cambridge (1902: 394) indicated a male type. However, he illustrated two different specimens (F. O. P.-Cambridge, 1902, fig. 14a–d); both are in the type vial and are here found to be heterospecific, differing considerably in palpal morphology. I here designate one of them as a LECTOTYPE (Fig. 19F, G), chosen as it matches the original drawing of O. P.-Cambridge (1896, pl. 21, fig 13). The other specimen belongs to *A. octavius* sp. nov. (see F. O. P.-Cambridge, 1902, fig. 14b–d).

Simon (1897) suggested that *A. jucundus* and *A. studiosus* are synonymous due to difficulty of telling the females apart (this would mean the *jucundus* and *studiosus* groups as treated here represent only a single species). F. O. P.-Cambridge (1902: 394) conceded that ‘I am unable as yet to satisfactorily distinguish between the females of *A. jucundus* and

A. studiosus'. He (F. O. P.-Cambridge, 1902: 395) agreed with Simon that 'It is possible, however, that both *T. studiosum*, Hentz, and *T. jucundum*, O. P.-Cambr. (as Simon thinks probable), the varieties here figured, and also those from Bogota, are all one and the same species, the larger and more highly developed examples being *T. jucundum*, the smaller and more slender being *T. studiosum* . . .'. However, another possibility was suggested by F. O. P.-Cambridge (1902: 395) ' [i]t is also possible, on the other hand, that there are several species of these social spiders, and that the varieties above noted may prove to be really good species. I cannot at present reconcile myself to either view, but must be content with giving drawings and descriptions of them'. Levi (1956: 418) closely followed F. O. P.-Cambridge, and remarked on the variation of what he called *A. jucundus*: 'There is considerable variation in the structure of the palpi. The epigynum of a number of specimens (from Michoacan: Pátzacuaro [Mexico]; Guatemala: Yepocapa, Antigua; Costa Rica: San José) lacked the deep groove . . . which usually distinguishes *A. jucundus*. These specimens, however, otherwise resemble this species. It is very likely that this is a distinct but similar species.' It seems clear now that the differences F. O. P.-Cambridge (1902) and Levi (1963) noted between specimens from different localities represented different species rather than intraspecific variation. This conservative and broad formulation of *A. jucundus* by F. O. P.-Cambridge and Levi is understandable given the difficulty of identifying these species. However, it has muddled subsequent work on *Anelosimus*, and as a result of a lack of voucher specimens in particular, it is now unclear what species some literature is referring to.

ANELOSIMUS OCTAVIUS SP. NOV.

(FIGS 19J–N, 25–26, 64B)

Types: Male holotype and female paratype from Costa Rica, San Jose Province, San Antonio de Escazu, 9°56′N, 84°08′W, J. Coddington, in NMNH.

Synonymies:
Anelosimus jucundus: F. O. P.-Cambridge, 1902: 394, pl. 37, figs 14b–d, 15a,b, ♂♀, not *A. jucundus* O. P.-Cambridge; Levi, 1956: 417, figs 27, 34–35, not *A. jucundus* O. P.-Cambridge (note that it is not certain that Levi's illustrations are of *A. octavius*); Stejskal, 1976: 344, figs 4.4, 5.4, 6.3, ♂♀ (note that Stejskal's photographs are not recognizable and it is therefore not clear what species he discusses).

Etymology: Octavius Pickard-Cambridge (1896) described *A. jucundus*, but the type vial contains two heterospecific males, one of which belongs to this new species. The species epithet is a noun in apposition in honour of O. P.-Cambridge.

Diagnosis: Males of *A. octavius* differ from other *Anelosimus*, except *A. jucundus*, by having a distinct ridge ectally on the Eb distal portion (facing the embolus base) (Fig. 19J, K). Males differ from *A. jucundus* in a less robust embolus fork, and in the entire embolus being more roundish. I have not found a reliable way of separating females from others of the '*jucundus* group'.

Male (from Mexico, Omilteme, Godman & Salvin, BM1905.4.28.1811–30 (part), in BMNH): Total length 3.77. Prosoma 1.82 long, 1.65 wide, 1.20 high, brown, slightly darkest centrally. Sternum 1.07 long, 0.91 wide, extending between coxae IV, brown. Abdomen 2.02 long, 1.62 wide, 1.73 high. Pattern as in *A. baeza*. Eyes subequal, about 0.08 in diameter. Clypeus height about 3.8 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.70, patella 0.72, tibia 2.34, metatarsus 2.08, tarsus 2.08. Femur about 8 times longer than wide, metatarsus I about 18 times longer than wide. Leg formula 1243. Leg base colour yellowish to brown, with distal tip of all segments darkened, and femur I dark. Tarsal organs distal (0.65–0.70) on tarsi I–II, proximal (0.40–0.45) on III–IV, most proximal on tarsus III. Four to five small trichobothria dorsally on all tibia, 4–5 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III slightly proximal (about 0.45–0.50), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 19J–L, 25A–F.

Female (paratype): Total length 5.01. Prosoma 1.95 long, 1.60 wide, 1.40 high, light brown. Sternum 1.17 long, 1.07 wide, extending between coxae IV, light brown. Abdomen 2.93 long, 2.84 wide, 2.64 high, pattern as in *A. baeza*. Eyes subequal, about 0.12 in diameter. Clypeus height about 3.5 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.60, patella 0.81, tibia 2.21, metatarsus 2.21, tarsus 0.88. Femur about 5 times longer than wide, metatarsus I about 13 times longer than wide. Leg formula 1423. Leg base colour yellowish with distal tip of all segments darkened, and a central band on tibia and femora, most distinct on femur I. Distal part of femur IV darker than others. Tarsal distal tarsi I (0.65–70) and II (0.60–0.65) proximal on III (0.35–4-) and IV (0.40–0.45). Five to eight small trichobothria dorsally on all tibia, 7 on tibia I, 6 on tibia III, tibia IV, unusually, with 8. Trichobothria on metatarsi I–III proximal (0.35–0.45), absent on metatarsus IV, distal (0.85) on palpal tarsus. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 19M, N, 26A.

Variation: Male total length 3.64–3.77, prosoma 1.8–1.85, femur I 2.70–2.86, female total length 3.77–5.01, prosoma 1.89–1.95, femur I 2.47–2.60.

Additional material examined: COSTA RICA. San José, San Antonio de Escazú (9°56′0″N, 84°8′0″W], 28–31.iii.1989, *c.* 1200 m (J. Coddington, NMNH), 1♂ [IA40532]; 30.iii.1989, holotype and paratype, and additional 1♂, 1♀ [IA40617]; 17.iii.1997 (L. Avilés, NMNH), 1♂, 1♀ [IA40535]. GUATEMALA. Alta Verapaz, Cobán [15°27′0″N, 90°22′0″W], vii.1947, 1300 m (C. & P. Vaurie, AMNH), 1♂ [cf. IA40738]. Chimaltenango, Yepocapa [19°30′0″N, 90°56′0″W], 27.vii.1949, 1400 m (T. H. Farr, AMNH), 1♂ [cf. IA40737]; iii–vi.1935 (E. Elishewitz, AMNH), 1♀ [cf. IA40744]. Quiché, Nebaj [15°24′0″N, 91°9′0″W], 9–10.viii.1947, 2000 m (C. & P. Vaurie, AMNH), 1♀ [cf. IA40739]. MEXICO. Chiapas, San Cristóbal de las Casas [16°44′0″N, 92°38′0″W], 22.vii .1947, 2200 m (C. & M. Goodnight, AMNH), 2♂, 1♀ [cf. IA40733]; 2.ix.1972, 2164 m (C. Mullinex, CAS), 1♂ [IA40784]. Hidalgo, 4 km NE. of Tlanchinol on Highway 105 (21°2′0″N, 98°39′0″W), 14.vi.1983, cloud forest and edge, 1500 m (W. Maddison, MCZ), 1♀ [IA40505]. Guerrero, Omiltemi [17°30′0″N, 99°40′0″W], *c.* 2800 m (Godman & Salvin, BMNH, in vial with *A. jucundus* holotype), 1♂.

Distribution: Mexico, Guatemala, Costa Rica (Fig. 64B), from altitudes of 1000–2800 m.

Natural history: The only information on the natural history of this species is from field label and notes from J. Coddington (pers. comm.). He found adult males and females in individual webs or wandering (males), and thus the species is probably a typical subsocial species with a solitary life phase after dispersal from the natal nest (during the time males are adult).

ANELOSIMUS BAEZA SP. NOV.

(FIGS 27A–M, 28–32, 64D)

Types: Male holotype and female paratype from Tena Road, 17 km S of Baeza, Napo administrative division, Amazon river basin, Ecuador, 0°37′S, 77°53′W, 3.viii.1999, L. Avilés, deposited in NMNH [IALA0601].

Synonymies:
Anelosimus jucundus: Levi, 1956: 417–418 (in part), fig. 26 (possibly also 27, 31–33); Levi, 1963: 35–36 (in part).
Anelosimus cf. *jucundus*: Agnarsson, 2004: figs 20A–F, 21A–G.

Etymology: The species epithet is a noun in apposition based on the name of the type locality.

Diagnosis: Males differ from all other *Anelosimus*, except *A. puravida*, in having an ectal tegular outgrowth (Fig. 27B, C) and in the shape of the Eb, with a distinct basal lobe pointing caudally, and an evenly broad, terminally ridged distal portion (Fig. 27B, C). Morphologically this species is extremely similar to *A. puravida*. Subtle differences in the male palp separate the two species, the ectal tegular outgrowth of *A. baeza* (Tr, Fig. 27B, C) is much broader than that of *A. puravida* (Fig. 27O), the connection of the distal hematodocha with the embolus is smaller. I have not found a reliable way of separating females from others in the *jucundus* group. *Anelosimus baeza* appears to be less social than *A. puravida*, and sex ratio is unbiased, but most likely female biased in *A. puravida*.

Male (holotype): Total length 2.86. Prosoma 1.43 long, 1.12 wide, 0.92 high, brown. Sternum 0.79 long, 0.73 wide, extending between coxae IV, brown. Abdomen 1.56 long, 1.07 wide, 1.04 high. Pattern as in Figure 27H, I, L, M. Eyes subequal, about 0.09 in diameter. Clypeus height about 3.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.92, patella 0.55, tibia 1.76, metatarsus 1.50, tarsus 0.68. Femur about 7 times longer than wide, tibia I about 18 times longer than wide Leg formula 1243 with legs two and four subequal. Leg base colour yellowish, distal tip of tibia I very slightly darker, femur I darker than other femora, their distal tip not noticeably darkened. Tarsal organs slightly distal (around 0.55) on tarsi I and II, proximal (0.40–0.45) on III and IV. Four to eight small trichobothria dorsally on all tibia, 7–8 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 27A–C, 28A–F, 29A–F, 30A–E.

Female (paratype): Total length 4.00. Prosoma 1.82 long, 1.45 wide, 0.99 high, brown. Sternum 1.19 long, 0.86 wide, extending between coxae IV, brown. Abdomen 2.47 long, 1.62 wide, 1.47 high. Pattern as in Figure 27J, K. Eyes subequal, about 0.09 in diameter. Clypeus height about 3.5 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.37, patella 0.72, tibia1 0.95, metatarsus 1.76, tarsus 0.91. Femur about 6 times longer than wide, tibia I about 16 times longer than wide. Leg formula 1423. Leg base colour light brown, tibia I with an indistinct ventral central band. Tarsal organs distal (0.60–0.65) on tarsi I and II, central (0.5) on III, slightly proximal (0.40) on IV, distal (0.85) on female palp, positions vary slightly between specimens. Five to eight small trichobothria dorsally on all tibia, 8 on tibia I, 5–6 on tibia III (variable between sides of the animal). Trichobothria on metatarsi I–III proximal (about 0.40–0.45, absent on metatarsus IV. Three dorsal trichobothria on female palpal tibia. Epigynum as in Figures 27D–G, 31A, but very variable, sometimes more distinctly ridged.

Additional material examined: BRAZIL. Rio de Janeiro, Parque Nacional Tijuca, Paineiras [22°57′0″S, 43°16′0″W], 1.iv.1987 (H. Levi, MCZ), 1♀ [IA0208]; 1♀ [IA0219]. São Paulo, São Paulo botanical garden [23°34′0″S, 46°37′0″W], 10.iii.1985, *c.* 600 m (H. & L. Levi, NMNH), 1♀ [cf. IA0205]; 1♀ [cf.IA0206]; 1♀ [cf. IA40666]; 9.iii.1985, 1♀ [cf. IA081101]; Serra do Japi, Jundiaí [23°15′0″S, 47°0′0″W], 4.ii.1998, *c.* 1100 m (M. O. Gonzaga, NMNH), 1♂, 1♀ [IA40540]. COLOMBIA. Antioquia, La Estrella [7°15′0″N, 75°57′0″W], 24.i.1974, 1720 m (P. Schneble, MCZ), 1♂ [IA0201]; v-vi.1973, 1720 m (P. A. Schneble, MCZ), 1♀ [cf. IA030101]; San Vicente [6°17′0″N, 75°20′0″W], 30.xii.1986, *c.* 2000 m (M. A. Serna, MCZ), 1♂ [IA0213]; 26.xii.1986, picked from leaves (M. A. Serna, MCZ), 1♀ [cf. IA030501]. Huila, 12 km E. of Santa Leticia (2°20′0″N, 76°6′0″W), hand collected (NMNH), 5♂, 1♀ [IA020701]. Valle, Cali-Bitura road (25 km) [3°25′0″N, 76°33′0″W], ix.1975, 1700 m (MCZ), 1♀ [IA023101]; 1♀ [IA022401]; Cali [3°25′0″N, 76°33′0″W], v.1976, *c.* 750 m (W. Eberhard, MCZ), 1♂, 2♀, 1juv [IA031401]; (around house) [3°25′0″N, 76°33′0″W], 28.ii.1973, 1000 m (H. Levi, MCZ), 1♀ [cf. IA022501]; Lago Colima, Río Colima [3°42′0″N, 76°33′0″W], vi.1976, looking up, 1400 m (W. Eberhard, MCZ), 1♀ [IA010201]; Río Calima [3°42′0″N, 76°33′0″W], v.1976, picked from colony (W. Eberhard, MCZ), 1♂ [IA023201]; iv.1976, 1400 m (W. Eberhard, MCZ), 1♀, 4juv [cf. IA031301]; vi.1976, 1400 m (W. Eberhard, NMNH), 1♀ [IA40509]. Mala Valley, 23.iv.1964 (M. Guerovich, CAS), 1♂, 1♀ [IA40780]. COSTA RICA. San José, San Antonio de Escazú (9°56′0″N, 84°8′0″W], 28–31.iii.1989, *c.* 1200 m (J. Coddington, NMNH), 1♂, 2♀ [cf. IA40511]; San José, [9°55′0″N, 84°4′0″W], 1150 m (E. Schmidt, AMNH), 1♀ [cf. IA40734]. ECUADOR. Manabí, Salaite [1°23’29’S, 80°45’29’W], 6.v.1994, hand collected (W. Maddison, MCP), 1♂ [IALA14]; Puerto Lopez (1°32′56″S, 80°48′36″W), 1–5.viii.2004, 5 m (W. Maddison, NMNH), 1♂ [IAV07]. Morona Santiago, km 4 from Limón to Gualaceo, Napo, Amazon river basin, 1.3 km S of Baeza (0°28′0″S, 77°53′0″W), 17.xii.2002 (L. Avilés, NMNH), 1♂ [IA40561]; 10.15 km S of Baeza (0°30′76″S, 77°52′73″W), 17.xii.2002, hand collected (L. Avilés, NMNH), 1♀ [IALA26]; 11.3 km S of Baeza (0°30′0″S, 77°52′0″W), 17.xii.2002, hand collected (L. Avilés, NMNH), 1♂ [IALA25]; 5.6 km S of Baeza (0°28′59″S, 77°52′17″W), 17.xii.2002, hand collected, *c.* 1500 m (L. Avilés, NMNH), 1♂ [IALA21]; 6 km S of Baeza (0°31′0″S, 77°53′0″W), 22.iv.1994, hand collected (V. Roth, MCP), 1♀,1♀ [IALA0801]; Baeza [0°27′0″S, 77°53′0″W], 13.viii.1999 (L. Avilés, NMNH, paratype), 1♀ [IA40625]; Las Caucheras, 16.6 km rd. to Sierra Azul, near Cosanga river (0°37′0″S, 77°55′0″W), 20.viii.1999 (L. Avilés, NMNH), 2♂, 2♀ [IA40560]; 5.3 km on road to Sierra Azul (0°37′0″S, 77°55′0″W), 20.viii.1999, hand collected, 2200 m (L. Avilés, NMNH), 2♂ [IALA28]; Las Caucheras, between Aliso & Cosanga rivers (0°33′5″S, 78°46′0″W), 6.i.2002, hand collected (L. Avilés, NMNH), 1♂ [IALA27]; Las Caucheras (0°37′0″S, 77°55′0″W), 20.viii.1999, hand collected, 2200 m (L. Avilés, NMNH), 2♂, 1♀, 3juv [IALA0401]; 3♂, 1♀, 1juv [IALA0501]; Oritoyacu, 8.4 km S of Baeza (0°29′98″S, 77°72′48″W), 17.xii.2002, hand collected, *c.* 2000 m (L. Avilés, NMNH), 2♂ [IALA24]; Road to Bermejo 0.52, 10 km S. of Baeza (0°30′97″S, 77°53′2″W), 17.xii.2002, hand collected, *c.* 1501 m (L. Avilés, NMNH), 1♂ [IALA23]; 10 km S. of Baeza (0°31′21″S, 77°53′85″W), 17.xii.2002, hand collected, *c.* 1500 m (L. Avilés, NMNH), 1♂, 1♀ [IALA22]; Tena Road, 17 km S of Baeza (0°37′0″S, 77°53′0″W), 3.viii.1997, hand collected, 2200 m (L. Avilés, NMNH, with holotype), 3♂, 2♀ [IALA0601]; 13.viii.1999, hand collected, 2200 m (L. Avilés, NMNH), 1♂, 1♀ [IALA0701]. Pichincha, near El Cisne, N of Pedro Vicente Maldonado (0°8′57.48″N, 79°1′54.12″W), 26.vii.2004, 600 m (I. Agnarsson *et al.*, NMNH), ♂♂♀♀ [IAV08]. Tungurahua, Baños [1°23′0″S, 78°25′0″W], iv.1939,1850–2000 m (W.C. Macintyre, MCZ), 1♂, 2♀ [IA050501]; 15–21.vi.1943 (MCZ), 1♀ [cf. IA051326]; 1–15.iii.1939, 1800 m (F. M. Brown, AMNH) [cf. IA40740]. EL SALVADOR. San Salvador, San Salvador [13°42′0″N, 89°12′0″W], i-iii.1954 (J. B. Boursot, AMNH), 1♀ [cf. IA40736]. GUATEMALA. Sacatepéquez, Antigua [14°33′0″N, 90°44′0″W], 16–17.viii.1947,1600 m (C. & P. Vaurie, AMNH), 1♀ [cf. IA40743]. HONDURAS. Atlántida, Lancetilla [15°41′0″N, 87°28′0″W], 1.vii.1929, 400 m (A. M. Chickering, MCZ), 1♀ [cf. IA011101]; vii.1929, 1♀ [cf. IA011301]. MEXICO. Hidalgo, 4 km NE of Tlanchinol on Highway 105 (21°2′0″N, 98°39′0″W), 14.vi.1983, 1500 m (W. Maddison, MCZ), 1♂ [IA010601]. Chiapas, Las Cruces Arriaga [16°17′0″N, 93°48′0″W], 15.ix.1947 (H. Wagner, AMNH), 3♀ [IA40516]; Rincón [16°28′0″N, 93°34′0″W], 6.iv.1953, *c.* 900 m (L. I. Davis, AMNH), 1♀ [cf. IA40522]; San Cristobal [16°44′0″N, 92°38′0″W], 21.vii.1950, *c.* 2200 m (C. & M. Goodnight, AMNH), 1♂ [cf. IA40513]. Guanajuato, Guanajuato [21°0′0″N, 101°16′0″W], 22.vii.1975, *c.* 2100 m (J. W. Burgess, AMNH), 1♀ [cf. IA40519]. Michoacán, Cerro Tancitare [19°25′0″N, 102°18′0″W], vii-viii.1941, Sweaping, 2377 m (H. Hoogstraal, MCZ), 1♀ [cf. IA010801]. Oaxaca, 7 miles S of Nochixtlan

[17°21′0″N, 97°17′0″W], 27.vi.1947 (L. I. & A. M. Davis, AMNH), 1♀ [cf. IA40521]. San Luis Potosí, Tamazunchale [21°15′0″N, 98°47′0″W], 20.v.1944, *c.* 200 m (C. Bolivar, AMNH), 1♂ [IA40515]. Veracruz, Fortín [18°54′0″N, 96°59′0″W], 22.vii.1955 (P. Vaurie, AMNH), 1♂ [IA40523]. PANAMA. Panamá, Canal Zone, Barro Colorado Island [9°9’17’N, 79°50’53’W], vi.1950 (A. M. Chickering, MCZ), 1♀ [IA0124]; 5.vii.1936, 1♀ [cf. IA022901]; 1–3.viii.1939, 1♀ [cf. IA40748]; 23–30.vi.1939, 1♀ [cf. IA023001]; viii.1950, 1♀ [IA010501]; 3.vii.1954, 1♀ [cf. IA032001]; 5.ii-4.iii.1958, 1♀ [IA011001]; 17–20.iii.1967 (Patterson expedition, MCZ), 1♂ [IA40569]; 16.v-15.vii.1934 (A. M. Chickering, NMNH), 1♀ [cf. IA0221]; 29.vii.1936 (MCZ), 1♀ [cf. IA40749]; Canal Zone, Ft. Sherman [9°22′0″N, 79°57′0″W], 15.viii.1939 (A. M. Chickering, MCZ), 1♀ [IA010701]; Perlas Islands, Isla San José (816′0″N, 79°6′0″W), 5.ii.1973, mangroves (MCZ), 1♂ [IA0210]; El llano (330) (8°24′0″N, 80°9′0″W), 28.v.1975 (F. Vollrath, MCZ), 1♂, 1juv [cf. IA033401]. Chiriqui, Boquete [8°46′0″N, 82°25′0″W], vii.1939 (A. M. Chickering, MCZ), 1♀ [cf. IA022701]; El Volcán [8°46′0″N, 82°38′0″W], 9–14.viii.1950 (A. M. Chickering, MCZ), 2♀ [IA0121]; La Fortuna [8°44′0″N, 82°15′0″W], 5.iv.1984, 1100–1200m (W. Eberhard, MCZ), 1♀ [cf. IA0202]; Road between Volcan-Concepción [8°38′0″N, 82°34′0″W], 28.x.1983, 1100 m (NMNH), 1♀ [cf. IA40504]. Bocas del Toro, Pipeline road [913′0″N, 82°30′0″W] 6.iv.1984 (NMNH), 1♀ [IA0216]. PERU. [?Piura], Chira road, Mallares [4°50′0″S, 80°26′0″W], 4.i.1942 (D. & H. Frizzel, CAS), 1♂, 1♀ [IA40781]. Cajamarca, San Andres de Cutervo [6°12′0″S, 78°40′0″W], 16.iii.1989, 2000 m (D. Silva, MHNSM), 2♀ [cf. IA40601]; 15.iii.1989, 1♀ [cf. IA40604]. Lima, Lima [12°2′0″S, 77°2′0″W], 31.v.1989 (D. Silva, MHNSM), 1♀ [cf. IA40548]. Urubamba, Machu Picchu, Pueblo Guzvo [13°9′0″S, 72°31′0″W], 20–22.iii.1947, 2400 m (J. C. Pallister, AMNH), 1♀ [cf. IA40741]. Pasco, Oxapampa [10°34′0″S, 75°23′0″W], 22.vi.1986 (D. Silva, MHNSM), 1♂, 3♀ [IA40590]; 5 km SE. of Oxapampa [10°40′0″S, 75°18′0″W], 20.vi.1986, 2000 m (D. Silva, MHNSM), 2♂, 1♀ [IA40552]. San Martín, Vilcapasa [7°6′0″S, 76°42′0″W], 7.i.1985, 2080 m (*A.* Delgado *et al.*, MCZ), 1♂, 7juv [IA030701]. SURINAM. Commewijne, Matapica Reserve [5°80′0″N, 54°50′0″W], 20.v.1986 (D. Smith Trail, NMNH), 3♂, 1♀ [IA40640]. VENEZUELA. Monagas, Café, Caripe [10°10′0″N, 63°30′0″W], 15.ix.1975 (W. Stejskal, NMNH), 1♀ [cf. IA0203]. [No locality data], 11.viii.1983 (H. & L. Levi, MCZ), 1♀ [cf. IA010101]. ?HONDURAS. Label only states ‘Dyer Tenne- ix.13 1917’. Unlikely from Dyer in Tennessee, USA as the species has never been found in USA. Possibly the collector is Dyer, whose other collections of *Anelosimus* all came from Honduras. 13.ix.1917 (AMNH), 1♂ [IA40742].

Variation: Male total length 2.65–4.10, prosoma 1.35–1.85, first femur 1.80 – 2.90. Female total length 3.80–6.10, prosoma 1.75–2.25, first femur 2.20–2.50. Coloration in general variable, some populations have very dark individuals, others lightly coloured individuals. Prosoma coloration varies from nearly uniformly brown to yellowish with darker areas in centre and around rim. Leg coloration varies from fairly unicolorous brown to yellowish-brown with distal tip of femora slightly darkened, tips and centre of tibia, and tip of metatarsus dark. Abdomen pattern and coloration also variable (Fig. 27H–M). The number of trichobothria on tibia 1 varies from 6 to 9 in male, and from 6 to 8 in female. Male palpal organ quite variable (Figs 27A–C, 28A–F, 29A–F, 30A–E), especially the shape of the distal portion of the Eb, the orientation of the E lobe and the size and shape of the weakly sclerotized area of the embolus where the distal hematodocha connects with it. Palpal coloration ranges from nearly white appearing lightly sclerotized to dark reddish-brown. A male (identified as *A.* cf. *baeza*) from San Antonio de Escazu, Costa Rica, has an abnormal left palp, appearing functional, but entirely different from any *Anelosimus* species (I. Agnarsson, unpubl. data). The right palp is similar to *A. baeza*, although differing in detail. Females collected with this male also differ from ‘normal’ *A. baeza*. Behaviour is also variable (see Natural history). Based on current evidence I consider this variation to be intraspecific, but further studies are necessary to understand this variation better, and *A. baeza* as here circumscribed may well represent two or more distinct species. Epigyna vary in the number and prominence of the ridges on the epigynal plate; no variation was observed in the internal female genitalia.

Distribution: From Panama to Peru (Fig. 64D), at a range of altitudes from *c.* 200 to 2500 m.

Natural history: At the type locality, *Anelosimus baeza* is subsocial, typically with single-mother and offspring association (Avilés *et al.*, 2001; L. Avilés, pers. comm.). The webs are a typical basket, the largest one encountered by Avilés *et al.* (2001) measured 20 × 15 × 10 cm. Of 13 webs documented by Avilés *et al.* (2001), four contained solitary adults, two contained an adult female and one or two males, two a mother with egg sac, three contained a group of juveniles or subadults, and two a mother and her offspring, up to 89 individuals of three cohorts. Sex ratios were not biased. Interestingly, in the nearby Las Caucheras *A. baeza* sometimes forms larger colonies containing offspring of several females (L. Avilés, pers. comm.). However, as at Baeza, sex ratios are not biased, which is unusual for colonies containing more than one adult female. The lack of sex ratio bias indicates outbreeding; males, females or both must exit their natal colony to seek mates. Given this behavioural difference, these possibly represent different species. However, no morphological characters have been found to separate the two, and further studies on behavioural variation and inbreeding are necessary to solve this issue adequately.

ANELOSIMUS PURAVIDA SP. NOV.

(FIGS 27N–Q, 33, 34, 63C)

Types: Male holotype and female paratype from Costa Rica, San José Province, San Antonio de Escazú, 1300 m, viii.1988, W. Eberhard, deposited in NMNH [IA40620].

Synonymy:
Anelosimus jucundus: Levi, 1956: 417–418 (in part); Levi, 1963: 35–36 (in part).

Etymology: The species epithet comes from the Costa Rican phrase 'pura vida' (literally 'pure life'). It translates to 'everything is fine', a cheerful salut characteristic of the 'Ticos'.

Diagnosis: Males differ from all other *Anelosimus*, except *A. baeza*, in having an ectal tegular outgrowth Tr (Fig. 27O) and in the shape of the Eb, with a distinct basal lobe pointing caudally, and an evenly broad, terminally ridged distal portion (Fig. 27O). Morphologically this species is extremely similar to *A. baeza*, but both sexes tend to be slightly larger. Subtle differences in the male palp separate the two species, the non-sclerotized region of the embolic base is typically larger in *A. puravida*, and the tegular outgrowth (Tr) is much narrower at its tip. The male of *A. puravida* also has a more strongly developed SPR. Behaviourally the two seem to differ: *A. puravida* seems to be prominently a social species with multiple adult spiders and a biased sex ratios (J. Coddington, pers. comm.), whereas *A. baeza* has equal sex ratios, but ranges from single-mother nests to nests containing several females. Apart from natural history I have not found any reliable way of distinguishing between females of the two.

Male (holotype): Total length 4.03. Prosoma 1.89 long, 1.65 wide, 1.16 high, brown, darker in centre and around rim. Sternum 1.20 long, 1.02 wide, extending between coxae IV, dark brown, darkest in centre and around rim. Abdomen 2.41 long, 1.65 wide, 1.65 high. Pattern as in *A. baeza*. Eyes subequal, about 0.11 in diameter. Clypeus height about 3.8 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.60, patella 0.75, tibia 2.37, metatarsus 2.11, tarsus 0.85. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1243. Leg base colour yellowish, distal tip of all segments slightly darkened, femur I darker than other femora, their distal tip not noticeably darkened. Tarsal organs slightly distal on tarsi I (0.60) and II (0.50–55), proximal on III (0.4–0.45) and IV (0.45–50). Six to seven small trichobothria dorsally on all tibia, 6 on tibia I, 6–7 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 27N, O, 33A–F.

Female (paratype): Total length 5.07. Prosoma 2.02 long, 1.73 wide, 1.25 high, brown, darker in centre and around rim. Sternum 1.29 long, 1.07 wide, extending between coxae IV, dark brown, darkest in centre and around rim. Abdomen 3.38 long, 2.48 wide, 2.72 high. Pattern as in *A. baeza*. Eyes subequal, about 0.10 in diameter. Clypeus height about 3.5 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.37, patella 0.81, tibia 1.98, metatarsus 2.24, tarsus 0.88. Femur about 5 times longer than wide, metatarsus I about 12 times longer than wide. Leg formula 1423 Leg base colour yellowish, distal tip of all segments slightly darkened, femur I darker than other femora, their distal tip not noticeably darkened. Tarsal organs slightly distal on tarsus I (0.55), proximal on tarsi II (0.45–0.50), III (0.40–0.45) and IV (0.35–40). Four to seven small trichobothria dorsally on all tibia, 4–5 on tibia I, 6 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Three dorsal trichobothria on female palpal tibia. Epigynum as in Figures 27P, Q, 34A.

Additional material examined: COSTA RICA. Cartago, Cartago [9°51′0″N, 83°55′0″W], xi.1953, *c.* 1400 m (N. *L.* Krauss, MCZ), 1♀ [cf. IA022601]. Puntarenas, 6 km S of San Vito (642′0″N, 83°0′0″W), 13–18.iii.1967 (OTS course, NMNH), 1♀, 4juv [IA0223]; Monteverde Cloud Forest Reserve [10°2′0″N, 83°27′0″W], 28.vii.1979, *c.* 1350 m (J. Coddington, NMNH), 1♀ [cf. IA40533]. San José, Pico Blanco (9°56′0″N, 84°8′0″W), iii.1988, 1500 m (W. Eberhard, MCZ), 1♀ [IA0212]; San Antonio de Escazú [9°56′0″N, 84°8′0″W], vi.1988, 1300 m (W. Eberhard, NMNH), 6♀ [cf. IA40634]; 28–31.iii.1989, *c.* 2300 m (J. Coddington, NMNH), 1♀ [IA40506]; viii.1988, 1300 m (W. Eberhard, NMNH), 1♂, 2♀ [IA40507]; 7♂, 43♀, 7juv [IA40512]. Chíral Paraíso (N. Banks, MCZ), 6♀ [cf. IA0209]. GUATEMALA. El Quiché, Chichicastenango [14°56′0″N, 91°6′0″W], 6–7.viii.1947, *c.* 2200 m (C. & P. Vaurie, AMNH), 1♀ [cf. IA40735]. PANAMA. Chiriqui, Boquete [8°46′0″N, 82°25′0″W], 10–25.vii.1939, *c.* 1100 m (A. M. Chickering, MCZ), 1♂, 7♀ [IA011201]. Panamá, El Valle [8°36′0″N, 80°8′0″W], 27.viii.1983 (T. Christenson, MCZ), 1♀ [cf. IA0214]; (T. Christenson, NMNH), 1♀ [cf. IA40508].

Variation: Male total length 3.90–4.50, prosoma 1.80 – 2.10, first femur 2.50 – 3.00. Female total length 4.70–6.20, prosoma 1.90–2.30, first femur 2.30–2.60.

Distribution: Central America from Guatemala to Panama (Fig. 63C), at altitudes of *c.* 1000–2200 m.

Natural history: *Anelosimus puravida* is apparently social. The types came from a nest containing in total 43 adult females, 7 adult males, 8 juveniles (several instars) and 9 egg sacs (collection label states that all were from the same nest, coll. W. Eberhard). The observed sex ratio (approximately 6 females per male) may not represent primary sex ratio bias, but would not be atypical for a social species.

THE *STUDIOSUS* GROUP

Diagnosis: Males of the *studiosus* group can be separated from the related *jucundus* group by a smaller, flat, embolic division b (e.g. Fig. 35H), which is distally much narrower than in species of the *jucundus* group. The basal lobe of the embolus never surpasses the hood of the subconductor, but is rather hooked in it, or orientated towards it, unlike in the *jucundus* group. Epigyna are very similar among species, and to those of the *jucundus* group, but differ from the latter in the strongly sclerotized part of the CD being directly below, or ventral to the ectalmost margin of the spermathecae (Fig. 49J). The external epigyna in the *studiosus* group range from weakly to strongly ridged (e.g. Figs 44C, I, 49C, I, M), whereas they are always strongly ridged in the *jucundus* group. Species of the *studiosus* group are generally smaller than those of the *jucundus* group, although the overlap is considerable. Palpal organs and epigyna are similarly smaller in the *studiosus* group than in *jucundus* the group.

Description: Males with a flat embolic division b that narrows gradually (or sometimes abruptly near the centre) towards tip, the E plus Eb covering only a portion of the tegulum (and other sclerites) ventrally. Tip of the Eb narrow compared with base. The lobe of the embolus usually indistinct not surpassing the hood of the SC. Epigyna are similar among species, but vary in having the epigynal plate weakly to strongly ridged. Strongly sclerotized part of the CD located directly below or ventral to the ectalmost margin of the spermathecae (e.g. Fig. 44D).

Phylogenetics: The *studiosus* group (*A. studiosus sensu* Levi, 1956, 1963) monophyly is supported by four unambiguous synapomorphies (Fig. 60), the following two of which have perfect fit to the cladogram: sclerotized region of copulatory duct, mesal to ectal margin of spermathecae (**10**-1, Fig. 44D), and embolic division b terminally narrow and snout-like (**75**-1, Fig. 44A).

Composition: In his treatment of *A. studiosus*, Levi (1956: 419) discussed the extensive geographical variation he observed under the subheading ‘subspecies’. It seems clear now that his *A. studiosus* included numerous related species and here the following eight species are treated: *Anelosimus studiosus*, *A. elegans*, *A. oritoyacu*, *A. pantanal*, *A. tungurahua*, *A. guacamayos*, *A. tosum* and *A. fraternus.*

Distribution: From north-eastern USA to Argentina (Figs 63C, 64C, E). Most speciose in Ecuador, particularly at altitudes of 1000 m or above.

Natural history: Species of the *studiosus* group range from subsocial to social.

ANELOSIMUS TOSUM CHAMBERLIN, 1916
(FIGS 35A–F, 36–38, 64E)

Types: Female holotype from Peru, Huadquiña, vi.1911, Yale Peruvian Expedition, in MCZ, examined

Synonymies:
Theridion tosum Chamberlin, 1916: 229, pl. 16, figs 1–4, ♂♀.
Anelosimus jucundus: Levi, 1956: 417, synonymy here rejected.

Etymology: Chamberlin (1916) did not explain the species epithet.

Diagnosis: *Anelosimus tosum* has stark contrasting dark and white spots within the dorsal band on the abdomen (Fig. 35E, F). Males differ from most other species of the *studiosus* group in having a large Eb and a distinctly lobed E base entering or slightly surpassing the SC (Fig. 35B). It differs from the closely similar *A. oritoyacu* in having a broader and more rugose Eb tip and a smaller E tip fork (Fig. 35B). Females are difficult to separate from others in the *A. studiosus* group, but have unusually numerous ridges on the epigynal plate, especially towards the posterior end (Fig. 37A). Morphologically this species shows some characters intermediate to the *studiosus* and *jucundus* groups.

Male (IA40618): Total length 3.58. Prosoma 1.63 long, 1.25 wide, 1.07 high, brown, broad thicker bands around rim, and centre. Sternum 0.99 long, 0.91 wide, extending between coxae IV, dark brown. Abdomen 2.08 long, 1.90 wide, 1.98 high. Pattern as in other Anelosimus. Eyes subequal, about 0.08 in diameter. Clypeus height about 3.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.41, patella 0.59, tibia 2.11, metatarsus 1.79, tarsus 0.81. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1423.

Leg base colour yellowish, with distal tip of all segments darkened, tibia also with darker central bands, and femur I slightly darker than other segments. Tarsal organs distinctly distal (0.65–0.70) on tarsi I–II, central on III (0.50), slightly distal on IV (0.50–0.55). Four to five small trichobothria dorsally on all tibia, 5 on tibia I and III. Trichobothria on metatarsi I–III proximal (about 0.40–0. 50), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 35A, B, 36A–F.

Female (IA40618): Total length 5.20. Prosoma 2.28 long, 1.82 wide, 1.40 high, brown, broad thicker bands around rim, and centre. Sternum 1.30 long, 1.07 wide, extending between coxae IV, dark brown. Abdomen 3.25 long, 2.48 wide, 2.64 high. Pattern as in Figure 35E, F. Eyes subequal, about 0.10 in diameter. Clypeus height about 4.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.28, patella 0.81, tibia 2.11, metatarsus 2.02, tarsus 0.98. Femur about 5 times longer than wide, metatarsus I about 13 times longer than wide. Leg formula 1423. Leg base colour yellowish with distal tip of all segments darkened, and a central band on femora and tibia, most distinct on legs I and II. Tarsal distal on tarsi I (0.70–0.75) and II (0.60–0.65), proximal on III (0.45–50) and IV (0.35–4.00). Six to seven small trichobothria dorsally on all tibia, 6–7 on tibia I, 6 on tibia III. Trichobothria on metatarsi I–III proximal (0.40–0.45), absent on metatarsus IV, distal (0.85) on palpal tarsus. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 35C, D, 37A.

Variation: Male total length 3.58–3.90, prosoma length from 1.5–1.69, first femur 2.21 – 2.60. Female total length 4.23–5.90, prosoma 1.85–2.28, first femur 2.21–2.60.

Additional material examined: BRAZIL. Rio de Janeiro, Teresopolis [22°24′0″S, 42°58′0″W], iii.1946, 900–1000 m (H. Sick, AMNH), 1♀ [cf. IA40696]. COLOMBIA. Antioquia, San Vicente [6°17′0″N, 75°20′0″W], 2.i.1985 (M. A. Serna, NMNH), 1♀ [cf. IA40662]. Boyacá, Santuario de Fauna y Flora Iguaque, near margin of Laguna Iguaque (5°41′20″N, 73°26′7″W), 5–8.ii.1998, canopy fogging, 3450–3650 m (J. Coddington *et al.*, NMNH), 1♂, 1♀ [IA111301]; 5♂ [IA1112]; 5–8.ii.1998, 2800 m (G. Hormiga *et al.*, NMNH), 1♂, 1♀ [IA40529]; 1♂, 1♀ [IA40618]; 29 juv [cf. IA40630]; Near visitors centre (5°42′5.3″N, 73°27′20.1″W), 5–8.ii.1998, 2850–3000 m (G. Hormiga *et al.*, NMNH), 2♀ [IA40409]; 4♂, 17♀ [IA40531]; 3♂, 4juv [IA40631]; 2♀ [IA40633]; 1♂, 1♀ [IA40639]; 1♀ [IA40637]; 5.ii.1998, 1♂, 2♀, 2juv [IA40638]; 8.ii.1998, 2800 m (G. Hormiga, NMNH), 1♀ [IA40632]. Cundinamarca, La Calera, Cerro del Chocolatero, *c.* 5 km NE of Bogotá [4°42′0″N, 73°58′0″W], 31.i.1998, 3000 m (G. Hormiga *et al.*, NMNH), 2♀, 15juv [IA40534]. Valle de Cauca, Atuncela [3°46′0″N, 76°42′0″W], 22.xi.1969, 300 m (MCZ), 1♀ [cf. IA40668]. ECUADOR, Chimborazo, *c.* 6 km NE of Chunchi on Panamerican Highway (2°15′48.96″S, 78°53′19″W), 10.vii.2004, 2380 m (I. Agnarsson *et al.*, NMNH), ♂♂♀♀ [IAV09]. Cañar, W of Suscal (2°28′1.2″S, 79°7′6.6″W), ♂♂♀♀ [IAV10]. EL SALVADOR. San Salvador, Santa Tecla [13°40′0″N, 89°17′0″W], 15.x.1949 (J. B. Boursot, AMNH), 1♀ [cf. IA40216]. MEXICO. Michoacán, Pátzcuaro [19°30′0″N, 101°36′0″W], 12.vi.1941 (A. M. Davis, AMNH), 1♀, 1juv [cf. IA40517]; Tancítaro [19°19′0″N, 102°21′0″W], vi-vii.1941, *c.* 2000 m (H. Hoogstraal, MCZ), 1♂ [IA0222]. PERU. Cajamarca, Cuttervo [6°22′0″S, 78°48′0″W], 22.vi.1956, 2900 m (V. Vegr., MCZ), 1♂, 8♀ [IA050201]. La Libertad, Pataz [7°43′0″S, 77°37′0″W], 26.iii.1988, 2000 m (D. Silva, MHNSM), 1♀, 8juv [IA40545]; Yalen [7°45′0″S, 77°33′0″W], 26.iii.1988 (D. Silva, MHNSM), 1♂, 2♀, 5juv [IA40551].

Distribution: Found from Mexico to Peru (Fig. 64E), most records from 2000 m or above.

Taxonomic history: Chamberlin (1916) described this species based on a single female from Peru. Levi (1956: 417) considered all females with a strongly ridged epigynal plate to be *A. jucundus* and thus synonymized it with *A. jucundus*. It is clear now that species of both the *jucundus* and the *studiosus* group can have strongly ridged epigynal plates, and although *A. tosum* females resemble *A. jucundus*, the resemblance is closer to specimens from Colombia (also based on colour pattern), which based on the male clearly belong to the *studiosus* group. Examination of the type female of *A. tosum* also suggests that it belongs to the *studiosus* group, as the strongly sclerotized portions of the CD appear (without dissection) to be relatively close together, rather than extending ectal to the ectalmost rim of the spermathecae as is typical in the *jucundus* group. Nevertheless, it is notoriously difficult to identify unaccompanied females, and matching the type female to the description series from Colombia represents nothing more than a best guess.

Natural history: Information on the natural history of this species comes from field labels, and field notes of G. Hormiga (pers. comm.), who collected the description series, and my personal observations made in Ecuador in 2004. Most colonies encountered consisted only of juveniles, or an adult female with juveniles. This appears to be a typical subsocial species with single-mother nests where the mother dies before the young reach adulthood. Colonies were common in forest gaps, along edges (trails) and in secondary growth, but were rare in the forest understory. Heteropteran commensals (*Ranzovius*) and argyrodine kleptoparasites were seen in some nests.

ANELOSIMUS ORITOYACU SP. NOV.

(FIGS 35G–J, 39–41, 63C, 66D)

Types: Male holotype, four male paratypes, and female paratype from Napo, Oritoyacu, 8.1 km S. of Baeza, Ecuador, 0°29.83′S, 77°52.43′W, 6.i.2002, L. Avilés, deposited in NMNH [IA40626].

Synonymy:
Anelosimus studiosus Levi, 1956 (in part); Levi 1963 (in part).

Etymology: The species epithet is a noun in apposition referring to the name of the type locality.

Diagnosis: Males can be diagnosed from all other *Anelosimus* of the *studiosus* group by the relatively large Eb and stout embolus fork (Fig. 35H); females are very difficult to separate from others, but may be identified by the epigynal plate being unusually high relative to its width (Fig. 35I).

Male (holotype): Total length 2.99. Prosoma 1.50 long, 1.17 wide, 0.91 high, brown, nearly covered with dark grey markings. Sternum 0.92 long, 0.81 wide, extending between coxae IV, brown nearly covered with dark grey markings. Abdomen 1.69 long, 1.24 wide, 1.16 high. Pattern similar to *A. guacamayos*. Eyes subequal, about 0.09 in diameter. Clypeus height about 3.4 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.08, patella 0.65, tibia 1.79, metatarsus 1.50, tarsus 0.75. Femur about 7 times longer than wide, metatarsus I about 15 times longer than wide. Leg formula 1243. Legs base colour light brown, femur I, distal half of femur II, and tips of other femora, tibia, patella and metatarsus dark brown. Tarsal organs distal (0.50–0.55) on tarsi I–II, proximal (0.35–0.40) on III–IV. Four to six small trichobothria dorsally on all tibia, 5 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 35G, H, 39A–F, 40A–F.

Female (paratype): Total length 3.51. Prosoma 1.63 long, 1.27 wide, 1.04 high, brown with dark grey markings. Sternum 1.06 long, 0.86 wide, extending between coxae IV, brown with dark grey markings. Abdomen 2.02 long, 1.60 wide, 1.65 high. Pattern similar to *A. guacamayos*. Eyes subequal, about 0.10 in diameter. Clypeus height about 3.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.95, patella 0.62, tibia 1.50, metatarsus 1.40, tarsus 0.72 . Femur about 5 times longer than wide, metatarsus I about 11 times longer than wide. Leg formula 1423. Legs pale brown with distal tips of femora, tibia, patella and metatarsus dark brown. Tibia I also with a central band ventrally. Tarsal organs distal (0.55–0.60) on tarsus I, central (0.50) on II, proximal (0.40–0.45) on III–IV. Five to six small trichobothria dorsally on all tibia, 5 on tibia I, 5 on tibia III. Trichobothria on metatarsi I and III proximal (about 0.40–0.45), central on II, absent on metatarsus IV. Three or four dorsal trichobothria on palpal tibia. Epigynum as in Figures 35I, J, 41A.

Variation: Male total length 2.80–3.05, prosoma 1.45–1.55, first femur 2.05–2.20. Female total length 3.35–3.70, prosoma 1.55–1.70, first femur 1.85–2.10. Female palpal tibia has three or four dorsal trichobothria; this variation can be asymmetric, i.e. differing between sides of the individual. Specimens from Jacala, Mexico, are large, 3.60 (male), 4.40 (female) but their identity is uncertain.

Additional material examined: ECUADOR. Chimborazo, 30 miles SW of Alausí [2°22′0″S, 79°4′0″W], 14.xi.1955, 2500 m (CAS), 1♂ [IA40778]; 2♂, 2♀ [IA40783]. Napo, 3.9 km S of Baeza (0°28′0″S, 77°71′9″W), 13.i.2002, hand collected, *c.* 1500 m (L. Avilés, NMNH), 2♂ [IALA29]; Oritoyacu 8.1 km S of Baeza (0°29′83′S, 77°52′43′W), 23.xi.2002, hand collected, *c.* 1500 m (P. Salazar & G. Iturralde, NMNH), 1♂, 1♀ [IALA30]. Pichincha, Tandayapa [0°1′0″S, 78°46′0″W], xi.1984, 1700 m (G. Onore, MCZ), 1♂, 9♀ [cf. IA40764]. MEXICO. Hidalgo, Jacala [21°1′0″N, 99°12′0″W], 13.vi.1936, *c.* 1600 m (Davis, AMNH), 1♂, 2♀ [cf. IA40218]. Guerrero, Taxco, *c.* 1800 m, [18°34′0″N, 99°37′0″W], 15.viii.1943 (Bolivar, Pelaez & Osorio, AMNH), 1♂ [IA40202]. Morelos, Cuernavaca, *c.* 1500 m, [18°55′0″N, 99°13′0″W] (N. Banks, NMNH), 1♂ [IA40510].

Distribution: Only known from Ecuador and Mexico (Fig. 63C). All collections made at altitudes around 1500 m or above.

Natural history: *Anelosimus oritoyacu* is social, with biased sex ratio. It seems to be mostly confined to the canopy, where it makes nests containing multiple adult males and females (L. Avilés, pers. comm.; my pers. obs.). As the sheet is placed in the canopy, the webs lack the aerial threads so typical of *Anelosimus* species, and rather resemble the webs of *A. rupununi* and *A. lorenzo* (Fig. 66D).

ANELOSIMUS TUNGURAHUA SP. NOV.
(FIGS 35K–Q, 42–43, 64D)

Types: Male holotype and female paratype from Ecuador, Tungurahua, Baños, 1800–2000 m, iii.1939, W. C. Macintyre (MCZ), examined.

Synonymy:
Anelosimus studious: Levi, 1956: 419 (in part).

Etymology: The species epithet is a noun in apposition after the type locality.

Diagnosis: Males can be distinguished from most species by the shape of the Eb, which narrows abruptly near the mid region, similar to *A. studiosus* (Fig. 35L). It differs from *A. studiosus* in the Eb being much flatter, with a narrower and less rugose distal tip. Females may be separated from others by the large epigynal lip, and relatively small epigynal plate (Fig. 35P).

Male (holotype): Total length 2.60. Prosoma 1.30 long, 1.04 wide, 0.79 high, brown, with centre darker. Sternum 0.83 long, 0.71 wide, extending between coxae IV, dark brown. Abdomen 1.43 long, 1.16 wide, 1.12 high. Pattern as in Figure 35M. Eyes subequal, about 0.10 in diameter. Clypeus height about 2.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.15, patella 0.55, tibia 1.82, metatarsus 1.66, tarsus 0.72. Femur about 7 times longer than wide, metatarsus I about 15 times longer than wide. Tarsus I with a ventral row of thickened setae. Leg formula 1243. Leg base colour yellowish-brown, distal tip of all segments darker, femur 1 darker than other femora. Tarsal organs distal (0.55) on tarsi I–II, proximal (0.40–0.45) on III–IV. Four to five small trichobothria dorsally on all tibia, five on tibia I and III. Trichobothria on metatarsi I–III proximal (0.35–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 35K, L, 42A–F.

Female (paratype): Total length 3.90. Prosoma 1.69 long, 1.20 wide, 0.99 high, yellowish-brown with centre and rim darker. Sternum 1.02 long, 0.89 wide, extending between coxae IV, dark brown. Abdomen 2.34 long, 1.90 wide, 2.03 high. Pattern as in Figure 35N, O. Eyes subequal, about 0.09 in diameter. Clypeus height about 3.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.02, patella 0.52, tibia 1.79, metatarsus 1.69, tarsus 0.78. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1423. Leg base colour yellowish-brown, distal tip of all segments darker, femora and tibia also with central bands, especially prominent on leg I. Tarsal organs distal on tarsi I (0.55–0.60) and II (0.50–0.55), proximal on III (0.45–50) and IV (0.40–0.45), distal (0.85) on female palp. Four to seven small trichobothria dorsally on all tibia, 6–7 on tibia I, five on tibia III. Trichobothria on metatarsi I–III proximal (0.40–0.45, absent on metatarsus IV. Three, or sometimes four (Fig. 43G), dorsal trichobothria on female palpal tibia. Epigynum as in Figures 35P, Q, 43A.

Variation: Male total length 2.28–3.12 prosoma 1.00–1.50, first femur 1.43–2.15. Female total length 3.19–4.50 mm, prosoma 1.43–1.69, first femur 1.83–2.02.

Additional material examined: ECUADOR. Tungurahua, Baños [1°23′0″S, 78°25′0″W], vii.1938 (W. C. Macintyre, MCZ), 17♂, 45♀, *c.* 1800 m, [IA050101]; 24.iv.1939, 1800 m, 3♂ [IA050701]; iii.1939, 1♂, 1♀ 10.iv.1939, 4♂, 8♀, 1juv [IA050301]; iv.1939, 1850–2000 m (W. C. Macintyre, MCZ), 1♂, 2♀ [IA050401]; iii.1939, 5♂, 16♀, 5juv [IA052401]; vii-viii.1938, 2000 m (W. C. Macintyre, MCZ), 3♂, 1♀ [IA051101]; 15–21.vi.1943 (MCZ), 3♂, 21♀ [IA051301].

Distribution: Only known from area of type locality (Fig. 64D), at altitudes of 1800–2000 m.

Natural history: Subsocial (L. Avilés, pers. comm.).

