Revision and phylogenetic analysis of American *ethicus* and *rupununi* groups of *Anelosimus* (Araneae, Theridiidae)

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Two species groups of the social spider genus *Anelosimus* are revised. The *ethicus* group contains six species found in South America, in an area ranging from the Guianas to southern Brazil and Argentina. Of these, *A. rabus* Levi, 1963, *A. ethicus* (Keyserling, 1884), and *A. nigrescens* (Keyserling, 1884) are redescribed, while *A. nigrescens* is removed from synonymy with *A. ethicus*. Three new species are described: *A. misiones* sp. nov., *A. sumisolena* sp. nov. and *A. inhandava* sp. nov. *Anelosimus ethicus* is reportedly either subsocial or solitary, while the behaviour of the other species in the group is unknown. The *rupununi* group contains two quasisocial species, *A. rupununi* Levi, 1956 and *A. lorenzo* Fowler & Levi, 1979, from the Caribbean and tropical South America. Both are redescribed here. A parsimony analysis of morphological characters provides support for the monophyly of both groups. In the phylogeny, subsociality optimizes to the base of *Anelosimus*, indicating that the common ancestor of the *ethicus* group was subsocial. Its members can thus be predicted to be subsocial, or secondarily solitary. Quasisociality arose *de novo* in the *rupununi* group, representing one of 6–7 independent origins in theridiids. Study of the biology of *Anelosimus* is important to advance our understanding of the evolution of sociality in spiders.

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Introduction

The cobweb spider genus *Anelosimus* (Theridiidae) is well known for containing numerous social species. Many of these have been intensively studied behaviourally (see Kullmann 1972, and Avilés 1997 for review), and the genus has played a key role in advancing our understanding of the evolution of spider sociality (e.g. Avilés 1993, 1997; Agnarsson 2002, 2004, in press; Agnarsson & Kuntner 2005; Bukowski & Avilés 2002; Powers & Avilés 2003). Research has been hampered by the notoriously complex taxonomy of the genus (F.O.P.-Cambridge 1902; Levi 1956, 1963; Agnarsson in press), augmented by the lack of recent revisionary work. Thus species identification is difficult and much diversity remains undescribed. Levi's (1956, 1963) revisions of American *Anelosimus* have been the only extensive taxonomic works on the genus, but covered only part of the regional diversity.

This paper is part of a series which sets out to clarify the taxonomy and phylogeny of *Anelosimus* worldwide (Agnarsson in press; Agnarsson & Kuntner 2005). According to the phylogenetic analysis of Agnarsson (in press), American *Anelosimus* belong to three isolated clades, with Old World species groups nesting in between them. One of these clades, the '*eximius* lineage', containing 20 social species, has been revised. Agnarsson & Kuntner (2005) have reported on social *Anelosimus* from Madagascar, the sister clade of the *eximius* lineage.

In this paper the two other American species groups are revised: the '*ethicus* group' with six species, and the '*rupununi* group' with two. This work completes the taxonomic revision and phylogenetic placement of all *Anelosimus* clades known to contain social species.

Materials and methods

For details of methodology see Agnarsson (2004, 2005, in press). Specimens were examined and illustrated using a Leica MZ Apo dissecting microscope and a Leica DMRM compound microscope, both with a camera lucida. Microscope images were taken using a Nikon DXM 1200 digital camera, and assembled with the Automontage software. Additional

photographs were taken on a Leo 1430VP scanning electron microscope.

All measurements are in millimeters and were made using a micrometer eyepiece. Prosoma and abdomen length and height were measured in lateral view, the width in dorsal view, all measured at the widest points. Leg segments were measured without detaching the legs from the prosoma and are thus approximations. The position of the metatarsal trichobothria and of the tarsal organs is expressed as linyphiid metatarsal trichobothria in Roberts (1985). Temporary mounts of palps were made in methyl salycilate (see Coddington 1983) and then photographed and drawn using a compound microscope with a camera lucida. Female genitalia were excised using microknives and sharp needles. The epigyna were then rendered transparent in methyl salycelate (Holm 1979). The internal genitalia were preserved in ethanol and photographed. All drawings were done in Adobe Photoshop and plates were assembled in Adobe Illustrator.