ANELOSIMUS ELEGANS NEW REPLACEMENT NAME
(FIGS 44A–E, 45, 46, 64E)

Types: *Anelosimus elegans* is a replacement name for *Enoplognatha dubia* Chamberlin, 1916, 60: 233, pl. 17, fig. 3, a junior secondary homonym of *Brattia* (?) *dubia* Tullgren, 1910 (=*Anelosimus dubius*, see Miller, 2004). Female holotype of *E. dubia* came from Sorontoy, Peru (7000 ft.), in MCZ, examined. Not *A. studiosus* (Hentz), contra Levi (1956: 419).

Synonymies:
Enoplognatha dubia Chamberlin, 1916, preoccupied by *Brattia* (?) *dubia* Tullgren, 1910 (=*A. dubius*, see Miller, 2004).
Anelosimus studiosus: Levi (1956: 419, in part), synonymy here rejected.

Etymology: The species epithet refers to their unusual and elegant posture, standing with legs in a plane parallel to the body, opened to the sides (L. Avilés, pers. comm.). The males of this species are also unusually shiny.

Diagnosis: Although differing in posture, colour intensity (shininess) and behaviour, this species is morphologically very similar to the sympatric *A. guacamayos*. The male is readily distinguished from most other *Anelosimus* by the gradually narrowing Eb (Fig. 44A), but is slightly less gradual than in *A. guacamayos*. Females are difficult to separate from others in the *studiosus* group, but have a relatively evenly broad epigynal plate (Fig. 44C), more gently curved than in, for example, *A. studiosus*. In *A. elegans* spermathecae are further apart than in other species of the *studiosus* group, so that the strongly sclerotized part of the CD is mesal to the spermathecae, instead of lying directly underneath them (Fig. 44D). *Anelosimus elegans* is apparently less social than *A. guacamayos*, having equal sex ratios and predominantly single female nests.

Male (IA40627): Total length 2.67. Prosoma 1.37 long, 1.04 wide, 0.86 high, dark shiny brown. Sternum 0.83 long, 0.71 wide, extending between coxae IV, dark brown. Abdomen 1.56 long, 1.16 wide, 1.07 high. Pattern as in Figure 44E. Eyes subequal, about 0.08 in diameter. Clypeus height about 3.0 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.79, patella 0.59, tibia 1.59, metatarsus 1.40, tarsus 0.65. Femur about 6 times longer than wide, metatarsus I about 14 times longer than wide. Leg formula 1243. Leg formula 1243. Leg base colour orange, femora I and II darker brown and distal tip of femora III–IV and tibia darker. Tarsal organs slightly distal (0.50–0.55) on tarsi I, proximal (0.30–0.45) on II–IV. Four to six small trichobothria dorsally on all tibia, 5 on tibia I, 5 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 44A, B, 45A–F.

Female (IA40627): Total length 3.77. Prosoma 1.89 long, 1.49 wide, 1.11 high, yellowish with sparse dusky grey markings, more concentrated in the cephalic region, and especially the thoracic groove. Sternum 1.16 long, 0.96 wide, extending between coxae IV, yellowish with dense dusky grey markings. Abdomen 2.02 long, 1.73 wide, 1.57 high. Pattern as in the male; see Figure 44E. Eyes subequal, about 0.09 in diameter. Clypeus height about 3.4 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.28, patella 0.72, tibia 1.95, metatarsus 1.79, tarsus 0.75. Femur about 5 times longer than wide, metatarsus I about 12 times longer than wide. Leg formula 1423. Leg base colour yellowish, distal tip of femora, patella, tibia and metatarsi slightly darkened. Tarsal organs distal (0.60) on tarsus I, central (0.50) on II, proximal (0.30–0.40) on III–IV, most proximal on IV. Five to seven small trichobothria dorsally on all tibia, 5–6 on tibia I, 5–6 on tibia III. Trichobothria on metatarsi I–III proximal (about 0.30–0.45), absent on metatarsus IV. Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 44C, D, 46A.

Variation: Male total length 2.47–2.67, prosoma 1.24–1.37, femur 1.66–1.79. Female total length 3.77–4.03, prosoma 1.83–1.89, first femur 2.02–2.28. A female identified as *A.* cf. *elegans* from San Geronimo, Mexico, measured 5.85 in total length, prosoma 2.15, first femur 2.67.

Additional material examined: BRAZIL. Rio Grande do Sul, Pelotas [31°46′0″S, 52°19′0″W], 2.iii.1964, *c.* 0–5 m (C.M. Biezanko, MCZ), 1♀ [cf. IA053201]. COLOMBIA. Putumayo, Sibundoy [1°10′0″N, 76°53′0″W], viii.1963, 2200 m (M L. Bristol, MCZ), 1♂, 2♀ [IA051701]. ECUADOR. Morona Santiago, km 20 from Limón to Gualaceo, cloud forest (3°0′15.84″S, 78°30′50″W), 11.vii.2004, 2270 m (I. Agnarsson *et al.*, NMNH), ♂♂♀♀ [IAV12]. Napo, Cordillera Guacamayos, Cocodrilo (0°38′75″S, 77°47′45″W), 11.xii.2002 (L. Avilés, NMNH), 2♂, 1♀ [IA40563]; 4♂, 3♀ [IA40627]. Pichincha, near Mindo, roadside (0°1′35.79′S, 78°47′20.39′W), 25.vii.2004, *c.* 1400–1800 m (I. Agnarsson and G. Iturralde, NMNH), ♀♀ [IAV11]. MEXICO. Guerrero, Taxco (18°34′0″N, 99°37′0″W), viii.1978, *c.* 1800 m (P. Klass, NMNH), 1♀ [cf. IA0218]. Morelos, Cuernavaca [18°54′0″N, 99°13′0″W], viii.1996, *c.* 1500 m, hand collected (W. Maddison, MCP), 1♂ [IALA13]. Oaxaca, San Geronimo [16°34′0″N, 95°6′0″W] (AMNH), 1♀ [cf. IA40524]. PERU. Junín, Utcuyacu [11°40′0″S, 75°0′0″W], iii.1948, *c.* 3500 m (F. Woytkowski, AMNH), 1♂, 10♀ [cf. IA40695]; 15♂, 40♀, 50juv [IA40746]. Pasco, 15 km SE. of Oxapampa on Carretera Nueva a Villa Rica, Pampa (10°40′0″S, 75°18′0″W), 20.vi.1986 (D. Silva,), 4♂, 1♀ [IA1109]. Pasco, Oxapampa, 15 km SE of Oxapampa [10°40′0″S, 75°18′0″W], 20.vi.1986, 2000 m (D. Silva, MHNSM), 1♂, 4♀ [cf. IA40596]; 1♂, 4♀, 65juv [cf. IA40602]; 4♂, 2♀ [IA40605].

Distribution: Occurs from Mexico to Peru (Fig. 64E). It is not certain that specimens from Mexico belong to this species; they are very large, but otherwise closely resemble specimens from other areas. Likewise the identity of the specimen from Brazil is in doubt, an unaccompanied female collected near sea level; all other records of *A. elegans* come from altitudes of 1300–3100 m.

Natural history: In Ecuador *A. elegans* is apparently subsocial, and has unbiased sex ratios (L. Avilés, pers. comm.; my pers. observ.). A sample from Peru contained *c.* 15♂, 40♀ and 50 juveniles, indicating that the level of sociality may differ between populations. The argyrodine *Faiditus caudatus* has been collected in the webs of *A. elegans*.

Taxonomic note: Based on subtle differences in morphology and different levels of social behaviour *A. elegans* and *A. guacamayos* are here treated as separate species. There is some evidence, however, that populations of *A. elegans* may be social (see Natural history) and further data are necessary to investigate if the observed variation is intra- or interspecific.

***ANELOSIMUS GUACAMAYOS* SP. NOV.**

(FIGS 44F–O, 47, 48, 63C, 66B)

Types: Male holotype and female paratype from Ecuador, Cordillera Guacamayos, Cocodrilo, 0°38.75′S, 77°47.45′W, 14.xii.2002, P. Salazar, deposited in NMNH [IA40624].

Synonymy:
Anelosimus studiosus: Levi (1956: 419, in part); Levi (1963: 36, in part).

Etymology: The species epithet is a noun in apposition based on the name of the type locality.

Diagnosis: *Anelosimus guacamayos* differs in behaviour from most species of the *studiosus* group, being social. Behaviour apart, separating this species from others in the *studiosus* complex is difficult. Males can be distinguished by the shape of the embolic apophysis, whose ectal edge is straighter than in other species (Fig. 44F–H). Some *A. guacamayos* males lack the fork at the embolus tip (Fig. 44H) reminiscent of *A. fraternus* from Haiti. I have not found a reliable way of separating the females morphologically from other species of the *studiosus* complex, except from *A. elegans* which has CD located more mesally in the internal epigynum.

Male (holotype): Total length 2.86. Prosoma 1.37 long, 1.09 wide, 0.84 high, brown, dusky grey markings most noticeable in centre, in streaks towards the rim and on rim. Sternum 0.86 long, 0.79 wide, extending between coxae IV, brown, dusky grey markings get denser closer to pedicel. Abdomen 1.63 long, 1.20 wide, 1.09 high, truncated in front. Pattern as in Figure 44M, O. Eyes subequal, about 0.10 in diameter. Clypeus height about 2.7 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.92, patella 0.49, tibia 1.69, metatarsus 1.56, tarsus 0.72. Femur about 9 times longer than wide, curved, metatarsus I about 17 times longer than wide. Leg formula 1243. Leg base colour brown, distal tip of tibia darker, coxae, trochanters and base of femora lighter than other parts. Tarsal organs central (0.50) on tarsus I, proximal (0.40–0.45) on II–IV. Five to seven small trichobothria dorsally on all tibia, five on tibia I, II and III. Trichobothria on metatarsi I–III proximal (0.35–0.40), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 44F, H, 47A–E.

Female (IALA34): Total length 4.05. Prosoma 1.80 long, 1.40 wide, 0.50 high, brown. Sternum 1.10 long, 0.90 wide, extending midway between coxae IV, brown. Abdomen 2.30 long, 1.65 wide, 1.70 high, pattern as in Figure 44L, N. Eyes subequal, about 0.10 in diameter. Clypeus height about 2.6 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.30, patella 0.65, tibia 1.80, metatarsus 1.80, tarsus 0.90. Femur I about 7 times longer than wide, tibia I about 14 times longer than wide. Leg formula 1423. Leg base colour light brown, distal tip of femur and tibia dark grey, femora also with a central band. Tarsal organs usually slightly distal (0.55) on tarsi I and II, slightly proximal (0.45) on III and IV, distal (0.85) on female palp (but the positions vary slightly among specimens). Five to seven small trichobothria dorsally on all tibia, five on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35), absent on metatarsus IV. Three dorsal trichobothria on female palpal tibia. Epigynum as in Figures 44I–K, 48A, B.

Variation: Male total length 2.34–2.95, prosoma 1.24–1.45, femur I 1.80–1.95. Males in some collections lack the fork at the embolus tip (compare Fig. 44G to 44H), a variation among, but not within colonies. It is uncertain if this represents intraspecific variation or if ‘forkless’ males belong to a different species. While provisionally treated as conspecifics here, the more common forked condition is scored in the data matrix as all those from the type locality have the fork. Female total length 3.70–4.42, prosoma 1.80–1.89, first femur 2.28–2.30.

Additional material examined: ECUADOR. Napo, Cordillera Guacamayos, Cocodrilo, 18.8 km S of Cosanga river (0°38’75′S, 77°51′0″W), 29.xi.2002, hand collected, *c.* 1500 m (P. Salazar, NMNH), 1♂, 2♀ [IALA31]; 11.i.2002 (L. Avilés, NMNH), 4♂, 2♀ [IALA32]; 7.i.2002, 1♀ [IALA33]; 15.5 km S. of Cosanga river [0°38′9′S, 77°47′4′W], 19.viii.1999, hand collected (L. Avilés, NMNH), 1♂, 1♀ [IALA34]; 17.6 km S. of Cosanga river [0°38′9″S, 77°47′4″W], 19.viii.1999, hand collected (L. Avilés, NMNH), 1♂, 4♀ [IALA35]; 16.65 km S of Cosanga (0°38’79′S, 77°47’45′W), 8.i.2002 (L. Avilés, NMNH), 6♂ [IA40556]; 17.6 km S of Cosanga, Cordillera de los Guacamayos (90°45′0″S, 77°51′0″W), 19.viii.1999, hand collected (L. Avilés, NMNH), 6♀ [IALA02]; 1♂, 5juv [IALA0301]; Cocodrilo (0°38′75″S, 77°47′45″W), 11.xii.2002 (L. Avilés, NMNH), 2♀ [IA40562]; NE of El Chaco, bridge at Rio Salado (0°12′9″S, 77°42′5″W), 19.vii.2004, 1290 m (I. Agnarsson *et al.*, NMNH), [IAV02], ♀♀. Morona Santiago, km 6.7 from Limón Indanza (2°59′33″S, 78°26′3″W), 12.vii.2004, 1415 m (I. Agnarsson, NMNH), ♂♂♀♀ [IAV01].

Distribution: Known from Ecuador (Fig. 63C). This appears to be a mid-elevation species, found between 1200 and 2000 m.

Natural history: *A. guacamayos* is social with distinct primary sex ratio bias (L. Avilés, pers. comm.; my pers. obs.). It makes large, typical basket-shaped nests (Fig. 66B), and forms colonies of up to 1000 or more individuals, including numerous adult females and their clutches.

Most nests are found in open areas, typically in clearings, for example old landslides where often a cluster of nests may be found.

Taxonomic note: Here, specimens lacking the fork at the embolus tip (Fig. 44H) are treated as synonymous with the type. Apart from this detail, 'forkless' males otherwise strongly resemble the holotype. Females collected with 'forkless' males are not separable from females collected with the more common ('normal') males. Based on this evidence I presume that this difference represents variation within a species, but further studies should explore the possibility of these being two distinct species.

ANELOSIMUS STUDIOSUS (HENTZ, 1850)
(FIGS 49A–F, 50, 51, 64C)

Types: Hentz's types of *Theridion studiosum*, from Alabama, USA, have been lost (Levi, 1956). Their identity is not problematic however; Hentz's description is recognizable, and other specimens from Alabama are very similar to specimens from across the USA.

Synonymies:
Theridion studiosum Hentz, 1850, 6: 274, pl. 9, fig. 5, ♀.
Theridion studiosum: Hentz 1875, 145, pl. 16, fig. 5, ♀ Keyserling, 1884, 1: 20, pl. 1, fig. 7, ♂♀ (in part); Marx, 1890, 12: 520; 1892, 2: 156; Simon, 1894a, 1: 540; 1894b, 521; 1897, 862; Banks, 1902, 11: 272; Banks, 1903, 55: 340; 1904, 56: 125; 1906, 22: 187; Simon, 1903, 2: 989; Petrunkevitch, 1911, 29: 207; 1925, 27: 68; Comstock, 1912, 350, fig. 250, ♀ 1940, 365, fig. 350 ♀ Bishop and Crosby, 1926, 41: 183; Chickering, 1936, 55: 452; Fox, 1940, 53: 43; Mello-Leitão, 1941, 13: 250; 1946, 11: 36; Roewer, 1942, 1: 501; Muma, 1945, 38: 29.
Anelosimus studiosus: F. O. P.-Cambridge, 1902, 2: 395, pl. 37, figs 16–17, ♂♀ (probably *A. studiosus*, drawings difficult to recognize); Banks, 1910, 72: 20; Mello-Leitão, 1942, 2: 385; 1943, 37: 171; 1944, 3: 313; 1948, 100: 382; Gertsch, 1949, 167. Kaston, 1948, 20: 99, figs 178–181, ♂♀ Levi, 1956, 75: 407–422 (in part), figs 21, 23, possibly also figs 37–39 ♂♀. Stejskal, 1976, 26: 344, fig. 4.2 ♀ (note that Stejskal's photos are not recognizable); Kaston, 1981, 890; Breene *et al*., 1993, 56, fig. 20A–C ♂♀ Platnick, 2006; Agnarsson, 2004, figs 24(A–G), 25(A–F) ♂♀.
Anelosimus textrix, Chamberlin and Ivie, 1944, 8(5): 37, probably an incorrect synonymy of *Linyphia textrix* Walckenaer, 1842, 2: 281. *L. textrix* was illustrated in an unpublished manuscript 'Spiders of Georgia' by J. Thomas Abbot, cited in Walckenaer as 'Abbot, 1792' and is considered valid, see Levi, 1956: 419; Platnick, 2006; Mello-Leitão, 1945, 4: 215; Archer, 1946, 22: 54; 1950, 30: 22, pl. II, fig. 5–6 ♂. Kaston, 1953, 166; Barnes, 1953, 23: 321.
Theridion magnificum Keyserling, 1884, 2(1): 47–48, pl. 2, fig. 26, ♂♀.

Diagnosis: Males can be distinguished by the sharp constriction of the Eb centrally, and a relatively broad Eb tip (Figs 49B, 50B). Females are difficult to separate from others of the *studiosus* group, but most specimens differ from all other *Anelosimus* by having a more strongly procurved genital plate (Fig. 49C; note however that this feature is not universal, see under Variation).

Male (IA40656): Total length 2.65, prosoma 1.30 long, 0.90 wide, 0.75 high, brownish-orange with scattered grey flecks, narrow rim around the edge slightly darker. Sternum 0.75 long, 0.65 wide, extending between coxae IV, yellowish, with a darker rim around edge. Abdomen 1.40 long, 1.10 wide, 1.20 high, pattern as in Figure 49E. Eyes subequal, about 0.08 diameter. Clypeus height about 2.3 times AME diameter. Chelicera with one large and two small prolateral teeth, three or four denticles retrolaterally. Legs pale yellow, part of femur I and distal tip of tibia I slightly darker. Leg formula 1243. Leg I femur 1.80, patella 0.55, tibia 1.65, metatarsus 1.40, tarsus 0.65. Femur I about 7 times longer than wide, tibia I about 12 times longer than wide, thickening somewhat towards distal end. Four to five small trichobothria dorsally on all tibia, five on tibia I and III. Trichobothria on metatarsus I (0.35), II (0.40) and III (0.40) proximal, absent on metatarsus IV. Tarsal organs on tarsus I (0.45), II (0.40), III (0.35), and IV (0.40) proximal.Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 49A, B, 50A–E.

Female (IA40503): Total length 4.40, prosoma 1.60 long, 1.25 wide, 1.00 high, brownish-orange with grey flecks in cephalic area and narrow rim along edges. Sternum 0.90 long, 0.80 wide, extending between coxae IV, brownish-yellow, mostly covered by dusky grey dots, with a darker rim around edge. Abdomen 2.85 long, 2.45 wide, 3.00 high, pattern as in Figure 49F. Eyes subequal, about 0.10. Clypeus height about 2.9 times AME diameter. Chelicera with one large and two small prolateral teeth, three denticles retrolaterally. Legs pale yellow, part of femur I and distal tip of tibia I slightly darker. Leg formula 1423. Leg I femur 2.00, patella 0.60, tibia 1.70, metatarsus 1.55, tarsus 0.75. Femur I about 6 times longer than wide, tibia I about 9 times longer than wide. Four to seven small trichobothria dorsally on all tibia, 6–7 on tibia I, five on tibia III. Trichobothria on metatarsus I (0.40), II (0.40) and III (0.40) proximal, absent on metatarsus IV. Tarsal organ central (0.50) on leg I, proximal on legs II (0.45), III (0.40), and IV (0.45), distal (0.85) on palpal tarsus. Epigynum as in Figures 49C, D, 50H.

Variation: Male total length 2.00–3.50, prosoma 1.10–1.55, femur I 1.40–2.30. Female total length 3.50–4.70, prosoma 1.35–1.90, femur I 1.80–2.40. A male from Chapala, Mexico, measured 3.90 mm in total length, but the identity of the specimen is dubious. Like in other species of the *studiosus* complex the female epigynum of *A. studiosus* is highly variable. In the majority of specimens the epigynal plate is narrower and more strongly procurved than in any other species. However, in some specimens the plate may be broader and less procurved, then very similar to *A. guacamayos* (e.g. Fig. 44I) and other species. The setae ventrally on metatarsus I are sometimes thickened in the males, sometimes not. Behaviour appears to be variable also, some populations prominently subsocial, others social.

Additional material examined: ARGENTINA. Córdoba, La Serrapita, Alta Garcia, Depto. Santa María [31°39′0″S, 64°25′0″W], 24.x.1967, *c.* 500 m (di Tada, MCZ), 1♂, 1♀ [cf. IA051001]. Santiago del Estero [27°47′0″S, 64°16′0″W], 2.iv.1965, *c.* 180 m (H. Levi, MCZ), 1♀ [cf. IA052701]. BRAZIL. Rio de Janeiro, Guanabara, Barra de Tijuca [23°0′0″S, 43°21′0″W], 16.iv.1965 (H. Levi, MCZ), 1♀ [cf. IA052801]; Petropolis [22°31′0″S, 43°11′0″W], 2–5.xi.1945, 850 m (H. Sick, AMNH), 2♂, 3♀ [IA40303]. Rio Grande do Sul, Canela (29°21′0″S, 50°48′0″W), 2–8.i.1992, *c.* 600 m, hand collected (J.W. Thome, MCP), 1♀ [cf. MCP02]; Cordilheira, Cachoeira do Sul [30°2′0″S, 52°53′0″W], 30.xii.1993, *c.* 60 m (R. G. Buss, MCP), 1♀ [cf. IA40611]; Fazenda Souza, nr. Caxias [29°7′0″S, 51°1′0″W], 3–5.xi.1994, hand collected (A. A. Lise, MCP), 4♂ [cf. MCP01]; 18–21.xi.1993, 2♂, 4♀ [cf. IA40609]; Pelotas [31°46′0″S, 52°19′0″W], 2.iii.1964, *c.* 0–5 m (C. M. Biezanko, MCZ), 2♀ [IA050801]; São Francisco de Paula [29°26′0″S, 50°34′0″W], 21–24.iii.1996, *c.* 600 m (A. A. Lise *et al.*, MCP), 4♀ [cf. IA40607]; Viamão (30°5′0″S, 50°58′0″W), 22.xi.1995, hand collected (A. A. Lise, MCP), 2♀ [cf. MCP03]. COLOMBIA. Magdalena, Gaira [11°10′0″N, 74°13′0″W], xii.1975, 10 m (W. Eberhard, MCZ), 2♀ [cf. IA40667]. Meta, Pto. Lieras, Lomalinda (3°18′0″N, 73°22′0″W), 300 m (B. T. Carrol, MCZ), 2♀ [IA40761]; Villavicencio [4°9′0″N, 73°38′0″W], 12.xii.1979, 470 m (M. Barreto, MCZ), 1♂ [IA40767]. Putumayo, Sibundoy [1°10′0″N, 76°53′0″W], viii.1963, 2200 m (M. L. Bristol, MCZ), 1♀ [IA053101]. Valle, above Piekindixii, 1972, 1800 m (MCZ), 1♀ [cf. IA052301]; Atuncala [3°46′0″N, 76°42′0″W], 17.xii.1969, *c.* 800 m (W. Eberhard, MCZ), 1♀ [cf. IA052101]; 1♂, 1♀ [IA051401]; 22.xi.1969, 1♀, 10juv [IA053001]; 23.xi.1969, 1♂ [IA051601]; Between Dagua and Loboguerrero [3°43′0″N, 76°40′0″W], 10.vii.1970, 800 m (H. Triana, MCZ), 1♂, 1♀ [IA051201]; Río Calima [3°42′0″N, 76°33′0″W], v.1976, 1400 m (W. Eberhard, MCZ), 2♂, 3♀ [IA050601]; nr. Pance, P. N. N. Farallones de Cali, Res. Nat. Hato Viejo (3°20′53″N, 76°40′16.7″W), 12.ii.1998, 2300 m (G. Hormiga, NMNH), 6♂, 2♀ [IA40661]. Western Cordillera, Between Queremal and Buenaventura, 12.ii.1935 (H. F. Schwarz, AMNH), 1♀ [IA40702]. COSTA RICA. Alajuela, near Esparta [9°59′0″N, 84°40′0″W], xi.1981, *c.* 300 m (MCZ), 1♂ [IA40771]; Grecia [10°4′0″N, 84°18′0″W], 27.xi.1955 (B. Malkin, AMNH), 1♂ [IA40108]. Cartago, Turrialba [9°54′0″N, 83°41′0″W], 10–17.iv.1944, 600 m (F. Schrader, AMNH), 1♀ [IA40112]; 23.vii-15.viii.1965 (A. M. Chickering, MCZ), 1♂ [IA40750]. Guanacaste, Comunidad [1033′0″N, 85°35′0″W], 19.ii.1967 (J. M. Nelson, MCZ), 1♀ [cf. IA0211]; Palo Verde, Bagaces [10°31′0″N, 85°15′0″W], 16–22 .i.1978 (W. Eberhard, MCZ), 1♂ [IA40765]. Heredia, Heredia, Universidad Nacional Autónoma (10°0′0″N, 84°7′0″W), 1–2.iv.1989 (J. Coddington, NMNH), 3♂, 3♀ [IA40559]. San José, San José [9°55′0″N, 84°4′0″W] (E. Schmidt, AMNH), 3♂ [IA40107]; Escazú [9°55′0″N, 84°8′0″W], 30.vii.1983,1300 m (H. Levi, MCZ), 1♀ [IA40772]; San Pedro de Montes de Oca [9°55′0″N, 84°2′0″W], iii.1983, 1000 m (W. Eberhard, MCZ), 1♀ [IA40756]; vii.1988 (W. Eberhard, NMNH), 6♀ [cf. IA40641]; 15 km N. of Puriscal [9°58′0″N, 84°19′0″W], vii.1988, 600 m (W. Eberhard, NMNH), 2♀ [cf. IA40635]. CUBA. Ciudad de La Habana, Siboney, Oriente [22°4′0″N, 82°27′0″W], 26.vi.1955 (A. F. Archer, AMNH), 1♀ [IA40572]. ECUADOR. Pichincha, Calderón [0°5′0″S, 78°26′0″W], 5.vii.1989, *c.* 2500 m (L. Avilés, NMNH), 1♂ [IALA16]; 1♂ [IALA18]; area no censada [0°5′0″S, 78°26′0″W], 5.vii.1989, *c.* 2500 m (L. Avilés, NMNH), 3♂ [IALA17]; Ilalo [0°3′0″S, 78°32′0″W], viii.1999, hand collected (L. Avilés, MCP), 3♂, 1juv [IALA09]; Pululahua Crater [0°3′0″S, 78°32′0″W], viii.1999 (L. Avilés, NMNH), 3♂ [IALA15]; San Antonio del Tingo [00′6′S, 78°27′0″W], 1.vii.1989 (L. Avilés, NMNH), 1♂ [IALA19]; 1♂, 3juv [IALA20]. Tungurahua, Río Pastaza between Baños and Mapoto [1°25′0″N, 78°10′0″W], viii.1938 (W. C. Macintyre, MCZ), 1♂ [IA050901]; Río Pastaza near Mapoto [1°25′0″N, 78°10′0″W], 2.iv.1938, 1300 m (W. C. Macintyre, MCZ), 1♀ [cf. IA051901]. EL SALVADOR. San Salvador, San Salvador [13°42′0″N, 89°12′0″W], iii.1954 (J. B. Boursot, AMNH), 1♀ [IA40104]. GUATEMALA. Baja Verapaz, Los Ramones [15°0′0″N, 90°12′0″W], 25.vii.1947 (C. & P. Vaurie, AMNH), 1♂ [IA40105]. HAITI. l'Artibonite, Carrefour [19°24′0″N, 72°4′0″W], 23vii.1955

(A. F. Archer, AMNH), 1♀ [cf. IA40576]. HONDURAS. Atlandida, Lancetillal [14°54′0″N, 89°7′0″W], vii.1929, 900 m (A. M. Chickering, MCZ), 1♀ [IA40751]. [no detailed locality] (Dyer, AMNH), 1♂ [IA40212]. JAMAICA. St. Andrew, [18°1′0″N, 76°54′0″W], xi-xii.1957 (A. M. Chickering, MCZ), 1♀ [IA40754]; Mona pasture [18°1′0″N, 76°54′0″W], 29.xi.1957 (MCZ), 3♂, 1♀, 15juv [IA40752]. St. Catherine, Spanish Town [17°59′0″N, 76°57′0″W], 15.viii.1974 (D. B. Jayasingh, MCZ), 1♀ [IA40753]; old harbor [17°58′0″N, 77°0′0″W], xi.1957 (A. M. Chickering, MCZ), 1♀ [IA40755]. Westmoreland, Negril [18°16′0″N, 78°20′0″W], 23–30.iii.1981, 90 m (H. & L. Levi, MCZ), 1♀ [IA40760]; Whitehouse [18°4′0″N, 77°59′0″W], 26.iii.1955 (A. M. Nadler, AMNH), 1♂ [IA40312]. MEXICO. Chiapas, Cintalapa [16°41′0″N, 93°42′0″W], 17.ix.1947 (H. Wagner, AMNH), 2♂ [IA40710]; Las Cruces Arriaga [16°17′0″N, 93°48′0″W], 18.ix.1947 (H. Wagner, AMNH), 2♂ [IA40678]; Ocosingo [16°54′0″N, 92°7′0″W], 25.vi.1950, 900 m (C. & M. Goodnight and L. J. Stannard, AMNH), 1♂ [IA40304]; Río de las Flores [17°10′0″N, 91°16′0″W], 15.ix.1947 (H. Wagner, AMNH), 1♂ [IA40713]; 1♂ [IA40715]; 16.ix.1947, 1♀ [IA40210]; Tuxtla Gutiérrez [16°44′0″N, 93°6′0″W], 9.ix.1947 (H. Wagner, AMNH), 2♂, 2♀ [IA40221]. Distrito Federal, Coyoacan [19°20′0″N, 99°10′0″W], 28.vii.1947 (H. Wagner, AMNH), 2♂ [IA40729]. Guerrero, Acapulco, El Mirador Hotel [16°51′0″N, 99°54′0″W], 5.vi.1943 (F. H. Pough, AMNH), 1♀ [IA40725]; Taxco, km. 100, Rd. Taxco [18°45′0″N, 99°48′0″W], 10.viii.1946 (Goodnight, Bolivar & Bonet, AMNH), 1♀ [IA40204]. Hidalgo, 6 mi. N. of Jacala [21°5′0″N, 99°11′0″W], 23.vi.1955 (C. & P. Vaurie, AMNH), 1♂ [IA40688]; Chapulhuacán [21°9′0″N, 98°53′0″W], 20.v.1952 (M. Cazier *et al*., AMNH), 1♂ [IA40716]; Ixmiquilpan [20°29′0″N, 99°13′0″W], 15.viii.1947 (H. Wagner, AMNH), 1♂ [IA40119]; Jacala [21°1′0″N, 99°12′0″W], 13.vi.1936, *c.* 1600 m (A. M. Davis, AMNH), 1♂, 1♀ [IA40218]. Jalisco, Chapala [20°17′0″N, 103°11′0″W], 22vi.1941, *c.* 1500 m (A. M. Davis, AMNH), 1♂ [cf. IA40213]. Michoacán, Tzararacua Falls, 7 mi. from Uruapan [19°20′0″N, 102°4′0″W], 14.vi.1941 (A. M. & L. I. Davis, AMNH), 1♂, 2♀ [IA40203]. [♀Michoacán],7 mi. S. of Hidalgo [19°36′0″N, 100°34′0″W], 3.vii.1936 (L. I. Davis, AMNH), 1♀ [IA40699]. Morelos, Cuernavaca [18°55′0″N, 99°13′0″W], 3.vii.1941 (A. M. & L. I. Davis, AMNH), 1♀ [IA40679]; x.1944 (N. L. H. Krauss, AMNH), 1♂ [IA40717]; Oaxtepec [18°54′0″N, 98°57′0″W], 17v.1942 (AMNH), 1♀ [cf. IA40686]. Nayarit, 15 mi. W. of Tepic [21°29′0″N, 105°5′0″W], 25.vii.1954 (W. J. Gertsch, AMNH), 2♀ [IA40703]; Jesús María Cortés [21°43′0″N, 104°53′0″W], 25–30.vii.1955 (B. Malkin, AMNH), 1♂ [IA40692]; Tepic [21°29′0″N, 104°53′0″W], 26.vii.1953 (P. & C. Vaurie, AMNH), 1♂ [IA40109]; 4.viii.1953, 1♂ [IA40120]; 2.viii.1947 (C. J. Goodnight, AMNH), 1♂, 1♀ [IA40217]; 2–7.viii.1947 (C. & M. Goodnight & B. Malkin, AMNH), 1♀ [IA40706]. Nuevo León, Horsetail Falls [25°21′0″N, 100°8′0″W], 11.vi.1936 (L. I. Davis, AMNH), 1♀ [IA40683]; Horsetail Falls, Cola de Caballo, San Juan R. Canyon [25°21′0″N, 100°8′0″W], 31.viii.1968 (J. E. Carico, NMNH), 1♀ [IA40401]; Linares [24°51′0″N, 99°33′0″W], 8.vii.1941 (L. I. Davis, AMNH), 1♂ [IA40215]. Oaxaca, Asunción, Nochixtlán [17°27′0″N, 97°17′0″W], 5.vii.1953, 2000 m (A. Robinson Jr., AMNH), 1♂ [IA40208]; Oaxaca [17°3′0″N, 96°43′0″W], 2.x.1946, 1550 m (H. Wagner, AMNH), 2♂, 1♀ [IA40727]. Puebla, Tecamalchalco [18°52′0″N, 97°43′0″W], 2.vii.1953, 2000 m (A. Robinson Jr., AMNH), 1♂ [IA40681]; Tehuacán [18°27′0″N, 97°23′0″W], 17–24.x.1944 (H. Wagner, AMNH), 2♀ [IA40205]. San Luis Potosí, Huichichuyán [21°30′0″N, 98°57′0″W], 19.v.1952 (AMNH), 1♂ [IA40707]; Nr. Ciudad del Maíz [22°24′0″N, 99°36′0″W], 19.viii.1947 (C. & M. Goodnight, AMNH), 1♀ [IA40207]; Tamazunchale [21°15′0″N, 98°47′0″W], 20.v.1952 (M. Cazier, W. Gertsch, & R. Schramme, AMNH), 2♂ [IA40201]; Valles [21°59′0″N, 99°0′0″W], vii.1959 (Steude, AMNH), 1♀ [IA40698]. Tamaulipas, 11 mi. N. of Victoria [23°54′0″N, 99°9′0″W], 22.v.1952 (M. Cazier *et al*., AMNH), 1♂ [IA40711]; 40 mi. S. of Linares [24°54′0″N, 98°14′0″W], 30.xi.1939 (A. M. & L. I. Davis, AMNH), 1♀ [IA40724]; Reynosa [26°4′0″N, 98°17′0″W], 2.v.1936 (J. Ruth, AMNH), 2♂, 1♀ [IA40712]. Veracruz, 14 mi. S. of Catemaco on Rt. 180 [18°13′0″N, 95°6′0″W], 23.vi.1982, 400 m (F. Coyle, MCZ), 1♂ [IA051501]; Aroyac [19°3′0″N, 96°6′0″W], 12.xi.1941 (F. Bonet, AMNH), 1♀ [IA40685]; Papantla de Olarte [29°27′0″N, 97°19′0″W], 12.x.1947 (H. M. Wagner, AMNH), 1♂ [IA40209]; pass above Orizaba [18°50′0″N, 97°5′0″W], 29.vi.1944, 1950 m (L. I. Davis, AMNH), 1♀ [IA40310]; Tecolutla [20°29′0″N, 97°0′0″W], 13.x.1947 (H. M. Wagner, AMNH), 1♂ [IA40705]; Tlapacoyan [19°58′0″N, 97°12′0″W], 7–8.vii.1946 (H. Wagner, AMNH), 1♀ [IA40206]. Taxco, viii.1978 (P. Klass, MCZ), 1♀ [IA40763]. [México♀], Cerro Gordo [19°9′0″N, 100°7′0″W], 22.vi.1936 (AMNH), 1♀ [IA40219]. NETHERLANDS ANTILLES. Curacao, Curacao [12°4′0″N, 68°34′0″W], 22.xii.1962 (B. deJong, MCZ), 2♂, 2♀ [IA090101]. PANAMA. Bocas del Toro, Bocas del Toro, Corriente grande (9°18′0″N, 82°32′0″W), 13–17.iii.1980, hand collected (R. Ibanez, NMNH), 1♀ [IA0204]. Chiriqui, Boquete [8°46′0″N, 82°25′0″W], 4–11.viii.1954, 1100 m (A. M. Chickering, MCZ), 1♂, 1♀ [IA40747]; Renacilmento, 10 km W. of Volcán [9°13′0″N, 83°32′0″W], 10.viii.1983,1300 m (H. & L. Levi, MCZ), 1♀ [IA40773]. Panamá, Canal Zone, Barro Colorado Island [9°9′17″N, 79°50′53″W], 20.iv.1953 (A. M. Nadler, AMNH), 1♀ [IA40220]; v.1964 (A. M. Chickering, MCZ), 1♂, 1juv [IA40766]; 18–29.viii.1939, 1♂, 1♀ [IA060101]; 16.vi.-15.vii.1930, 3♀ [IA071001]; 3♀ [cf. IA40541]; Panama Canal Zone, Colon humid forest (9°21′0″N, 79°54′0″W), 2–14.vii.1979, canopy fogging, tree 4 (E. Broadhead *et al.*, NMNH), 1♀ [IA40414]; tree 6 (E. Broadhead *et al.*, NMNH), 2♂ [IA40416]; Panama City [8°57′0″N, 79°32′0″W], 15–30.vii.1979, canopy fogging (E. Broadhead *et al.*, NMNH), 1♂ [IA40406]. TRINIDAD. Victoria, Gasparillo [10°19′0″N, 61°25′0″W], 4.xi.1944 (R. H. Montgomery, AMNH), 1♀ [cf. IA40704]. URUGUAY. Montevideo, Montevideo [34°54′0″S, 56°9′0″W], x-xi.2000 (F. Costa & C. Viera, NMNH), 1♂, 1♀ [IA40568]. USA. Alabama, Baldwin Co., Lagoon [30°21′0″N, 87°35′0″W], 12.x.1951 (A. F. Archer, AMNH), 1♂, 1♀ [IA40694]; Mobile Co., Dauphin Island [30°14′0″N, 88°6′0″W], 20.iv.1948 (A. F. Archer, AMNH), 2♀ [IA40574]; Tuscaloosa Co., Tuscaloosa [33°12′0″N, 87°34′0″W] (A. F. Archer, AMNH), 5♀, 9juv [IA40571]. Connecticut, Cobalt [41°33′0″N, 72°33′0″W], 2.viii.1939 (B. J. Kaston, NMNH), 1♂ [IA40652]. District of Colombia, Washington DC, Rock Creek Park (38°56′0″N, 77°2′0″W), 16.vii.1985, hand collected (J. Coddington, NMNH), 1♂ [IA1108]; (38°53′0″N, 77°1′0″W), 24.vi.1982, hand collected (J. Coddington, NMNH), 1♂ [IA1106]; National Arboritum [38°54′0″N, 76°58′0″W], 15.vi.1989 (J. Coddington, NMNH), 4♂, 2♀ [IA40503]. Florida, 5 mi. W. of Marianna [30°46′0″N, 85°19′0″W], 17.xi.1972 (*A.* Moreton, MCZ), 3♀ [IA042301]; 7 mi. E. of Apopka [28°40′0″N, 81°24′0″W], 20.viii.1944 (M. Ninenberg, AMNH), 1♀ [IA40118]; Alachua [29°47′0″N, 82°29′0″W], 10.v.1941 (H. K. Wallace, AMNH), 2♂, 3♀ [IA40106]; 28.iv.1937 (AMNH), 1♂ [IA40113]. Florida, Alachua Co. [29°42′0″N, 82°21′0″W], 8.iv.1938 (AMNH), 1♀ [IA40308]; Auburndale, Polk Co. [28°3′0″N, 81°47′0″W] (N. Banks, MCZ), 1♀ [IA041501]; Biscayne Bay [25°41′0″N, 80°9′0″W] (N. Banks, MCZ), 1♀ [IA041301]; Charlotte co., Punta Gorda [26°56′0″N, 82°3′0″W], 1–16.i.1946 (S. Rounds, AMNH), 1♀ [IA40690]; Clay Count's Hammock, Alachua Co. [29°42′0″N, 82°21′0″W], 30.iii.1939 (H. Wallace, AMNH), 1♂ [IA40301]; Collier Co., Naples [26°8′0″N, 81°47′0″W], 18.i.1946 (S. Rounds, AMNH), 1♀ [IA40674]; Cox's Hammock, Dade Co. [25°38′0″N, 80°30′0″W], 28.xii.1940 (Archer, AMNH), 1♀ [IA40102]; Dunedin [28°1′0″N, 82°47′0″W], 1924 (W. S. Blatchley, MCZ), 1♀ [IA40777]; Earmra SE. Isl. Everglades National Park, Dade Co. [25°14′0″N, 80°51′0″W], 28.i.1973 (A. Sheldon, MCZ), 1♂ [IA040701]; Dade co., Everglades, 28.xii.1950 (A. M. Nadler, AMNH), 1♂ [IA40693]; (in hammock area), [25°38′0″N, 80°24′0″W], 19.vi.1975 (L. Roth, MCZ), 1♂, 1♀ [IA042101]; Kendall [25°41′0″N, 80°19′0″W], 4.iii.1953 (A. M. Nadler, AMNH), 1♀ [IA40211]; 31.iii.1953 (A. M. Nadler, AMNH), 1♂, 1♀ [IA40684]; La Belle [26°45′0″N, 81°26′0″W], 25.xii.1952 (B. J. Kaston, NMNH), 2♀ [IA40654]; Lake Okeechobee [26°56′0″N, 80°47′0″W], 17.ii.1943 (W. Proctor & M. Cazier, AMNH), 1♀, 1juv [IA40111]; Lake Placid, Highlands Co. [27°17′0″N, 81°21′0″W], 25.ii.1976 (H. Levi, MCZ), 1♂, 1♀ [IA041401]; 3.ii.1943 (M. Cazier, AMNH), 1♀ [IA40114]; 25.i.1943, 1♀ [IA40115]; 1943, 1♀ [IA40101]; 3.ii.1943, 2♀ [IA40302]; 26.i.1943, 6♀ [IA40314]; Leesburg, Lake co. [28°48′0″N, 81°52′0″W], 1–11.iii.1954 (M. Statham, MCZ), 5♂, 1♀, 7juv [IA041901]; Matheson Hammock, 1/2 M south of Dade Co. [25°44′0″N, 80°18′0″W], 1952 (P. Porter, MCZ), 1♀ [IA041201]; Miakka River State Park, nr. Sarasota [27°20′0″N, 82°31′0″W], 6.iv.1936 (Gertsch, AMNH), 1♀ [IA40117]; Miami Beach [25°48′0″N, 80°7′0″W], vi.1944 (*A.* Bacon, AMNH), 1♀ [IA40116]; Naples [26°8′0″N, 81°47′0″W] (AMNH), 1♀ [IA40110]; Nassau Co. [30°36′0″N, 81°43′0″W], 28.iv.1935 (H. K. Wallace, AMNH), 1♀ [IA40676]; Orange Co., Orlando [28°33′0″N, 81°22′0″W], 11–14.xi.1946 (A. F. Archer, AMNH), 1♂, 6♀ [IA40575]; Orange Park, Trismen Estate [30°10′0″N, 81°43′0″W], 13.xi.1942 (MCZ), 1♀ [IA40775]; Orlando [28°33′0″N, 81°22′0″W], 15–30.viii.1944 (M. Nirenberg, AMNH), 1♀ [IA40103]; Pine Crest off Tamiami Trail [25°44′0″N, 80°66′0″W], 1.iii.1936 (S. C. Bishop, AMNH), 1♀ [IA40313]; Royal Palm Hammock [25°59′0″N, 81°35′0″W], 21.i.1946 (S. Rounds, AMNH), 1♂, 3♀ [IA40675]; Sebastian [27°49′0″N, 80°29′0″W], 30.xi.1931 (G. Nelson, MCZ), 1♂ [IA041801]; Tampa, Mac Dill Field [27°57′0″N, 82°27′0″W], 15–19.iii.1943 (B. Malkin, AMNH), 3♂ [IA40311]; Tavernier [25°0′0″N, 80°31′0″W], 29.xi.1952 (A. M. Nadler, AMNH), 1♀ [IA40214]; Wewahitchka, Dead Lake [30°6′0″N, 85°12′0″W], 6.iv.1927 (MCZ), 1♂ [IA041001]; Winter Park [28°35′0″N, 81°21′0″W], 11.iv.1938 (W. J. Gertsch, NMNH), 1♂ [IA40656]; (N. Banks, MCZ), 3♂, 5♀ [IA042401]. Georgia, 5 mi. N. of Macon [32°54′0″N, 83°38′0″W], 15.vi.1939 (W. J. Gertsch, AMNH), 1♂ [IA40691]; Bar-M-Ranch, S. of Boston [30°45′0″N, 83°47′0″W], 25.vi.1978 (H., L. & F. Levi, MCZ), 1♀ [IA40776]; Gainesville [34°17′0″N, 83°49′0″W], 28.v.1943 (B. J. Kaston, AMNH), 2♂ [IA40309]; 8.vi.1940, 1♂ [IA40653]; Rabun Co., Talullah [34°43′0″N, 83°23′0″W], 20.viii.1961 (J. E. Carico, NMNH), 1♀ [IA40659]; St. Simons Island [31°8′0″N, 81°24′0″W], v.1911 (S. C. Bishop, AMNH), 1♂ [IA40307]. Kansas, Elk Lake City, Montgomery Co. [37°17′0″N, 95°54′0″W], 10.ix.1994 (H. Guarisco, MCZ), 10♂, 4♀, 14juv [IA040201]. Louisiana, Saint Tammany Co., Mandeville [30°21′0″N, 90°4′0″W] (R. V. Chamberlin, MCZ), 1♀ [IA40774]; Cheniere au Tigre, Vermilion Par [29°34′0″N, 92°12′0″W], 27.iv.1974 (D. *A.* Rossman, MCZ), 1♀ [IA052501]. Maryland (Drury, AMNH), 2♂ [IA40315]. Mississippi, Wilkinson Co., Centreville [31°5′0″N, 91°4′0″W], 1944 (A. F. Archer, AMNH), 1♂, 3♀ [IA40573]. North Carolina, Apex, Wake Co. [35°43′0″N, 78°51′0″W], 28.ix.2000 (I. Agnarsson, NMNH), 7juv [IA40403]; Ashville [35°35′0″N, 82°34′0″W], 8.vii.1933 (W. J. Gertsch, AMNH), 1♂, 1♀ [IA40682]; Carteret co. [34°49′0″N, 76°46′0″W], 29.vii.1950 (R. B. Barnes, AMNH), 50 juv. [IA40687]; Raleigh [35°47′0″N, 78°38′0″W], viii.1912 (C.S. Brimley, MCZ), 1♀ [IA040801]; (C. S. Brimley, NMNH), 1♀ [IA40501]; Schenck forest, Raleigh [35°47′0″N, 78°38′0″W], 20.ix.2000 (I. Agnarsson, NMNH), 15 juv [IA40402]; Swan Co., Oconolufte visitor centre [35°29′0″N, 83°19′0″W], 21.vii.1998 (F. Coyle & I. Agnarsson, NMNH), 2♀ [IA40657]; Sylva [35°22′0″N, 83°13′0″W], 16.iv.1938 (B. B. Fulton, AMNH), 5 juv [IA40306]; Wake Co., Apex [35°43′0″N, 78°51′0″W], 28.ix.2000 (J. Perry, NMNH), 21 juv [IA40660]. South Carolina, Charleston [32°47′0″N, 79°56′0″W], 15–30.vi.1943 (B. Malkin, AMNH), 1♀ [IA40680]; Horrey Co., Socastee, Maccaman River [33°41′0″N, 79°0′0″W], 3.vii.1961 (J. E. Carico, NMNH), 2♀ [IA40658]; McClellanville [33°5′0″N, 79°27′0″W], vii-viii.1945 (P. Vaurie, AMNH), 1♂ [IA40305]. Tennessee, Martel [35°48′0″N, 84°14′0″W], 8.vii.1950 (M. Cazier, NMNH), 1♀ [IA40677]. Texas, 3 mi. E. of Edinburg [26°18′0″N, 98°6′0″W], 12.iv.1937 (S. Mulaik, AMNH), 1♂, 1♀ [IA40721]; 7 mi. E. of Edinburg [26°17′0″N, 98°3′0″W], 14.x.1936 (S. M., AMNH), 2♀ [IA40316]; Beaumont [30°5′0″N, 94°7′0″W], iv-vi.1946 (E.D. Parmer, MCZ), 1♂, 1♀ [IA041601]; Beeville, Bee Co. [28°24′0″N, 97°44′0″W], 25.iv.1982 (D. Bickel, MCZ), 1♂ [IA040401]; Cameron Co. [41°26′0″N, 78°11′0″W], ix.1933 (S. Mulaik, NMNH), 1♂, 1♀, 8juv [IA40655]; i-iii.1936 (L. I. Davis, AMNH), 1♀ [IA40728]; Corpus Cristi [27°46′0″N, 97°24′0″W], 21.iii.1936 (AMNH), 1♂ [IA40697]; Cotulla [28°26′0″N, 99°13′0″W], 8.vii.1936 (L. I. Davis, AMNH), 3♀ [IA40719]; Dallas, Denton Co [32°46′0″N, 96°47′0″W], 11.x.1947 (S. E. Jones, MCZ), 1♀ [IA040901]; Edinburg [26°17′0″N, 98°9′0″W], 10.xii.1935 (Stockton, AMNH), 1♀ [IA40708]; 1.xii.1936 (S. Mulaik, AMNH), 1♀ [IA40720]; 10.x.1935 ([collector unknown], AMNH), 1♀ [IA40722]; 15.xi.1935 (J. L. Ledbetter, AMNH), 2♀ [IA40730]; Goose Island State Park, Aransas Co. [28°1′0″N, 97°2′0″W], 16.vi.1961 (A.R. Brady, MCZ), 3♂, 1♀ [IA042001]; Harlingen [26°11′0″N, 97°41′0″W] (AMNH), 1♂, 1♀ [IA40714]; 25.x.1936 (S. Mulaik, AMNH), 1♀ [IA40732]; Kingsville [27°30′0″N, 90°51′0″W], x.1934 (AMNH), 1♀ [IA40718]; 4.xi.1934 (S. Mulaik, AMNH), 4♀, 2juv [IA40731]; Liberty [30°3′0″N, 94°47′0″W], 12.vi.1937 (AMNH), 1♀ [IA40723]; Newton [30°50′0″N, 93°45′0″W], 13.viii.1938 (L. I. Davis, AMNH), 1♀ [IA40701]; S. of Pharr [21°11′0″N, 98°11′0″W], 5.iv.1936 (M. Welch, AMNH), 3♂, 1♀ [IA40689]; Stony Oaks, Denton Co. [33°13′0″N, 97°7′0″W], 11.vi.1944 (MCZ), 1♀ [IA041701]; Zapata Co. [27°1′0″N, 99°14′0″W], 10.iv.1936 (Welch, AMNH), 1♂ [IA40726]. Virginia, 1407 N. Garland, Fayetteville, Arlington [36°4′0″N, 94°9′0″W], 9.xi.1986 (Richard Leschen, MCZ), 1♀, 25juv [IA040101]; Dismal swamp W. of Lake Drummond, 7 mi. S of Suffolk, Nansemond Co. [36°38′0″N, 76°31′0″W], 18–19.v.1968 (E. Sabath, MCZ), 25♂, 9♀, 10juv [IA042201]; Great Falls [38°59′0″N, 77°17′0″W] (N. Banks, MCZ), 2♂ [IA041101]; Hampden-Sydney, Prince Edward Co. [37°14′0″N, 78°27′0″W], 20.vi.1982 (H. Levi, MCZ), 1♀ [IA040501]; Waynesboro, Augusta Co. [38°4′0″N, 78°53′0″W], 3.viii.1981, from webs (L. & H. Levi, MCZ), 11♀ [IA040601]. VENEZUELA. Mérida, Mérida, [8°36′0″N, 71°9′0″W] (Y. Lubin, MCZ), 3♀ [cf. IA030901]. Monagas, Jusepín [9°45′0″N, 63°31′0″W], xi.1974 (MCZ), 15♀ [IA052901]. Patos, 24.ix.1944 (R. H. Montgomery, AMNH), 1♀ [IA40745].

Distribution: USA to Argentina. Widespread and common over a large portion of the Americas from 39°N to 33°S and altitudes of 0–2500 m. In a range of habitats, but apparently not in lowland tropical rainforests.