The data matrix in Agnarsson (in press) includes *A. ethicus*, *A rabus*, *A. rupununi* and *A. lorenzo*. Here the other four species of the *ethicus* group are added. Three new characters that reflect informative variation within the ethicus group have been added and scored for all taxa:

148. *Embolic division b orientation*: (0) normal, orientated towards palpal tip (Figs 1A, 2C); (1) orientated towards palpal tibia (Figs 7A,E, 9A).

149. *Post embolic division b notch*: (0) absent; (1) present.

150. *Embolus base – theridiid tegular apophysis relation*: (0) embolus base touching TTA; (1) embolus base surpassing TTA.

The character data were analysed in NONA (Goloboff 1993) through the WinClada shell (Nixon 2002) using parsimony with all characters unordered and equally weighted. Node support was estimated using Bootstrapping (Felsenstein 1985; Farris *et al*. 1996) and Bremer support (Bremer 1988, 1994). For further detail on phylogenetic methodology see Agnarsson (2004). Character coding for the four species was as follows:

Anelosimus nigrescens 101100010-1000100011---01000111100-0100112200000-00200100000001000010-010000010-0000000000000111101120110011100 1-0101100111110110010000111?????????010

Anelosimus misiones 101100010-1000100011---01000111100-0100112200000-000---00000001000010-010000010-0000000000000111101120110011101?1-0101100111110110010000111?????????110

Anelosimus inhandava ??????????1000100011---01000111100-????112200000-002001000 00001000010-010000010-0000000000000111101120110011101?1-01??10??1?11?11?0???0???1?????????111

Anelosimus sumisolena 101100010-??0000000011110 1?????????1??1-01011?01?1??01?0010000111????????????

The full matrix is available at http://www.theridiidae/cladogramsi.html, and on request from the author. The matrix will also be submitted to Treebase (treebase.com).

The new taxon names *A. arizona*, *A. baeza*, *A. elegans*, *A. guacamayos*, *A. may*, *A. octavius*, *A. oritoyacu*, *A. pantanal*, *A. puravida*, *A. sallee*, and *A. tungurahua* referred to in Fig. 16 follow Agnarsson & Kuntner (2005) and Agnarsson (in press); they are here disclaimed and made unavailable for nomenclatural purposes (ICZN Art. 8.3). Agnarsson & Kuntner (2005) and Agnarsson (in press) provide diagnoses, descriptions, type designations and formal synonymy for these species.

Abbreviations

Anatomical

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
AME	anterior median eyes
C	conductor
CY	cylindrical gland spigot(s)
E	embolus
Eb	embolic division b
MA	median apophysis
mAP	minor ampullate gland spigot(s)
SC	subconductor
ST	subtegulum
T	tegulum
TTA	theridiid tegular apophysis

Institutional

AMNH	American Museum of Natural History, New York, USA
BMNH	British Museum of Natural History, London, UK
CAS	California Academy of Sciences, San Francisco, USA
HDO	Hope Department of Entomology, Oxford University, UK
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium
MCP	Museu de Ciencias da PUCRS, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard, USA
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
NMV	Naturhistorisches Museum, Vienna, Austria

Results and discussion

Systematic treatment

Family Theridiidae Sundevall, 1833.

Genus *Anelosimus* Simon, 1891.

Anelosimus Simon, 1891, 60: 11. Type species: *Anelosimus socialis* Simon, 1891, by original designation [= *Anelosimus eximius* (Keyserling 1884)]. See Agnarsson (2004, in press) for taxonomic treatment of the genus.