Natural history: Extensive literature is available about the natural history and various aspects of the biology of *Anelosimus studiosus* (e.g. Simon, 1891; Brach, 1977; Buskirk, 1981; Avilés, 1987, 1993, 1999; Avilés & Maddison, 1991; Avilés & Gelsey, 1998; Furey, 1998; [note that Stejskal's (1976) report from Venezuela cannot be specifically linked to *A. studiosus*]). It is typically characterized as a predominantly subsocial species, with a single mother and offspring in each nest. Yet, some populations have up to several hundreds of individuals building large communal webs with extensive co-operation (Furey, 1998). Apparently the behaviour of this species is thus highly variable. Brach (1977) discusses *A. studiosus* in Florida. He found that the majority of colonies consisted of a single female and its brood of the same or adjacent instar. The juveniles were fed by regurgitation at first but then started catching prey in the mother's web. The mother usually disappeared by the time her juveniles reached the 5th instar. Eventually most of the offspring dispersed from their natal nest (often after mating there), but sometimes a single female or a female and a couple of juveniles (and males) stayed and started a new colony in the old nest. As they mature, the offspring are pursued out of the web by the mother, if still alive, but otherwise by the first female to mature. Males are always tolerated, but contribute little and can only handle tiny prey. The mother lays a single egg case at the time containing 31–47 eggs. Individuals may wander around the web in search of small prey, but when a large prey item becomes entangled it is usually attacked first by the mother and then juveniles converge to feed on it. Juveniles were dependent on the mother and could not survive without her until after the third instar. Conspecific juveniles were never attacked (introduced or not) but juveniles of other theridiids were killed and eaten within a day of having been introduced. Introduced adult females were accepted by the brood but vigorously attacked by the mother. Brach (1977) attempted to create colonies by putting several adult females together, but these would show no co-operation and high aggression resulting in frequent cannibalism. Sometimes they killed prey together, but did not feed communally.

Furey (1998) studied *A. studiosus* in Tennessee, and as for Brach (1977) found that the majority of nests were single female plus offspring, but some nests had more than one female, with up to 29 adults in a nest. Although multi-female nests are fewer, contrary to Brach's study, Furey (1998) found that 80% of *A. studiosus* females he encountered lived in groups. Females in solitary webs drove out other females whereas those in social webs accepted most of them and in general showed inter-attraction. He established multiple female nests with non-sibling females that lasted 3 years. In multi-female nests mothers did not discriminate between egg sacs (own and others).

Furey (1998) found female-biased sex ratio ranging between 4 and 6 females per male and concluded that the Tennesse populations are social.

Given that the studies were made on different populations, this may represent interspecific rather than intraspecific variation. However, I have not found any consistent morphological differences between specimens collected in subtropical versus northern temperate USA and all are thus treated as conspecific here.

Several mirid bugs of the genus *Ranzovius* have been reported living in the nests of *A. studiosus*, including *R. contubernalis* Henry, *R. clavicornis* (Knight), *R. fennahi* Carvalho, and *R. stysi* (Henry, 1984, 1999; Wheeler & McCaffrey, 1984).

Taxonomic note: *Anelosimus studiosus* as here circumscribed is both highly variable and very widespread, despite greatly limiting Levi's (1956, 1963) concept of the species. The possibility that *A. studiosus* as currently delimited still represents a number of species certainly deserves further scrutiny. Conversely, it is also possible that the within-species variation is greater yet, and e.g. *A. fraternus* and *A. tungurahua* may represent further variation rather than biologically separate species. Behavioural and molecular work is urgently needed to compare both syn- and allopatric populations from the entire species range.

ANELOSIMUS PANTANAL SP. NOV.

(FIGS 49G–J, 52–54, 63C)

Types: Male holotype and female paratype from Brazil, Pantanal, Mato Grosso do Sul, Cuiaba, Poconé, Rodovia Transpantaneira (hasta Pousada PIXAIM), Fazenda Araras, approximately 17°37′S, 57°28′W, 5.ix.1996, G. Hormiga and J. Coddington, deposited in MNR [IA40619].

Etymology: The species epithet is a noun in apposition, referring to the type locality, the wonderful swamplands of Pantanal, Brazil.

Diagnosis: The males can be easily separated from other species of the *studiosus* group by the relatively small Eb and absence of a distal E fork (Fig. 49H). Females are difficult to separate from others of the *studiosus* group, but differ in having a small, weakly procurved, epigynal plate, the ectal margins barely extending beyond the ectal margin of the spermathecae (Fig. 49J).

Male (holotype): Total length 2.47. Prosoma 1.17 long, 0.87 wide, 0.66 high, yellowish, darker in centre and around rim. Sternum 0.71 long, 0.64 wide, extending between coxae IV, yellowish, darker around rim. Abdomen 1.30 long, 1.09 wide, 1.16 high. Pattern as in *A. studiosus*. AME slightly the largest, other eyes subequal, about 0.08 in diameter. Clypeus height about 2.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.85, patella 0.42, tibia 1.69, metatarsus 1.53, tarsus 0.72. Femur about 8 times longer than wide, metatarsus I about 16 times longer than wide. Leg formula 1243. Leg base colour yellowish with distal tips of all segments slightly darker. Tarsal organs central distal (0.50) on tarsi I and II, proximal on III (0.35–0.40) and IV (0.40–0.45). Four to five small trichobothria dorsally on all tibia, five on tibia I, four on tibia III. Trichobothria on metatarsi I–III proximal (about 0.35–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figures 49G, H, 52A–F.

Female (paratype): Total length 3.58. Prosoma 1.37 long, 1.04 wide, 0.91 high, yellowish, darker in centre and around rim. Sternum 0.87 long, 0.78 wide, extending between coxae IV, yellowish, darker around rim. Abdomen 2.93 long, 1.73 wide, 1.82 high. Pattern as in *A. studiosus*. Eyes subequal, about 0.07 in diameter. Clypeus height about 2.1 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.98, patella 0.52, tibia 1.72, metatarsus 1.63, tarsus 0.68. Femur about 7 times longer than wide, metatarsus I about 16 times longer than wide. Leg formula 1423. Leg base colour yellowish, distal tip of femora, patella, tibia and metatarsi slightly darkened. Tarsal organs distal (0.55) on tarsus I, slightly proximal (0.40–0.45) on II–IV. Five to seven small trichobothria dorsally on all tibia, 5 on tibia I and III. Trichobothria on metatarsi I–III proximal (about 0.40), absent on metatarsus IV.

Three dorsal trichobothria on palpal tibia. Epigynum as in Figures 49I, J, 53A–C.

Variation: Male total length 2.35–2.55, prosoma 1.10–1.20, first femur 1.80–1.90, female total length 3.50–3.65, prosoma 1.35–1.45, first femur 1.95–2.10.

Additional material examined: BRAZIL. Mato Grosso do Sul, Pantanal, Poconé, Rodovia Transpantaneira (hasta Pousada PIXAIM), Fazenda Araras, [17°37′0″S, 57°28′0″W], 5.vii.1996, *c.* 150 m (G. Hormiga, MNR), 8♀ [IA40530]; Porto Cercado [17°25′0″S, 52°27′0″W], 2.viii.1992 (A. A. Lise & A. Braoul Jr, MCP), 1♀ [IA40612]; Pantanal [17°38′0″S, 57°29′0″W], 4–10.viii.1992 (A. A. Lise & A. Braoul Jr, MCP), 1♀ [IA40614]; Fazienda Sta. Inés, Poconé [16°16′0″S, 56°37′0″W], 4–10.viii.1992 (A. A. Lise & A. Braoul Jr, MCP), 2♀ [IA40616].

Distribution: Brazil, in lowland swamps of Mato Grosso (Fig. 63C).

Natural history: Field notes of J. Coddington (pers. comm.) indicate that *A. pantanal* is a typical subsocial species.

ANELOSIMUS FRATERNUS BRYANT, 1948
(FIG 49K–N, 63C)

Types: Male holotype from Haiti, Ennery [19°28′0″N, 72°29′0″W], 10.ix.1934, Darlington, in MCZ, examined [IA40768]. The specimen lacks the first pair of legs, except the femur on the left side, leg III is also missing from the left side.

Synonymies:
Anelosimus fraternus Bryant, 1948: 381–382, figs 55, 57, ♂.
Anelosimus studiosus: Levi, 1956: 419 (in part) not *Theridion studiosum* Hentz, synonymy here rejected.

Etymology: Bryant did not explain the etymology; one may speculate that the species epithet refers to web sharing (fraternus = brotherhood), but the biology of this species is unknown.

Diagnosis: *Anelosimus fraternus* differs from most species of the *studiosus* group by having the embolus tip entire (lacking E-fork, Fig. 49L). It differs from *A. pantanal* by a larger Eb, from fork-less specimens of *A. guacamayos* by a smaller, medially constricted Eb, and from both by having a more extensive row of abdominal stridulatory picks (about 14–16 on each side).

Male (holotype): Total length 2.28. Prosoma 1.17 long, 0.83 wide, 0.66 high, pale brown, darker in centre and around rim. Sternum 0.68 long, 0.59 wide, extending between coxae IV, pale brown with dusky markings. Abdomen 1.37 long, 1.07 wide, 1.07 high. Pattern as in *A. studiosus*. Eyes subequal, about 0.08 in diameter. Clypeus height about 2.3 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.50, the type specimen is lacking other segments of legs I. When described (Bryant 1948: 381) the legs were seemingly intact and she described the first pair of legs as ‘very long’. Femur about 7 times longer than wide. Leg formula 1423. Leg base colour yellowish with, femora slightly darker than other segments. Tarsal organs proximal (0.35–45) on tarsi II–IV. Three to five small trichobothria dorsally on tibia, 4 on tibia III. Trichobothria on metatarsi II–III proximal (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Figure 49K, L.

Female (IA40769): Total length 4.36. Cephalothorax 1.82 long, 1.22 wide, 1.11 high, brown, darker in centre and around rim. Sternum 0.99 long, 0.86 wide, extending between coxae IV, pale brown with dusky markings. Abdomen 2.73 long, 2.43wide, 2.56 high. Pattern as in *A. studiosus*. Eyes subequal in size about 0.08 in diameter. Clypeus height about 2.2 times AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.95, patella 0.62, tibia 10.59, metatarsus 1.46, tarsus 0.68. Femur about 6 times longer than wide, metatarsus I about 9 times longer than wide. Leg formula 1243. Leg base colour yellowish with femora slightly darker than other segments. Tarsal organs distal (0.55–60) on tarsus I, proximal on tarsi II (0.45–50), and III–IV (0.40–0.45). Five small trichobothria dorsally on all tibia. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Three dorsal trichobothria on palpal tibia. Epigynum as in Figure 49M, N.

Variation: Male only known from holotype. Female total length 4.30–4.50, prosoma 1.80–1.85, first femur 1.90–2.00.

Taxonomic note: Females collected on Hispaniola (Isla Española, Haiti plus Dominican Republic) differ slightly from typical *A. studiosus*, and are here considered conspecific with the holotype male from Haiti. Due to the variability of *A. studiosus*, the limited specimen availability of *A. fraternus*, and absence of other than geographical evidence matching sexes, the validity and circumscription of this species certainly needs further scrutiny.

Additional material examined: HAITI. Ouest, Port-au-Prince [18°32′0″N, 72°20′0″W] (MCZ), 1♀ [cf. IA40932]; Carrefour [19°24′0″N, 72°4′0″W], 23.vii.1955 (A. F. Archer, AMNH), 1♀ [cf. IA40576]. DOMINICAN REPUBLIC. Sánchez Ramírez, Mina Pueblo Viejo, nr.

Hatillo [18°56′0″N, 70°15′0″W], 21.iii.1984, 100 m (H. & L. Levi, MCZ), 1♀ [cf. IA40769].

Distribution: Haiti and Dominican Republic (Fig. 63C), between *c.* 100 and 400 m.

Natural history: Unknown.

MISPLACED TAXA

CHROSIOTHES EPISINOIDES (LEVI, 1963), **COMB. NOV.**

Synonymy:
Anelosimus episinoides Levi, 1963: 40, figs 20–24, ♂♀

Types: Male holotype from Chile, Lineres, Fundo Malcho, Cord., Parral, ii.1958, in KBIN, examined.

Comments: The affinities of this species are not clear, but it most closely resembles species of the genus *Chrosiothes* (see Levi, 1964b), where it also keys out in the key of Agnarsson (2003a). The triangular-shaped, humpy, abdomen overhanging spinnerets, dark dorsal band on carapace and conformation of palp and epigynum all indicate affinity with *Chrosiothes* (Levi, 1963: figs 20–24). It differs from *Anelosimus* by abdomen shape and coloration, prosoma shape and coloration, and labium without a seam.

STEMMOPS OSORNO (LEVI, 1963), **COMB. NOV.**

Synonymy:
Anelosimus osorno Levi, 1963: 47, fig. 58–61, ♂.

Types: Male holotype from Chile, Osorno, Lago Puyehue, 16.ii.1957, L. Peña, in KBIN, examined.

Comments: This small (1.5 mm) species is transferred to *Stemmops*. It has a distinctly round prosoma (Levi, 1963: figs 58, 59), characteristic of *Stemmops* (see Levi, 1964b). It bears a large colulus with a pair of setae, and has a hooded cymbial lock system, a combination unique to some species of *Stemmops*, and a few spintharines, albeit the latter normally have a small colulus (note that *Stemmops* groups with spintharines in the study of Arnedo *et al*., 2004, not with Pholcommatines as in the study of Agnarsson, 2004). It further differs from *Anelosimus* in having only two promarginal cheliceral teeth, with the outer one larger, by having AME smaller than other eyes, and by having a light central band dorsally on the abdomen. The palpal conformation is unlike that of any *Anelosimus* (Levi, 1963: figs 60–61), but resembles *Stemmops bicolor*, the type of the genus.

STYPOSIS CAMOTEENSIS (LEVI, 1967), **COMB. NOV.**

Synonymy:
Anelosimus camoteensis Levi, 1967: 15, figs 30–32, ♂♀.

Types: Female holotype and male paratype from Chile, Juan Fernández Islands, Más a Tierra, Valle Ansón, Plazoleta del Yunque, 200–250 m, Camote side, 1–28.iv.1962, B. Malkin, in AMNH, examined.

Comments: This small (1.2–1.5 mm) species is transferred to *Styposis*. It has a large leaf-like colulus, characteristic of *Styposis* and *Pholcomma* (see Levi, 1964a; Agnarsson, 2004). Like other *Styposis* the lateral eyes and PME are large and close together, while the AME are small. The abdomen lacks a dorsal band, but has dark- and light-pigmented spots on dorsum. Both general habitus and genitalia strongly resemble other *Styposis* species. It is not clear why Levi placed this species in *Anelosimus* as he correctly states (Levi, 1967: 15): 'This very small, large-eyed species resembles species of *Mysmena* . . .The palpus . . . except for a mesal sclerite, is lightly sclerotized and unlike that of any other *Anelosimus* species, except the larger *A. tepus*.' *Anelosimus tepus* Levi, 1967 (= *Styposis tepus*) is described from a female in the same paper (Levi, 1967) but interestingly, although comparing the males of the two species, Levi did not describe the male of *S. tepus*, which remains known only from the female.

STYPOSIS TEPUS (LEVI, 1967), **COMB. NOV.**

Synonymy:
Anelosimus tepus Levi, 1967: 15, figs 28–29, ♀

Types: Female holotype from Chile, Osorno, Termas de Puyehue, 240 m, 14.iii.1965, H. Levi, in MCZ, examined.

Comments: This medium-sized (2.2 mm) species is transferred to *Styposis*. It clearly belongs to Pholcommatinae, having a large colulus with two setae, and AME smaller than other eyes. It differs from *Anelosimus* by having a single trichobothrium dorsally on female palpal tibia, and epigynum a transparent plate without ridges. Furthermore, as pointed out by Levi (1967: 15): 'This species is readily separated from most other *Anelosimus* by the unusual coloration . . .', the abdomen lacks a dorsal band, but has dark-pigmented spots on dorsum. Its placement in *Styposis* (instead of the similar *Selkirkiella*) is speculative based on the female alone, but is congruent with Levi's statement (see above) on the similarity of the palps of *S. camoteensis* and *S. tepus*. The female, furthermore, has a simple copulatory duct, while the many similar sympatric species of *Selkirkiella* have tightly spiralling copulatory ducts.

NOMINA DUBIA

Anelosimus nigrobaricus Barrion & Litsinger 1995: 453, fig. 273a–f, ♀.
The original description lacks sufficient detail to allow identification, and the female holotype was not found

at the Rice Institute in the Philippines. It is thus here treated as a *nomen dubium*.

Anelosimus salaensis Barrion & Litsinger, 1995: 452, fig. 272a–h, ♀.
The original description lacks sufficient detail to allow identification. Female holotype in the Rice Institute, Philippines, examined. In very bad condition, lacks abdomen and chelicerae, but epigynum is in a microvial. Not *Anelosimus*, possibly a Pholcommatine.

Theridion fasciatum Holmberg, 1876: 4, 12, fig. 13, ♀.
The original description is clearly of *Anelosimus*, but lacks sufficient detail to allow further identification. The type came from Argentina, presumably deposited in either Paris, or Copenhagen, and presumed lost (see Levi, 1956).

Theridion sordidum Holmberg, 1876: 4, 12, fig. 14, ♀.
As *T. fasciatum*.

NOTES ON *SELKIRKIELLA*

SELKIRKIELLA ALBOGUTTATA BERLAND, 1924

Selkirkiella alboguttata Berland, 1924: 430, figs 20–24, ♂♀, transferred to *Anelosimus* by Levi, 1972. Transfer rejected by Agnarsson (2004) who again recognized *Selkirkiella*, *S. alboguttata*, a senior synonym of *A. portazuelo*, is the type species of *Selkirkiella*. The examination of the holotype of *A. portazuelo* here, corroborates the synonymy.

Synonomy:
Anelosimus portazuelo Levi, 1967: 14, fig. 34–36, ♂♀, synonymized by Levi, 1972: 536. Types in AMNH, examined.

SELKIRKIELLA CARELMAPUENSIS (LEVI, 1963)

Synonymies:
Anelosimus carelmapuensis Levi, 1963: 45, figs 45–48, ♀, Levi, 1967: 13, fig. 33, ♂.
Selkirkiella carelmapuensis Agnarsson, 2004.

Types: Female holotype from Chile, Llanquehue, Carelmapu, 21–28.ii.1957, L. Peña, in KBIN, examined.

Comments: The species was transferred to *Selkirkiella* by Agnarsson (2004) and the examination of the type specimen confirms this transfer. It has a prominent colulus with two setae, small AME, and the epigynum is characteristic of *Selkirkiella*, with a small opening and copulatory ducts winding and encircling itself lateral to the copulatory opening.

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APPENDIX 1

CHARACTER DESCRIPTIONS AND COMMENTS

Characters taken from Agnarsson (2004) whether modified or not, are marked with a bold A04, followed by the character number (e.g. **A04**-26 is character 26 in Agnarsson, 2004). These characters are not described in detail here unless modified (modified characters have underlined character numbers).

1. *Epigynal ventral margin*: (0) entire (Figs 3B, 5C, 7C, I, M); (1) with scape (Fig. 55A). **A04**-1.

Among theridiid spiders, a ventral (posterior) epigynal scape is only present in a few *Anelosimus* species, here it is a synapomorphy of the 'epigynal scape clade'.

2. *Epigynal external structure*: (0) epigynal plate on a broad depression, copulatory openings not visible (Figs 3B, 22A, 24B); (1) copulatory openings clearly visible ventrally, flush with abdominal cuticle, or on a depressed epigynal plate, sometimes slit like (see Agnarsson, 2004, fig. 45F).

In *Anelosimus* and relatives the copulatory openings are not visible ventrally on the distinctly depressed epigynal plate.

3. *Epigynal plate*: (0) narrow, ectal margins extending at most slightly ectal to ectal margin of spermathecae (Fig 1C-D, I); (1) wide (at least twice as wide as high), ectal margin extending beyond spermathecal ectal margin by at least one spermathecae diameter (Figs 19C, D, 44C, D, I–K).

A wide epigynal plate is characteristic for *Anelosimus* (excluding the new species from Australia) and is here a synapomorphy of clade 29.

4. *Epigynal plate surface*: (0) smooth, or with a single broad ridge (Fig. 5C); (1) ridged, with rows of parallel horizontal ridges (Figs 22A, B, 24B). **A04**-3.

Typically in *Anelosimus* the epigynal plate is distinctly ridged; here a synapomorphy of the Eb clade, and convergently of the *rupununi* group.

5. *Epigynal septum*: (0) absent (Figs 3B, 26A); (1) present (Fig. 55B).

Uniquely in the Madagascar group of *Anelosimus* a conspicuous plate (septum) arises from the anterior margin of the epigynal plate (see Agnarsson & Kuntner, 2005).

6. *Epigynal plate anterior margin*: (0) entire, broadly transverse; (1) medially acute. **A04**-6
7. *Copulatory duct-spermathecal junction*: (0) posterior; (1) lateral or anterior. **A04**-7.
8. *Copulatory duct loops relative to spermathecae*: (0) apart; (1) encircling. **A04**-9.
9. *Copulatory duct (CD) terminal sclerotization*: (0) as rest of duct (Figs 7D, J, N, 16D); (1) distinctly sclerotized, clearly more than rest of duct (Fig. 27D, F-G).

The copulatory duct is distinctly sclerotized terminally in all species of the *analyticus*, *studiosus* and *jucundus* groups. On this cladogram this sclerotization arose convergently in the *analyticus* group and in the 'sclerotized copulatory duct clade' (*studiosus* plus *jucundus* groups) .

10. *Sclerotized copulatory duct region*: (0) mostly or entirely ectal to the ectal rim of the spermathecae (Fig. 27G); (1) caudal to the spermathecae, mesal to ectal margin of spermathecae (Fig. 44D).

Mesally positioned sclerotized copulatory duct region is a synapomorphy of the *studiosus* group.

11. *Male palpal tibial rim*: (0) uniform or only slightly asymmetric; (1) strongly and asymmetrically protruding, scoop-shaped. **A04**-15.
12. *Male palpal tibia prolateral trichobothria*: (0) one; (1) none. **A04**-19.
13. *Cymbial ridge ectal setae*: (0) unmodified (e.g. Fig. 21D, E); (1) strongly curved towards the palpal bulb (*Kochiura aulica*, Fig. 55F).

In *Kochiura aulica* and some other *Kochiura* species (my pers. obs.) the setae forming a row on the ectal cymbial ridge are distinctly curved towards the palpal bulb.

14. *Cymbial distal promargin*: (0) entire; (1) with an apophysis. **A04**-24.
15. *Cymbial mesal margin*: (0) entire (Agnarsson, 2004, fig. 46A); (1) incised (Agnarsson, 2004, fig. 22A); (2) deeply notched (Figs 23A, B, 29A, 33A). **A04**-25.

Here a state has been added to **A04**-25, distinguishing between slight and deep incisions of the cymbial mesal margin. A slightly incised margin is a synapomorphy of clade 29, while a deeply notched margin unites the *eximius* group and the Madagascar group (clade 19). As both states 1 and 2 share the condition 'incised' this character could arguably be ordered. Doing so results in the same strict consensus tree, but support for several nodes goes up.

16. *Cymbial tip sclerotization*: (0) like rest of cymbium; (1) lightly sclerotized, appears white. **A04**-26.

On this cladogram a lightly sclerotized cymbial tip is a synapomorphy of the *eximius* group, and convergently the *Tanzania* group.

17. *Cymbial tip setae*: (0) like other setae; (1) some setae at tip thick and strongly curved. **A04**-27.
18. *Cymbial sheath*: (0) absent; (1) present. **A04**-28.
19. *Bulb to cymbium-lock placement*: (0) distal; (1) central. **A04**-32.

A centrally placed cymbial hood (the cymbial part of the bulb to cymbium-lock) is a synapomorphy uniting clade 23 (*Anelosimus nelsoni* plus the epigynal scape clade).

20. *Lock mechanism*: (0) hook; (1) hood. **A04**-33.

Hooded lock mechanism is here corroborated as an unreversed (perfect fit) synapomorphy of the lost colulus clade (see Agnarsson, 2004).

21. *Cymbial hook orientation*: (0) facing proximal; (1) facing terminal. **A04**-34.
22. *Cymbial hook location*: (0) inside cymbium; (1) ectal cymbial margin **A04**-35.
23. *Cymbial hook distal portion*: (0) blunt; (1) tapering to a narrow tongue. **A04**-37.
24. *Cymbial hood size*: (0) narrow; (1) broad. **A04**-38.
25. *Cymbial hood region*: (0) translucent, hood visible through cymbium; (1) opaque, hood not visible. **A04**-39.
26. *Alveolus shape*: (0) circular or oval; (1) with a mesal extension. **A04**-43.

27. *Tegulum ectal margin*: (0) entire; (1) protruded. **A04**-46.

Agnarsson (2004) found a protruded tegular margin (ectal tegular process, ETP) in a single undescribed *Anelosimus* (= *A. baeza*) species, but included the autapomorphy anticipating its use in *Anelosimus* phylogeny. Here the character provides evidence for the sister relationship of *Anelosimus baeza* and *A. puravida* (Figs 27B, C, O, 28C, 30A, 33C).

28. *Tegular groove*: (0) absent; (1) present. **A04**-47.
29. *Sperm duct trajectory switchback I (SDT SBI)*: (0) separate; (1) touching. **A04**-52.

The two arms of SB I touching is here a synapomorphy of the epigynal scape clade.

30. *Sperm duct trajectory post-switchback II turn*: (0) gradual; (1) 90°. **A04**-54 (Fig. 57D–F).

A sharp (90°) dive of the sperm duct into the tegulum after switchback II is a synapomorphy of the *eximius* group.

31. *Sperm duct trajectory switchback I & II reservoir segment alignment*: (0) divergent; (1) parallel. **A04**-55 (Fig. 57E, G).

Parallel switchback I & II segments is here a synapomorphy of the curved stridulatory pick row clade.

32. *Sperm duct trajectory switchback I & II orientation*: (0) in plane of first loop from fundus; (1) out of plane of first loop, against tegular wall. **A04**-56. (Fig. 57D–G)
33. *Sperm duct trajectory reverse switchback I & II*: (0) absent; (1) present. **A04**-57.
34. *Sperm duct trajectory switchback III*: (0) absent; (1) present. **A04**-58.
35. *Sperm duct trajectory switchback IV*: (0) absent; (1) present. **A04**-59.

Given the presence of switchback III, in some cases an additional switchback occurs between switchback III and the embolus (switchback IV, see Agnarsson, 2004: fig. 93E).

36. *Conductor shape*: (0) simple, round or oval, short (Fig. 56A); (1) fan shaped, narrow base and broad tip (*Selkirkiella*, *Kochiura* (Fig. 56B)); (2) *Enoplognatha* (Fig. 56C); (3) *Argyrodes* (Fig. 55D); (4) *Achaearanea* (Fig. 56D); (5) *Theridion* (Fig. 56E); (6) '*rupununi*' (Fig. 56F); (7) 'Tanzania' (Fig. 56G); **(8)** 'cup-shaped' (e.g. *A. jucundus* Fig. 56H)).

The shape of the conductor in theridiid varies so much that homology statements at the genus level are very difficult. Here I adopt an exemplar approach where each conductor form is a different character state and is associated with a specific taxon and described with an image (see Fig. 56A–H). Hormiga *et al*. (1995) and Griswold *et al*. (1998) adopted the same strategy dealing with the complex form of the araneoid paracymbium. This has the advantage of being explicit, and allowing the inclusion of at least some of the information contained in conductor shape. However, it comes at the cost of ignoring (due to difficulty) variation at a finer level.

On this cladogram a simple round conductor is the primitive condition, but has been modified multiple times. Within *Anelosimus* the cup-shaped conductor is of special interest, a synapomorphy of the sclerotized copulatory duct clade, and convergently of the *analyticus* group.

37. *Conductor*: (0) with a groove for embolus; (1) entire, lacking groove. **A04**-64.
38. *Conductor surface*: (0) smooth; (1) ridged. **A04**-65.
39. *Conductor tip sclerotization*: (0) like base; (1) more than base. **A04**-67.
40. *Subconductor*: (0) absent; (1) present. **A04**-70.

The subconductor on this cladogram is a synapomorphy of the embolic division b clade.

41. *Subconductor pit upper wall*: (0) entire, or slightly protruding (Figs 4B, 50C); (1) forms a regular oval lip (Figs 20C, 25C, 27B, C, O).

The subconductor forms a groove (pit) that may overhang a portion of the embolus spiral, or the embolus base may fit into it. In some *Anelosimus* the portion of the subconductor overlying the pit may be more or less straight (entire), or alternatively oval (e.g. the *jucundus* group).

42. *Subconductor at conductor base*: (0) narrows abruptly before conductor base (Figs 1B, 4B, 49G, 52D, E); (1) narrows gradually along its entire length (Figs 27B, C, O, 28B, 33C); **(3)** broad at base, conductor arises from the subconductor before it narrows (before it joins the tegulum) (Fig. 17E).

Where a subconductor is present the conductor arises directly from it (not from the tegulum; the subconductor is a modified outgrowth of the tegulum), usually at the base of the subconductor. The subconductor is usually much broader distally than basally, and may narrow abruptly near its base (0), gradually along its length from tip to base (1), or hardly narrow at all (2). In *A. eximius* and convergently in members of clade 23 the subconductor is uniformly wide, and the conductor arises from the subconductor before it joins the tegulum.

43. *Embolus base-subconductor relation*: (0) hooked in, or orientated towards subconductor (Figs 2C, 4B, 7F, 36C, 39C, 40B); (1) surpasses subconductor (Figs 16B, 17B, 19B, G, J, 20C); (2) behind embolus base.

In many cases the basal lobe of the embolus fits into the subconductor pit and is either hooked in or orientated towards it. In *A. eximius* and the *jucundus* group the embolus lobe surpasses the subconductor pit and the latter overhangs a portion of the embolus spiral. In the epigynal scape clade the subconductor pit lies behind the embolus base and it is unclear which (if any) part of the embolus interacts with it.

44. *Tegulum ectally*: (0) occupying less than half of the cymbial cavity; (1) occupying more than half of the cymbial cavity.

In the Asian *Anelosimus*, which based on descriptions form a monophyletic group, the tegulum is typically voluminous, in an ectal view occupying more than half of the cymbial cavity. A similar condition occurs convergently in *Anelosimus* sp. 1.

45. *Median apophysis and sperm duct*: (0) sperm duct loop not inside median apophysis; (1) sperm duct loop inside MA. **A04**-72.
46. *Median apophysis-tegular membrane connection*: (0) broad; (1) narrow. **A04**-74.
47. *Median apophysis form*: (0) unbranched; (1) two nearly equally sized branches. **A04**-75.
48. *Median apophysis distal tip*: (0) entire; (1) hooded. **A04**-78.
49. *Median apophysis hood form*: (0) narrow, pit-like; (1) scoop-shaped. **A04**-79.
50. *Theridiid tegular apophysis form*: (0) entire; (1) grooved. **A04**-83.
51. *Theridiid tegular apophysis*: (0) bulky (e.g. Fig.17E); (1) prong shaped (see Agnarsson, 2004 fig. 26(A–B).

An unusually shaped, long and thin (prong shaped) theridiid tegular apophysis is present in *Anelosimus nelsoni*, *A. vittatus* and *A. pulchellus*.

52. *Theridiid tegular apophysis distal tip*: (0) entire or gently curved (Fig. 55C); (2) *Argyrodes* (Fig. 55D); (3) hooked (branched, Figs 1A, 17A, 19A, F, 20A, 23B, 27A, 35A, 45A). **A04**-85 (in part).

The distal tip of the theridiid tegular apophysis in many *Anelosimus* is strongly hooked (or folded on itself), which may play some role in fixing the bulb in the epigynum. In *Argyrodes* a short and simple fold is present (Fig. 55D), but in many *Anelosimus* the theridiid tegular apophysis hook is long and overhangs a second short branch (the hook base).

53. *Theridiid tegular apophysis hook distal branch*: (0) barely exceeding lower branch (Figs 16A, 35A, G, K); (1) extending beyond lower branch (Fig. 19A, F).

In the *jucundus* group the theridiid tegular apophysis hook is especially long and extends beyond the lower ‘branch’ (or hook base) of the theridiid tegular apophysis tip (Fig. 19A).

54. *Theridiid tegular apophysis hook distal branch*: (0) thick (Fig. 19A); (1) thin, finger-like (Fig. 7A, K).

In the *domingo* group the theridiid tegular apophysis hook is thin and finger-like.

55. *Theridiid tegular apophysis hook proximal branch*: (0) blunt, broad (Fig. 19A); (1) flattened, blade-like (Fig. 57B); (2) cylindrical, elongated (Fig. 57A).
56. *Theridiid tegular apophysis surface subterminally*: (0) smooth (Fig. 55C, D); (1) ridged (Figs 2B, 42C). **A04**-86 (in part)

In the *eximius* group the surface of the theridiid tegular apophysis is ridged subterminally, inside the groove formed by the two branches of the theridiid tegular apophysis hook (Fig. 2B). Here these subterminal ridges are not considered homologous to ridges on the theridiid tegular apophysis tip (see character 57). Agnarsson (2004) considered any theridiid tegular apophysis ridges as potentially homologous, but on his cladogram ridges evolved several times. Apart from differing in topology, here the homology of subterminal and terminal ridges is rejected by the cladogram (Fig. 60), and by conjunction as both are present in *Theridion*. Subterminal ridges are here a synapomorphy of the *eximius* group.

57. *Theridiid tegular apophysis tip surface*: (0) smooth (Fig. 2A); (1) ridged (Fig. 55D). **A04**-86 (in part). See also character 56.
58. *Embolus and theridiid tegular apophysis*: (0) loosely associated with or resting in theridiid tegular apophysis shallow groove; (1) parts of embolus entirely enclosed in theridiid tegular apophysis. **A04**-87.
59. *Embolus tip surface*: (0) smooth; (1) denticulate (e.g. Fig. 28E).

Most species of the *jucundus* and *studiosus* complexes have distinct denticulation near the embolus tip, and the character is here a synapomorphy uniting these groups.

60. *Embolus spiral curviture*: (0) gentle (Figs 1B, 27B, C, O); (1) whip-like (Figs 7A, B, E, F, K, L, 9B, C, E); (2) corkscrew (Fig. 55E).

In most *Anelosimus*, and other theridiids, the embolus spirals gently and evenly. In the *domingo* group, however, the embolus is whip-like, changing directions along the spiral (Figs 7A, B, 9B, C). In *Anelosimus* sp. 1 the embolus is shaped like a corkscrew (Fig. 55E) similar to some *Theridula*.

61. *Embolus tip*: (0) entire (Figs 1B, G, K, 7A, B, E, F, K, L); (1) bifid (Figs 23F, 25F, 28E, 39E). **A04**-88.
62. *Embolus origin*: (0) ectoventral on tegulum; (1) retrolateral (ectal), partially or completely hidden by cymbium. **A04**-89.
63. *Embolus ridges*: (0) absent; (1) present. **A04**-90.
64. *Embolus shape*: (0) short to moderately elongate (fewer than 2 spirals); (1) extremely long, > 2 spirals. **A04**-91.
65. *Embolus spiral width*: (0) thin, much of E spiral subequal to E tip (Fig. 1B, G, J, K); (1) thick, entire E spiral much broader than tip (Fig. 23F). **A04**-92.

A thick (bulky) embolus spiral is here a synapomorphy of the 'bulky E clade'.

66. *Embolus distal rim*: (0) entire (normal); (1) deeply grooved. **A04**-95.
67. *Embolic terminus*: (0) abrupt; (1) with a distal apophysis. **A04**-96.
68. *Embolus base*: (0) entire, smooth; (1) distinct, lobed. **A04**-98.

A lobed embolus base is here a synapomorphy of clade 29.

69. *Embolus-dh connection grooves*: (0) absent (Figs 2C, 4B); (1) present (Figs 35B, H, L, 36C, 39B, C).

In theridiids the embolus connects to the tegulum via the distal hematodocha. This connection is usually not visible ventrally, and is 'seamless'. In most species of the *eximius* group, by contrast, the connection between the embolus and distal hematodocha is visible ventrally, marked by paired grooves near the embolus lobe (Fig. 36C). On this cladogram these grooves are an unreversed (perfect fit) synapomorphy of clade 14.

70. *Embolus-distal hematodocha grooves*: (0) deep, extend into the embolus base more than twice longer than the distance between them (Fig. 39C); (1) short, extend into the embolus base about as long, or slightly longer than the distance between them (Fig. 20C).
71. *E spiral subterminally*: (0) relatively thin or filiform, cylindrical (Fig. 1B); (1) thick, not cylindrical (Figs 20E, 23F); (2) *rupununi*/*lorenzo* like (see Agnarsson, 2004, fig. 22B–D).

Theridiid emboli are typically thin and cylindrical subterminally. In some *Anelosimus*, however, the distal portion is not cylindrical, but somewhat flattened and robust. Here this condition is a synapomorphy of the bulky embolus clade. *A. rupununi* and *A. lorenzo* have a unique embolus (see Agnarsson, 2004, fig. 22B–D).

72. *Embolus spiral*: (0) entire (Fig. 56D); (1) bipartite (Eb, Figs 1B, 7B, F, L, 19A, B, F, G, I, J); (2) 'pars pendula' (Figs 16B, 17B). **A04**-99 (in part).

In theridiids the embolus spiral is typically sclerotized and entire (e.g. Fig. 56D). In many *Anelosimus*, however, the embolus spiral is bipartite, forming the embolus main branch through which the sperm duct exits, and embolic division b (Eb), which often closely follows, and may support, the embolus (the terminology of Eb is taken from Levi, 1956). The embolic division b is variable in size, degree of sclerotization, orientation and rugosity. It is here not considered a potential homologue of other embolic apophysis (e.g. in *Argyrodes* and *Steatoda*, see Agnarsson, 2004), as it is dissimilar, differs distinctly in topology (branching off the embolus spiral, rather than off the embolus base) and presumably differs in function. The phylogeny supports this conclusion. The embolus spiral of *A. eximius* is autapomorphic in having an outer sclerotized rim and an inner membraneous part. Analogous membraneous parts are often termed 'pars pendula', but the term may be misleading as it does not seem to be used to imply homology across taxa.

73. *Embolic division b orientation*: (0) towards embolus tip (Fig. 19B); (1) towards tibia.

In most *Anelosimus* the embolic division b is orientated towards the tip of the palp, but in a few, e.g. *A. vittatus*, it is orientated towards the tibia (see Agnarsson, 2004, fig. 26B).

74. *Embolic division b*: (0) separates early from embolus (Figs 1B, 56A); (1) Embolus and embolic division b tightly associated over the entire spiral (Fig. 19B, G, J).

Tight association between the embolus and Eb is here a synapomorphy of the sclerotized copulatory duct clade.

75. *Embolic division b terminally*: (0) broad, does not narrow abruptly (Fig. 27B, C, O); (1) narrow, embolic division b narrows abruptly subterminally, terminus snout-like (Figs 44A, F, 49B, G, H, K, L).

The embolic division b of the *studiosus* group is narrow and snout-like distally compared with basally.

76. *Embolic division b distal portion*, *ectal marginl*: (0) level, not raised (Fig. 19B); (1) with a distinct ridge (Fig. 19F, G, J, K).

Anelosimus jucundus and *A. octavius* are united by a distinct ridge distally on embolic division b ectal side (Fig. 19J, K)

77. *Embolic division b form, basally*: (0) flat, in ectal view (Fig. 28D); (1) globose, inflated, distinctly rounded in ectal view (Fig. 20D).

In some species of the *jucundus* group the embolic division b is globose basally, so that when viewed ectally the embolus is grossly thickened (Fig. 20D). Here a globose embolic division b is a synapomorphy of clade 7 (*A. arizona* (*A. jucundus*, *A. octavius*)).

78. *Eb form*: (0) distinct, clearly separate apophysis (Fig. 36B); (1) short, confined to first section of spiral, barely separate (Fig. 57C).

In the *ethicus* group the embolus has a subbasal ridged area, presumably homologous to the embolic division b of related taxa. It differs in barely separating from the embolus spiral.

79. *Embolus spiral tip*: (0) separated from other parts of the embolus (Figs 1B, 56A); (1) embolic division b and embolus tips juxtaposed (Fig. 19F, G); (2) embolus tip rests on embolic division b 'cup' (Fig. 7B, E, F, L).
80. *Embolic division b snout*: (0) short, snug with embolus spiral (Fig. 42C); (1) long, separate from embolus spiral (Fig. 39E, F).

81. *Distal portion of embolic division b*: (0) entire (Figs 27B, 28B); (1) with a cup-shaped apophysis (Figs 7B, E, L, 9E, 11D, 13E); (2) with a raised ridge (Fig. 20B, E, F).

In the *domingo* group the Eb distally has a distinctly cup-shaped apophysis (Fig. 7B, F, L). In some species of the *jucundus* group (Fig. 20F) a distinct mesal ridge is present.

82. *Embolus tail*: (0) lobe simple, not reaching ectal margin of embolic division b (Fig. 27B, C, O); (1) lobe bifurcate, nearly touching ectal margin of embolic division b (Fig. 23D).

In clade 7 (*A. arizona* (*A. jucundus*, *A. octavius*)) the embolus tail is uniquely bifurcate and reaches the ectal margin of the embolic division b (Fig. 23D).

83. *Extra tegular sclerite*: (0) absent; (1) present. **A04**-101.
84. *Median eyes (male)*: (0) flush with carapace; (1) on tubercle. **A04**-103.
85. *Anterior median eye size (male)*: (0) subequal or slightly larger than ALE; (1) clearly smaller than anterior lateral eyes. **A04**-104.
86. *Cheliceral posterior margin*: (0) toothed; (1) smooth. **A04**-110.
87. *Cheliceral posterior tooth number*: (0) three or more; (1) two; (2) one. **A04**-111.
88. *Cheliceral furrow*: (0) smooth; (1) denticulate. **A04**-112.
89. *Carapace hairiness*: (0) sparsely or patchily hirsute (Figs 5E, 10D, 14F, G); (1) uniformly hirsute (Figs 12E, 18G, 24E, F, 26D, 34F). **A04**-127.

The carapace of species of the *jucundus* and *studiosus* group, and *A. eximius*, appear to be more hirsute than in most other theridiids.

90. *Carapace pars stridens*: (0) irregular; (1) regular parallel ridges. **A04**-128.
91. *Interocular area*: (0) more or less flush with clypeus; (1) projecting beyond clypeus. **A04**-130.
92. *Clypeus*: (0) concave or flat (Figs 10C, 12F, 15C, D, 26E); (1) with a prominent projection. **A04**-131.
93. *Ocular and clypeal region setae distribution (male)*: (0) sparse; (1) in a dense field, or fields. **A04**-132.
94. *Labium-sternum connection*: (0) visible seam; (1) fused. **A04**-135.
95. *Sternocoxal tubercles*: (0) present; (1) absent. **A04**-138.
96. *Pedicel location*: (0) anterior; (1) medial. **A04**-140.
97. *Abdominal folium pattern*: (0) bilateral spots or blotches; (1) distinct central band. **A04**-144.
98. *Abdomen folium*: (0) irregular or straight; (1) distinctly notched (Figs 7G, 27H–J, 35E, O, 44E, L, M, 49E, F).

The abdomen colour pattern of *Anelosimus* is distinct, a dark red in live specimens, distinctly notched, dorsal band, edged by a narrow white notched band. This pattern is alone sufficient to place species in the genus; it is a synapomorphy of clade 29 (only absent in *Anelosimus* sp. 1, which is sister to all other *Anelosimus*). However, colour patterns are difficult to code objectively as characters, a combination of features contribute to the typical *Anelosimus* dorsal band and their independence is not clear. Here, in order not to inflate the number of synapomorphies for *Anelosimus*, the regular dorsal band notches (on dark band) exemplify this characteristic *Anelosimus* abdomen coloration (potential additional characters with the same distribution include red coloration, notched white band, ventrolateral white blotches etc.).

99. *Dorsal band*: (0) dark edged by white; (1) light edged by dark; (2) light edged by white. **A04**-145.
100. *Abdominal pigment*: (0) silver; (1) non-reflective, dull. **A04**-146.
101. *Stridulatory pick form*: (0) weakly keeled; (1) strongly keeled and elongate. **A04**-151.
102. *Stridulatory pick row pick number*: (0) 1–4; (1) 6–28; (2) >30. **A04**-152 (in part).
103. *Stridulatory pick insertion*: (0) flush with abdominal surface; (1) on a ridge. **A04**-154.
104. *Stridulatory pick row mesally-orientated picks*: (0) absent; (1) present. **A04**-156.
105. *Stridulatory pick row mesally-orientated picks relative to sagittal plane*: (0) angled dorsally; (1) perpendicular or angled ventrally (Fig. 26C). **A04**-157.
106. *Stridulatory pick row*: (0) straight or slightly irregular; (1) distinctly curved (Figs 3C, 24C, 46D); (2) argyrodine, dorsal picks set aside from others. **A04**-159.

Curved stridulatory pick rows are here a synapomorphy of clade 25, or the ‘curved stridulatory pick row clade’

107. *Stridulatory pick row dorsal pick spacing*: (0) subequal to ventral pick spacing; (1) distinctly compressed (Figs 14E, 18B). **A04**-160.

The compression of stridulatory pick rows picks is another synapomorphy of the curved stridulatory pick rows clade, reversed in the epigynal scape clade.

108. *Stridulatory pick row relative to pedicel*: (0) lateral; (1) dorsal (Fig. 10F). **A04**-161.
109. *Stridulatory pick row setae*: (0) separate; (1) tight.

In most *Anelosimus* the stridulatory pick row setae are usually tightly arranged on the abdomen, so that the distance between setae is less than the width of the setal bases. Typically in other theridiids, and basal *Anelosimus*, the stridulatory pick row setae are more separate. Here tight stridulatory pick row setae are a synapomorphy of clade 27.

110. *Supra pedicillate ventrolateral (4 o'clock) proprioreceptor*: (0) absent; (1) present (e.g. Figs 3F, 12B). **A04**-164.
111. *Epiandrous spigot arrangement*: (0) in one pair of sockets (Figs 3A, 5D, 10E, 11F, 26B); (1) in a row. **A04**-169.
112. *Epiandrous spigot pair number*: (0) = >9 (Figs 11F, 26B); (1) 6–8; (2) 4–5 (Figs 10E, 46B); (3) 1. **A04**-170.
113. *Colulus*: (0) present; (1) absent. **A04**-172.

The results again corroborate the secondary loss of a colulus as a strong, unreversed, synapomorphy of the lost colulus clade.

114. *Colulus size*: (0) large and fleshy; (1) small, less than half the length of its setae. **A04**-173.
115. *Colular setae*: (0) present; (1) absent. **A04**-174.
116. *Colular setae number (female)*: (0) three or more; (1) two. **A04**-175.
117. *Palpal claw dentition (female)*: (0) dense, > half of surface covered by denticles; (1) sparse < half of surface with denticles. **A04**-178.
118. *Palpal tibial dorsal trichobothria (female)*: (0) four; (1) three; (2) two; **(3)** five. **A04**-179 (in part).

The presence of three dorsal tibial trichobothria is a synapomorphy of *Anelosimus* (Figs 15G, 48D). However, a few species of the *jucundus* and *studiosus* groups have four, and uniquely in the Madagascar group, five trichobothria are present.

119. *Femur I relative to II and IV*: (0) subequal (Fig. 7H); (1) robust, clearly larger than femur II and IV (Fig. 55G). **A04**-182.

Most basal *Anelosimus* have robust femora I, but a reversal to 'normal' femora I defines the *eximius* group.

120. *Leg IV relative length (male)*: (0) Leg IV 3rd longest (typical leg formula 1243); (1) Leg IV 2nd longest (typical leg formula 1423). **A04**-184.
121. *Leg IV relative length (female)*: (0) Leg IV 3rd longest; (1) Leg IV 2nd longest. **A04**-185.
122. *Femur vs. metatarsus length (female)*: (0) metatarsus longer; (1) metatarsus shorter. **A04**-186.
123. *Femur vs. metatarsus length (male)*: (0) metatarsus longer; (1) metatarsus shorter.
124. *Metatarsus vs. tibia length (female)*: (0) metatarsus longer; (1) metatarsus shorter. **A04**-187.
125. *Metatarsus vs. tibia length (male)*: (0) metatarsus longer; (1) metatarsus shorter.
126. *Metatarsal ventral macrosetae*: (0) like other macrosetae; (1) thick compared with other macrosetae (Fig. 22G). **A04**-188.

Several *Anelosimus* have a row of notably thick macrosetae ventrally on the metatarsus I, but this condition is highly homoplasious (CI = 0.16).

127. *Tarsus IV comb serrations*: (0) simple, straight; (1) curved hooks. **A04**-195.
128. *Tarsal organ size*: (0) smaller than setal sockets (normal); (1) enlarged. **A04**-198.
129. *Tarsus IV central claw vs. laterals (male)*: (0) short, at most subequal; (1) elongate, longer (Fig. 15E). **A04**-199.
130. *Tarsus IV central claw vs. laterals (female)*: (0) weak and at most slightly longer (Fig. 15F); (1) stout and distinctly longer. **A04**-200.
131. *Spinneret insertion*: (0) abdominal apex; (1) subapical, abdomen extending beyond spinnerets. **A04**-201.
132. *PLS flagelliform spigot length*: (0) subequal to PLS cylindrical; (1) longer than PLS cylindrical. **A04**-206.
133. *PLS, PMS cylindrical spigot bases*: (0) not modified, subequal or smaller than ampullates; (1) huge and elongated, much larger than ampullates. **A04**-208.
134. *Cylindrical shaft surface*: (0) smooth; (1) grooved. **A04**-209.
135. *PLS aciniform spigot number*: (0) five or more; (1) four or fewer. **A04**-211.
136. *PLS flagelliform spigot*: (0) present; (1) absent. **A04**-212.
137. *PLS posterior aggregate spigot shape*: (0) normal, round; (1) flattened (Figs 3E, 10B, 18C). **A04**-216.
138. *PLS theridiid type aggregate position*: (0) more or less parallel; (1) end-to-end. **A04**-218.
139. *PMS minor ampullate (mAP) spigot shaft length*: (0) short, subequal to cylindrical shaft; (1) clearly longer than any cylindrical shaft. **A04**-223.
140. *Web form*: (0) sheet; (1) cobweb; (2) network mesh web – with foraging field below (*rupununi*/*lorenzo*); (3) dry line-web. **A04**-225.

Web characters (140–142) scored based on personal observations (I. Agnarsson), personal communication (J. Coddington, W. Eberhard) and literature (Wiehle, 1931, 1937; Nielsen, 1932; Holm, 1939; Nørgaard, 1956; Levi, 1956, 1963, 1972; Bristowe, 1958; Kullmann, 1959a, b, 1960, 1971; Szlep, 1965; Lamoral, 1968; Cutler, 1972; Eberhard, 1972, 1977, 1979, 1981, 1982, 1991; Vollrath, 1977, 1979; Carico, 1978; Kaston, 1981; Roberts, 1985, 1995; Lubin, 1986; Nentwig & Christenson, 1986; Whitehouse, 1986, 1987; Hormiga, 1994; Hormiga, Eberhard & Coddington, 1995; Avilés & Gelsey, 1998; Avilés & Salazar, 1999; Avilés, 2000; Avilés *et al.*, 2001; Griswold *et al.*, 1998; Bukowski & Avilés, 2002; Benjamin, Düggelin & Zschokke, 2002; Benjamin & Zschokke, 2002, 2003, 2004). Most social *Anelosimus* make sheet webs with vertical knock-down lines (e.g. Nentwig & Christenson, 1986; Bukowski & Avilés, 2002), but *A. rupununi* and *A. lorenzo* make a mesh network without knock-down lines (Levi, 1972; Avilés & Salazar, 1999). Although here the sheet web is a synapomorphy of clade 19 (Madagascar group plus the *eximius* group) this is probably an artefact of poor knowledge of webs of Old World *Anelosimus*. The optimization of this web type is likely to change when the webs of more species have been documented.

141. *Knock-down lines*: (0) absent; (1) present.
142. *Sticky silk in web*: (0) present; (1) absent. **A04**-226.

On this cladogram absence of sticky silk in web is an ambiguous synapomorphy (ACCTRAN) of *Anelosimus*. Most reports on *Anelosimus* webs that discuss the issue state that the webs are without sticky silk; however, this needs to be verified as sticky silk may be easily overlooked, especially in older webs. Marques *et al*. (1998), for example, found sticky silk on the knock-down lines of *A. jabaquara* and *A. dubiosus*; as these build typical *Anelosimus* sheets, the absence of sticky silk in other species webs is suspect.

143. *Egg sac surface*: (0) spherical to lenticular; (1) stalked. **A04**-230.
144. *Egg case structure*: (0) suboval or roundish; (1) basal knob. **A04**-231.
145. *Web construction*: (0) solitary; (1) communal. **A04**-234.

The participation of several individuals in web construction is one of the features that define web-sharing sociality, beyond maternal care, and is here a synapomorphy of *Anelosimus*.

146. *Mating thread*: (0) present; (1) absent. **A04**-240.
147. *Adult females per nest*: (0) one; (1) multiple.

Another steppingstone on the road to sociality is the presence of multiple adult females per web (tolerance between adults). Some subsocial and all social species have (at least sometimes) nests containing two to numerous adult females. Here the ability to build multi-female webs is a synapomorphy of clade 14 (*domingo* group plus the bulky E clade), the very group containing most of the social species.

[148. *Cooperative behaviour*: (0) solitary; (1) subsocial; (2) permanent sociality.]

Sociality is typically discussed under the categories 'subsocial' and 'quasisocial' (or semi-permanent social). As is discussed here, these categories are somewhat arbitrary and may obscure the various behavioural components that differ both within and among group-forming species. Although social species are in general quite similar, the behaviour of subsocial species ranges enormously and lumping them all under a single character state is oversimplified. Here these categories are therefore not used to reconstruct relationships (this character is excluded from the main analysis). However, it is of interest to explore how many times sociality has arisen in *Anelosimus*. The conclusion of multiple independent origins of sociality is strengthened if these are presumed a priori to be homologous (including sociality as a character); alternatively this character could be considered a proxy for some characteristics all social *Anelosimus* species seem to share, such as inbreeding and biased sex ratios. The effect of including this character was explored with special reference to the evolution of sociality.

APPENDIX 2

MATERIAL EXAMINED FOR PHYLOGENETICS

The list includes species other than those revised here and not included in Agnarsson's (2004) phylogeny. For species also included in Agnarsson (2004) the same specimens were used for character coding, for species here described, see list of material examined for each species.

Sp. 1 Australia: [no locality data], in NMNH.

A. biglebowski: Tanzania: Iringa, Mufindi District, Uzungwa Scarp Forest Reserve Tanzania, 8°30′S 35°52′W, 1515 m, 3.iii.1996, canopy fogging in rainforest, N. Scharff *et al*. (5♂, 4♀), in NMNH.

A. dude: Tanzania: Iringa, Mufindi District, Uzungwa Scarp Forest Reserve Tanzania, 8°30′S 35°52′W, 1515 m, 3.iii.1996, canopy fogging in rainforest, N. Scharff *et al*. (5♂, 4♀), in NMNH.

A. kohi: Singapore: [no locality data], in NMNH.

A. nelsoni: South Africa: South Africa, KwaZulu-Natal, St. Lucia Estuary, Fanies Island, 28°06′41″S 32°25′51″E, 25m, 4.iv.2001, I. Agnarsson *et al*. (2♂, 2♀), in NMNH.

Anelosimus may: Madagascar, Toamasina Province, Périnet Special Reserve (Parc National Andasibe Mantadia), 900–1000 m, 18°56′S, 48°25′E, 7–8.v.2001, I. Agnarsson and M. Kuntner (4♂, 2♀), in NMNH.

Anelosimus sallee: Madagascar, Toamasina Province, Périnet Special Reserve (Parc National Andasibe Mantadia), 900–1000 m, 18°56′S, 48°25′E, 24.xii.1999, M. E. Irwin *et al*. (1♂ holotype and 1♀ paratype), in CAS.

A. ethicus: Brazil, Rio Grande do Sul: Alto dos Casemiros, Cachoeira do Sul, *c.* 61 m, 30°2′0″S, 52°53′0″W, 3.i.1994, R. G. Buss (3♂, 8♀), in MCP.

A. nigrescens: Brazil, Rio de Janeiro: Petrópolis, 850 m, 22°31′0″S, 43°11′0″W, 2–5.xi.1945, H. Sick (2♀, 3♀), in AMNH.

A. rabus: Brazil, Santa Catarina, Nova Teutonia, 27°11′S, 52°23′W, xi.1957, F. Plaumann (♂ holotype, 3♀ paratypes), in KBIN.

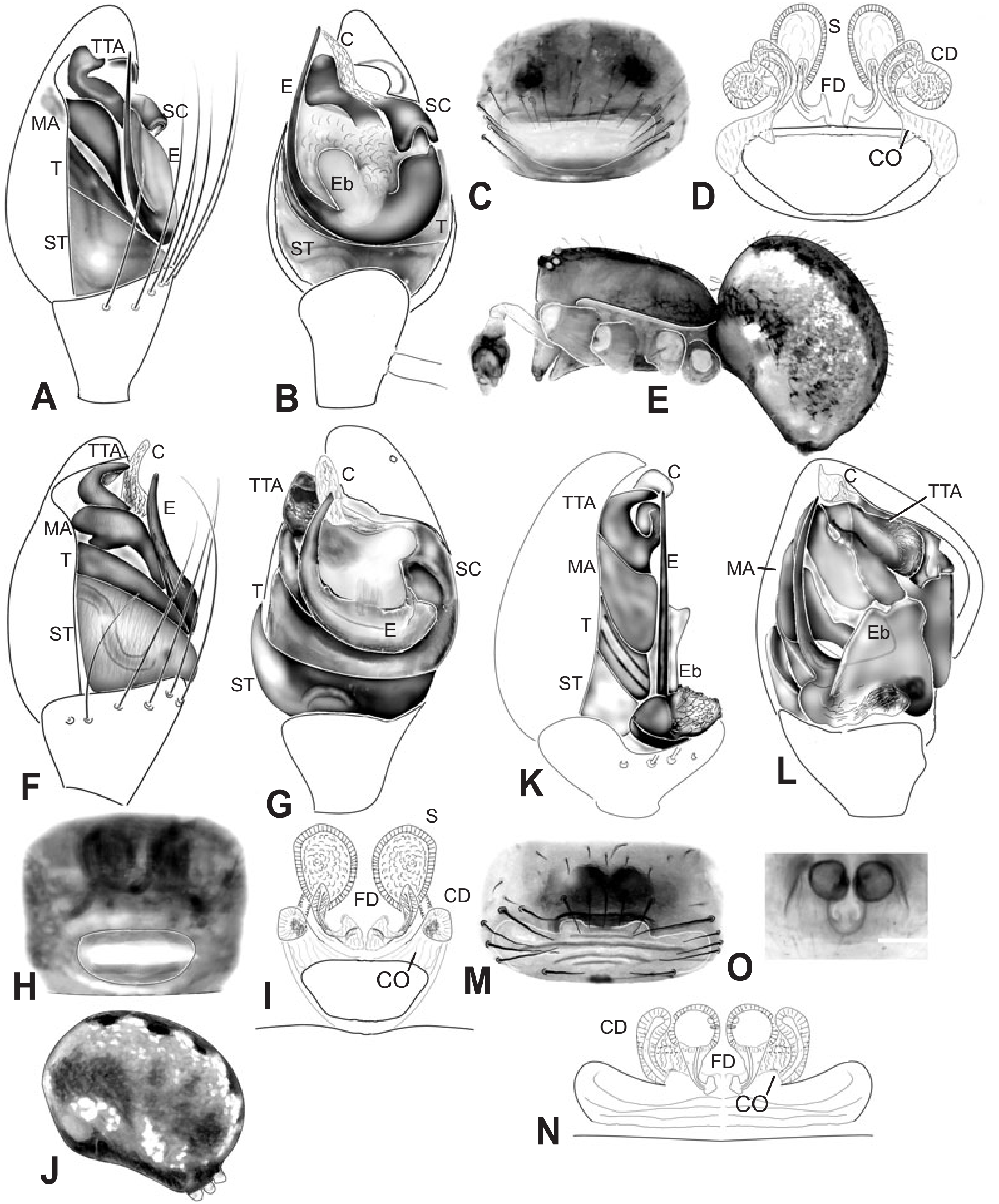

Figure 1. The '*analyticus* group'. A–E, *Anelosimus analyticus*. A, male palp mesal; B, same, ventral view; C, epigynum; D, internal epigynum dorsal; E, male habitus. F–I, *Anelosimus chickeringi*. F, male palp mesal; G, same, ventral view; H, epigynum; I, internal epigynum dorsal; J, female abdomen. K–O, *Anelosimus pacificus*. K, male palp mesal; L, same ventral view; M, epigynum; N, internal epigynum dorsal; O, digital photograph of spermathecal area of cleared epigynum.

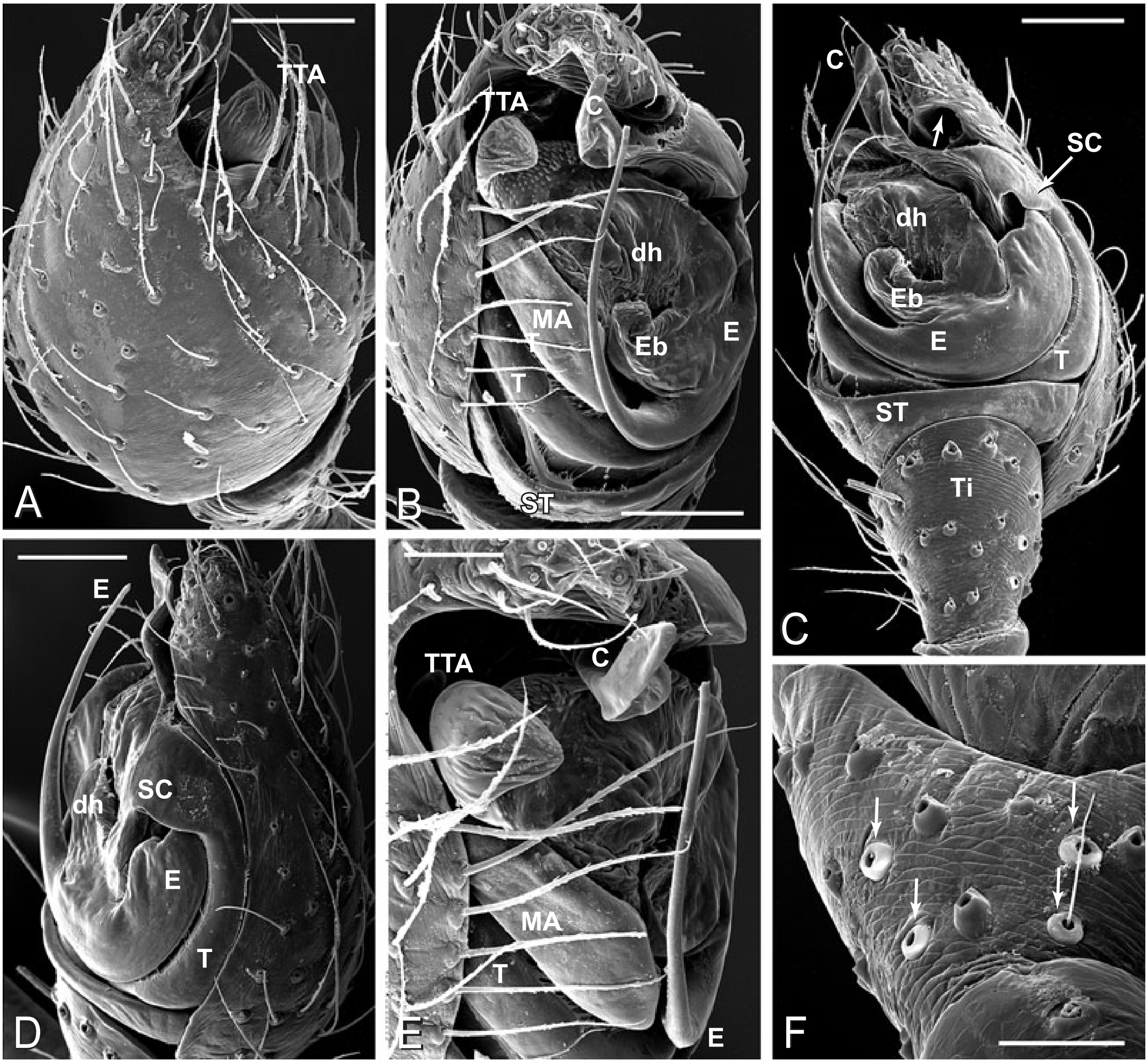

Figure 2. *Anelosimus analyticus*, male palp. A, dorsal; B, submesal; C, ventral, note the small embolic division b (Eb), and the cymbial hood (upper arrow). In this species the embolic lobe fits snugly under the subconductor (SC); D, ectal; E, apical view of tip, mesal side; F, part of palpal tibia, unusually with four trichobothria (arrows). Scale bars: A–D, 100 μm; E,F, 50 μm.

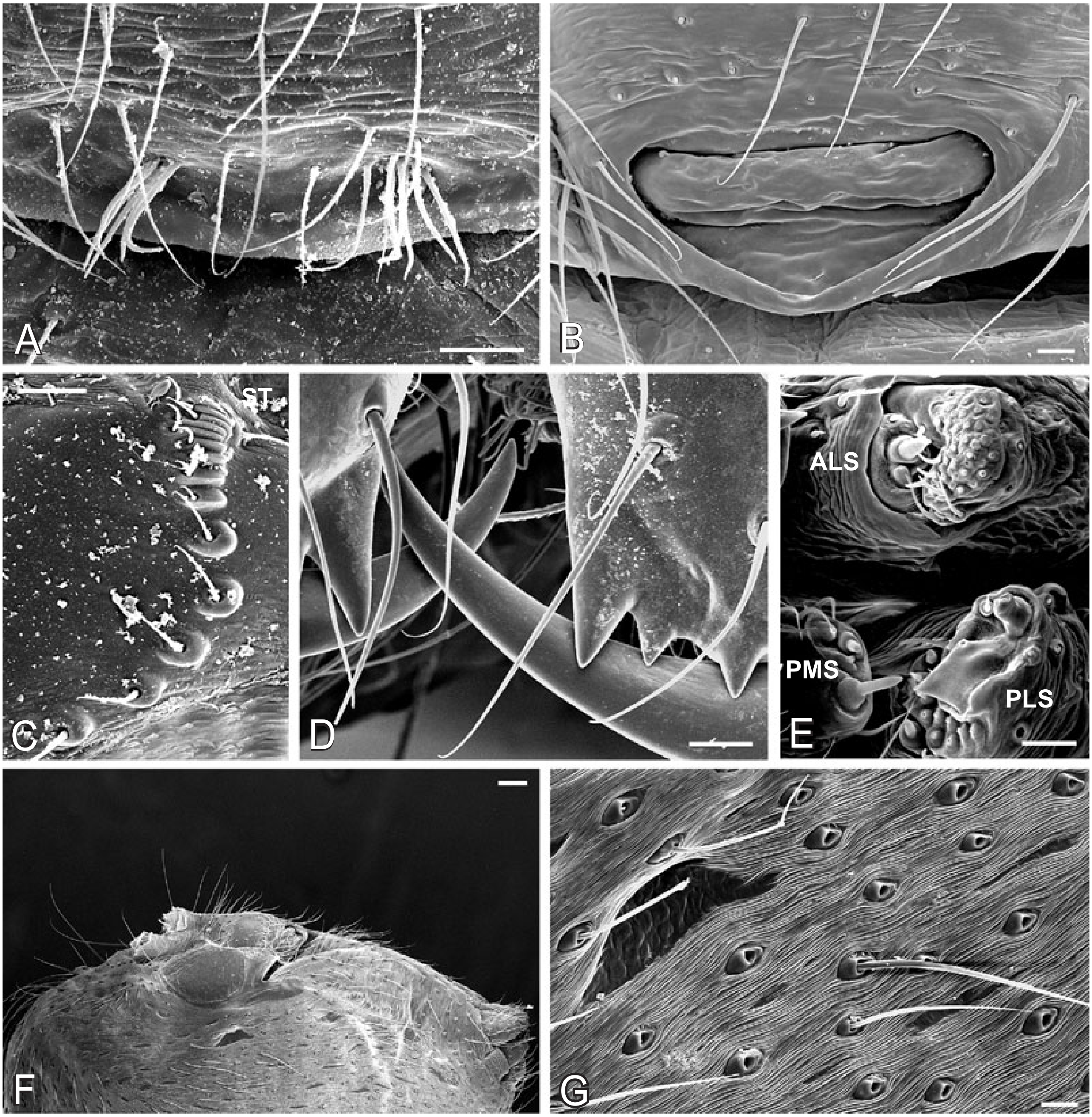

Figure 3. *Anelosimus analyticus*. A, epiandrous gland spigots; B, epigynum; C, male stridulatory pick row (left); D, female cheliceral promarginal teeth; E, female spinnerets; F, female abdomen ectal view; G, female abdominal surface. Scale bars: A–E,G, 20 μm; F, 100 μm.

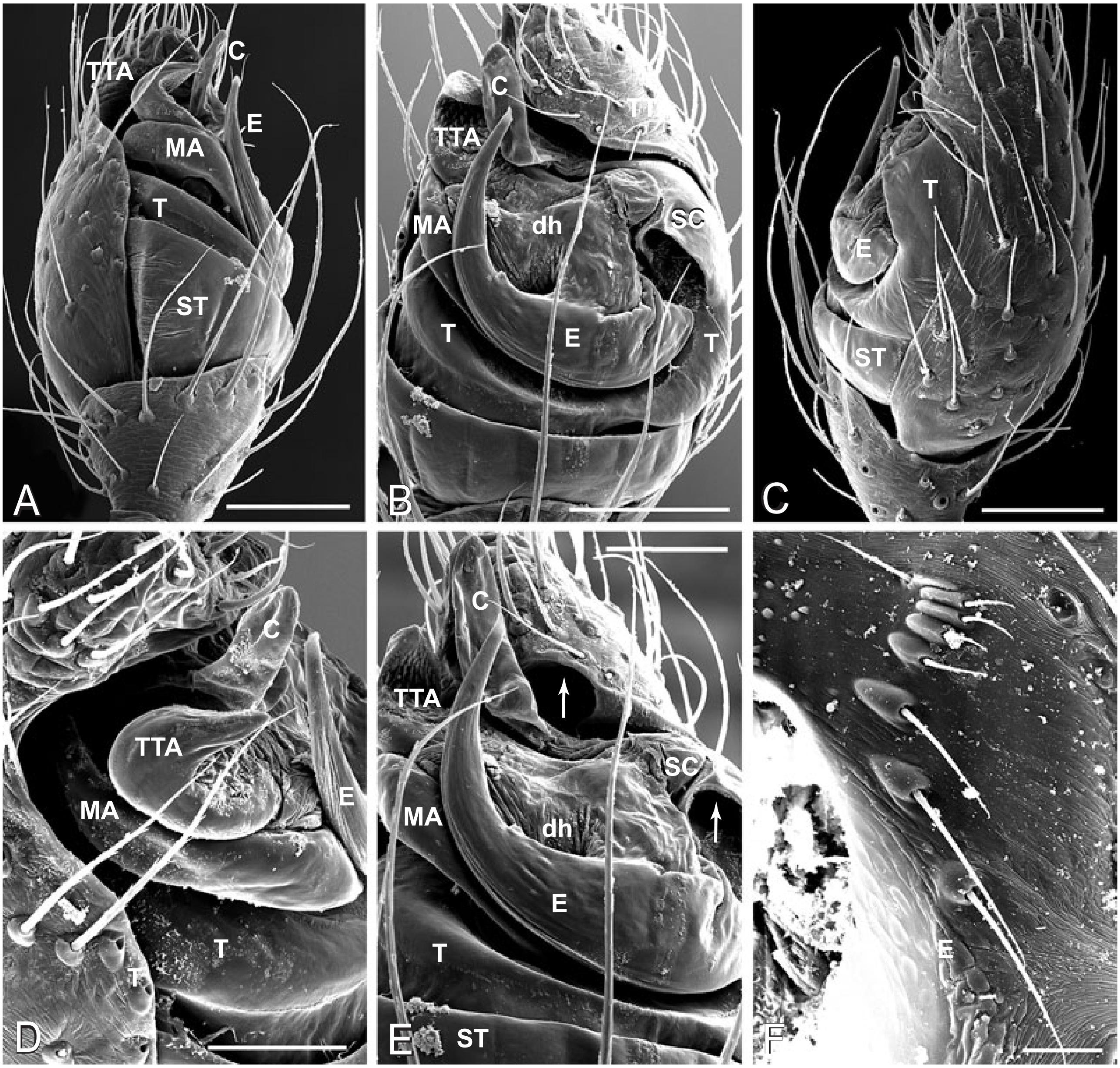

Figure 4. *Anelosimus chickeringi*, male. A–E, palp. A, mesal; B, ventral; C, ectal; D, apicomesal; E, details of sclerites, note the cymbial hood (upper arrow) and the hood formed by the subconductor (lower arrow); F, male stridulatory pick row. Scale bars: A–C, 100 µm; D,E, 50 µm; F, 20 µm.

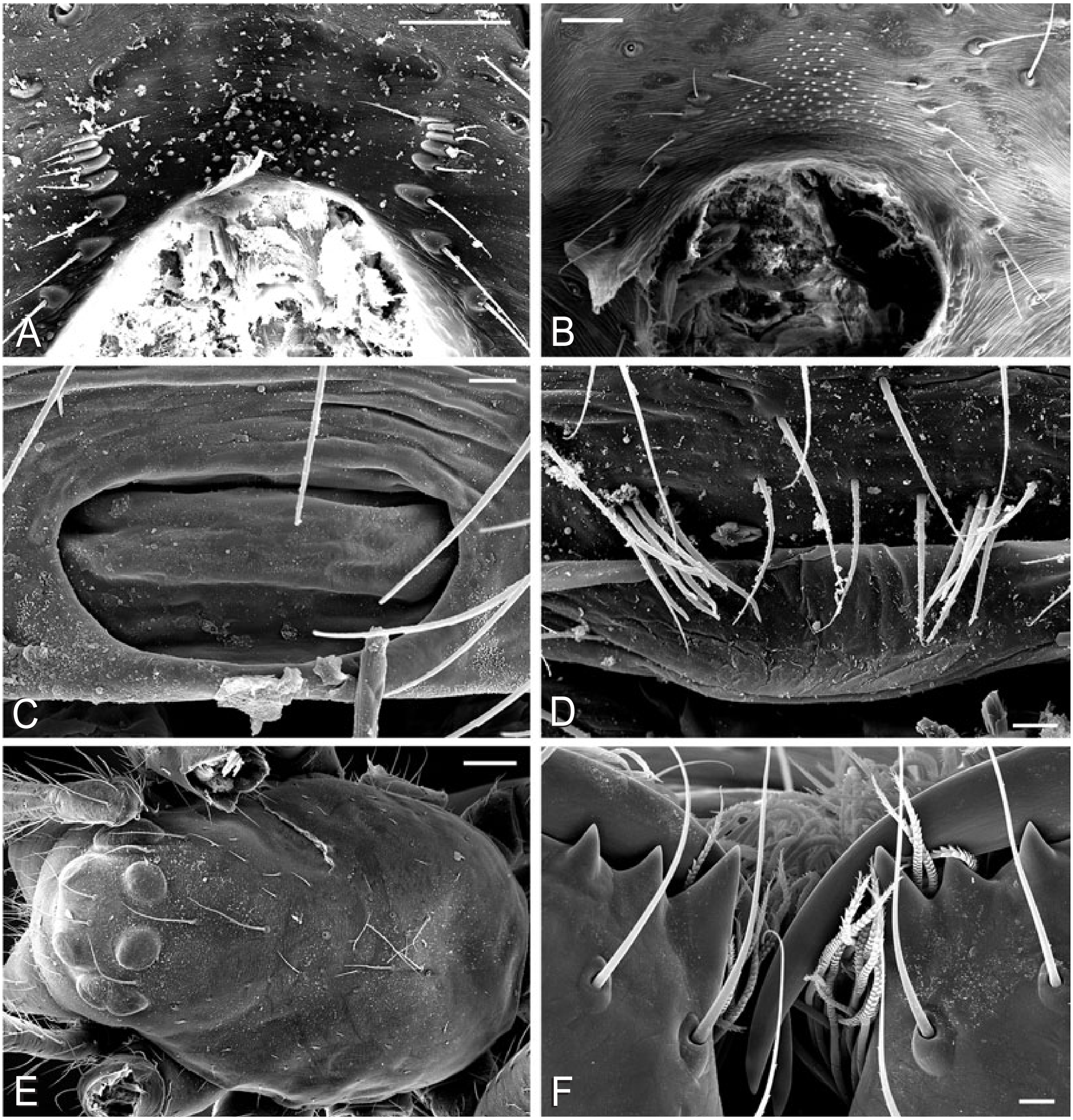

Figure 5. *Anelosimus chickeringi*. A, male pedicel area; B, female pedicel area; C, epigynum; D, epiandrous gland spigots; E, female carapace dorsal; F, female promarginal cheliceral teeth. Scale bars: A,B, 50 µm; C,D,F, 10 µm; E, 100 µm.

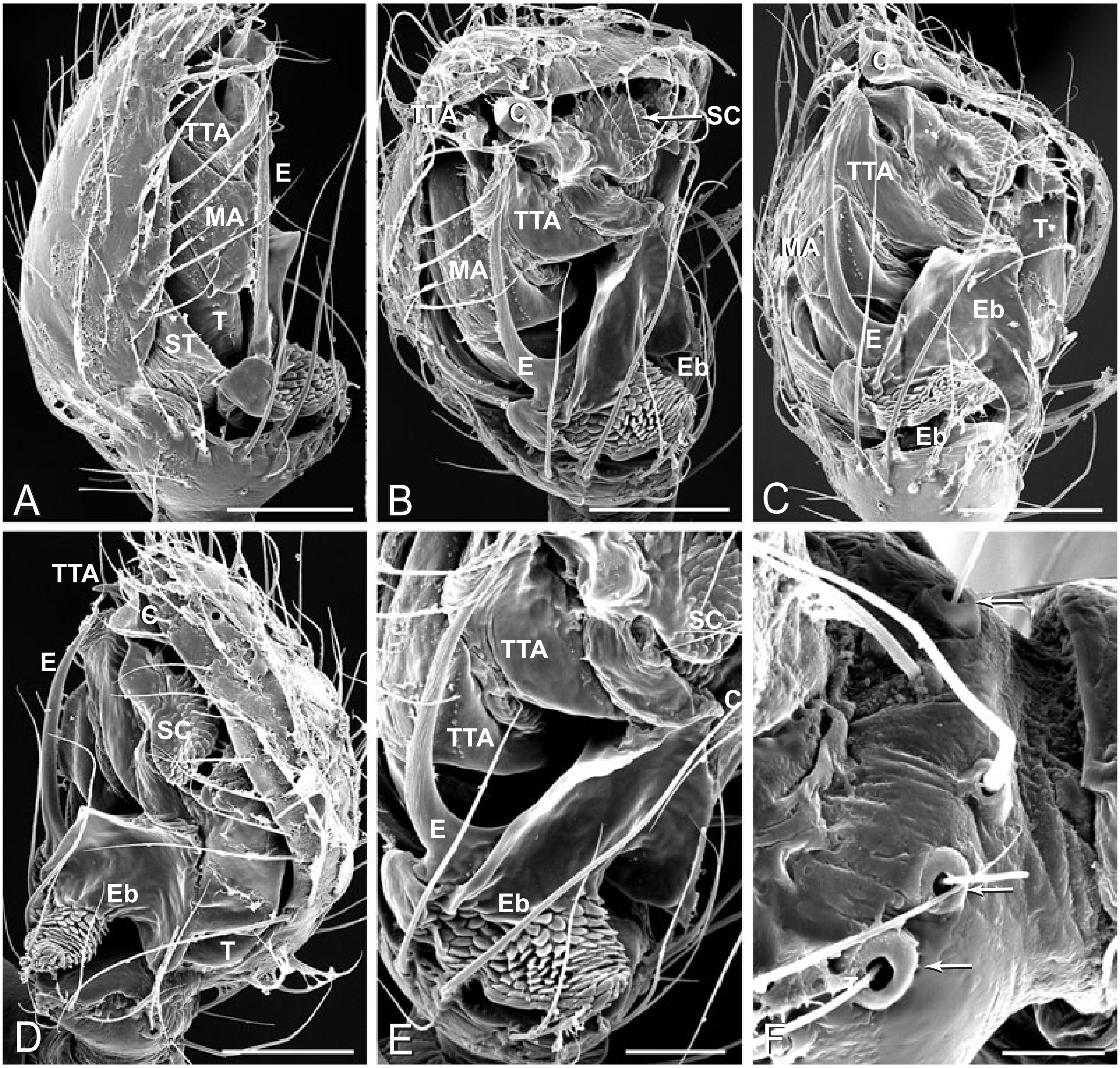

Figure 6. *Anelosimus pacificus*, male palp. A, mesal; B, mesoapical; C, ventral; D, subectal; E, details of embolus; F, tibia, showing three trichobothria (arrows). Scale bars: A–E, 100 μm; F, 20 μm.

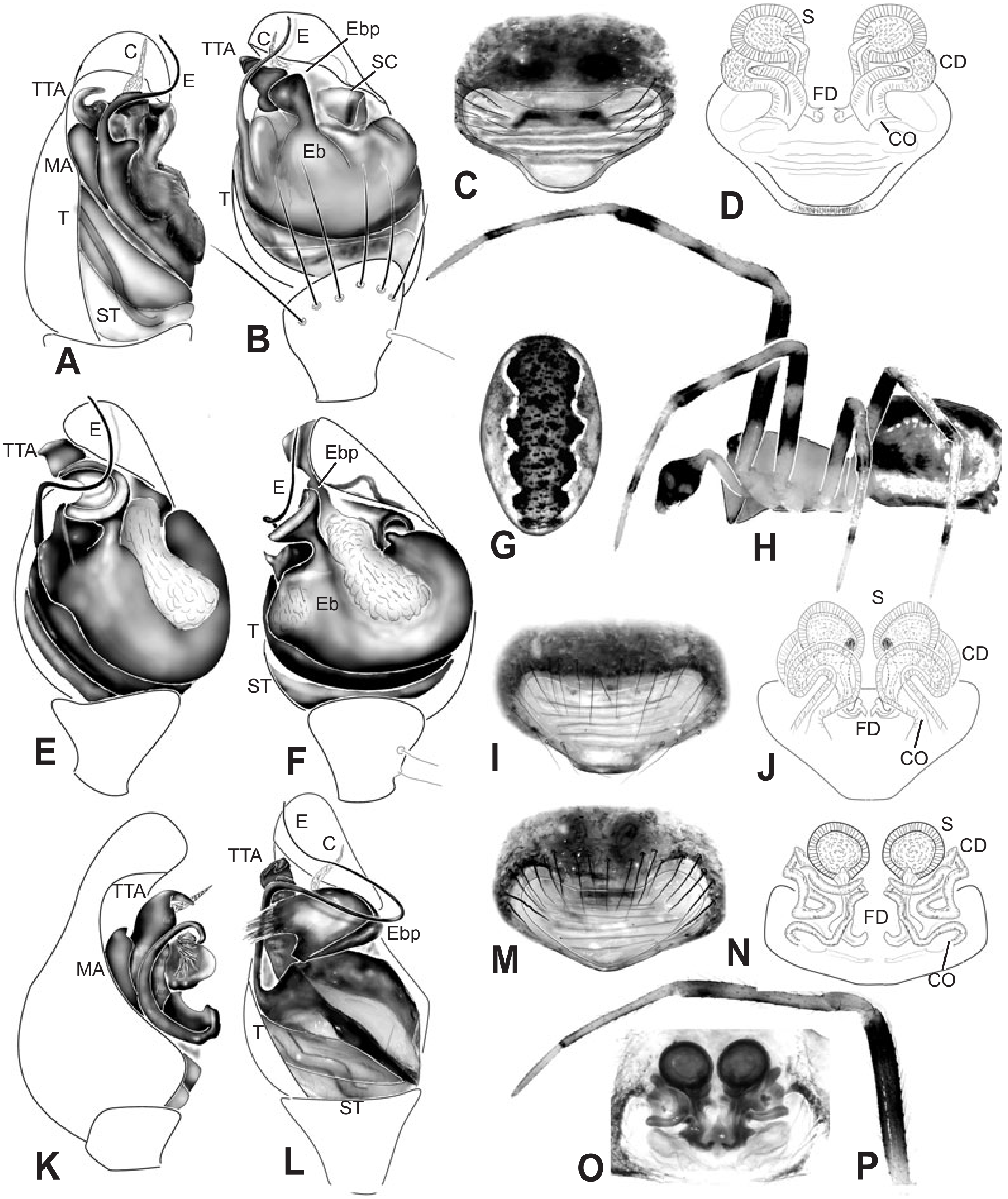

Figure 7. The '*domingo* group'. A–D, *Anelosimus domingo*. A, male palp mesal; B, same ventral; C, epigynum; D, internal epigynum dorsal. E–J, *Anelosimus jabaquara*. E, male palp submesal; F, same ventral; G, female abdomen; H, male habitus; I, epigynum; J, internal epigynum dorsal. K–P, *Anelosimus dubiosus*. K, male palp mesal; L, same ventral; M, epigynum; N, internal epigynum dorsal; O, digital photograph of internal epigynum dorsal; P, male first leg.

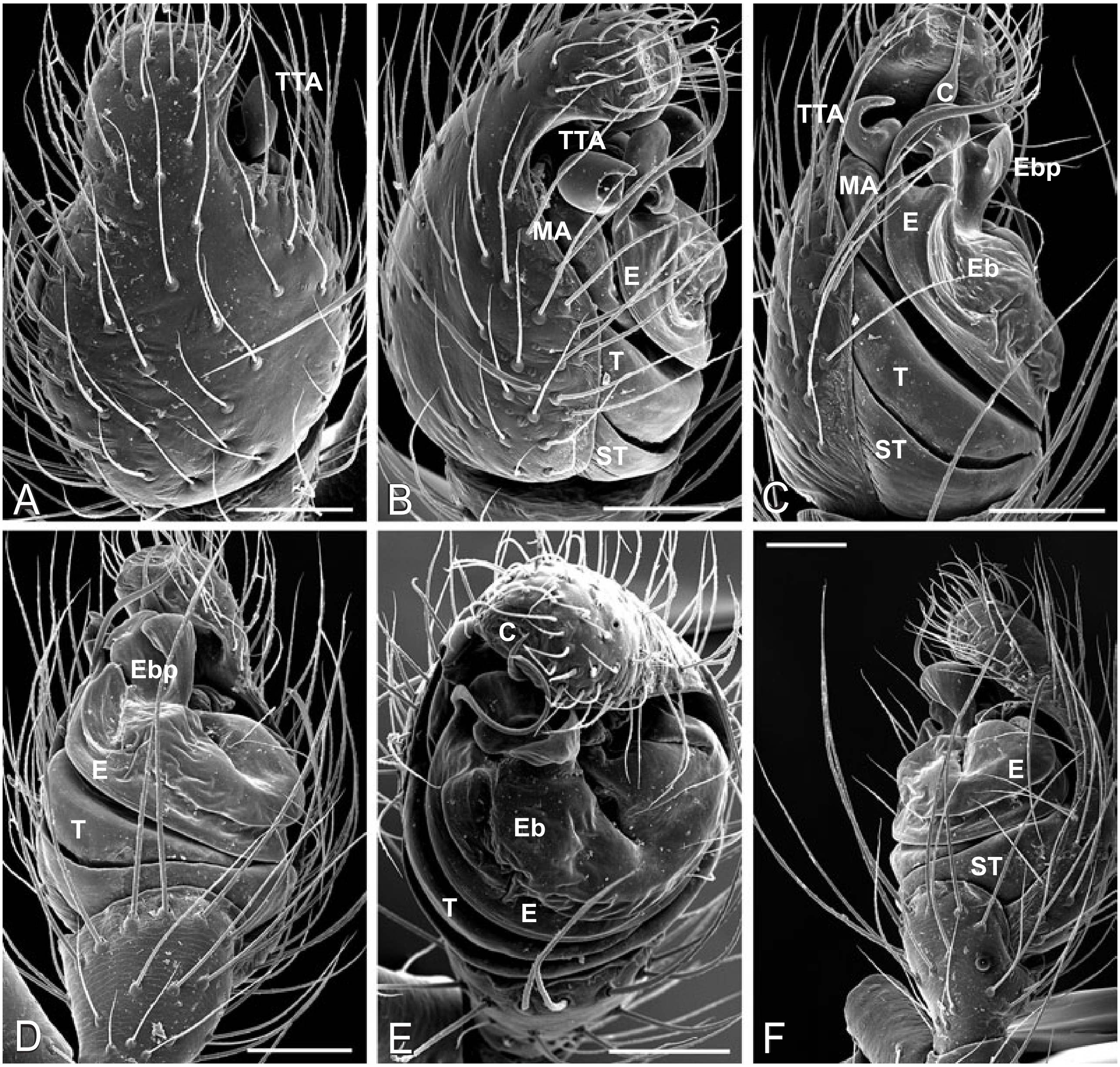

Figure 8. *Anelosimus domingo*, male palp from Peru. A, dorsal; B, apicomesal; C, mesal; D, ventral; E, apicoventral; F, ectal. Scale bars: 100 μm.

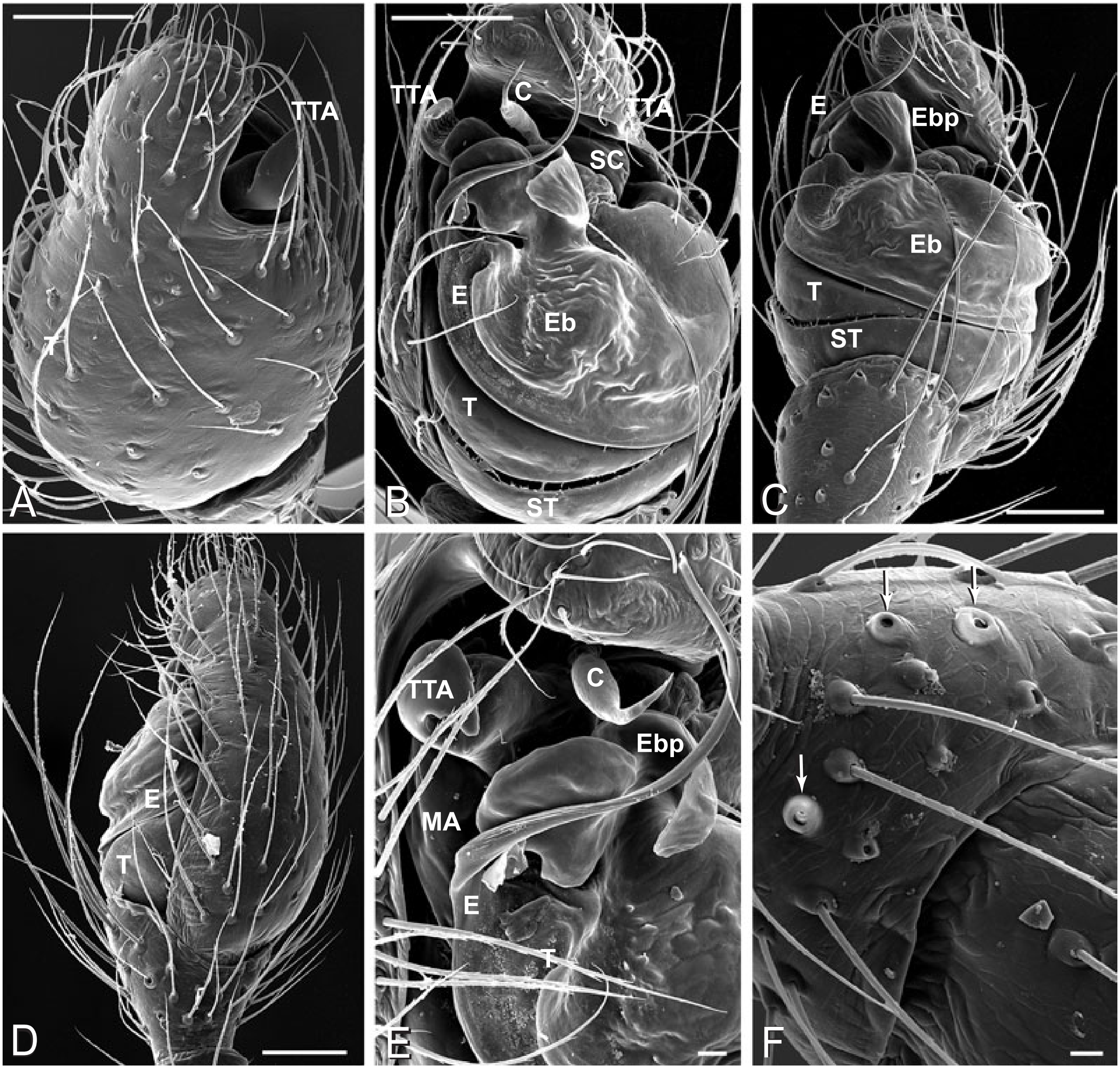

Figure 9. *Anelosimus domingo*, male palp from Ecuador. A, dorsomesal; B, subapical; C, mesal; D, ectal; E, details of sclerites, apical view; F, tibia, with three trichobothria (arrows). Scale bars: A–D, 100 μm; E,F, 10 μm.

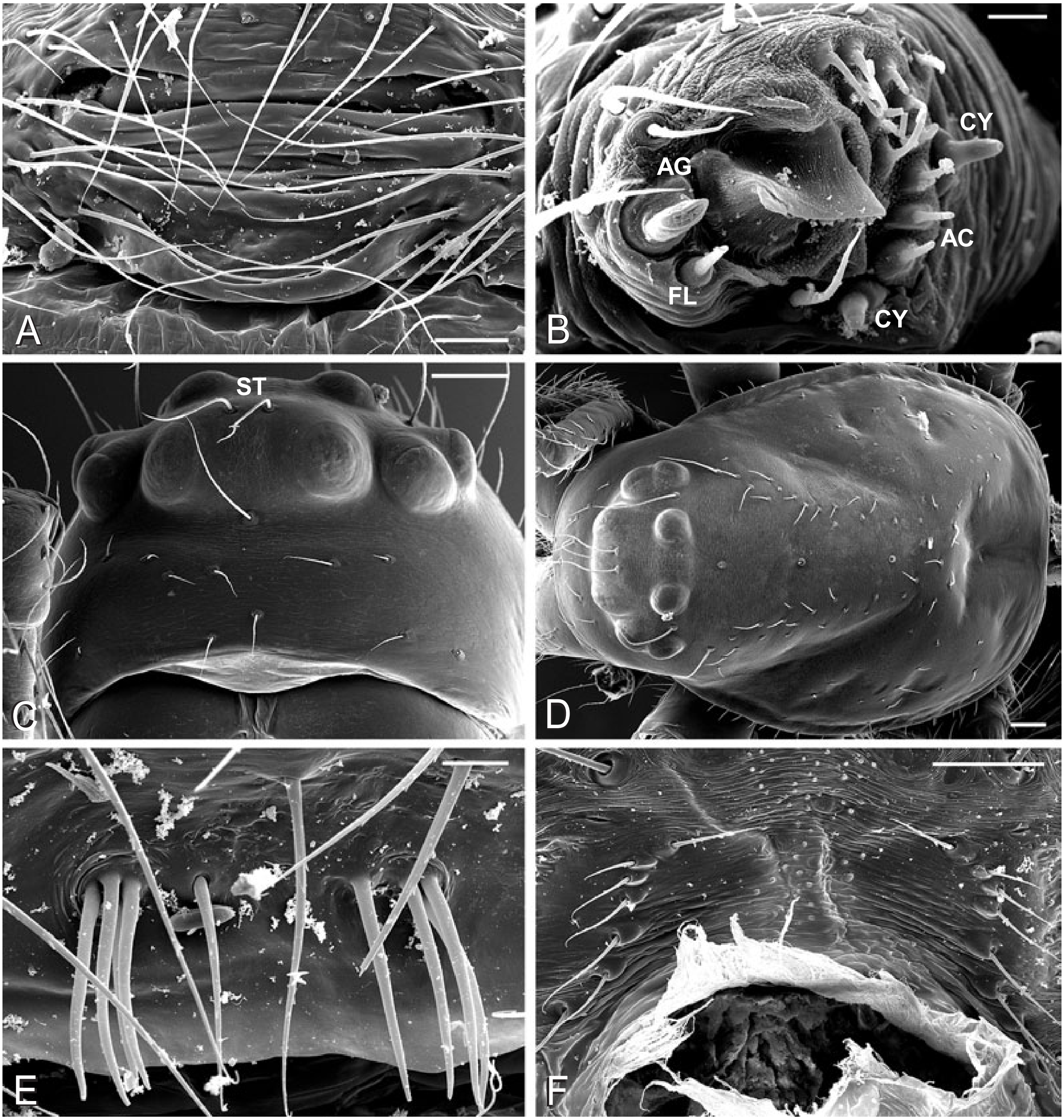

Figure 10. *Anelosimus domingo*. A–D, female. A, epigynum; B, posterior lateral spinneret, anterior is left; C, clypeus; D, carapace; E, epiandrous gland spigots; F, male stridulatory pick row. Scale bars: A,F, 50 µm; B,E, 10 µm; C,D, 100 µm.

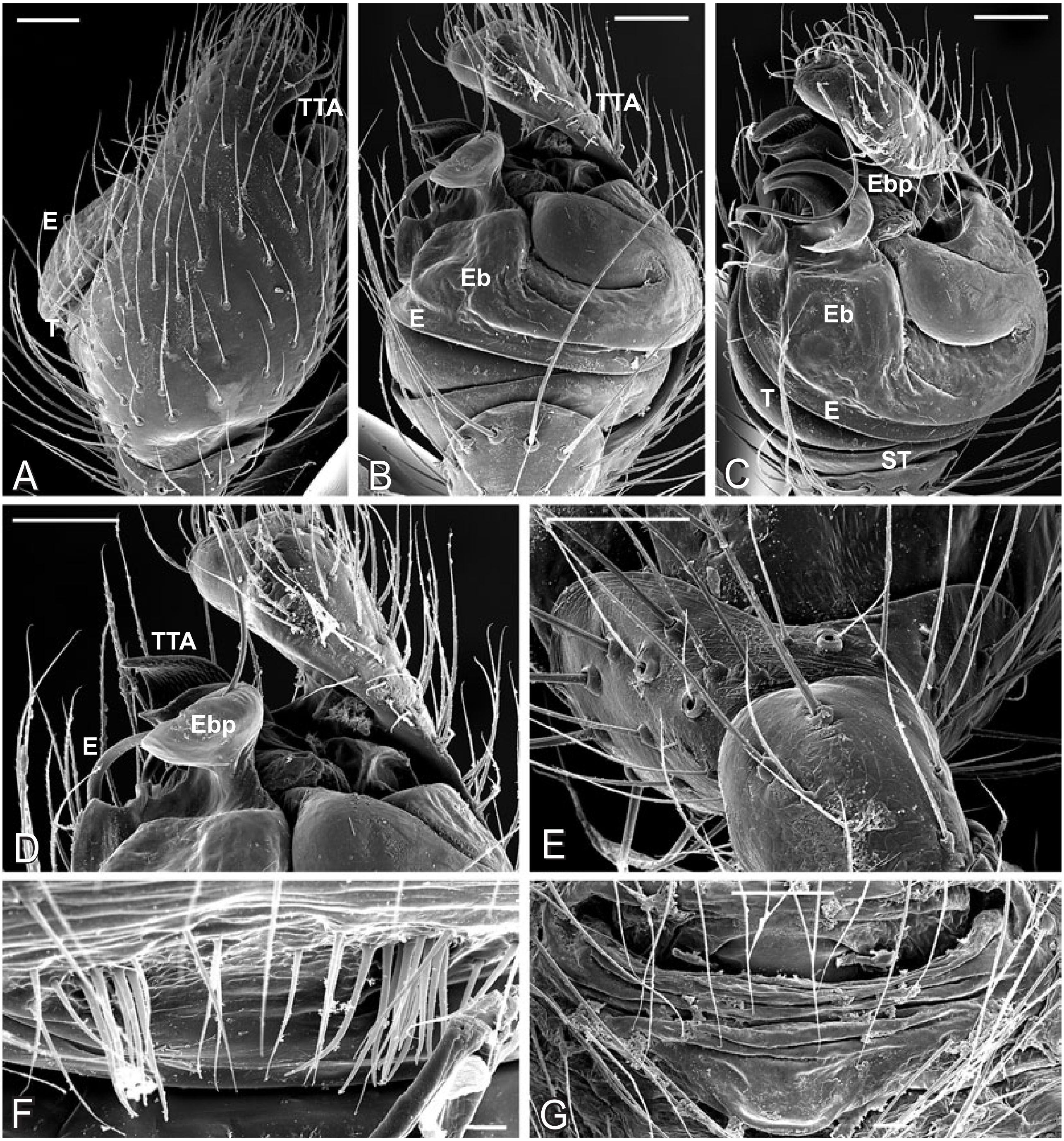

Figure 11. *Anelosimus jabaquara*. A–E male palp. A, dorsal; B, ventral; C, apical; D, palpal tip; E, palpal tibia; F, epiandrous gland spigots; G, epigynum. Scale bars: A–E, 100 µm; F, 10 µm; G, 50 µm.

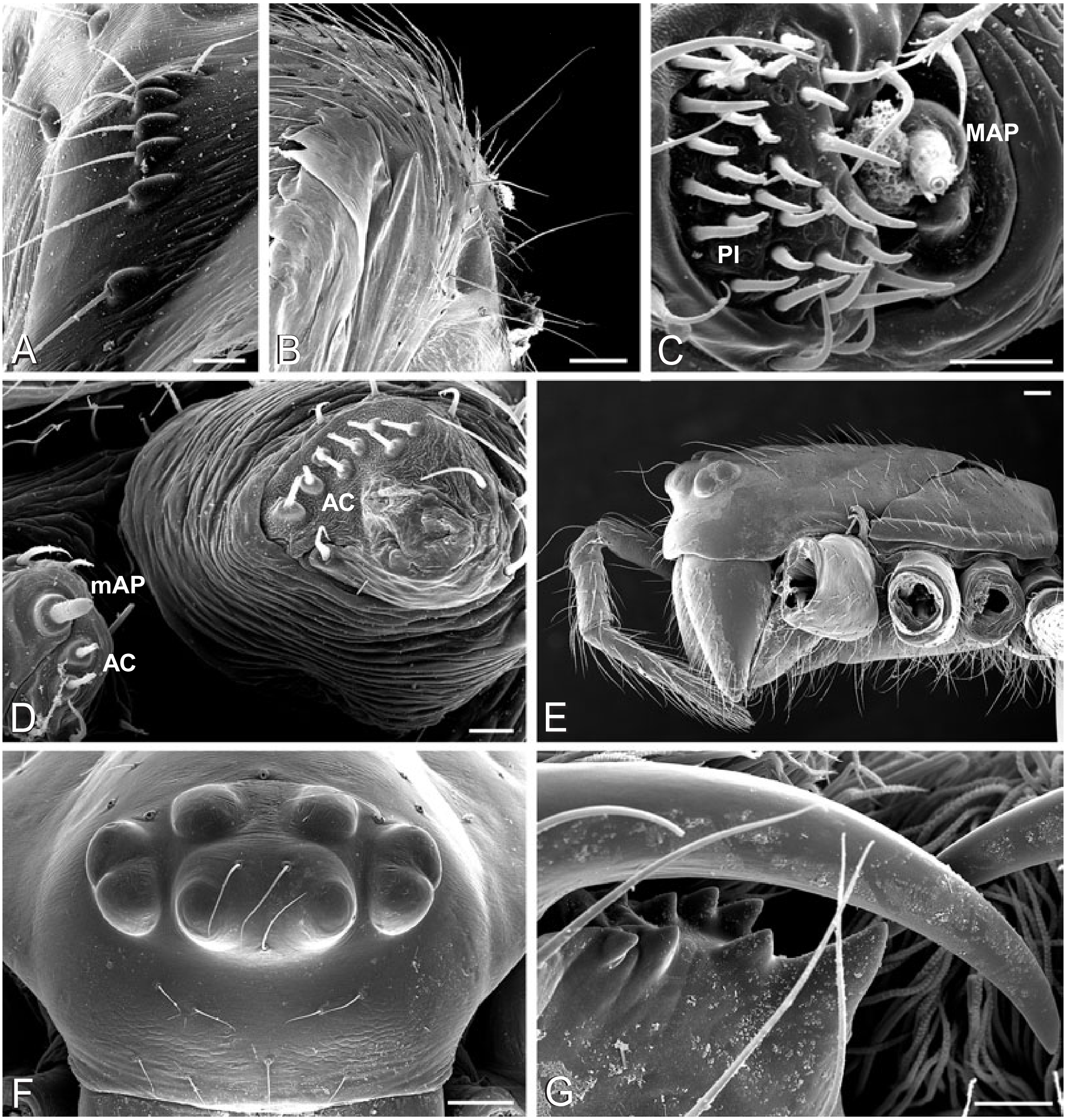

Figure 12. *Anelosimus jabaquara*. A–D, male. A, stridulatory pick row; B, pedicel area, ectal view, showing proprioreceptic setae; C, anterior lateral spinnerets, anterior is left; D, posterior median and posterior lateral spinnerets; E–G, female. E, female prosoma profile; F, ocular region and clypeus; G, cheliceral promargin, anterior view, both promarginal teeth and retromarginal denticles are visible. Scale bars: A,G, 20 µm; B,E,F, 100 µm; C,D, 10 µm.