The ethicus group

Diagnosis. The *ethicus* group can be separated from most other *Anelosimus* (except other members of the epigynal scape clade, see Agnarsson 2005) by a modification of the male stridulatory system, with a straight row of tightly spaced, numerous, stridulatory picks on the abdomen (Fig. 3G), and by the presence of a small epigynal scape (Figs 3A, 6A). Females can be separated from all other *Anelosimus* by copulatory ducts encircling spermathecae (Figs 1D,L, 7D,G–H). Males differ from other *Anelosimus* by a bulky, distally hooked theridiid tegular apophysis, and a simple short embolic division b (Figs 1A,B, 2A–C).

Description. Medium sized (2.50–4.50) *Anelosimus* spiders with characteristic abdomen pattern and coloration, a dark (red in live specimens) dorsal longitudinal band edged with white (Fig. 1G,N). Femur I noticeably robust compared to other femora, especially in the male (Figs 6F, 9D), male metatarsi with thickened setae ventrally (Fig. 1M). Males with a long, thin, embolus and a simple short embolic division b, hardly separate from the embolus (Fig. 2C). Conductor small and transparent (Fig. 4C), or absent. Female epigyna with ridged epigynal plates and a small ventral scape (Fig. 3A).

Phylogenetics. Unambiguous synapomorphies of the *ethicus* group (see below, bold numbers refer to characters, followed by state number) include: copulatory ducts encircling spermathecae (**8**–1), a bulky TTA (**51**–0), with a distal hook (**52**–0), and a simple short Eb (**78**–1).

Composition. Six species: *A. ethicus*, *A. nigrescens*, *A. misiones*, *A. sumisolena*, *A. inhandava* and *A. rabus*.

Distribution. The Guianas to southern Brazil and Argentina, mostly in lowland tropical forests.

Natural history. Almost no data exist on the natural history of the *ethicus* group species. Stejskal (1976) indicated that *A. ethicus* was subsocial. Stejskal's study mentioned several species, but doubts remain about their identification (see Agnarsson, 2005). Gonzaga & Vasconcellos-Neto (2001) found some specimens of *A. ethicus* in a survey of their study plot, and indicated that they were in individual webs (also observed by L. Avilés, pers. Comm.). Given the phylogenetic position of the *ethicus* group, it would be more parsimonious to predict subsocial than solitary behaviour in these species (see also Agnarsson 2004, in press; Agnarsson & Kuntner 2005).

Anelosimus ethicus (Keyserling, 1884) (Figs 1A–G, 2A–F, 3A–G)

Theridion ethicum. Keyserling, 1884: 44, pl. 2, fig. 24♂; Simon 1894, 1: 540; Petrunkevitch 1911, 29: 201; Roewer 1942, 1: 492; Mello-Leitão 1947, 6: 237.

Anelosimus ethicus. Levi, 1956: 416 (in part), fig. 30 (not 25, 28 or 29; see Taxonomic history).