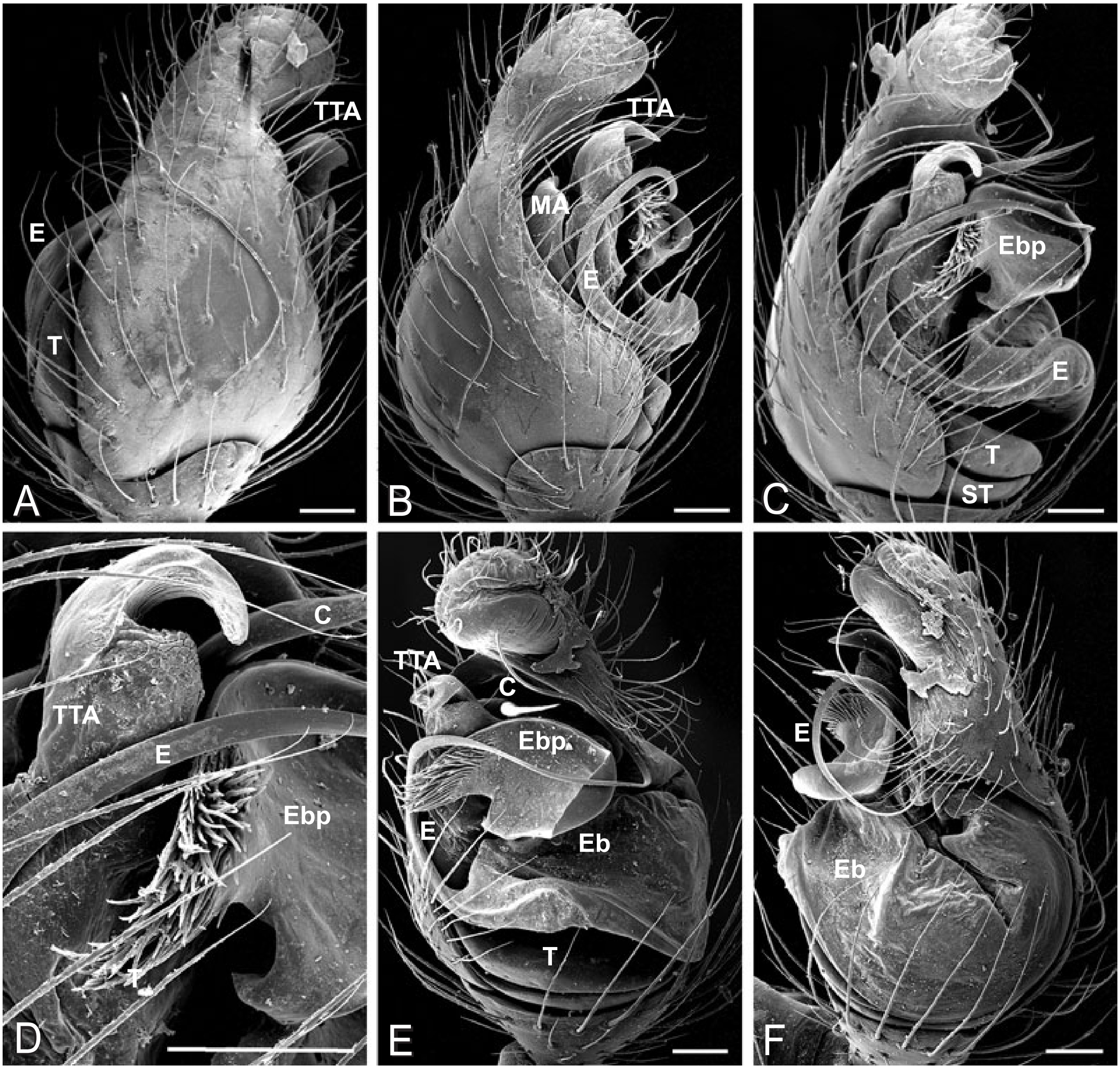

Figure 13. *Anelosimus dubiosus*, male palp. A, dorsal; B, dorsomesal; C, subventral; D, details of theridiid tegular apophysis and C; E, ventral; F, ectal. Scale bars: 100 μm.

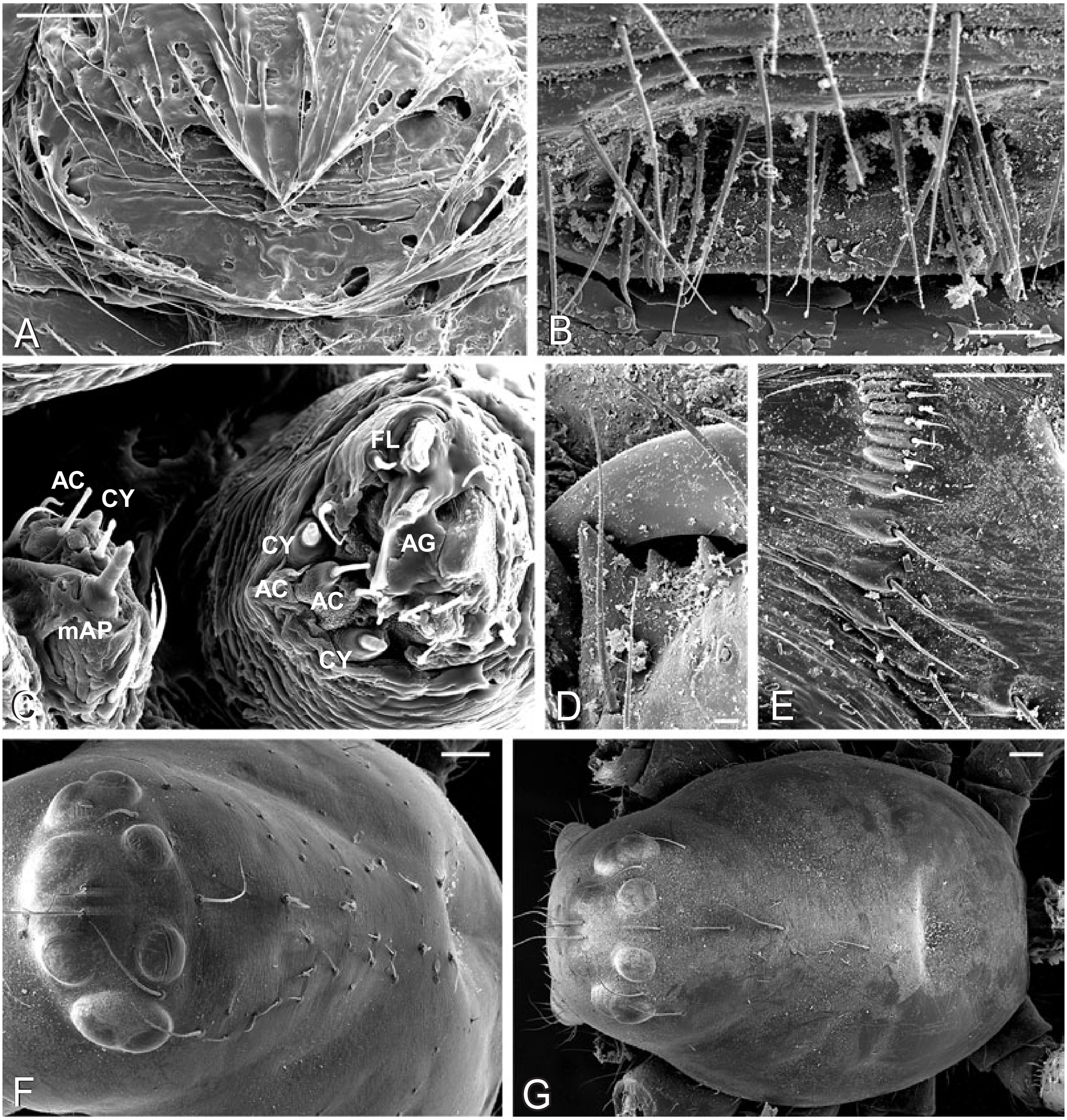

Figure 14. *Anelosimus dubiosus*. A, epigynum; B, epiandrous gland spigots; C, female posterior median and posterior lateral spinnerets; D, female prolateral cheliceral teeth; E, male stridulatory pick row; F, male prosoma dorsal; G, female prosoma dorsal. Scale bars: A,D,F,G, 100 μm; B, 20 μm; C, 10 μm; E, 50 μm.

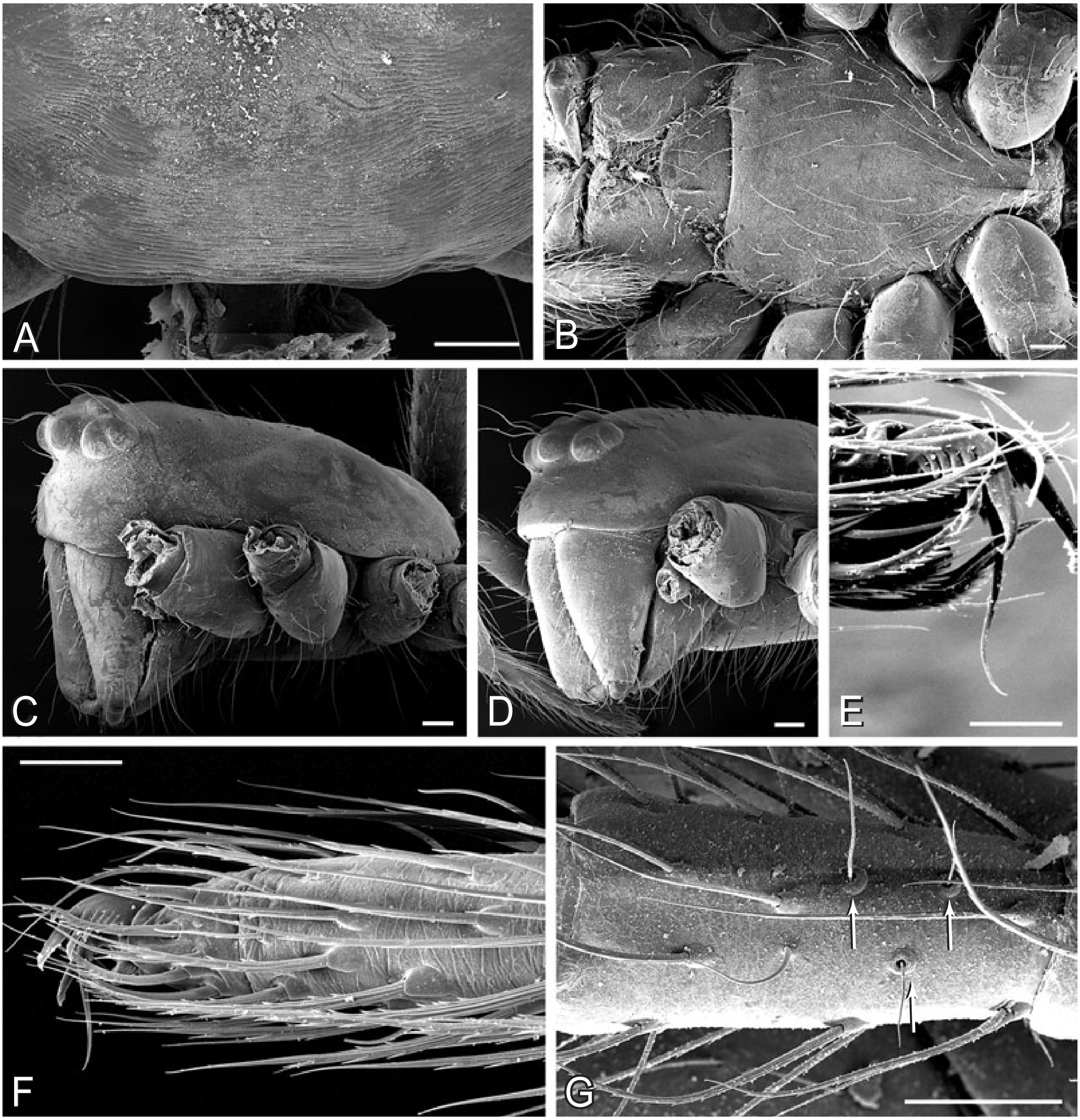

Figure 15. *Anelosimus dubiosus*. A, male prosomal stridulatory ridges; B, female sternum; C, male prosoma; D, female prosoma; E, male fourth tarsal claws; F, female tip of fourth tarsus; G, female palpal tibia, as typical for *Anelosimus* with three dorsal trichobothria (arrows). Scale bars: A–D, 100 µm; E, 20 µm; F,G, 50 µm.

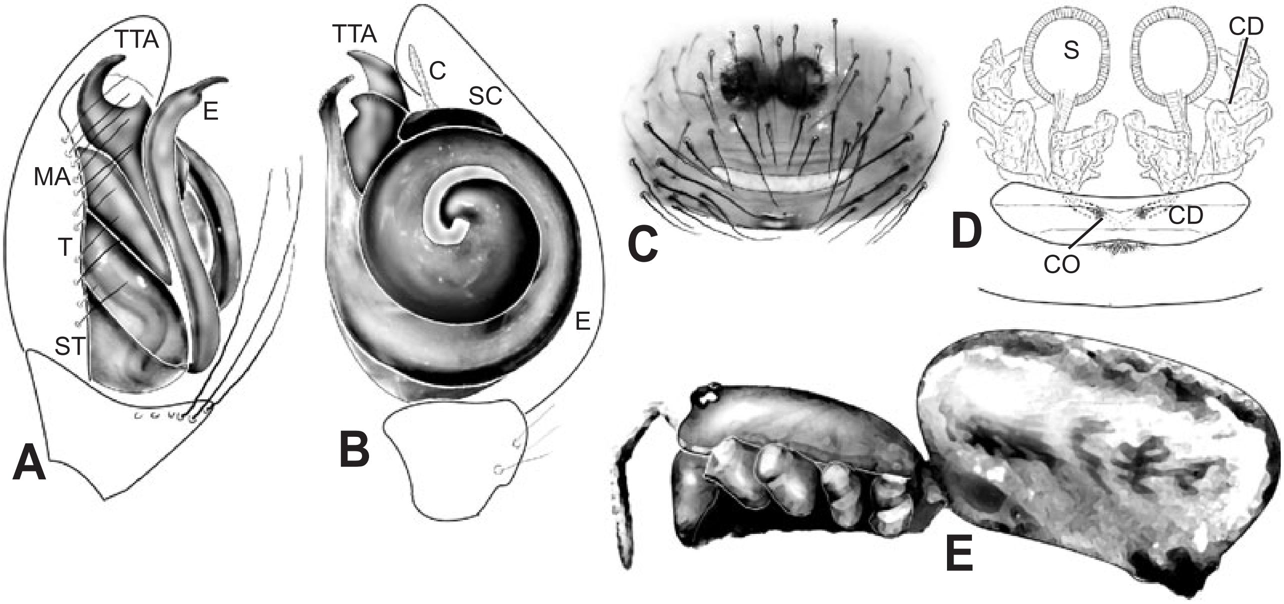

Figure 16. *Anelosimus eximius*. A, male palp mesal; B, same ventral; C, epigynum; D, internal epigynum, ventral, the complex folding is difficult to interpret and the pathway of the fertilization duct remains poorly understood; E, female habitus.

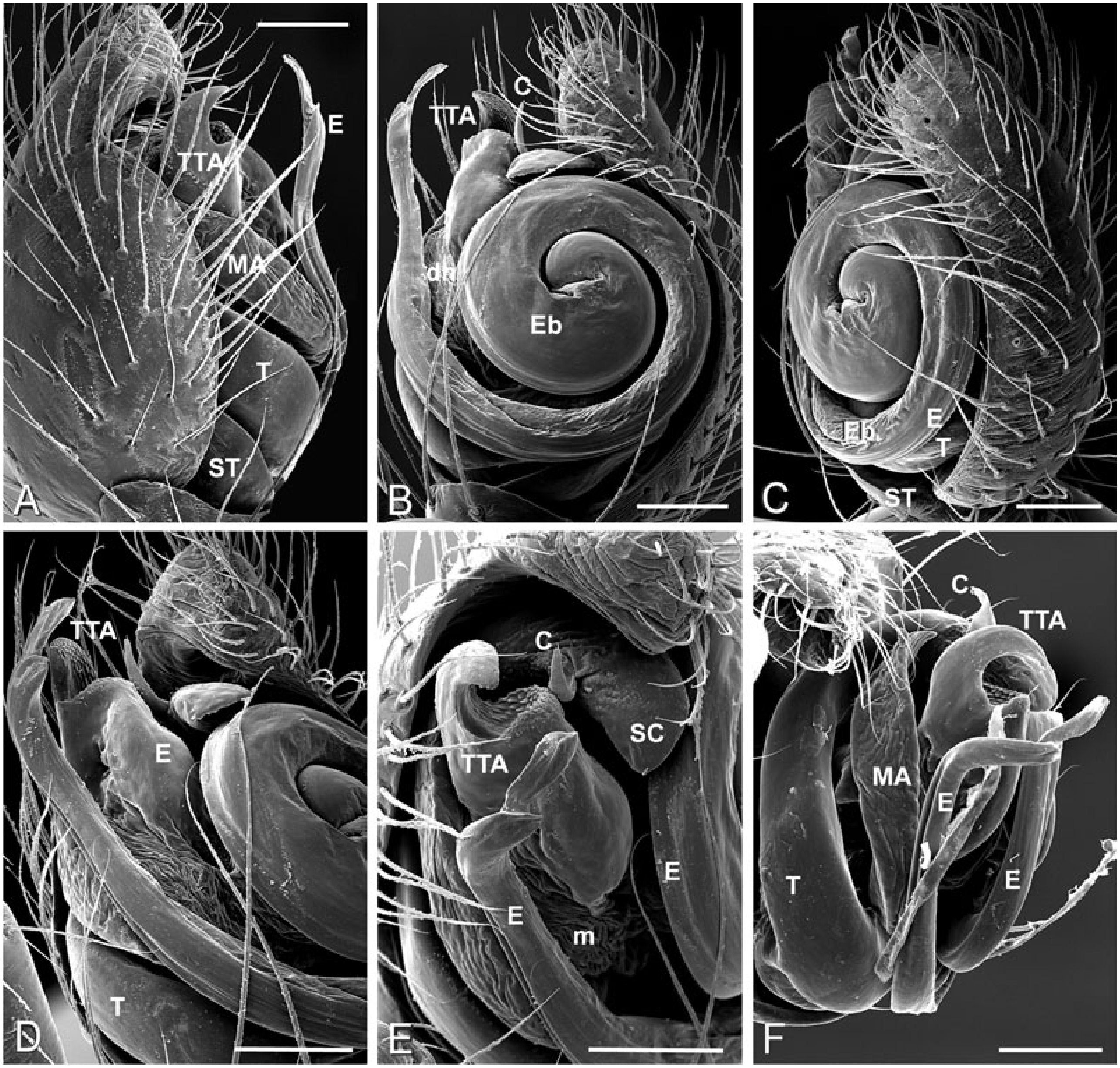

Figure 17. *Anelosimus eximius*, male palp. A, mesal; B, ventral; C, ectal; D, details of conductor, subconductor and embolus tip; E, same, apical view; F, mesal view of sclerites in an expanded palp. Scale bars: 100 µm.

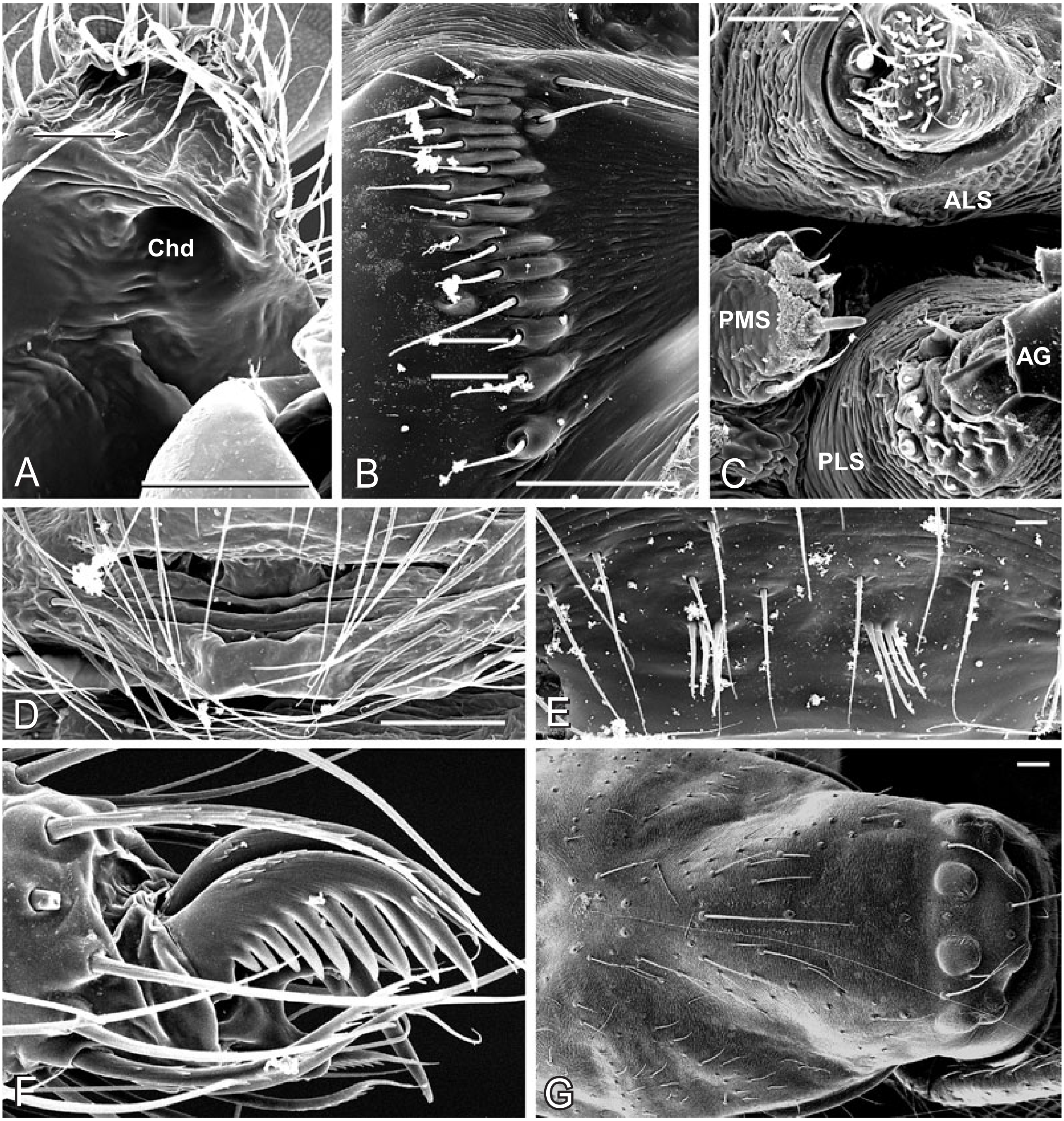

Figure 18. *Anelosimus eximius*. A, distal part of cymbium of an expanded palp, note the wrinkled tip (arrow); B, male stridulatory pick row, right side; C, female left spinning field; D, epigynum; E, epiandrous gland spigots; F, male second tarsal claws; G, female prosoma dorsal. Scale bars: A,D,G, 100 µm; B,C, 50 µm; E, 10 µm.

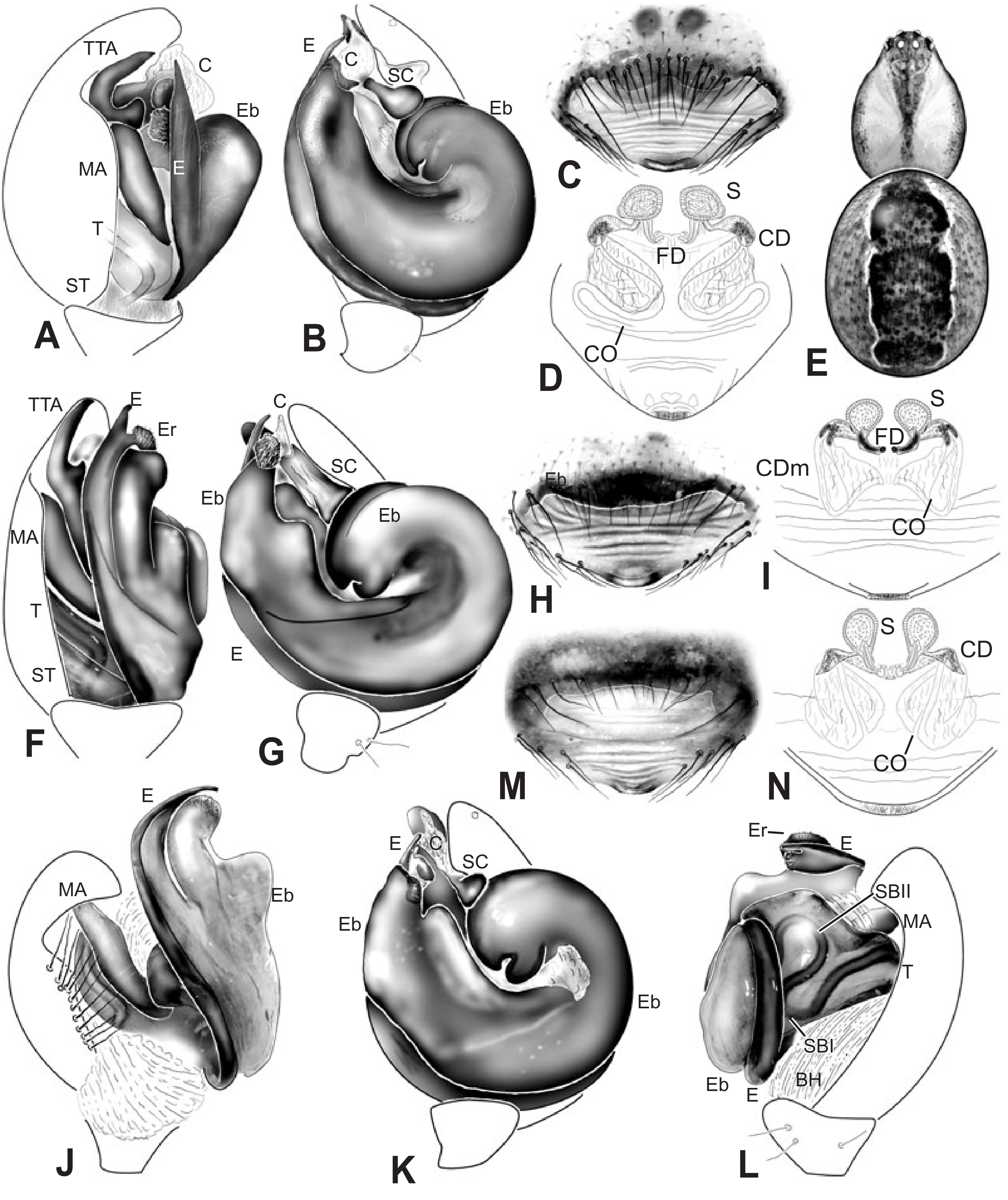

Figure 19. The '*jucundus* group'. A–E, *Anelosimus arizona*. A, male palp mesal, arrow points to the eb-ridge, larger in this species than in any other *Anelosimus*; B, same ventral; C, epigynum; D, internal epigynum dorsal; E, female habitus. F–I, *Anelosimus jucundus*. F, male palp mesal; G, same ventral; H, epigynum; I, internal epigynum dorsal. J–N, *Anelosimus octavius*. J, male palp expanded, mesal; K, male palp ventral; L, male palp expanded, ectal; M, epigynum; N, internal epigynum dorsal.

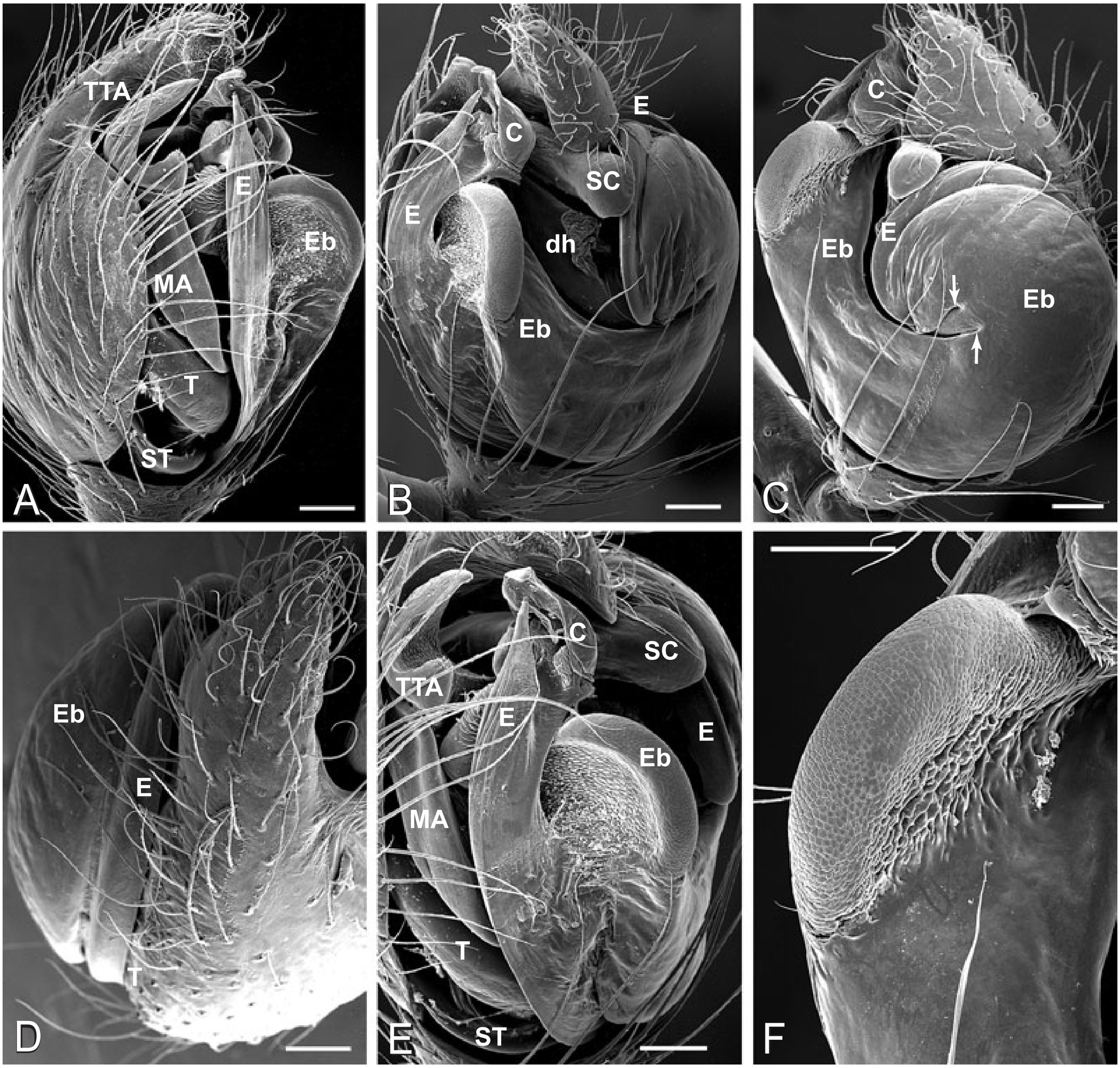

Figure 20. *Anelosimus arizona*, male palp from Huachuca Mountains, Arizona. A, mesal view; B, submesal; C, ventral, note the huge embolic division b (Eb) with a large ridge, and the shallow embolus-distal hemaodocha grooves (arrows); D, ectal view, note the swollen embolic division b; E, apical view of tip, mesal side; F, details of the large Eb ridge. Scale bars: A–E, 100 µm; F, 50 µm.

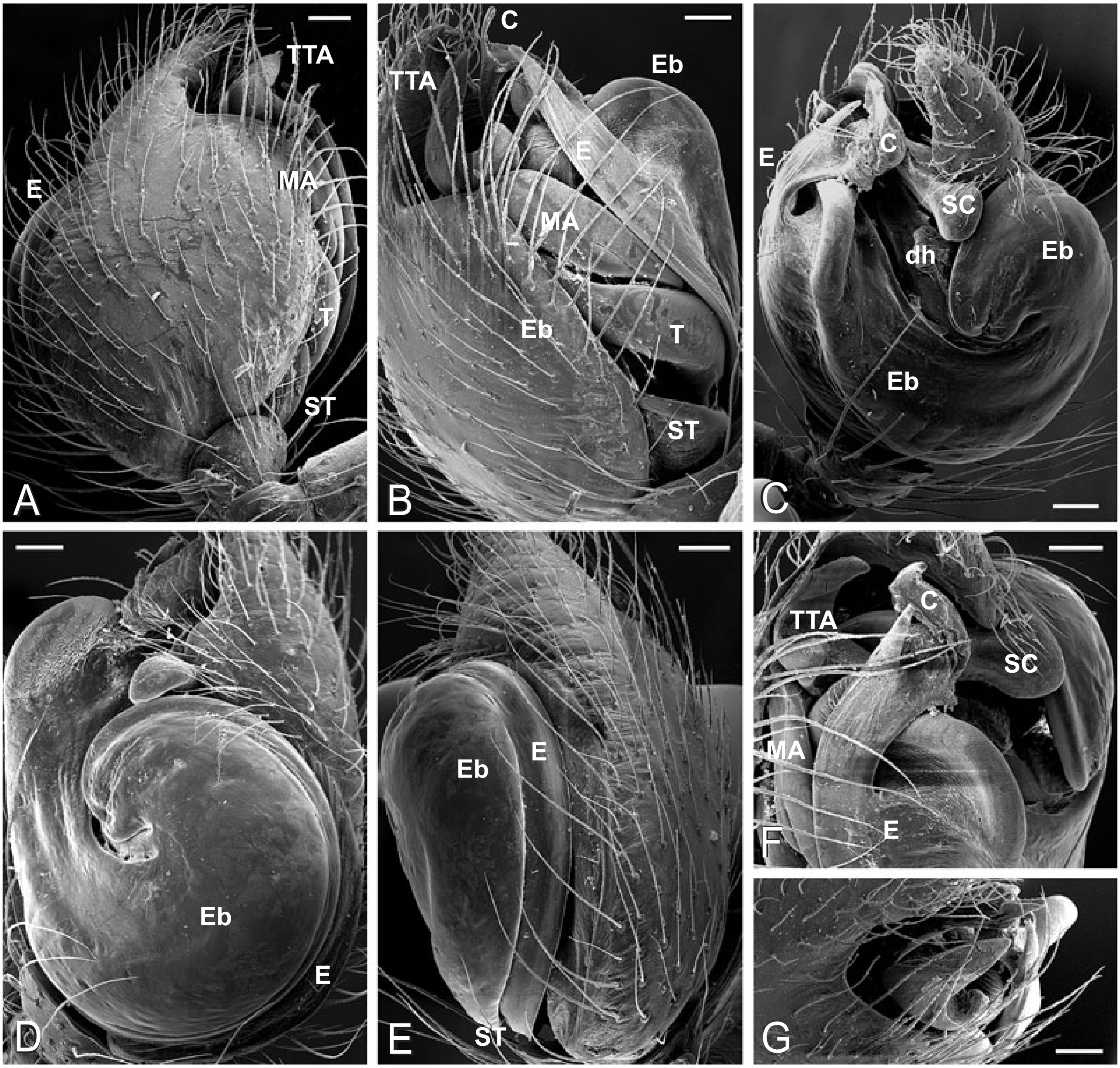

Figure 21. *Anelosimus arizona* male palp from Patagonia Mountains, Arizona. A, dorsal; B, mesal; C, apical; D, ventral; E, ectal; F, details of distal sclerites; G, apical view of mesal cymbial incision, showing the theridiid tegular apophysis. Scale bars: 100 µm.

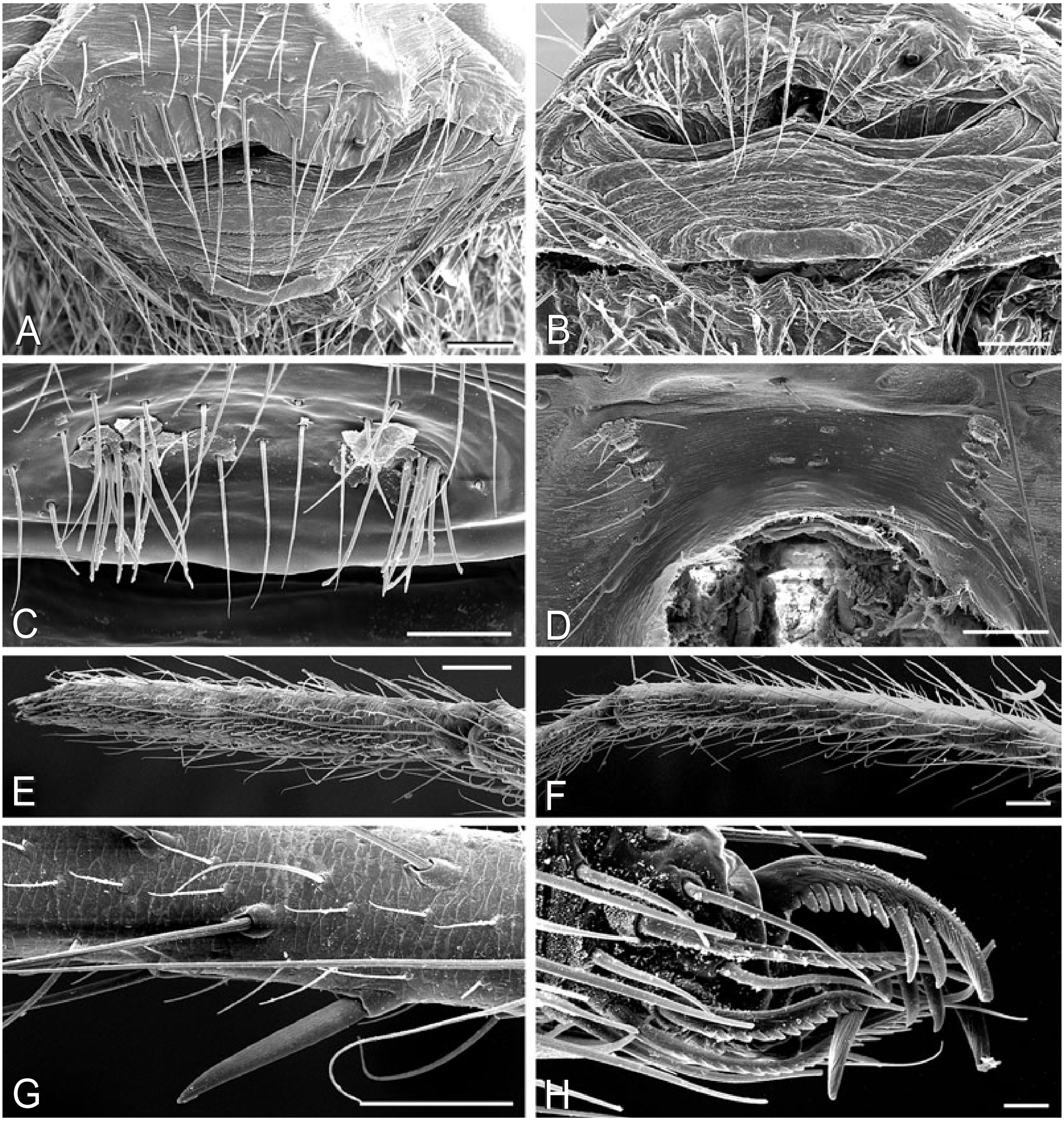

Figure 22. *Anelosimus arizona*. A, epigynum ventral; B, epigynum subcaudal; C–H, male. C, epiandrous gland spigots; D, stridulatory pick row; E, tarsus I ventral; F, metatarsus I ventral; G, details of thick setae on metatarsus I; H, tarsus I claws. Scale bars: A,B,D,G 100 μm; C, 50 μm; H, 10 μm.

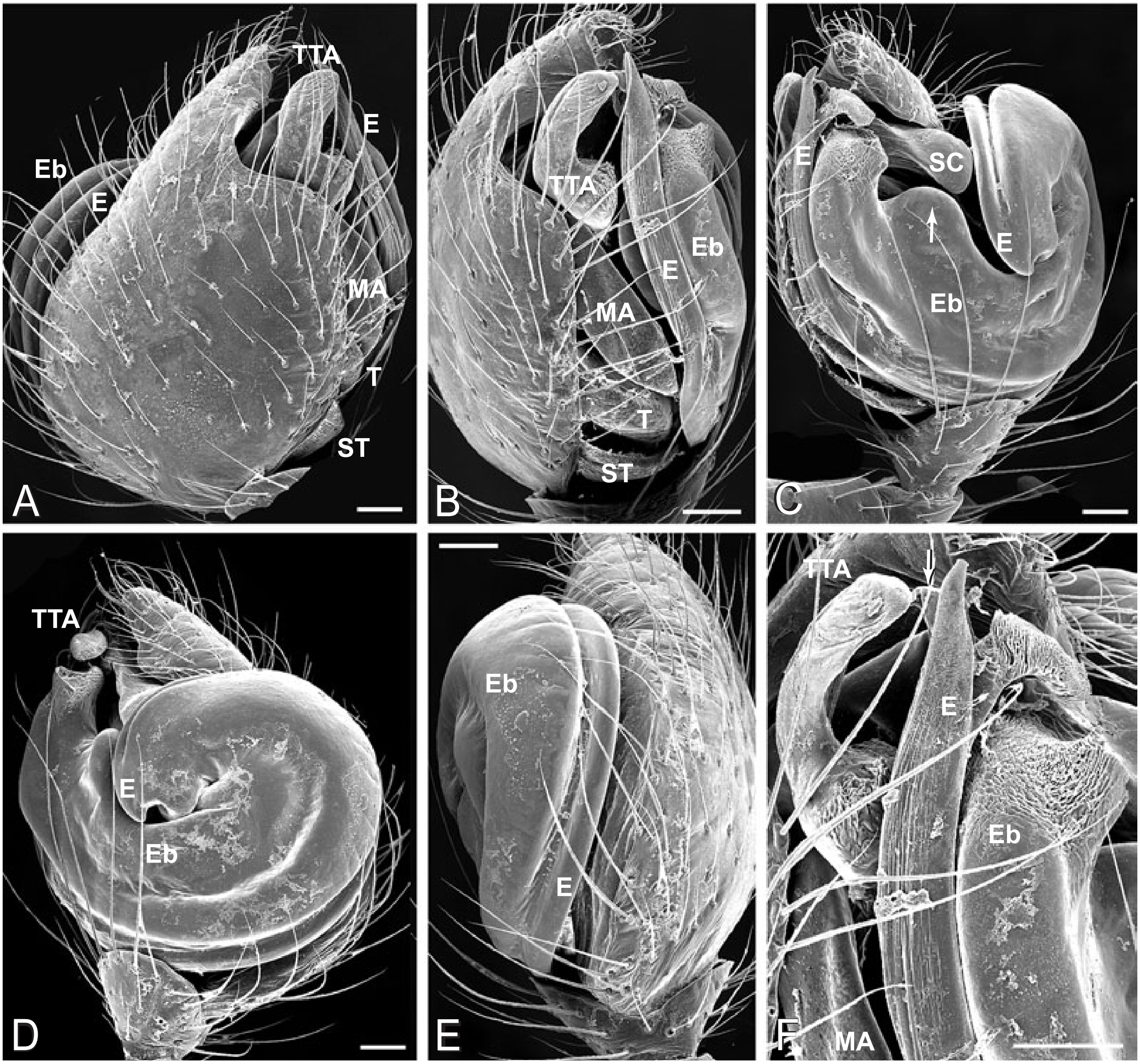

Figure 23. *Anelosimus jucundus*, male palp. A, dorsal view; B, mesal; C, submesal, the conspicuous embolus division b ridge (arrow) is a synapomorphy uniting *A. jucundus*, *A. octavius* and *A. arizona*; D, ventral; E, ectal, subcaudal view; F, details of E tip, the small conductor can be detected in the background (arrow). Scale bars: 100 μm.

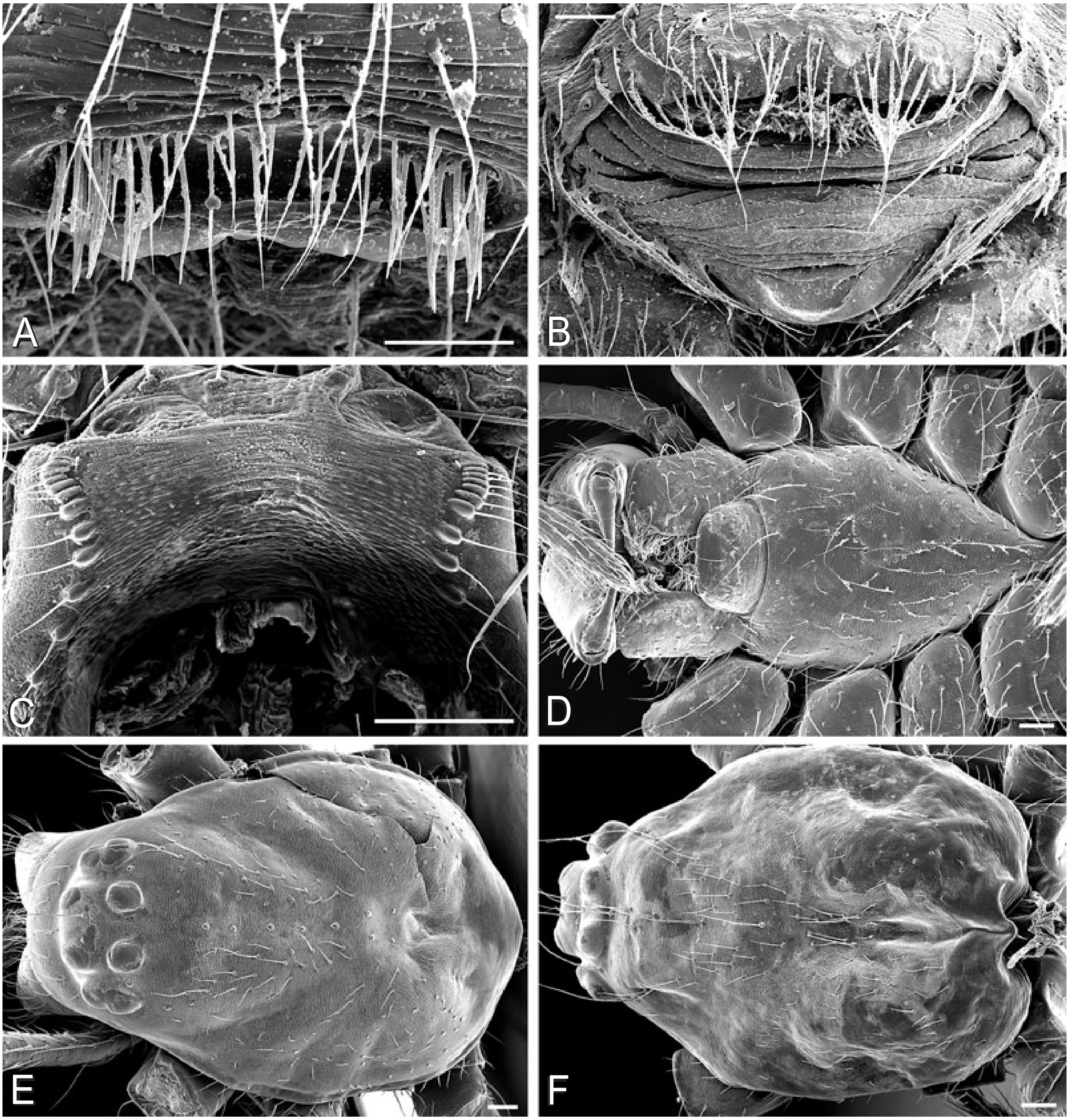

Figure 24. *Anelosimus jucundus*. A, epiandrous gland spigots; B, epigynum; C, male stridulatory pick row; D, female prosoma ventral; E, female prosoma dorsal; F, male prosoma dorsocaudal. Scale bars: A, 50 µm; B–F, 100 µm.

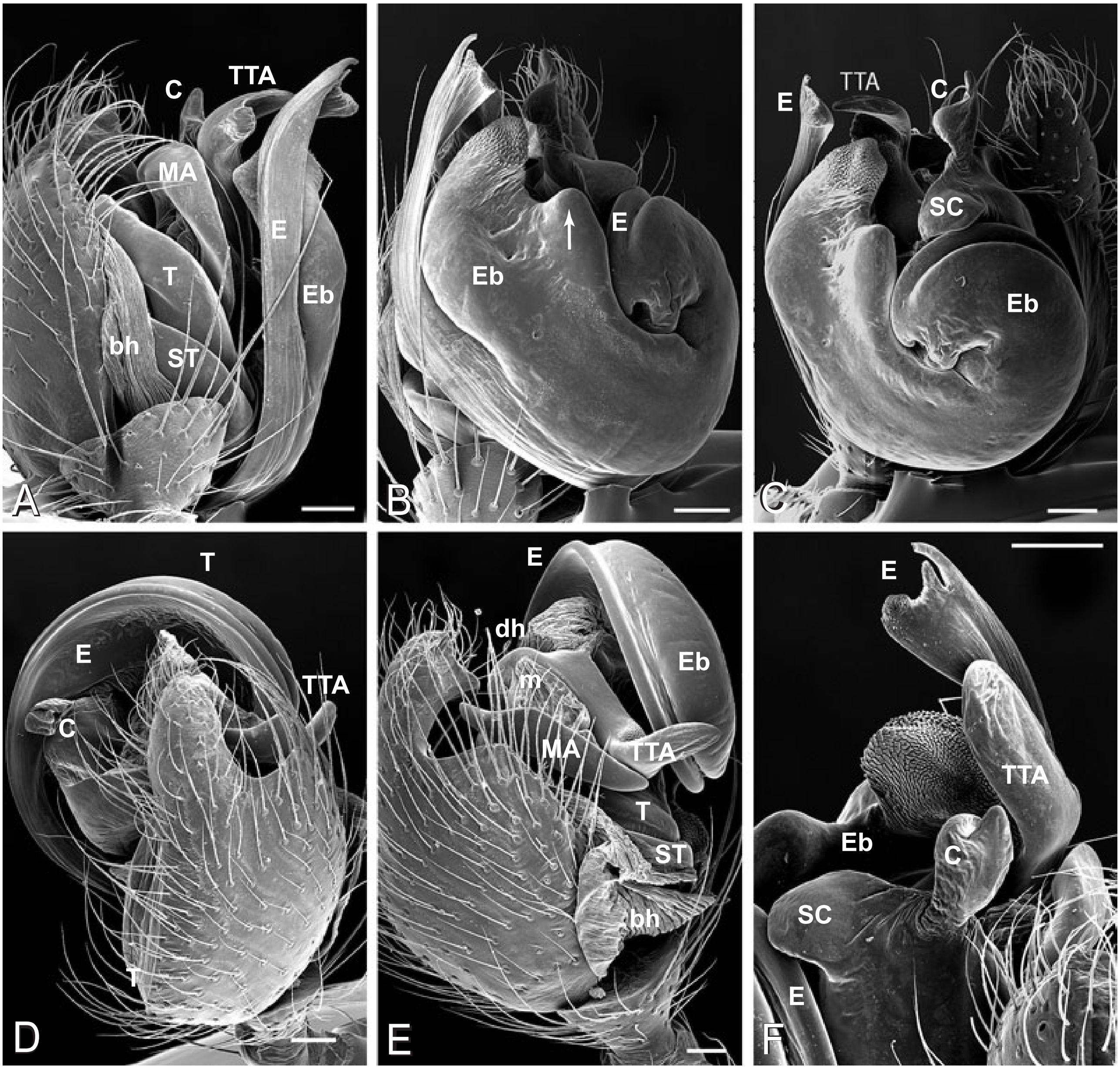

Figure 25. *Anelosimus octavius*, male palp, A–C,F, slightly expanded, D,E fully expanded. A, mesal view; B, ventral, the central ridge on the embolic division b (arrow) is diagnostic for this species; C, subectal viewl; D, dorsal; E, mesal; F, details of distal sclerites. Scale bars: 100 μm.

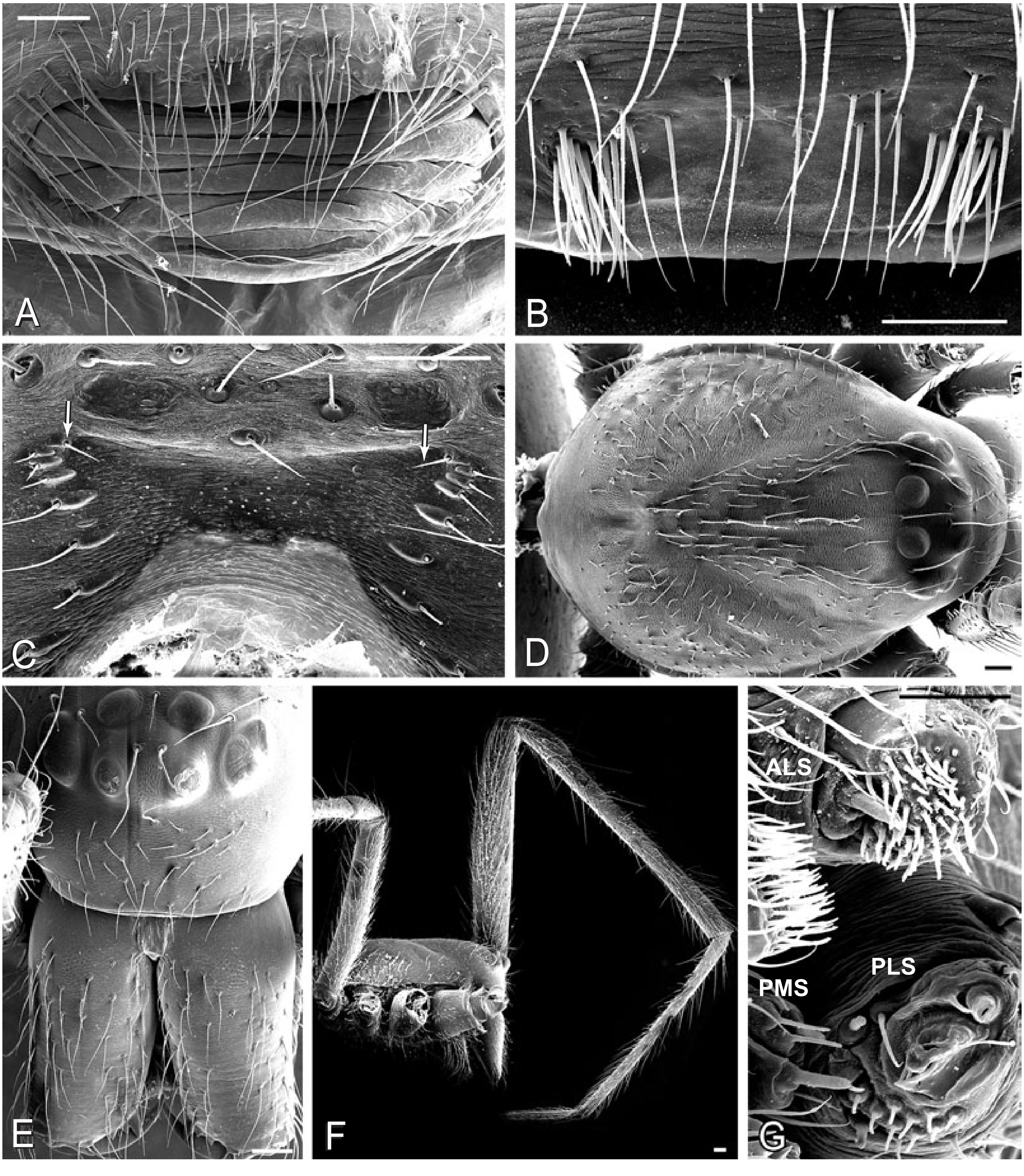

Figure 26. *Anelosimus octavius*. A, epigynum; B, epiandrous gland spigots; C, male stridulatory pick row, note dorsally angled, mesally orientated, picks (arrows); D, female prosoma dorsal; E, female prosoma front; F, male carapace with leg I and femur IV; G, female left spinning field. Scale bars: A,C–G 100 µm; B, 50 µm.

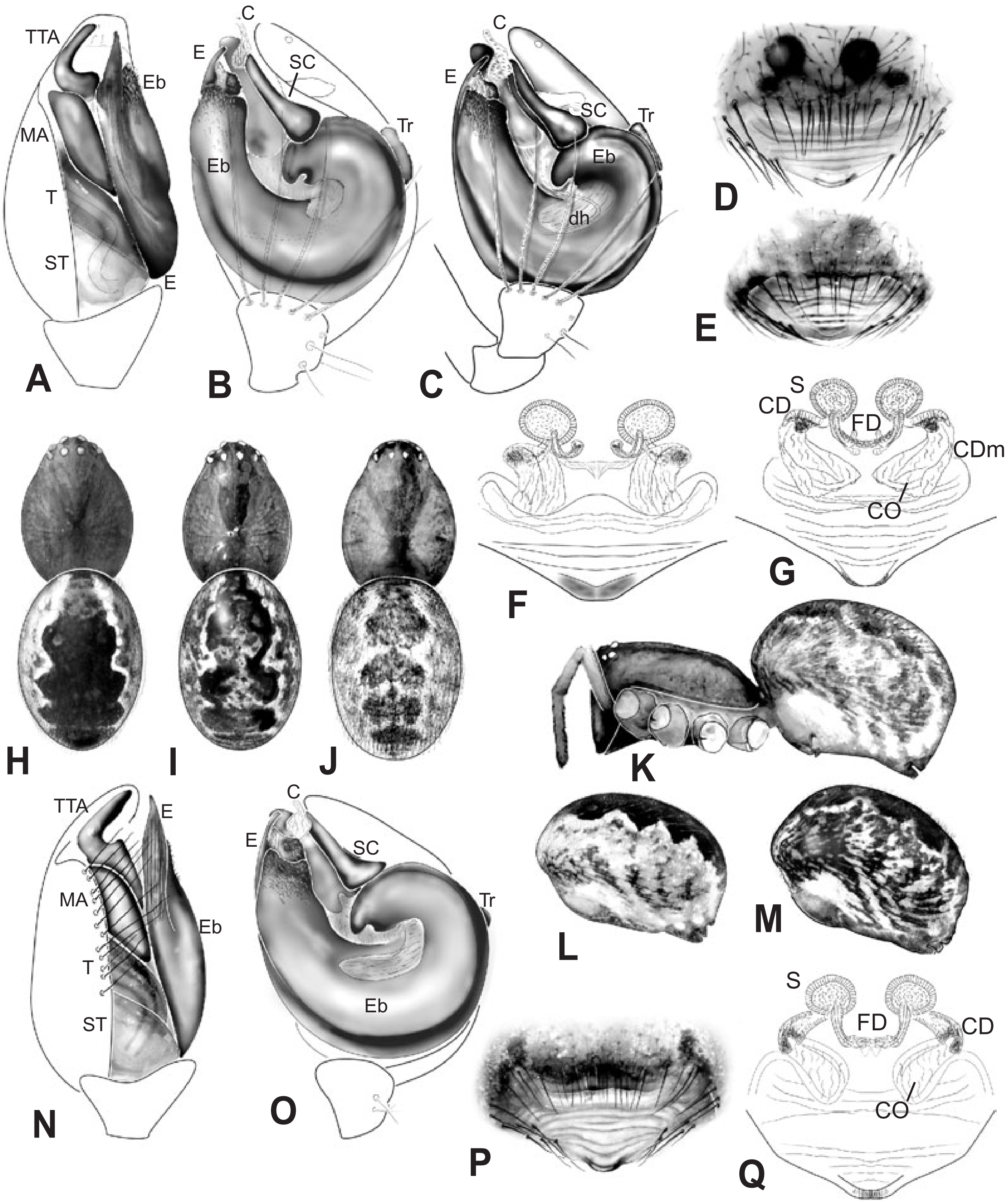

Figure 27. The '*jucundus* group'. A–M, *Anelosimus baeza*. A, male palp mesal, from Baeza, Ecuador; B, same, ventral view; C, male palp ventral, from Colombia; D, epigynum, from Baeza, Ecuador; E–G, epigynum, from Las Caucheras, Ecuador. E, ventral view; F, internal epigynum, ventral; G, internal epigynum dorsal; H, male habitus, from Baeza; I, male habitus, from Las Cuacheras; J, female habitus, from Las Caucheras; K, same, profile; L, ectal view of male abdomen, from Baeza; M, ectal view of male abdomen, from Las Caucheras. N–Q, *Anelosimus puravida*. N, male palp mesal; O, same, ventral; P, epigynum; Q, internal epigynum dorsal.

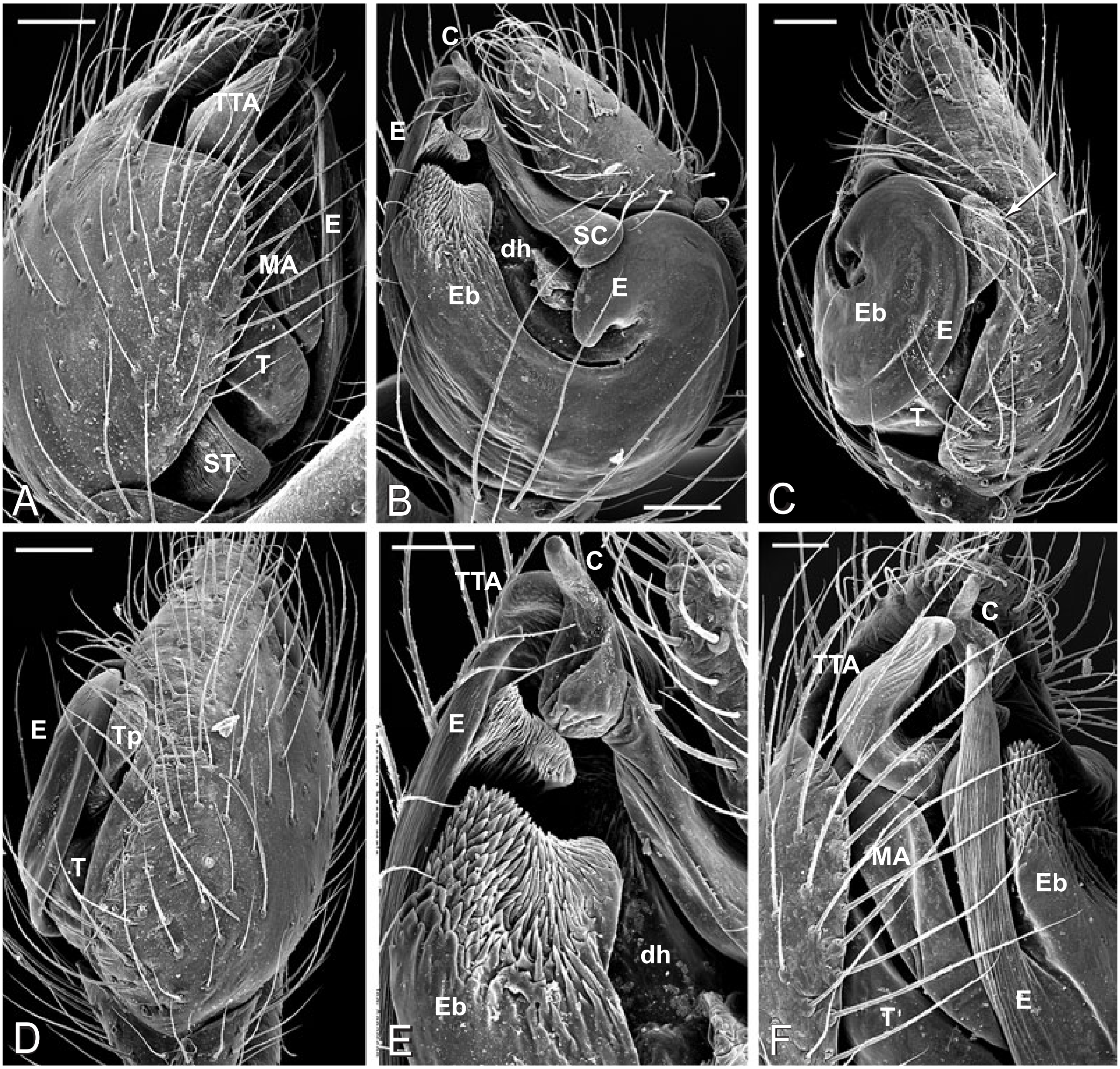

Figure 28. *Anelosimus baeza* from Baeza, male palp. A, mesal; B, ventral; C, subectal, note the ectal tegular process (arrow); D, ectal; E, details of conductor and embolus tip, ventral; F, same, mesal view. Scale bars: A–D, 100 µm; E,F, 50 µm.

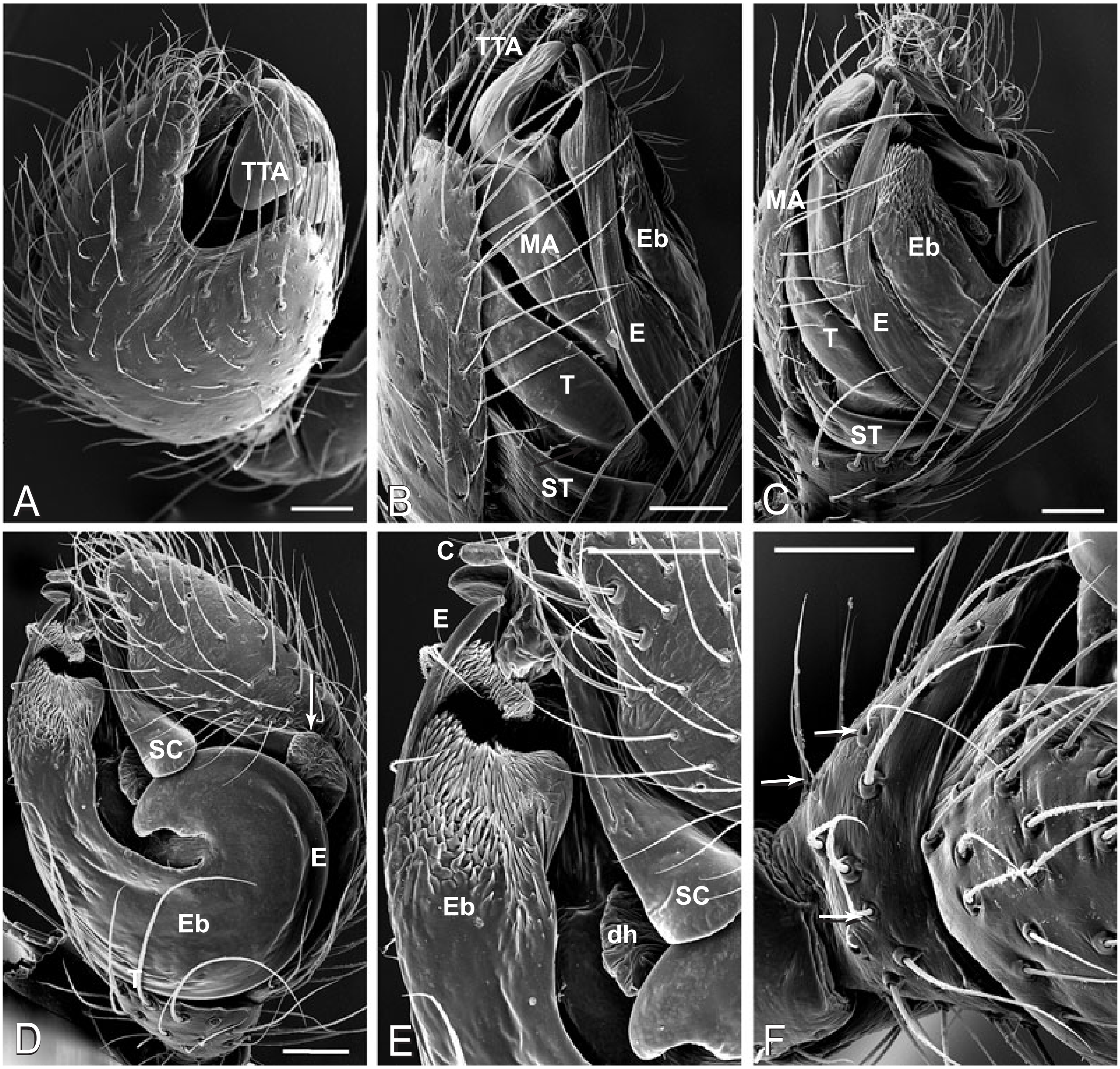

Figure 29. *Anelosimus baeza* from Las Caucheras, male palp. A, dorsoapical view; B, mesal; C, submesal, apical view; D, ventral, note a conspicuous ectal tegular process (arrow); E, details of conductor, subconductor and embolus tip, ventral; F, palpal tibia, with three trichobothria (arrows). Scale bars: 100 µm.

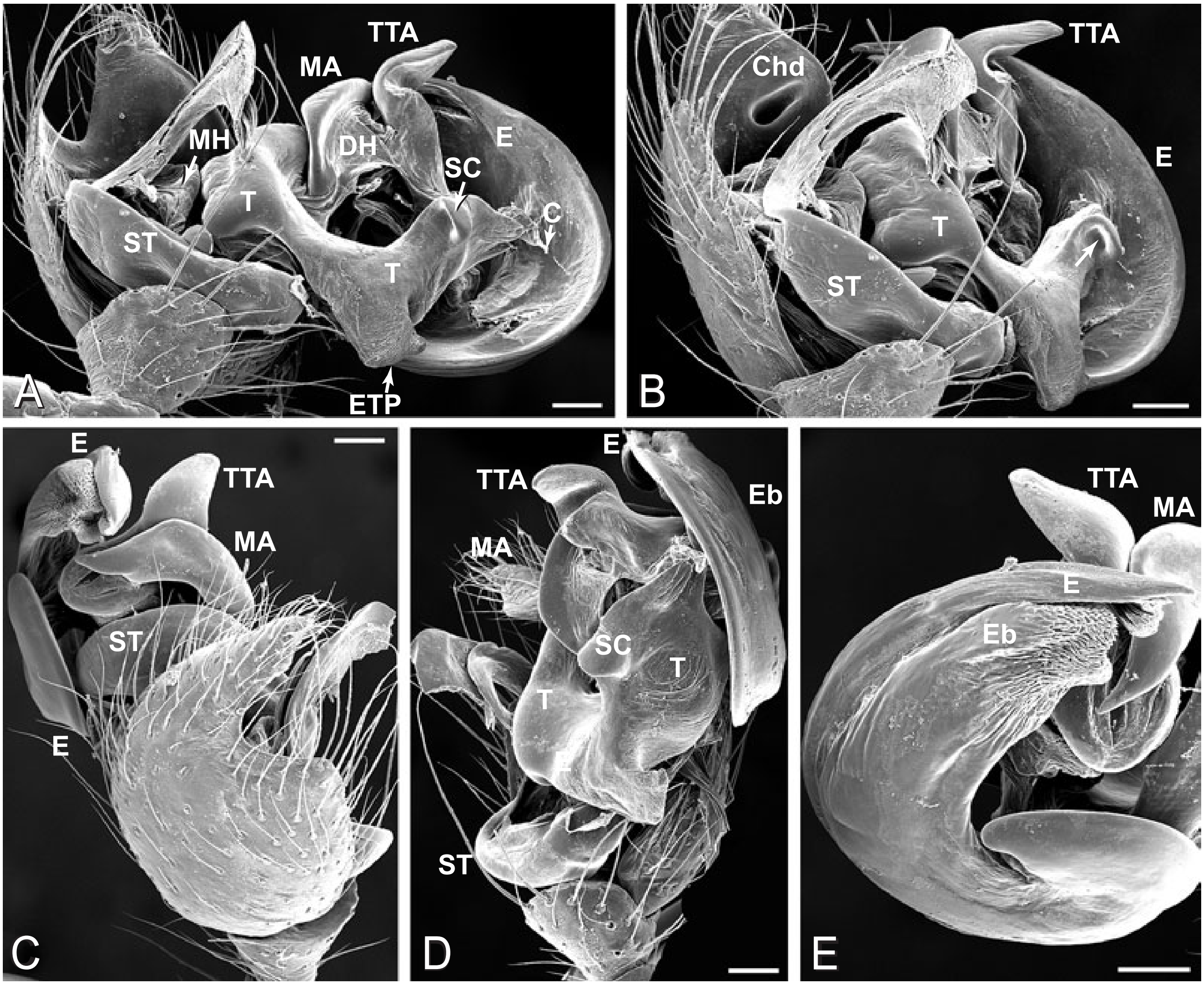

Figure 30. *Anelosimus baeza*, male palp expanded. A, mesal view; B, submesal, the arrow indicates the subconductor hood; C, dorsal; D, ectal; E, details of embolus. Scale bars: 100 µm.

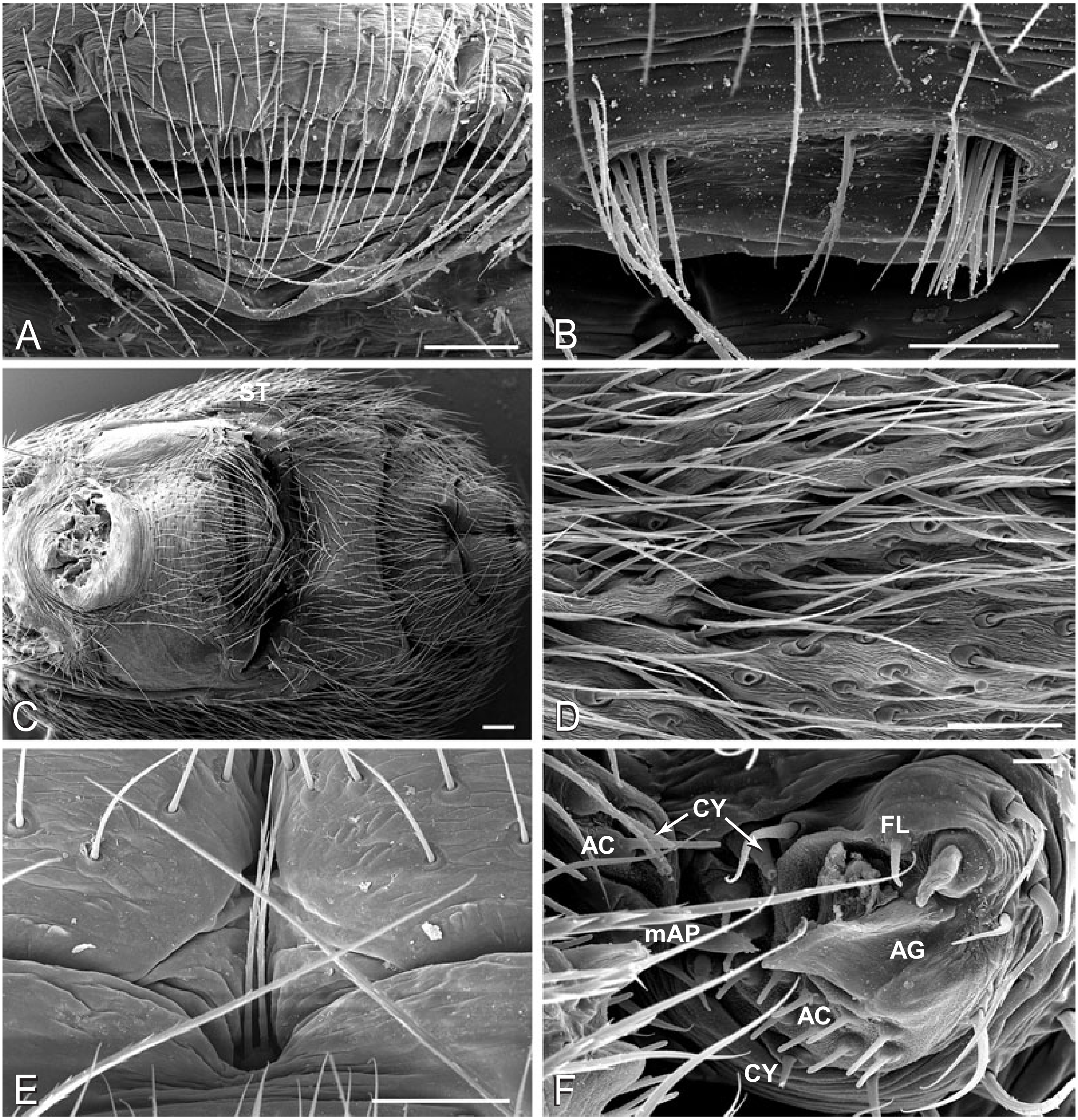

Figure 31. *Anelosimus baeza* from Las Caucheras. A, epigynum; B, epiandrous gland spigots; C–F, female. C, abdomen ventral; D, abdomen surface; E, colular setae; F, posterior median and posterior lateral spinnerets. Scale bars: A,C,D, 100 µm; B,E, 50 µm; F, 10 µm.

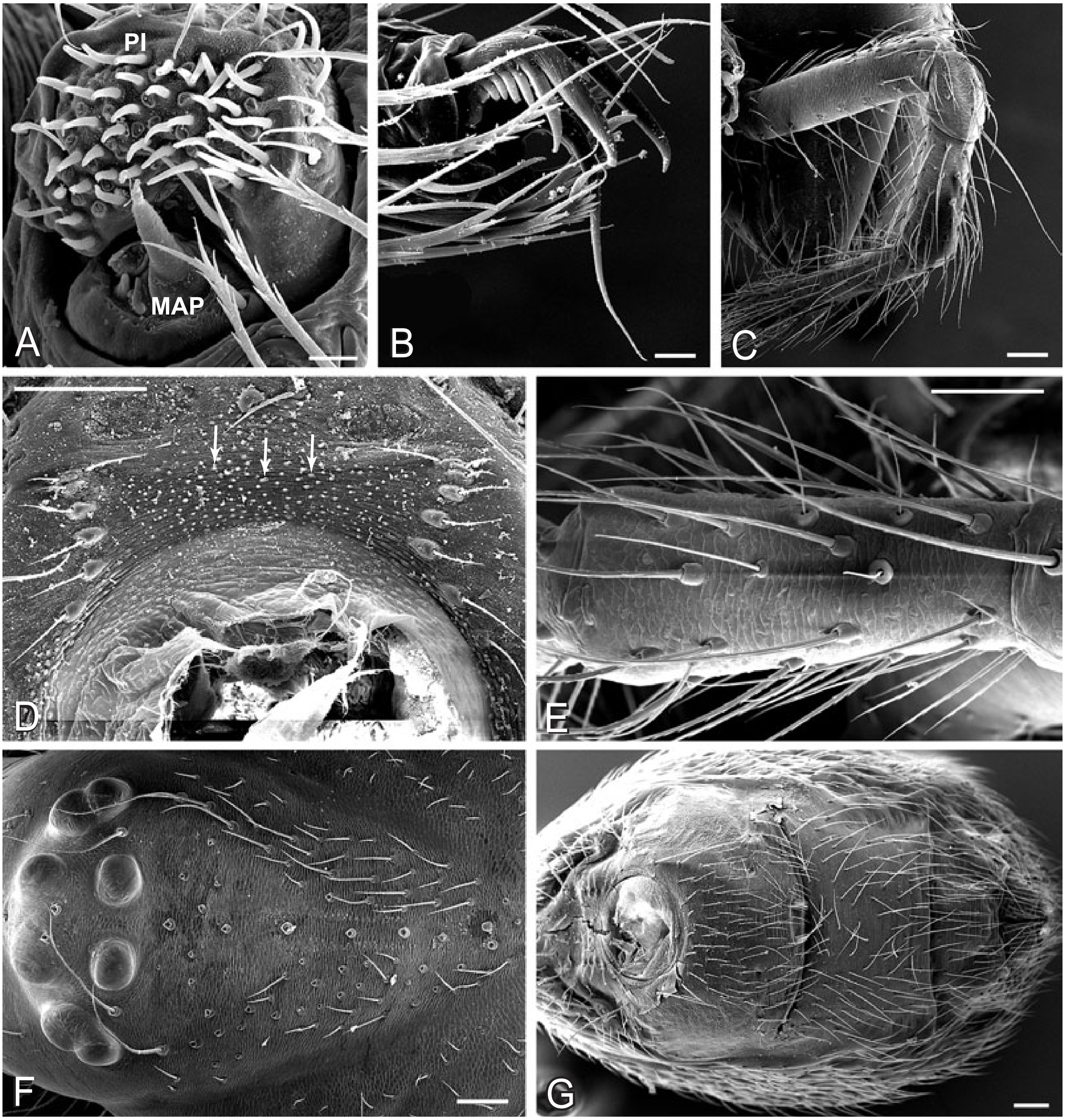

Figure 32. *Anelosimus baeza* from Las Caucheras. A, female anterior lateral spinnerets; B, male fourth tarsal claws; C, female palp; D, male stridulatory pick row, arrows indicate a couple of the stridulatory nubbins interspersed in the area between the rows of picks; E, female palpal tibia; F, female cephalic region; G, male abdomen ventral. Scale bars: A,B, 10 µm; C–G, 100 µm.

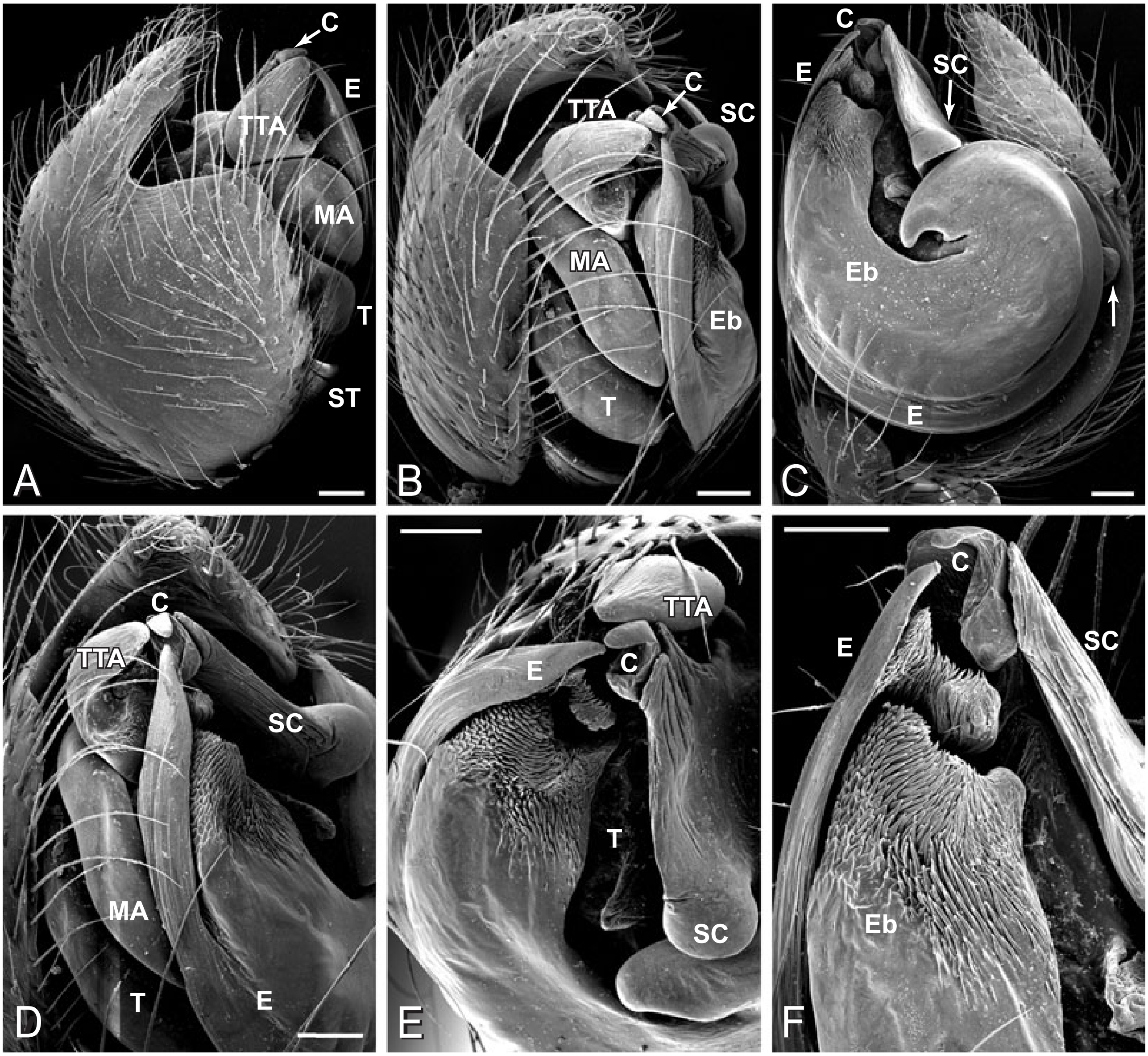

Figure 33. *Anelosimus puravida*, male palp. A, dorsomesal view; B, apical, submesal; C, ventral; D, ectal, tip of palpus; E, apical, tip of palpus; F, details of embolus tip and conductor. Scale bars: 100 μm.

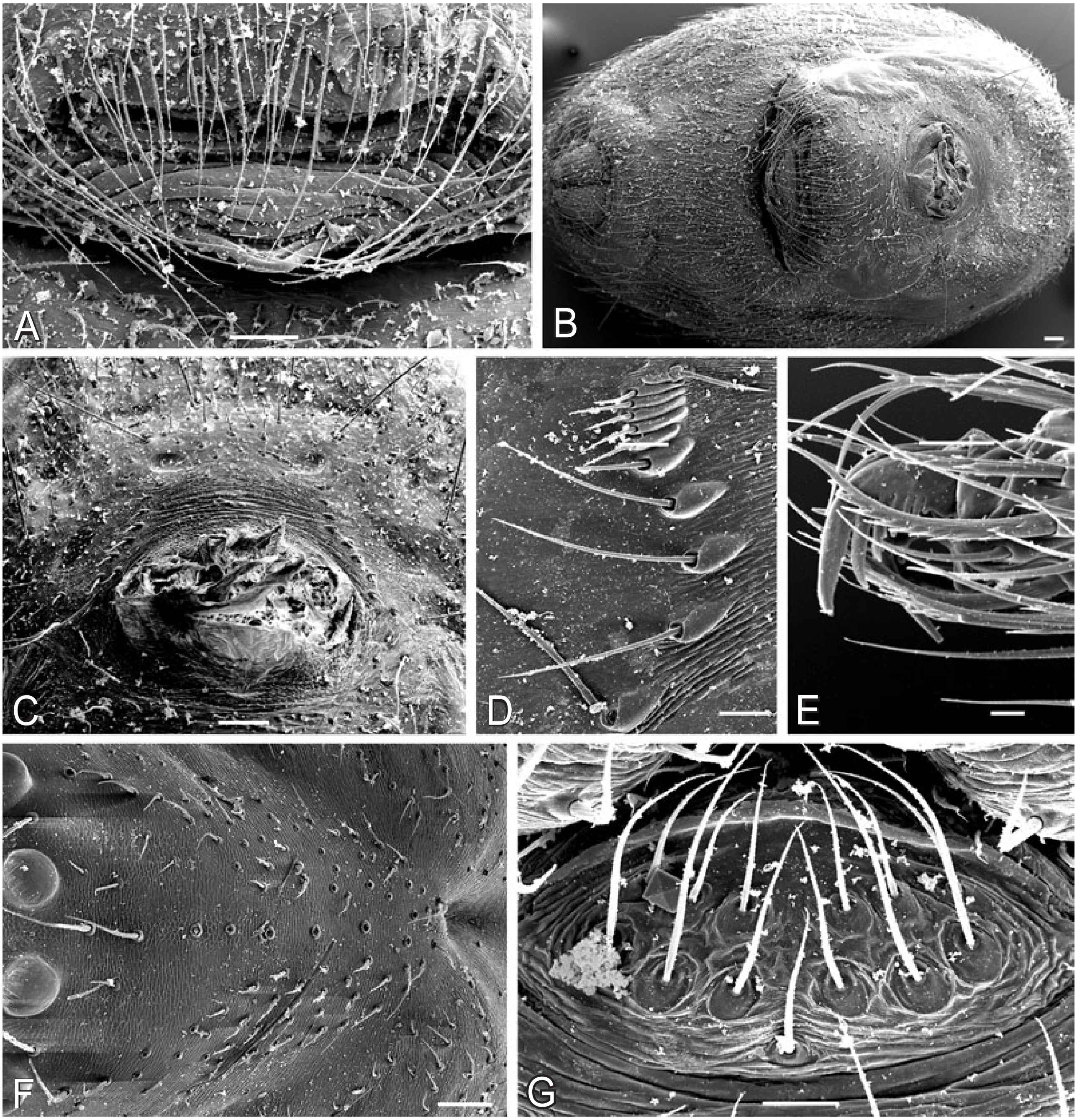

Figure 34. *Anelosimus puravida*. A–C, female. A, epigynum; B, abdomen ventral; C, abdominal pedicel area. D, male stridulatory pick row, right side; E, female fourth tarsal claws; F, female prosoma dorsal; G, male anal tubercle. Scale bars: A–C,F, 100 μm. D, 20 μm; E,G, 10 μm.

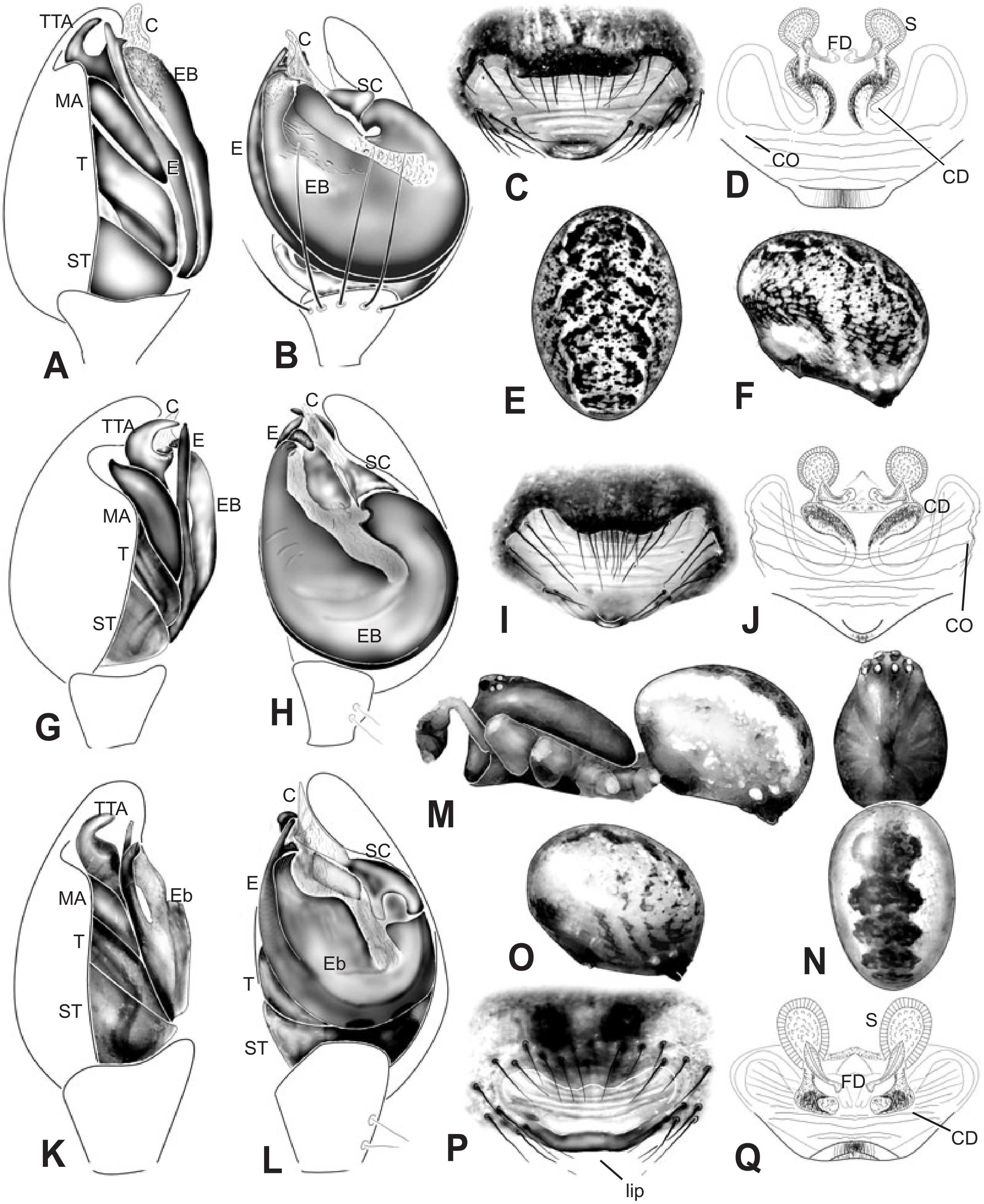

Figure 35. The '*studiosus* group'. A–F, *Anelosimus tosum*. A, male palp mesal; B, same ventral; C, epigynum; D, internal epigynum dorsal; E, female abdomen dorsal; F, same ectal. G–J, *Anelosimus oritoyacu*. G, male palp mesal; H, same ventral; I, epigynum; J, internal epigynum dorsal. K–Q, *Anelosimus tungurahua*. K, male palp mesal; L, same ventral; M, male habitus ectal; N, same, dorsal; O, female abdomen ectal; P, epigynum; Q, internal epigynum dorsal.

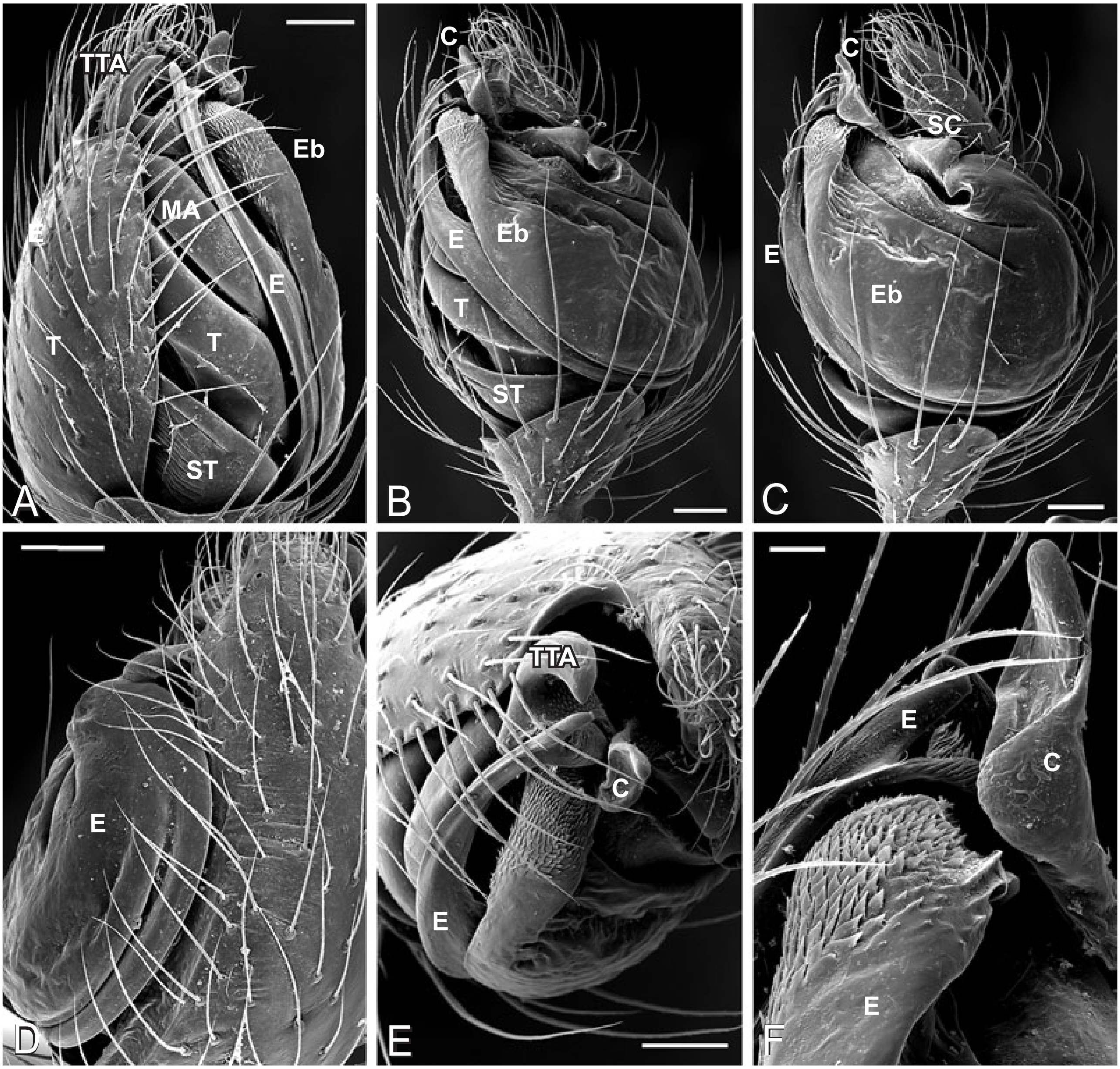

Figure 36. *Anelosimus tosum*, male palp. A, mesal view; B, submesal; C, ventral; D, ectal; E, apicoventral; F, details of embolus tip and conductor. Scale bars: 100 μm.

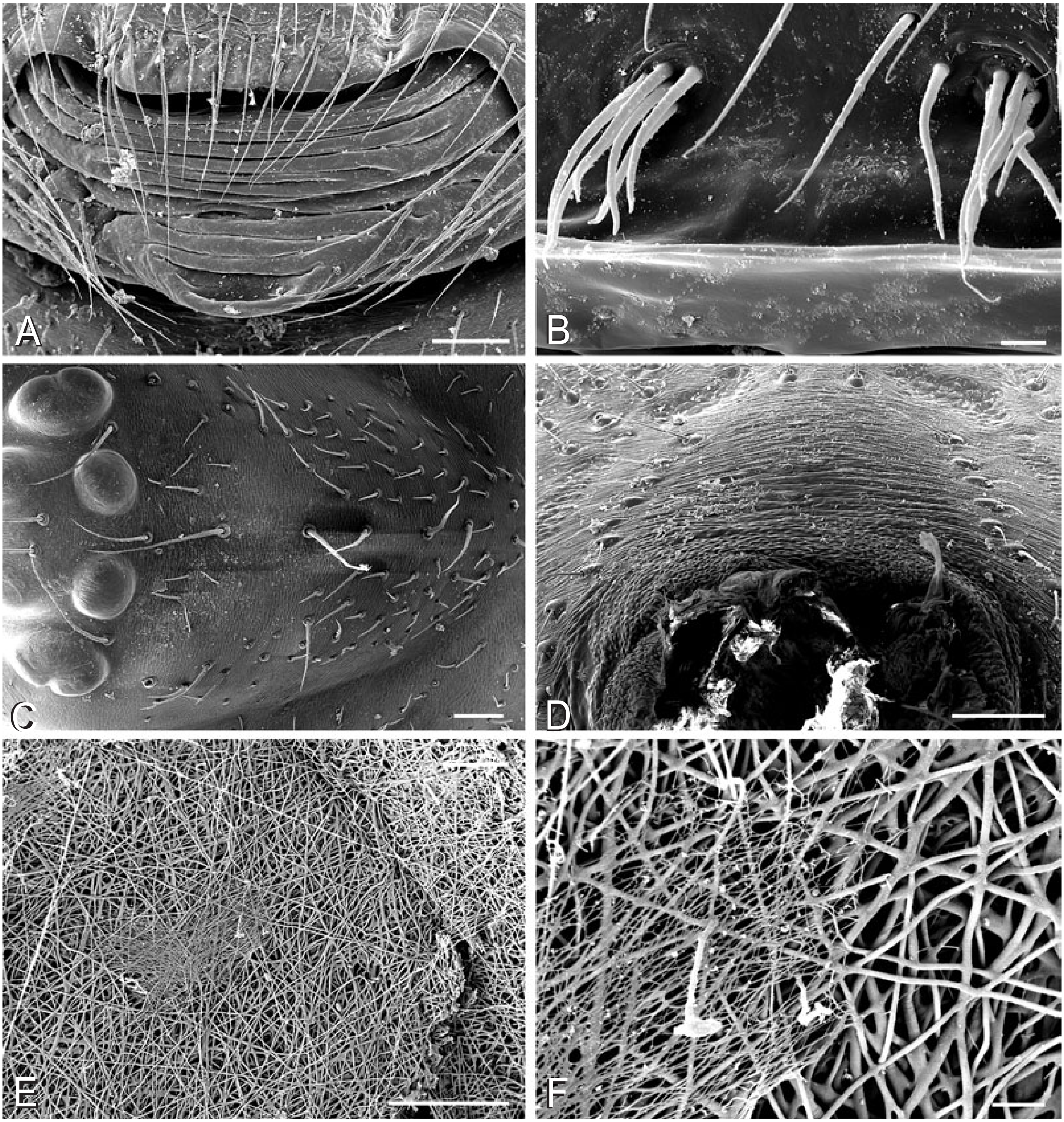

Figure 37. *Anelosimus tosum*. A, epigynum; B, epiandrous gland spigots; C, female prosoma dorsal; D, female stridulatory pick row; E, egg sac fibres; F, higher magnification of egg sac fibres. Scale bars: A,C–E, 100 μm; B,F, 10 μm.

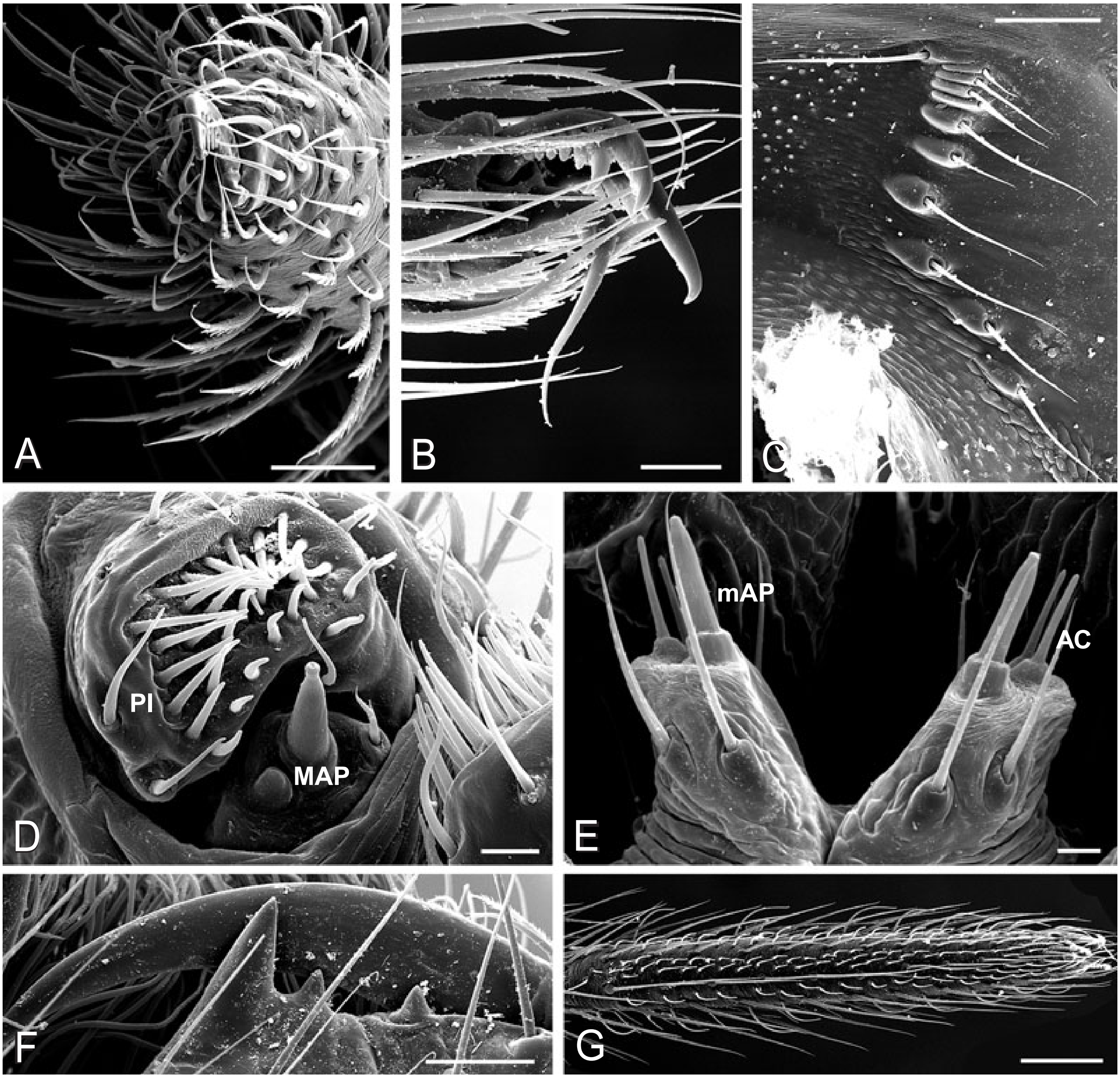

Figure 38. *Anelosimus tosum*. A, female palpal claw. B–G, male. B, fourth tarsal claws; C, stridulatory pick row; D, anterior lateral spinneret; E, posterior median spinnerets, anterior view; F, cheliceral promarginal teeth; G, first tarsus ventral. Scale bars: A,C,F, 50 μm; B, 20 μm; D,E, 10 μm; G, 100 μm.

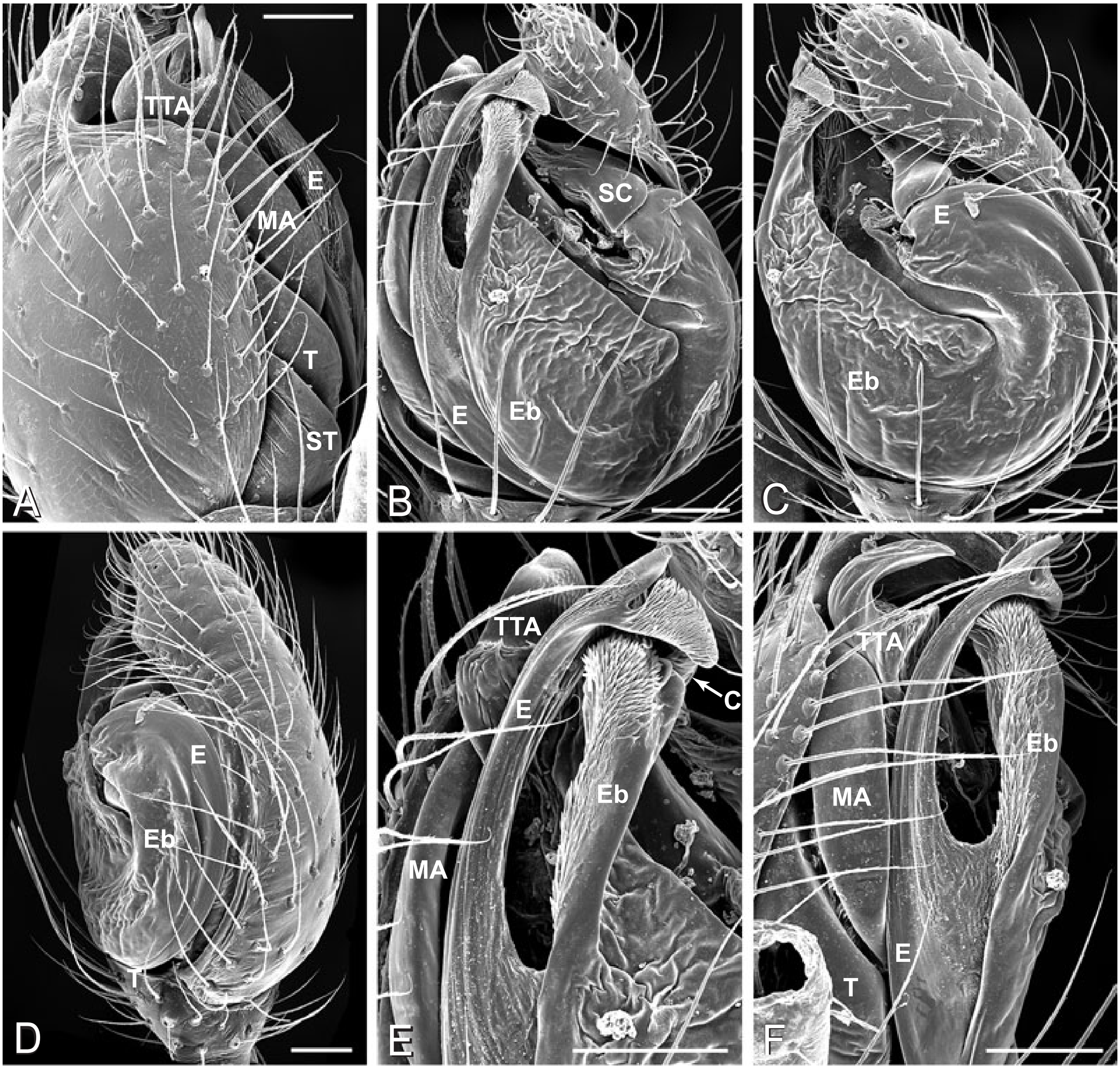

Figure 39. *Anelosimus oritoyacu* Ecuador, male palp. A, mesal view; B, submesal; C, ventral; D, ectal; E, details of distal sclerites, ventral; F, mesal view of distal sclerites. Scale bars: 100 µm.

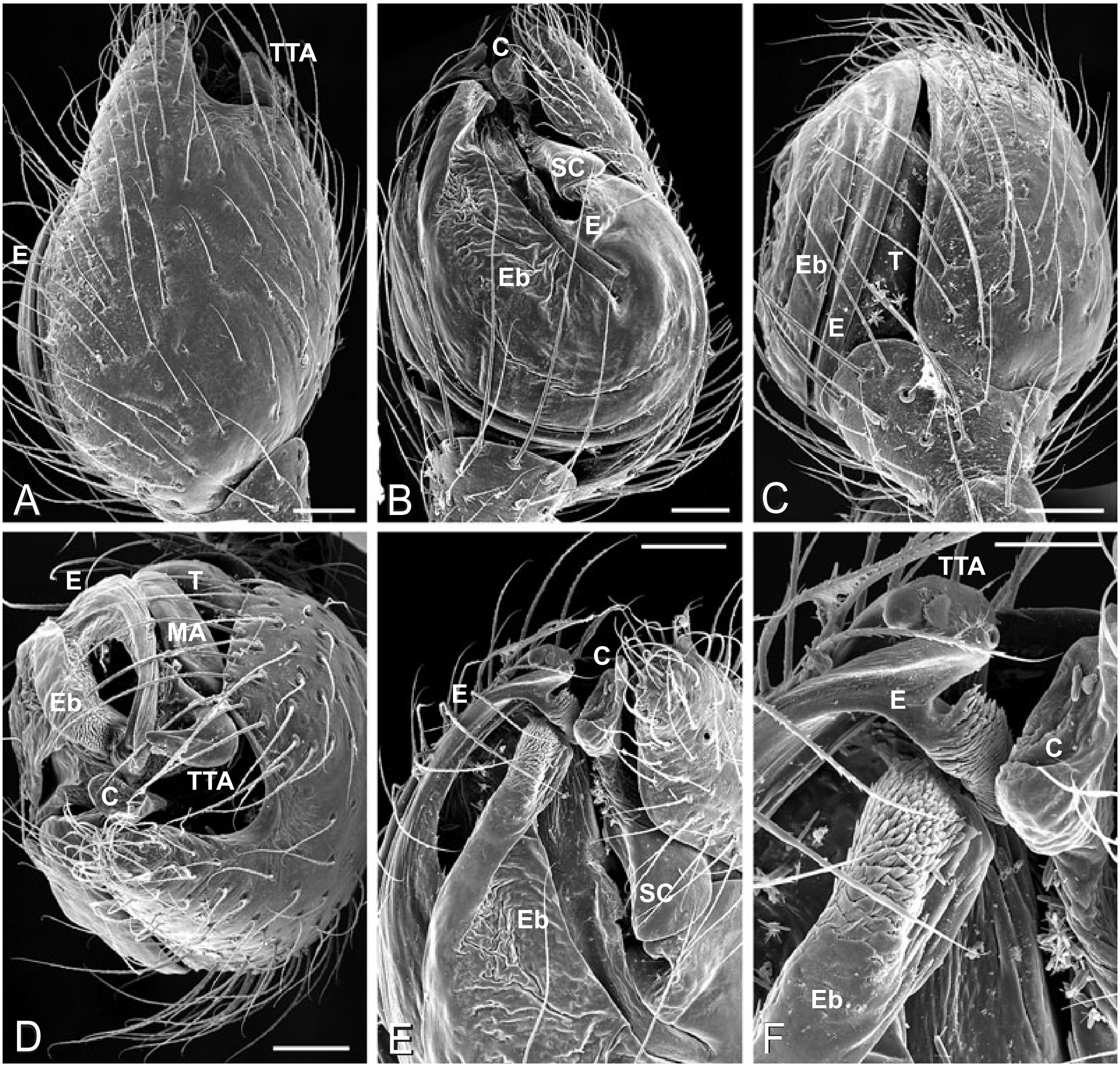

Figure 40. *Anelosimus oritoyacu* Peru, male palp. A, dorsal view; B, ventral; C, caudoectal; D, apical; E, details of distal sclerites; F, close up of distal sclerites. Scale bars: A–E, 100 µm; F, 50 µm.

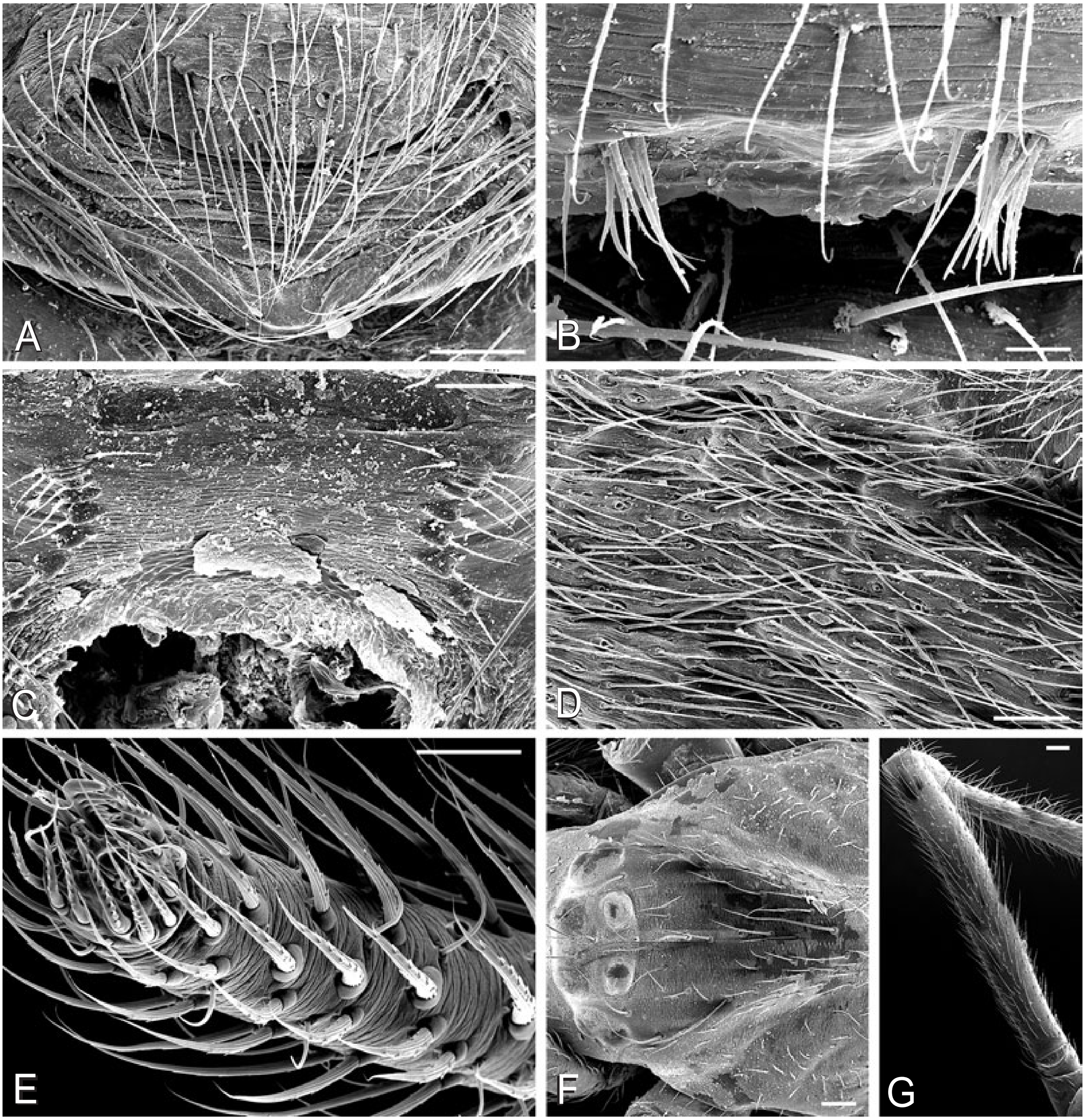

Figure 41. *Anelosimus oritoyacu*. A, epigynum; B, epiandrous gland spigots; C, male stridulatory pick row; D, female abdomen surface; E, female tarsus IV; F, female prosoma dorsal; G, male femur I. Scale bars: A,D,F,G, 100 µm; B, 20 µm; C,E, 50 µm.

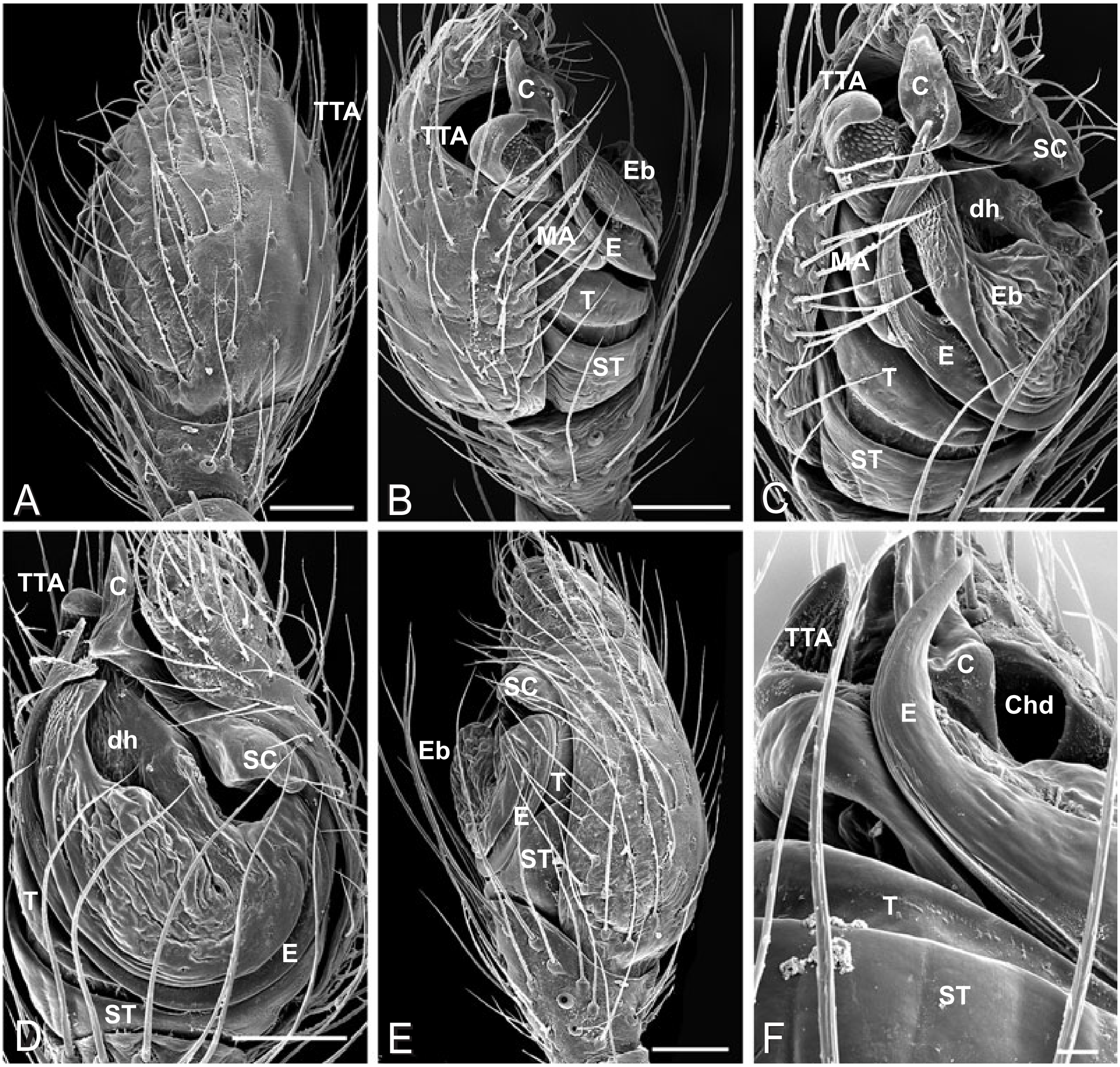

Figure 42. *Anelosimus tungurahua* male palp. A, dorsal view; B, mesal; C, apical; D, ventral; E, ectal; F, details of embolus tip. Scale bars: A–E, 100 µm; F, 10 µm.

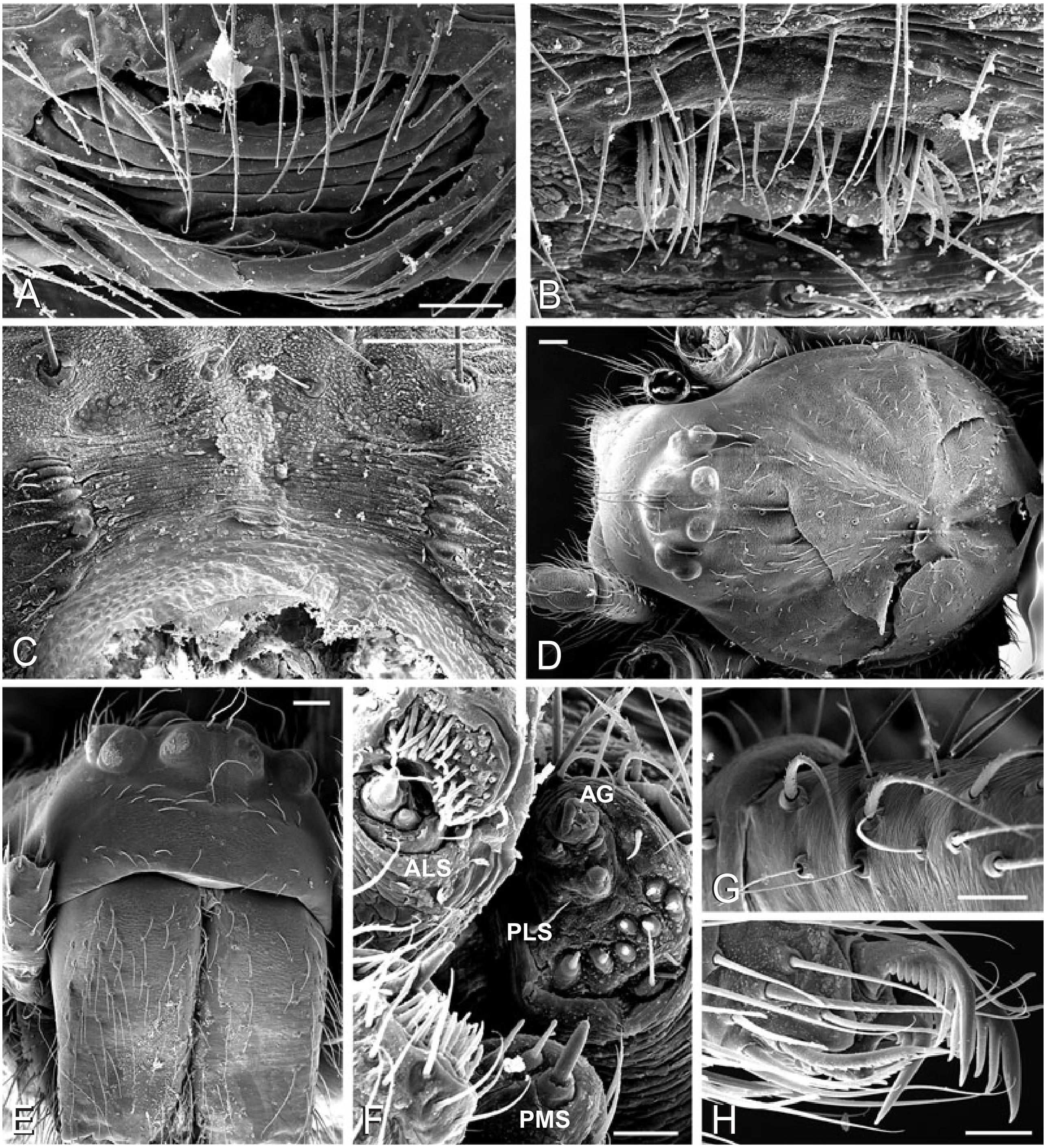

Figure 43. *Anelosimus tungurahua*. A, epigynum; B, epiandrous gland spigots; C, male stridulatory pick row; D, female prosoma dorsal; E, same, front; F, male spinnerets, anterior is left; G, female palpal tibia dorsal; H, male tarsus I claws. Scale bars: A,B,F, 50 μm; C–E, 100 μm; G,H, 20 μm.

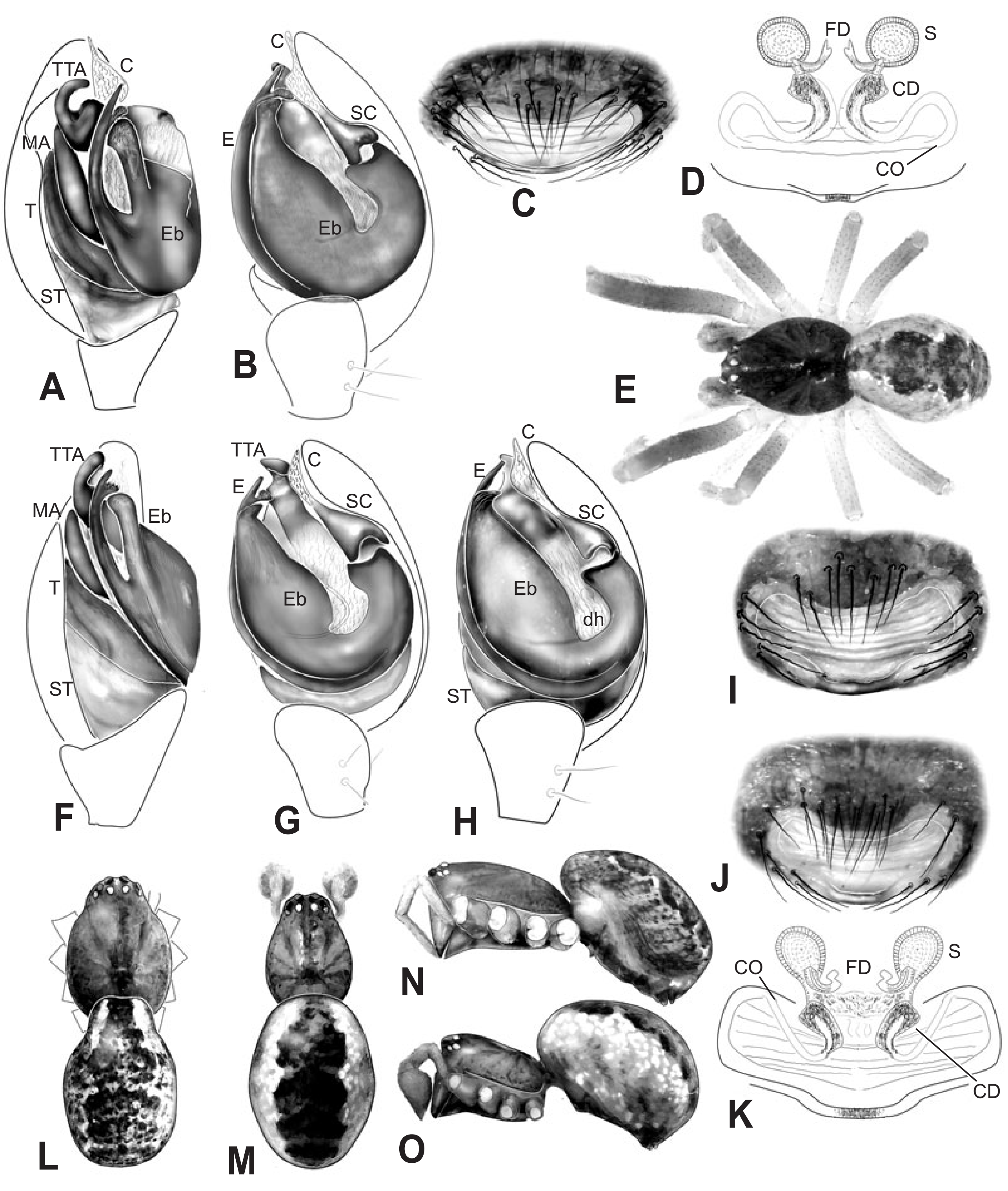

Figure 44. The '*studiosus* group'. A–E, *Anelosimus elegans*. A, male palp mesal; B, same ventral; C, epigynum; D, internal epigynum dorsal; E, digital photograph of male holotype. F–O, *Anelosimus guacamayos*. F, male palp mesal; G, same ventral; H, male palp lacking distal E fork; I, epigynum; J, epigynum, female collected with 'forkless' male; K, internal epigynum dorsal; L, female habitus dorsal; M, male habitus dorsal; N, female habitus ectal; O, subadult male habitus ectal.

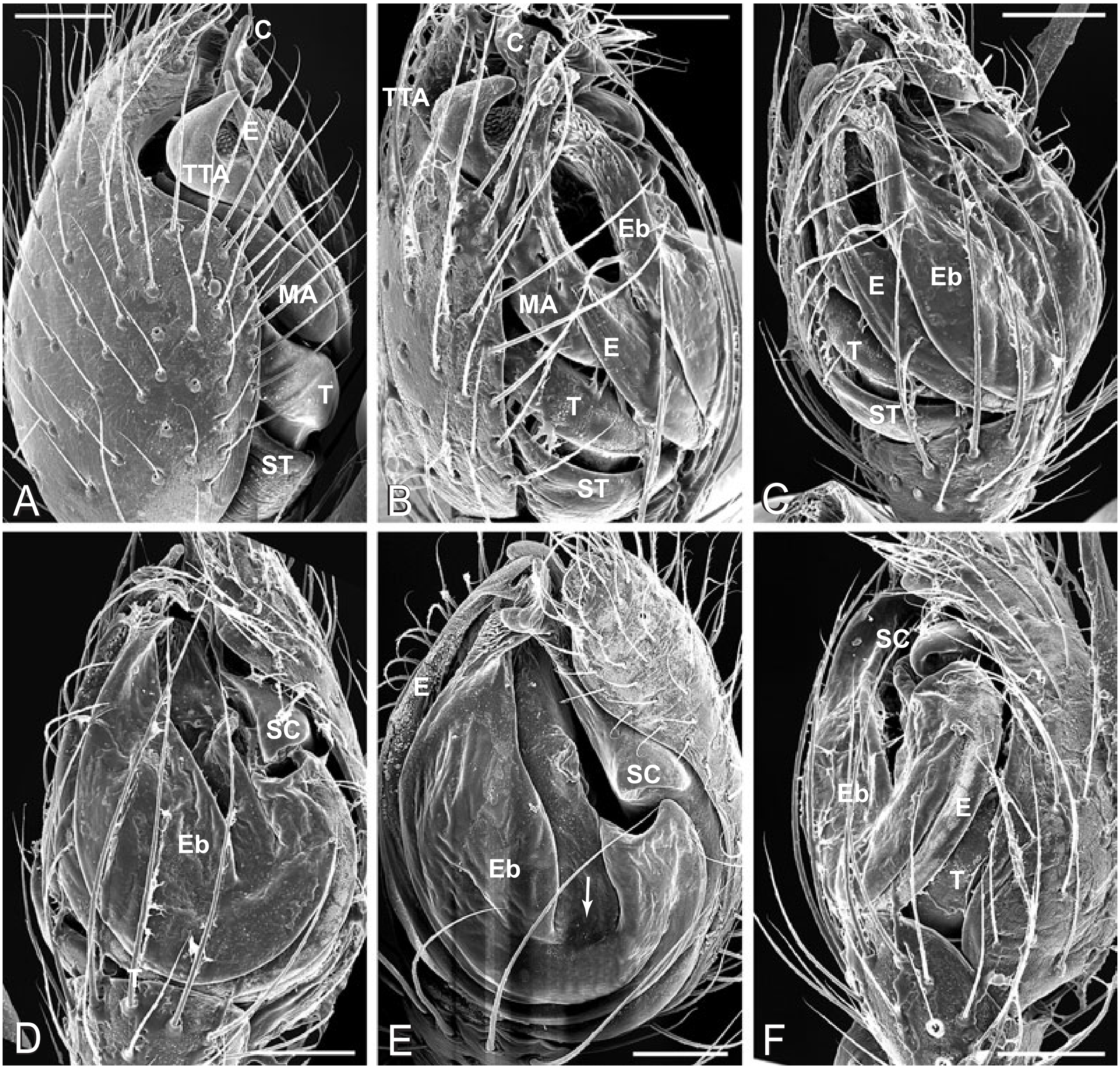

Figure 45. *Anelosimus elegans*, male palp (B–D,F, specimen 1; A,E, specimen 2). A, dorsomesal; B, mesal; C, submesal; D, ventral; E, ventral view, note deeper and broader incision of the distal hematodocha (arrow) as compared with specimen 1; F, ectal. Scale bars: 100 μm.

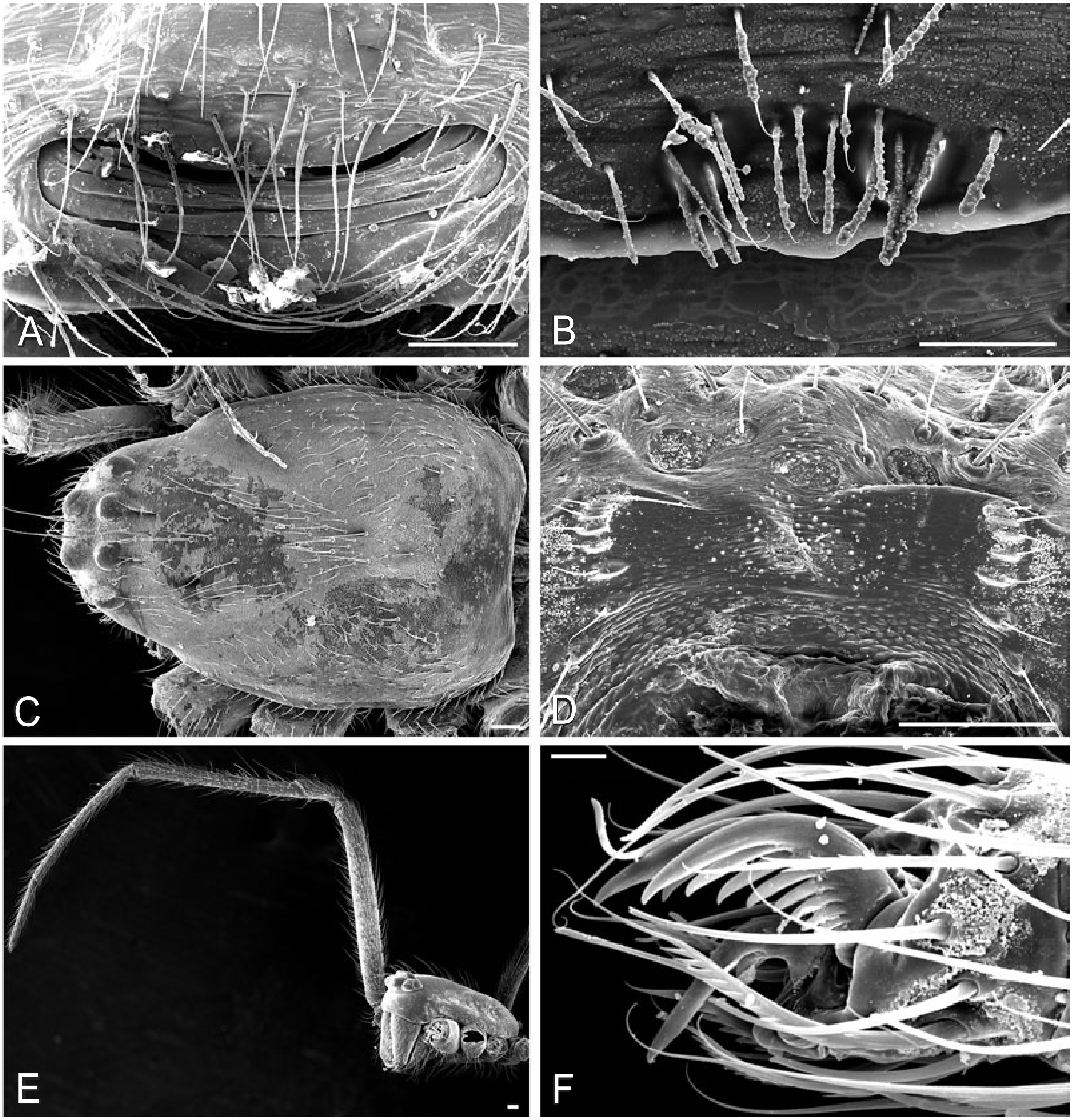

Figure 46. *Anelosimus elegans*. A, epigynum; B, epiandrous gland spigots; C, female prosoma dorsal; D, male stridulatory pick row; E, male prosoma and leg I; F, male tarsus I claws. Scale bars: A,C–E, 100 µm; B, 50 µm; F, 10 µm.

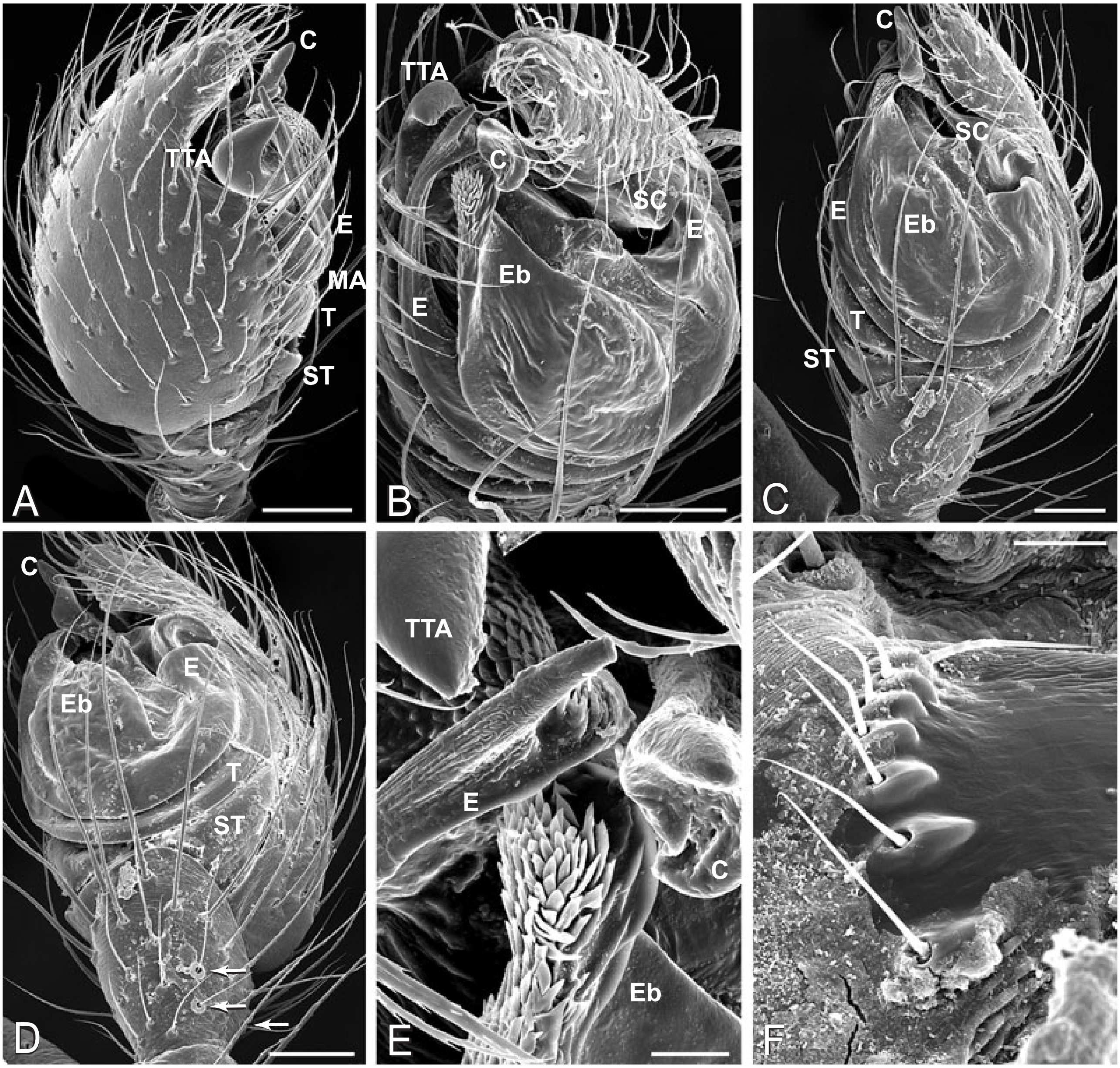

Figure 47. *Anelosimus guacamayos*. A–E male palp. A, mesal; B, apical; C, ventral; D, ectocaudal, arrows indicate the tibial trichobothria; E, details of embolus tip and conductor. F, male stridulatory pick row, right side. Scale bars: A–D, 100 µm; E,F, 20 µm.

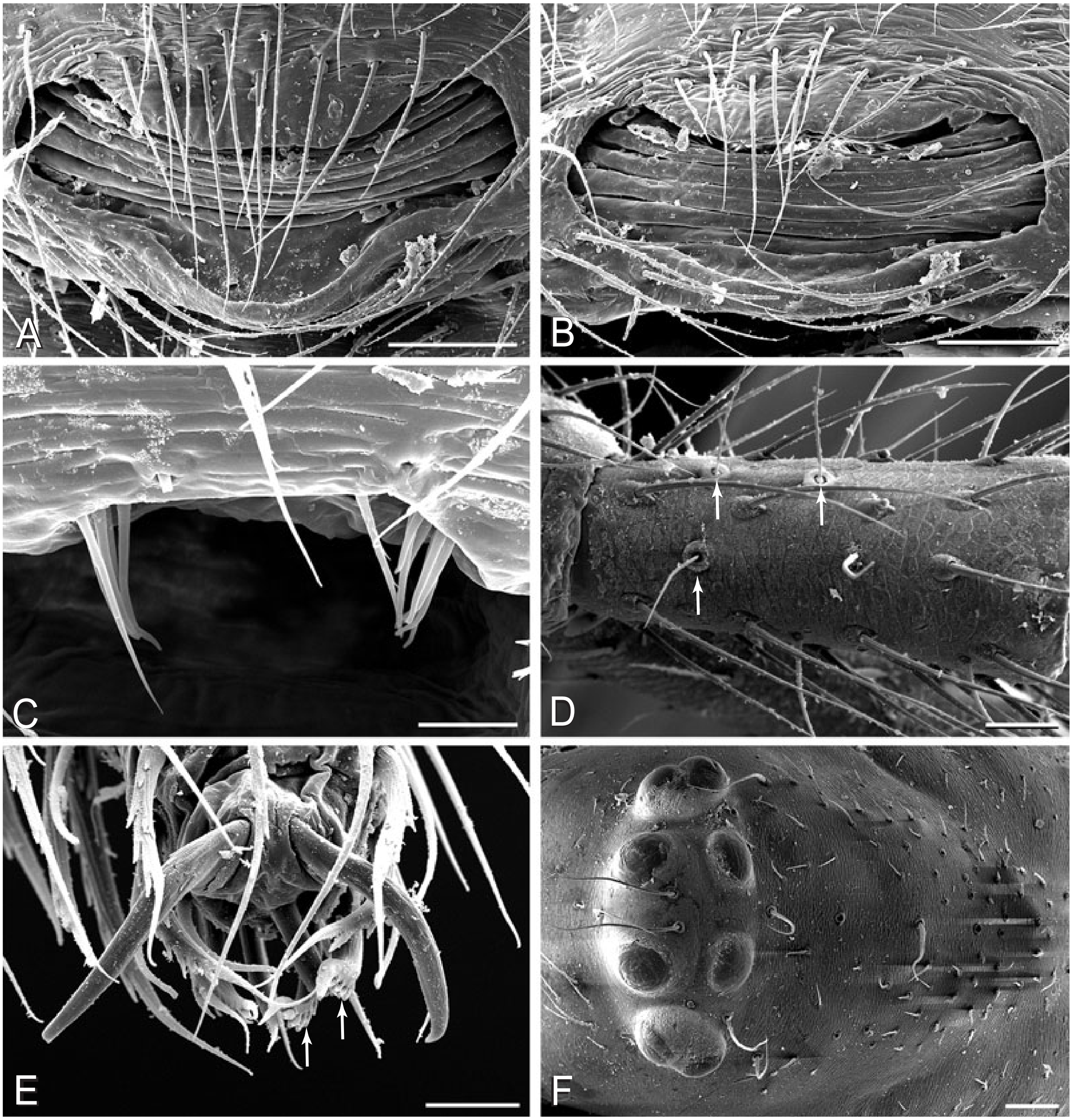

Figure 48. *Anelosimus guacamayos*. A,B, epigynum. A, ventral; B, subcaudal. C, epiandrous gland spigots; D, female palpal tibia, dorsal view showing the three trichobothria (arrows); E, female fourth tarsal claws, central claw removed – note strong accessory claws (arrows); F, female cephalic region. Scale bars: A,B,F, 100 μm; C,E, 20 μm; D, 50 μm.

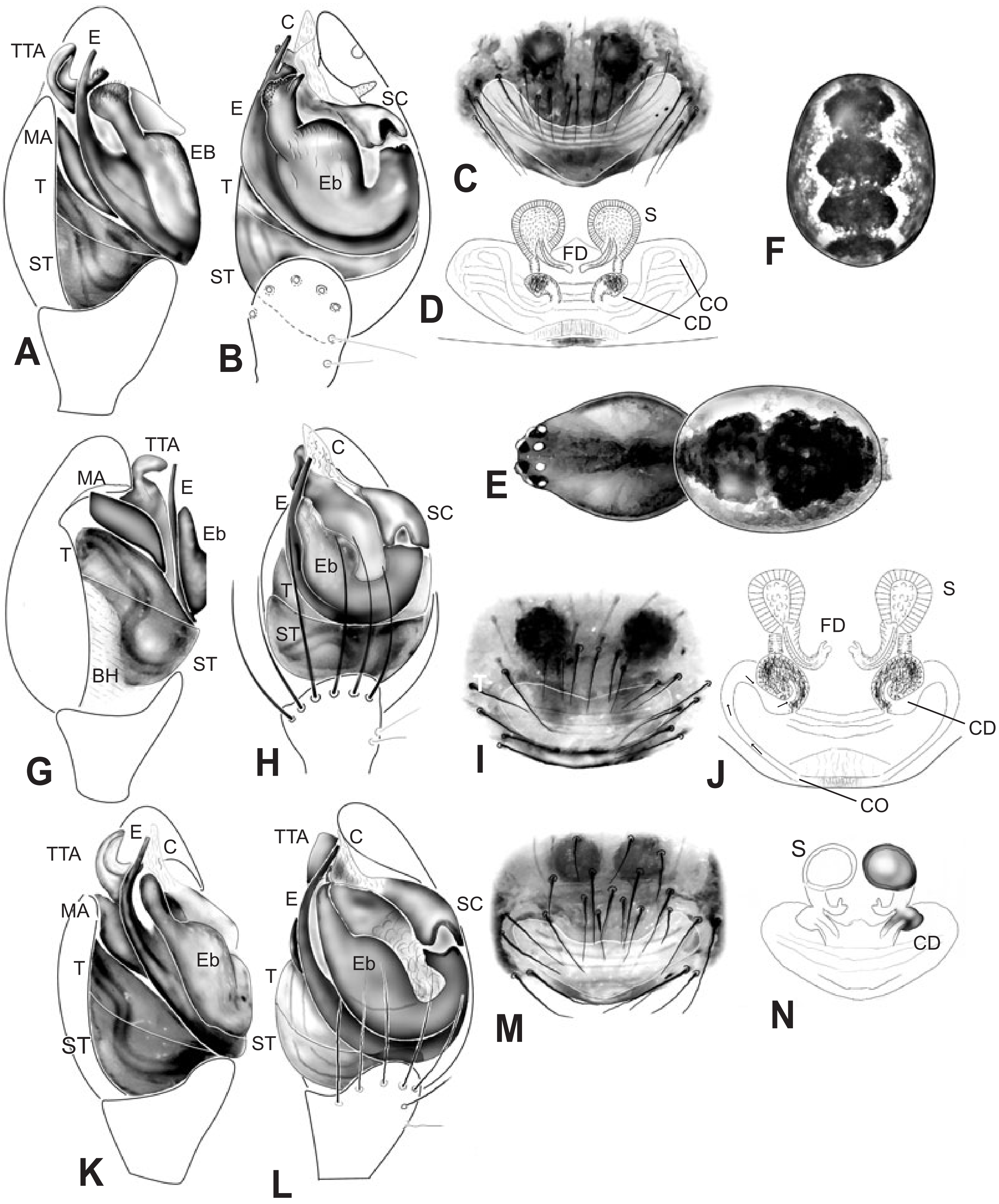

Figure 49. The *studiosus* group. A–F, *Anelosimus studiosus*. A, mesal view of male palp; B, ventral view of male palp; C, epigynum; D, internal epigynum dorsal; E, male habitus dorsal; F, female abdomen dorsal. G–J, *Anelosimus pantanal*. G, male palp mesal; H, same ventral; I, epigynum; J, internal epigynum dorsal. K–N, *Anelosimus fraternus*. K, male palp (holotype) mesal; L, same ventral; M, epigynum; N, internal epigynum dorsal.

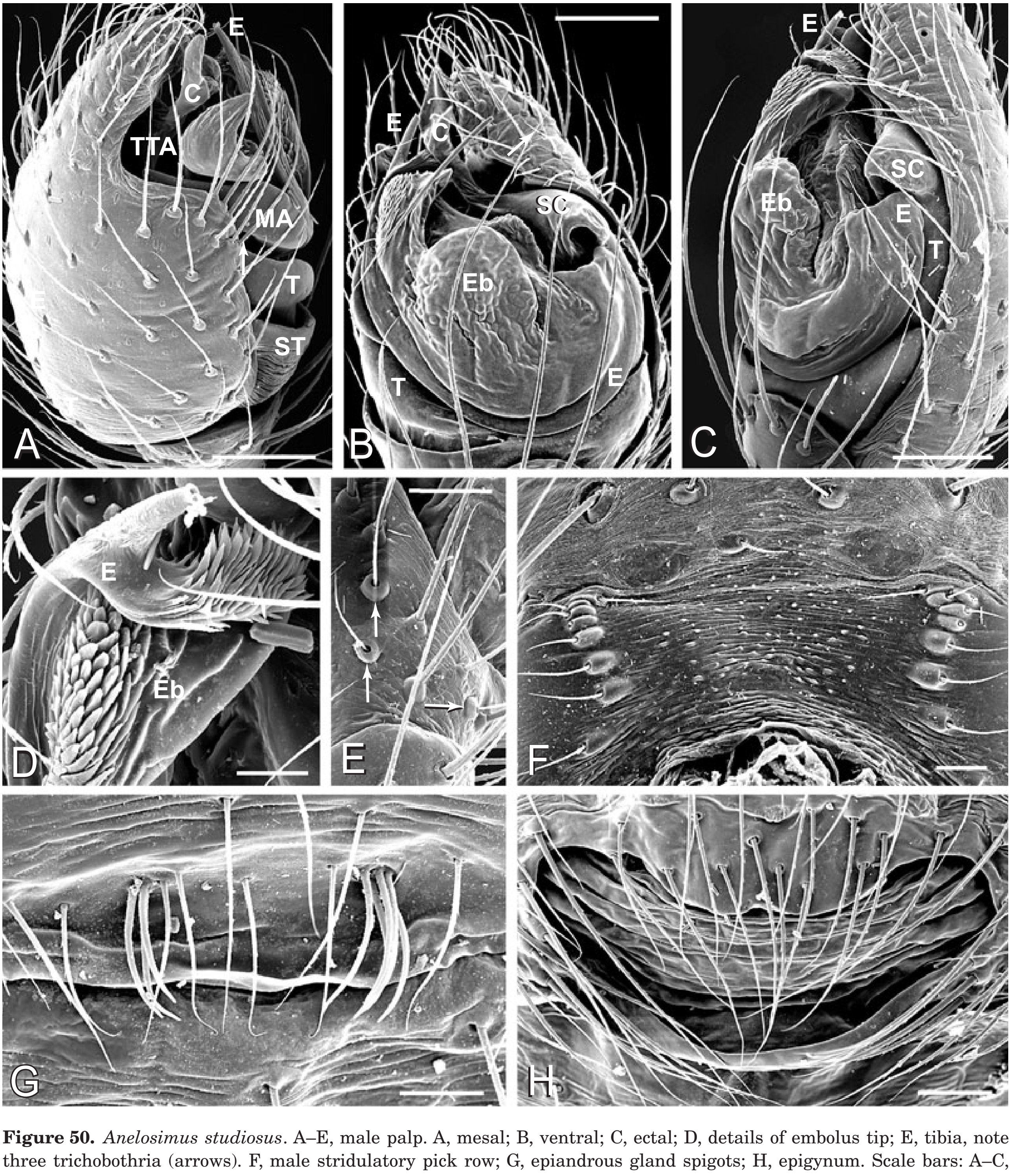

Figure 50. *Anelosimus studiosus*. A–E, male palp. A, mesal; B, ventral; C, ectal; D, details of embolus tip; E, tibia, note three trichobothria (arrows). F, male stridulatory pick row; G, epiandrous gland spigots; H, epigynum. Scale bars: A–C, 100 μm; E,H, 50 μm; D,F,G, 20 μm.

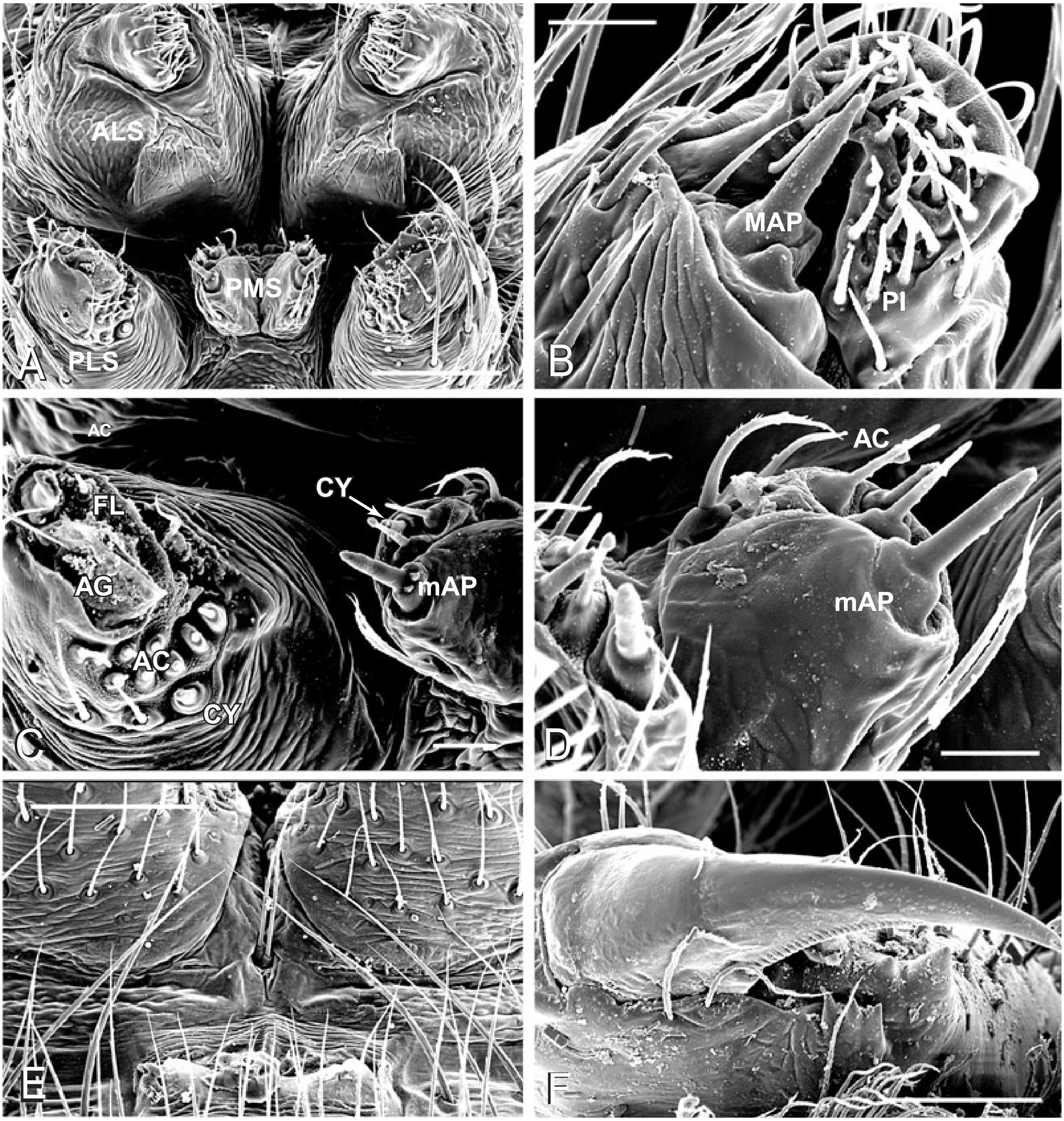

Figure 51. *Anelosimus studiosus* female. A, spinnerets; B, anterior lateral spinneret, anterior is right; C, posterior lateral, and posterior median spinnerets, right side; D, posterior median spinnerets, submesal view; E, colular setae (arrow), note absence of colulus; F, cheliceral teeth posterior view. Scale bars: A,E,F, 100 μm; B–D, 20 μm.

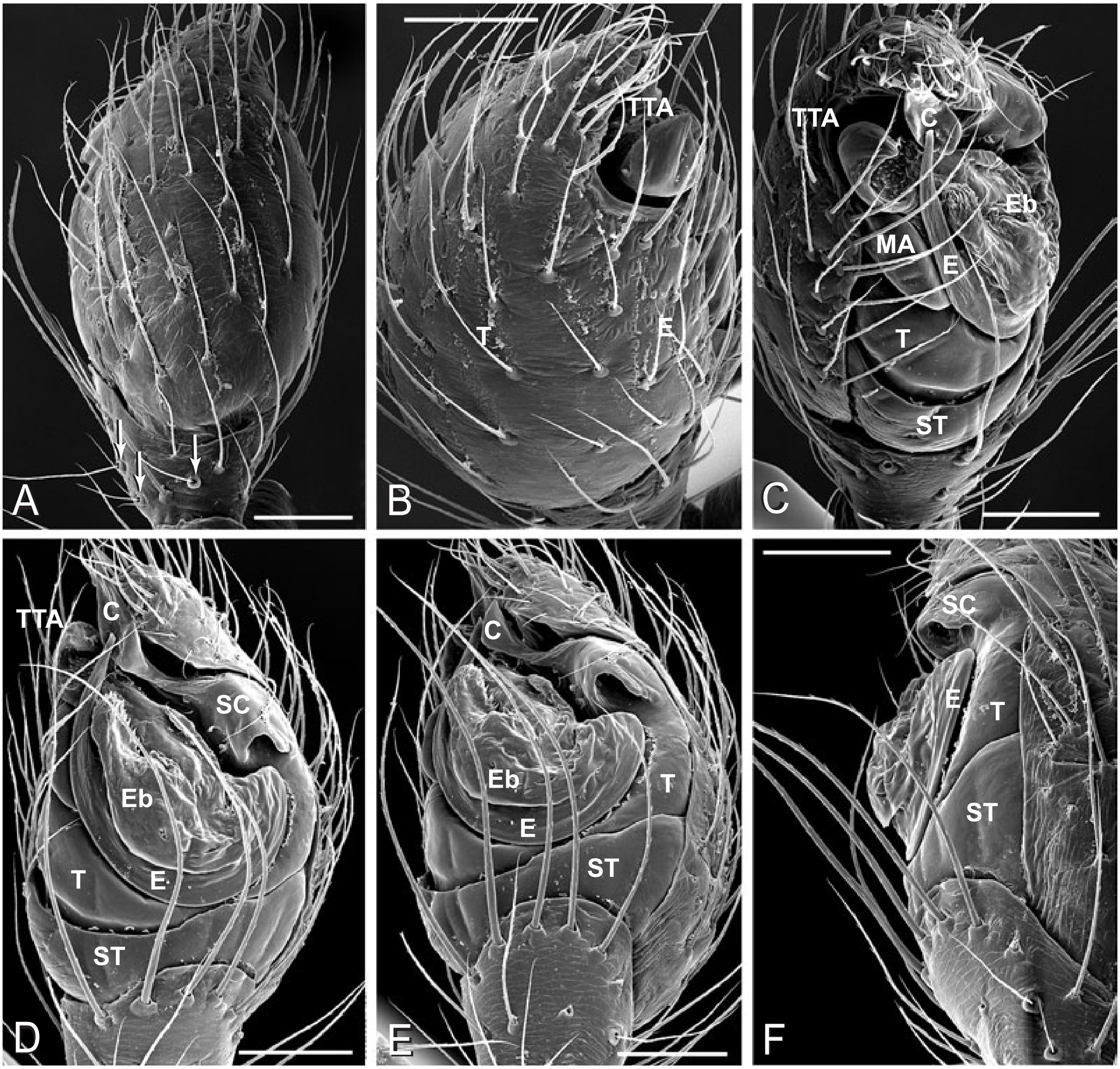

Figure 52. *Anelosimus pantanal* male palp. A, dorsal, note three tibial trichobothria (arrows); B, apicomesal; C, mesal; D, ventral; E, ventrocaudal; F, ectal. Scale bars: 100 µm.

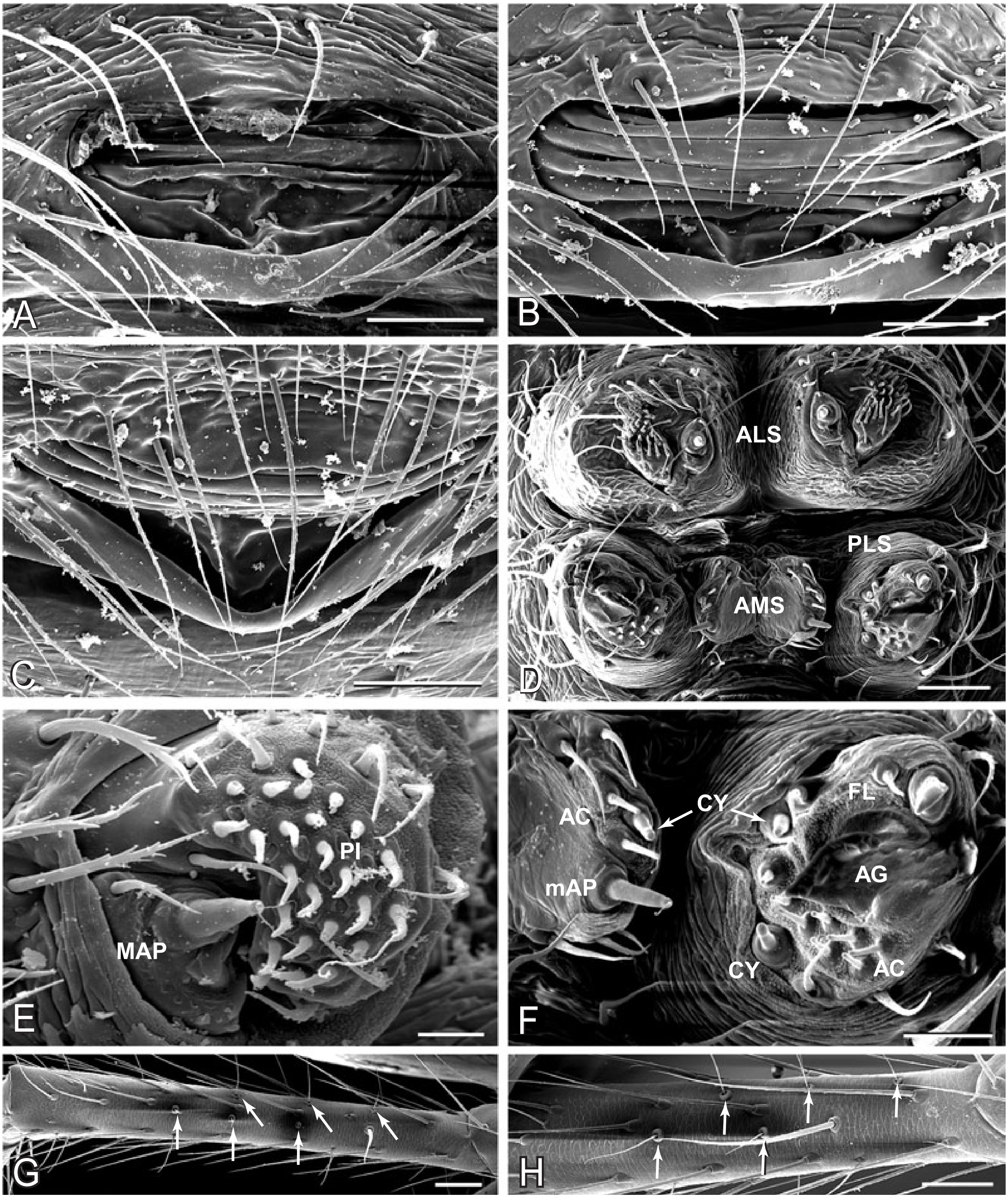

Figure 53. *Anelosimus pantanal*, female. A, epigynum ventral; B, epigynum, different specimen from same colony; C same, anterior view. D–F, spinnerets. D, all; E, anterior lateral spinneret, anterior is right; F, posterior lateral and posterior median spinnerets. G, fourth tibia, bearing six dorsal trichobothria (arrows); H, third tibia, bearing five dorsal trichobothria (arrows). Scale bars: A–D, 50 μm; E, 10 μm; F, 20 μm; G,H, 100 μm.

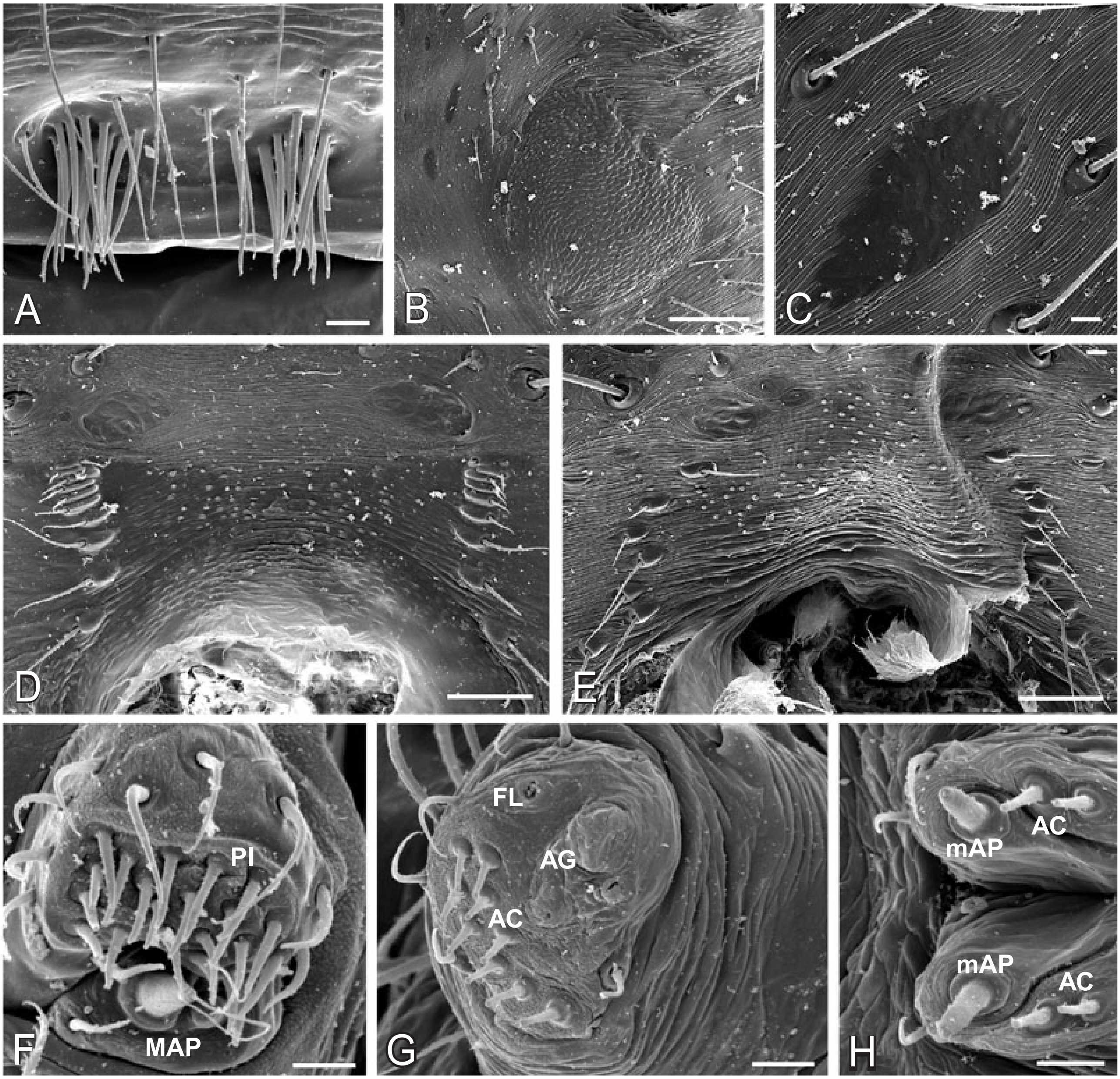

Figure 54. *Anelosimus pantanal*. A, epiandrous gland spigots; B, male booklung cover; C, male abdominal apodeme; D, male stridulatory pick row; E, female stridulatory pick row; F, anterior lateral spinneret; G, posterior lateral spinneret, right side; H, posterior median spinnerets, anterior is right. Scale bars: A,F–H, 10 µm; B,C, 100 µm; D, 50 µm; E, 20 µm.

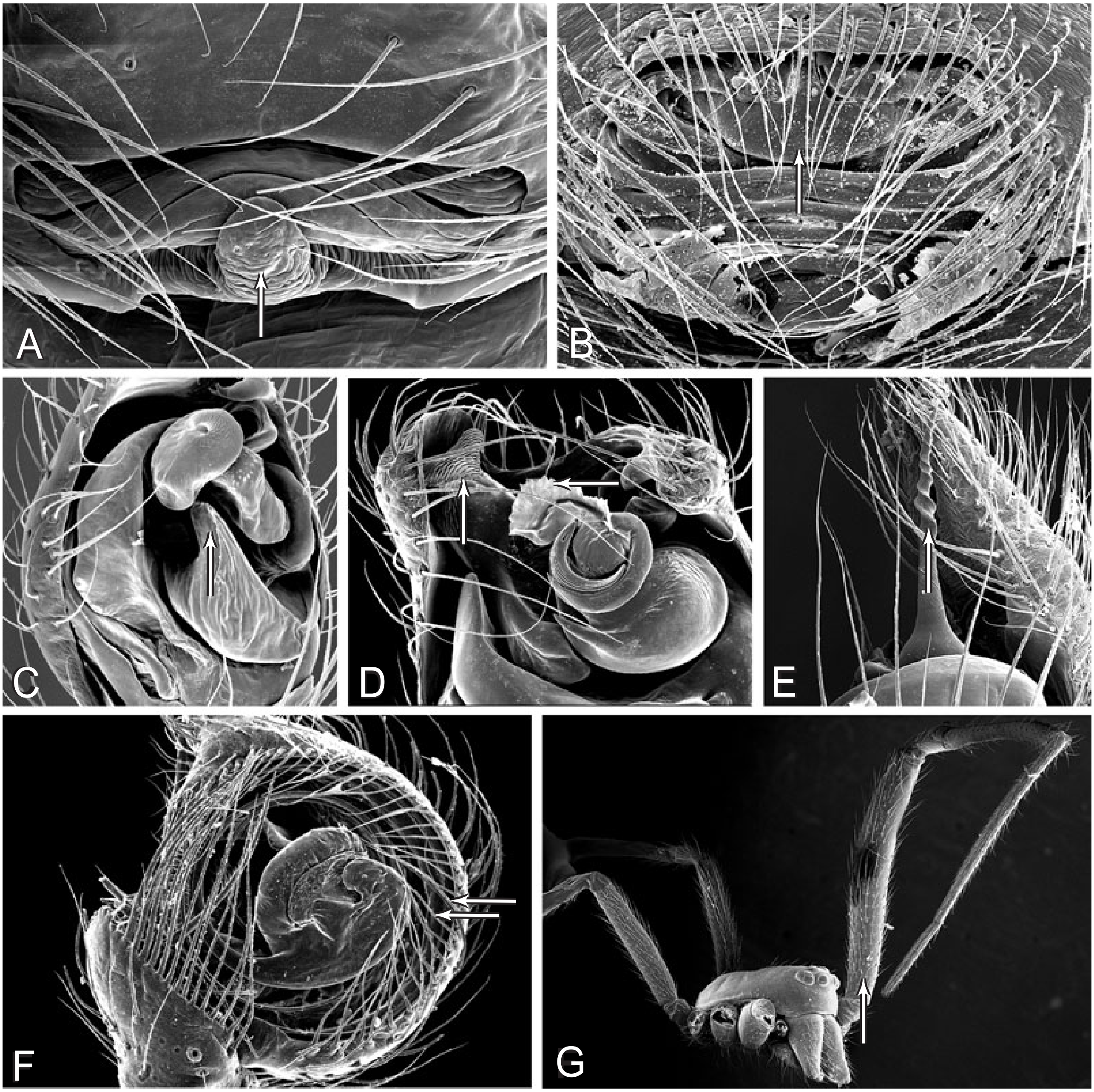

Figure 55. Characters I. A, *Anelosimus ethicus* epigynum, note scape (arrow); B, *Anelosimus may* epigynum, note anterior septum (arrow); C, *Enoplognatha ovata* male palp, note unmodified terminal portion of the theridiid tegular apophysis (arrow); D, *Argyrodes argyrodes* male palp, note simple terminal hook on the theridiid tegular apophysis (vertical arrow) with terminal ridges, and the unique *Argyrodes* conductor (horizontal arrow); E, *Anelosimus* sp. 1 (Australia), male palp with a 'corkscrew' embolus (arrow); F, *Kochiura aulica*, male palp, note cymbial marginal setae strongly bent towards the palpal bulb (arrows); G, *Anelosimus ethicus* male prosoma, note robust femur I (arrow) compared with femur IV.

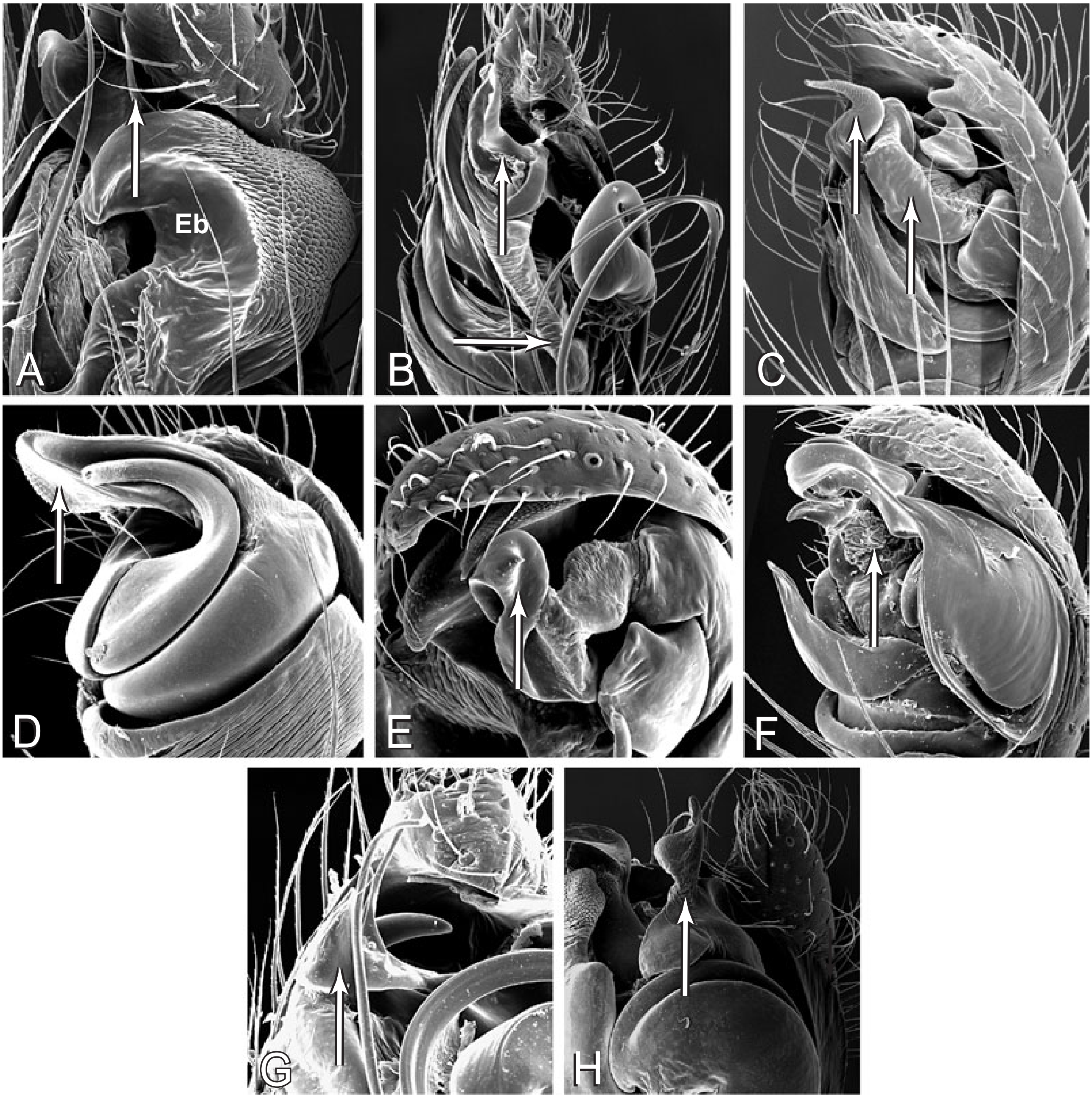

Figure 56. Characters II, conductor types (arrows). A, *Anelosimus* sp. 5 (South Africa), with simple round conductor; B, *Kochiura rosea*, with an elongated fan-shaped conductor; C, *Enoplognatha ovata*, with a complex, spiralling, and distally sclerotized conductor; D, *Achaearanea tepidariorum*, with a large, distinctly grooved conductor; E, *Theridion varians*, with a complex distally membraneous conductor; F, *Anelosimus rupununi*, with a small, membraneous, ball-like, conductor; G, *Anelosimus biglebowski*, with a simple, subtriangular, conductor; H, *Anelosimus octavius*, with a 'cup-shaped' conductor, a synapomorphy of the sclerotized copulatory duct clade and the *analyticus* group.

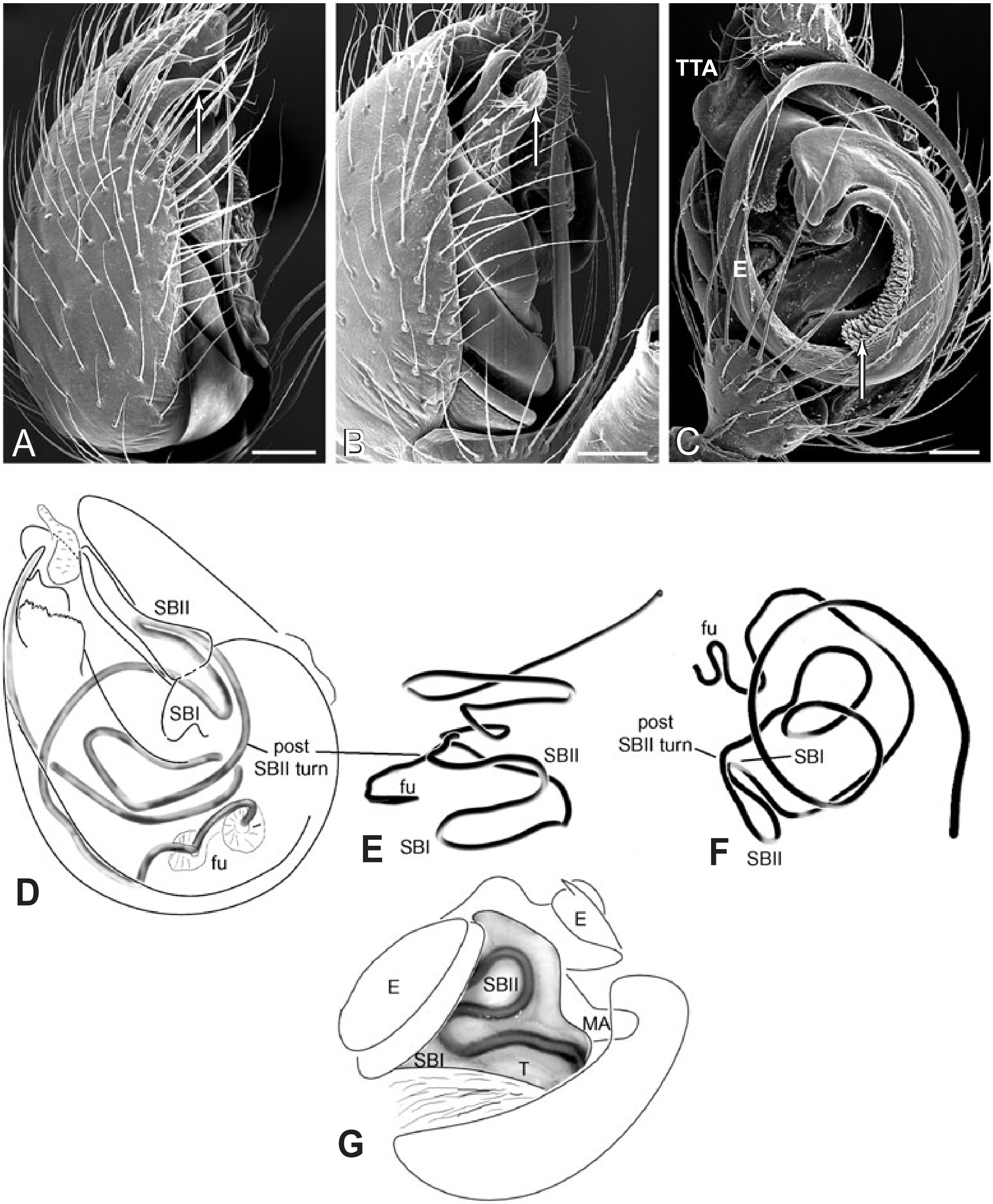

Figure 57. Characters III. A, *Anelosimus nelsoni*, note a finger-shaped lower branch of the theridiid tegular apophysis hook (arrow); B, *Anelosimus nigrescens*, note a blade-like lower branch of the theridiid tegular apophysis hook (arrow); C, *Anelosimus ethicus*, with a small, barely separate embolic division b (arrow); D, *Anelosimus baeza* male palp, ventral view, showing the sperm duct trajectory in the tegulum relative to position of sclerites; E, *Anelosimus eximius*, a schematic view of the sperm duct trajectory from ectal view (view as in G), F, *Anelosimus eximius* from above; G, *Anelosimus baeza* ectal view, showing switchbacks I and II.

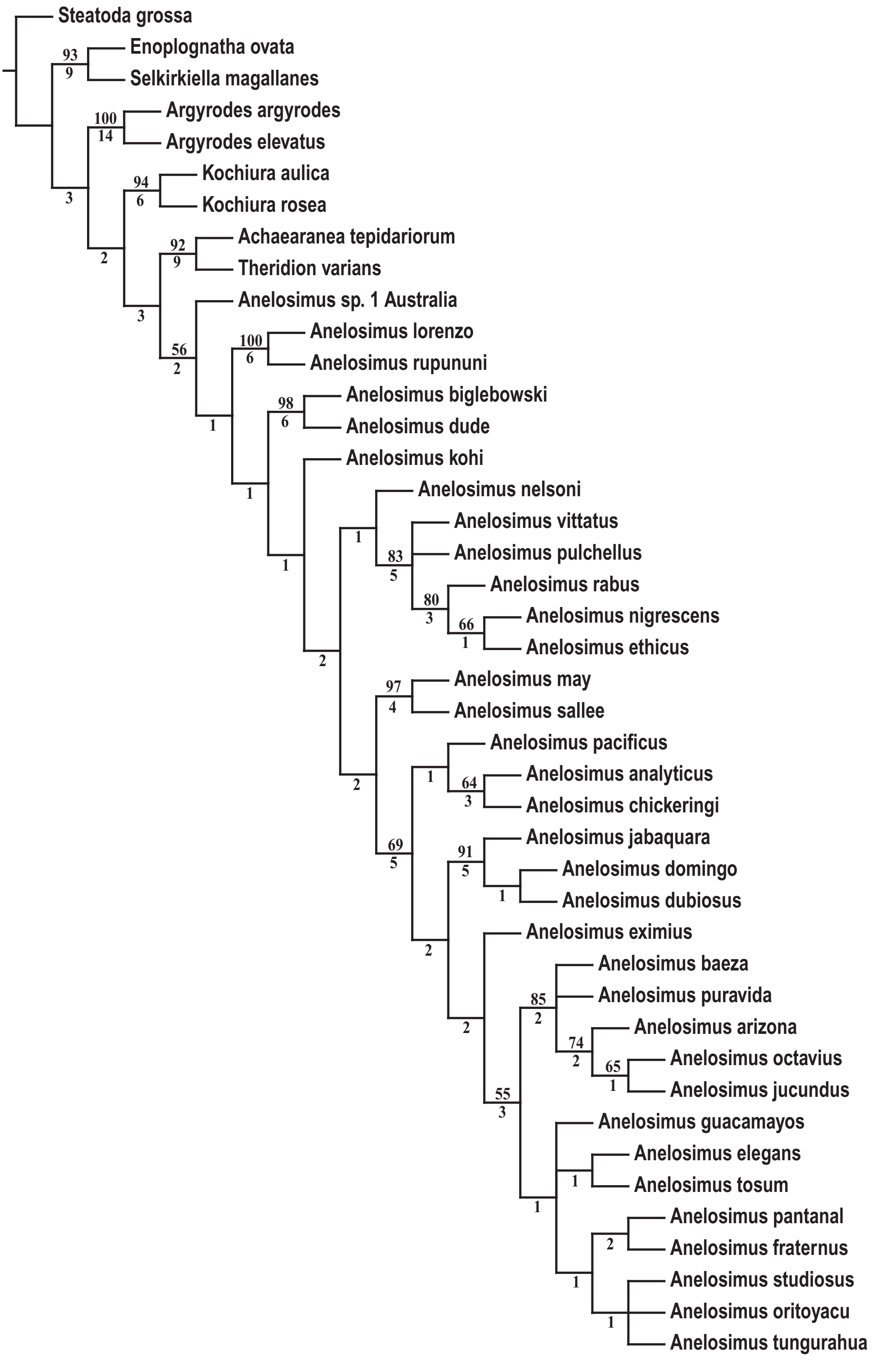

Figure 58. A strict consensus of the two most parsimonious cladograms (L = 298, CI = 58, RI = 88). Numbers below branches indicate Bremer support, while those above branches are bootstrap values (above 50%); parsimony jackknife scores were nearly identical to the bootstrap scores and are not shown.

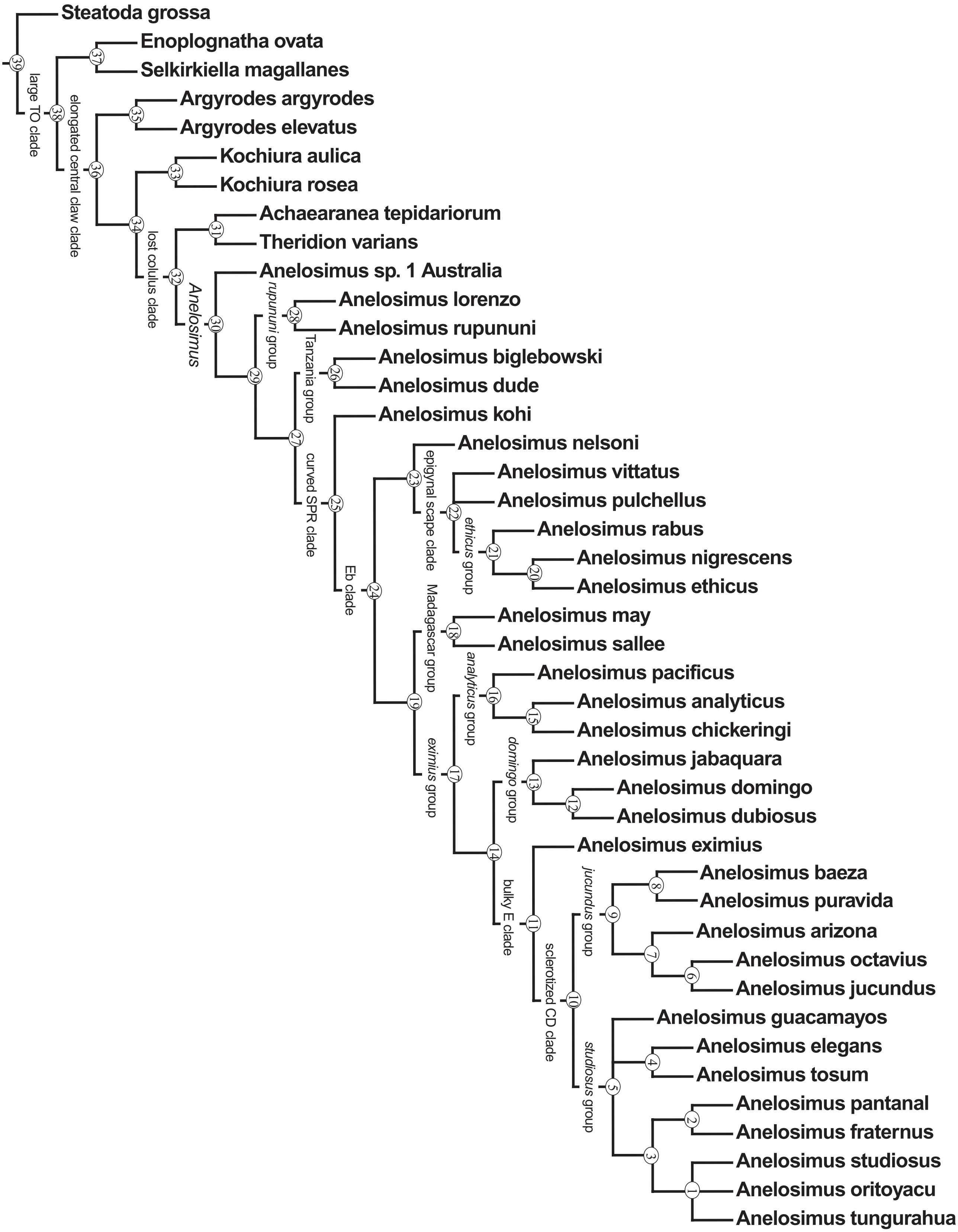

Figure 59. The preferred phylogeny with informal clade names and clade numbers in circles at the nodes.

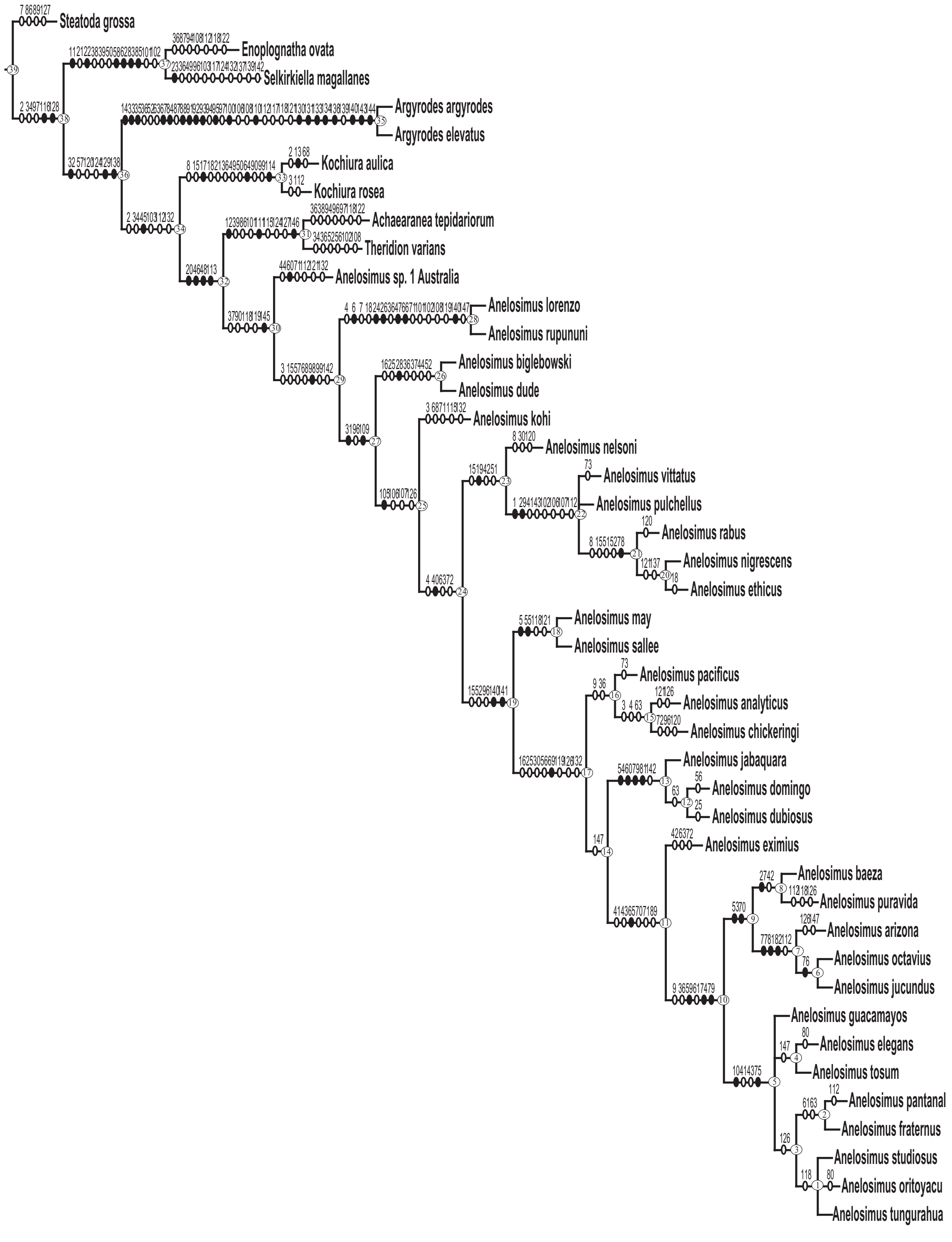

Figure 60. Character optimization on the preferred phylogeny, with clade numbers in circles at the nodes. Numbers above branches indicate characters changing on that node, filled circles indicate characters with perfect fit to the cladogram. All changes are shown; ambiguous character optimization was generally resolved in favour of parallel losses, over parallel gains of structures (see Methods).

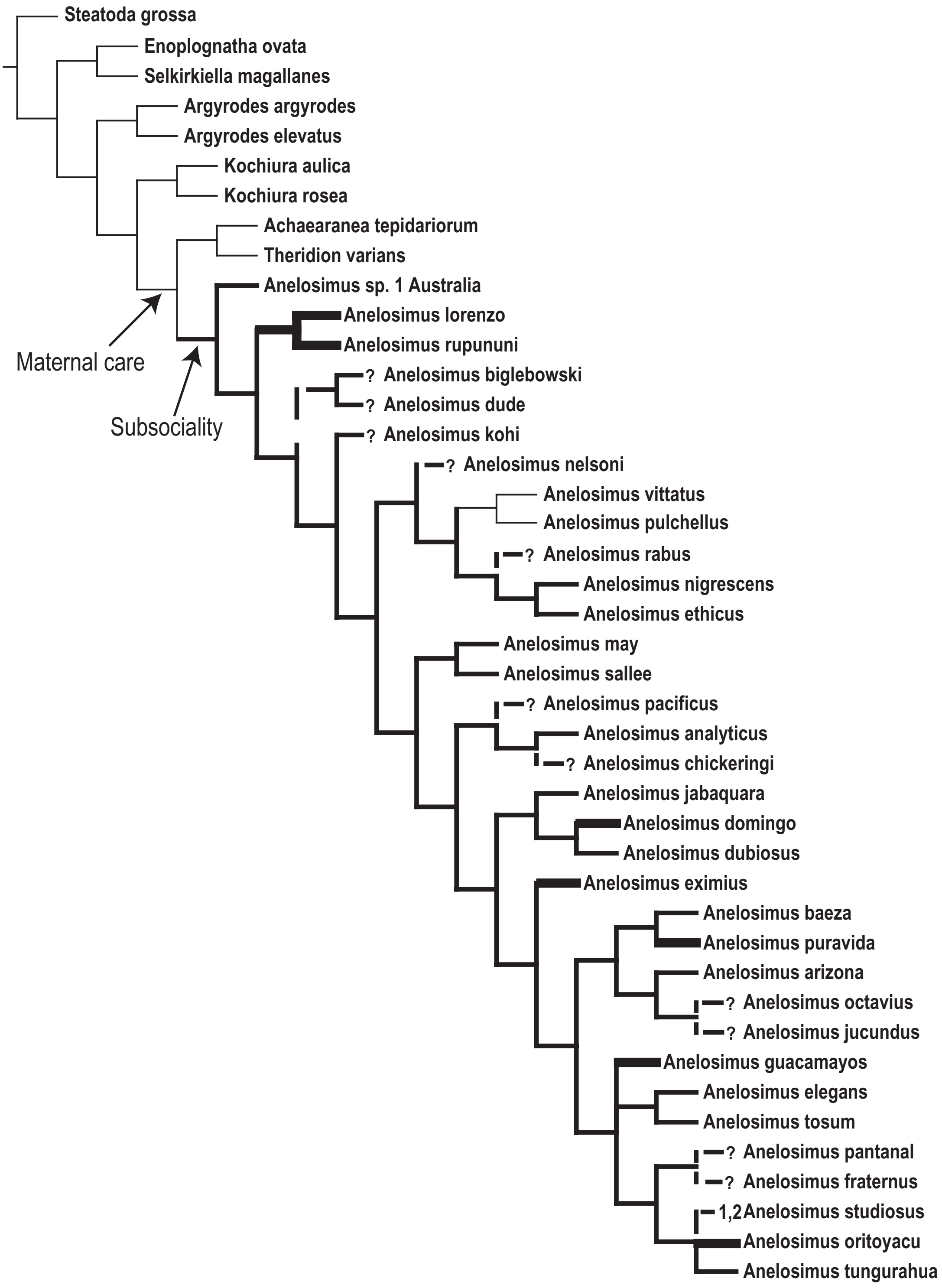

Figure 61. The evolution of sociality. Three categories, solitary (thin lines), subsocial (intermediate lines) and social (thick lines) are mapped on the preferred phylogeny. Question marks indicate unknown behaviour; broken lines indicate ambiguous optimization, '1,2' indicate polymorphism. Subsociality evolved at the node leading to *Anelosimus*; sociality has arisen repeatedly; 7–8 origins are inferred within the genus (depending on interpretation of *A. studiosus*, which is polymorphic for this character). Sociality is always preceeded by subsociality (subsociality evolves at a more inclusive node), and subsociality in turn is preceeded by maternal care, which optimizes to the node leading to the lost *colulus* clade (see Agnarsson, 2004).

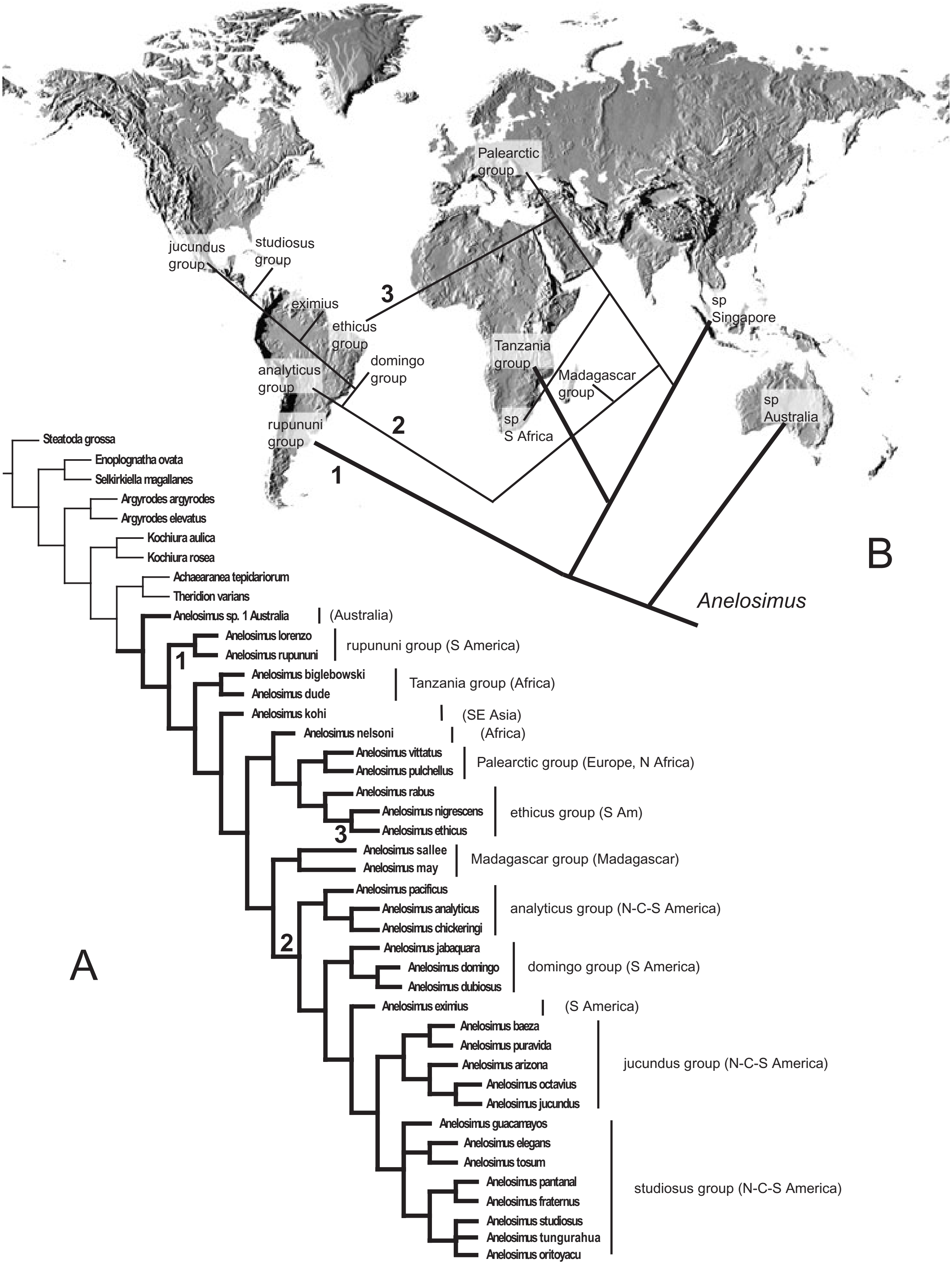

Figure 62. Biogeography. A, The geographical distribution of *Anelosimus* groups – numbers refer to the three lineages found in the Americas; B, taxa replaced with geographical regions on an area cladogram. The most basal *Anelosimus* occur in the Old World while three separate clades are found in the New World. Three independent dispersal events (numbers) appear to be the most parsimonious explanation of this distribution.

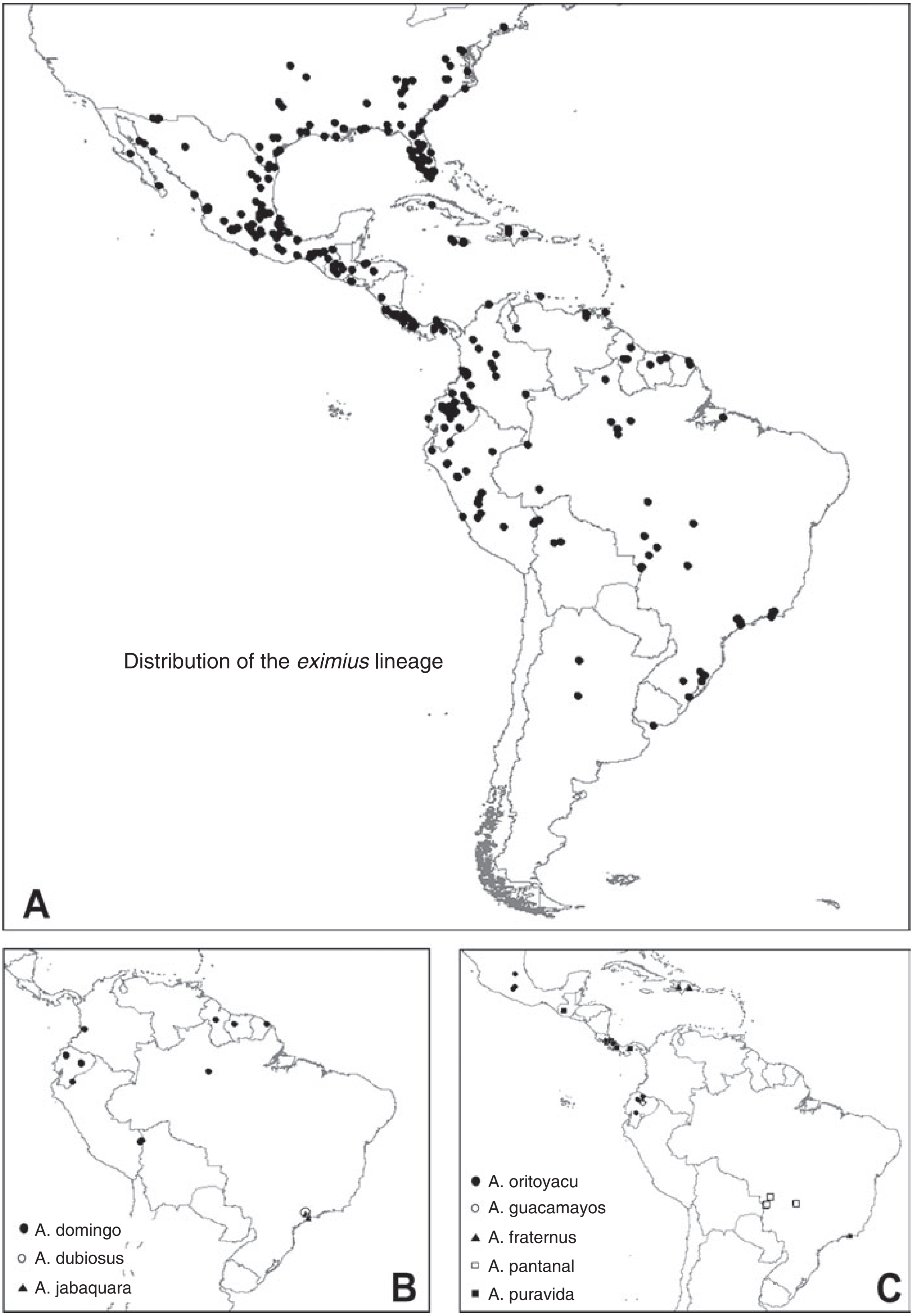

Figure 63. A, Distribution of the *Anelosimus* lineage; B, distribution of *A. domingo*, *A. dubiosus* and *A. jabaquara*; C, distribution of *A. oritoyacu*, *A. guacamayos*, *A. fraternus*, *A. pantanal* and *A. puravida*.

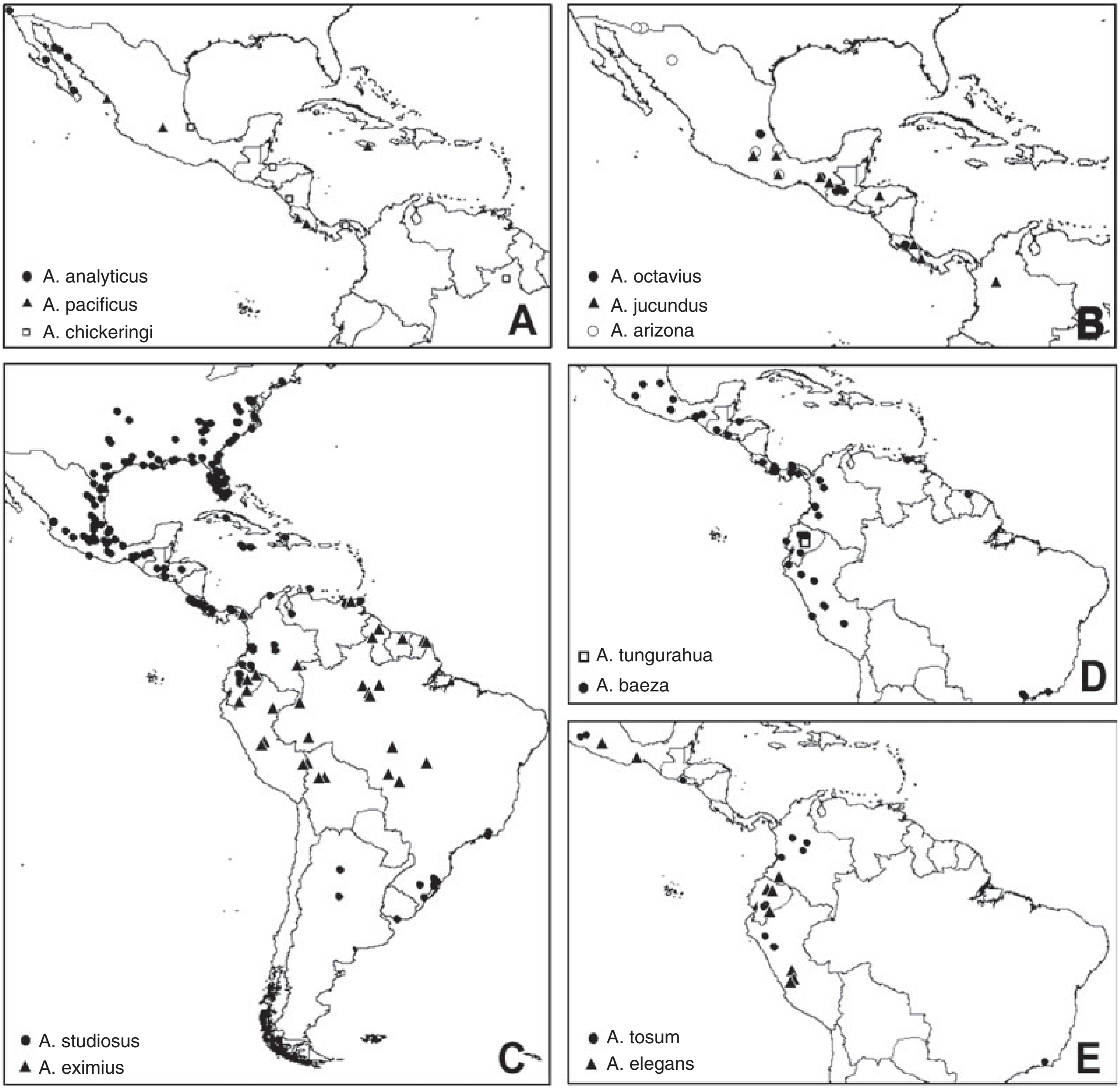

Figure 64. A, distribution of *A. analyticus*, *A. pacificus* and *A. chickeringi*; B, distribution of *A. octavius*, *A. jucundus* and *A. arizona*; C, distribution of *A. studiosus* and *A. eximius*; D, distribution of *A. baeza*; E, distribution of *A. tosum* and *A. elegans*.

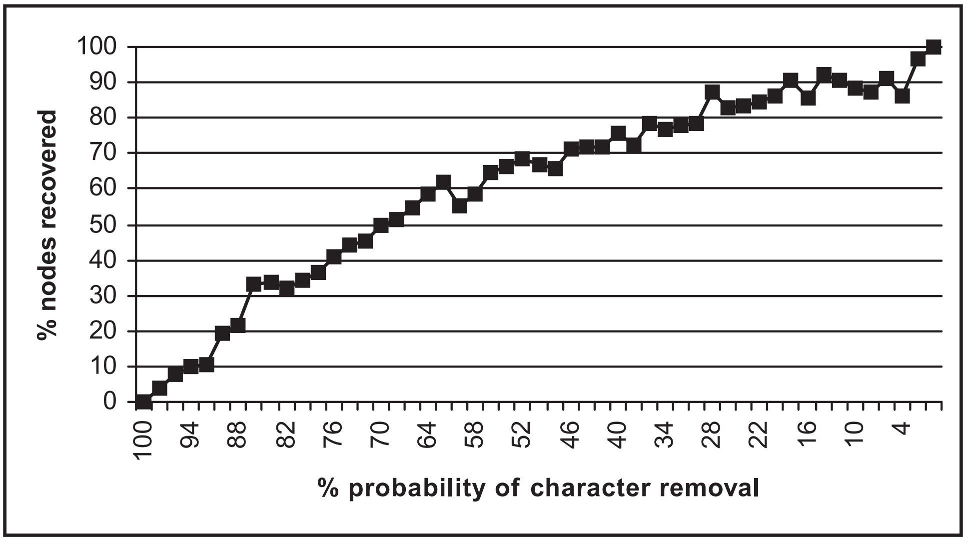

Figure 65. Results of the Continuous Jacknife Function Analysis.

Figure 66. *Anelosimus* webs, all from Ecuador. A, *A. studiosus*; B, *A. guacamayos*; C, *A. eximius*; D, *A. oritoyacu*; E, *A. domingo*.