Material examined. Male holotype from BRAZIL, Rio de Janeiro, August 1896 (NMV, coll. Musei Vindobonensis, Inv. no. 719, Koelbel's Nachlass, 1896.VIII.529). Other specimens: BRAZIL. Espírito Santo: Vitória [20°18′0″S, 40°18′0″W], vi.1954, *c.* 20 m, N. I. H. Krauss (1♀, AMNH), [IA40993]. Rio de Janeiro: Parque Nacional Tijuca, Paineiras [22°57′0″S, 43°16′0″W], 1.iv.1987, H. Levi (1♀, MCZ) [cf. IA080601]; Rio de Janeiro [23°54′0″S, 43°11′0″W], vii.1954, N. I. H. Krauss (1♀, AMNH), [IA40994]; São Conrado, Rio de Janeiro [22°57′0″S, 43°15′0″W], 29–31.iii.1987, H. & L. Levi (1♀, MCZ), [IA070401]. Rio Grande do Sul: Alto dos Casemiros, Cachoeira do Sul [30°2′0″S, 52°53′0″W], 3.i.1994, *c.* 61 m, R. G. Buss (3♂, 8♀, MCP), [IA40952]; same data but 26.ix.1992 (5♂, 2♀), [IA40955]; same data but 26.xi.1992 (1♀), [IA40966]; same data but 14.ix.1992 (1♀), [IA40969]; same data but 14.xi.1992 (6♀), [IA40971]; same data but 25.iv.1993 (3♀), [IA40984]; same data but 8.viii.1992 (1♂, 5♀), [MCP0501]; same data but 13.xii.1996 (1♂), [IA40934]; same data but 25.iv.1993 (1♂), [IA40960]; same data but 13.xii.1996 (2♂), [IA40978]; Campo Born, [29°34′0″S, 51°5′0″W], 26.x.1987, *c.* 50 m, C. J. Becker (1♀, MCP), [IA40987]; Capã Grande, Cachoeira do Sul [30°2′0″S, 52°53′0″W], 10.x.1992, *c.* 60 m, R. G. Buss (2♂, 4♀, MCP), [IA40933]; Capaneunho, Cachoeira do Sul [30°2′0″S, 52°53′0″W], 29.viii.1992, *c.* 60 m, R. G. Buss (2♂, 1♀, MCP), [IA40936]; Capão Novo, Capão da Canoa [25°45′0″S, 50°2′0″W], 17–18.vii.1993, 0–5 m, A. A. Lise (2♂, 1♀, MCP), [IA40937]; Cidreira [30°11′0″S, 50°12′0″W], 28.viii.1994, *c.* 0–5 m, L. Koch (2♀, MCP), [IA40968]; Guaíba [30°7′0″S, 51°19′0″W], 29.x.1994, *c.* 50 m, A. A. Lise *et al.* (2♂, 2♀, MCP), [IA40949]. Same data but 3.vi.1994 (9♂, 4♀), [IA40950]; same data but 3.x.1995 (1♀), [IA40965]; same data but 28.iv.1995, *c.* 50 m (1♀), [IA40970]; Lagoa do Leste, Osório, [29°53′0″S, 50°15′0″W], ii.1959, *c.* 60 m, S. Rosa (3♂, MCP), [IA40941]; Lami, Porto Alegre, [30°2′0″S, 51°13′0″W], 13.iv.1999, E. Cordeiro (4♀, MCP), [IA40954]; Pelotas, [31°46′0″S, 52°19′0″W], i.2000, 0–5 m, E. Rodrigues (2♂, 1♀, MCP), [IA40938]; same data but 16.xi.1991, 0–5 m, V. Wolff (1♀, MCP), [IA40975]; Porteira Sete, Cachoeira do Sul [30°2′0″S, 52°53′0″W], 31.x.1992, *c.* 60 m, R. G. Buss (1♂, MCP), [IA40951]; Santa Cruz do Sul [29°43′0″S, 52°25′0″W], 6.iii.1994, *c.* 150 m, R. Ott (1♀, MCP), [IA40986]; Santo Antônio da Patrulha [29°49′0″S, 50°32′0″W], 27.viii.1994, L. Koch (2♂, 1♀, MCP), [IA40980]; São Sepé [30°9′0″S, 53°35′0″W], 26.vi.1994, *c.* 130 m, I. Jungueira (1♂, MCP), [IA40939]; Tavares, [31°12′0″S, 51°1′0″W], 10.xii.1990, *c.* 100 m, N. Silveira (1♂, 3♀, MCP), [IA40943]; [30°5′0″S, 50°58′0″W], 2.xii.1994, *c.* 50 m, A. A. Lise *et al.* (1♂, 1♀, MCP), [IA40935]; Viamão [30°5′0″S, 50°58′0″W], 7.vii.1995, *c.* 50 m, A. A. Lise *et al.* (2♀, MCP), [IA40940]; same data but 5.xii.1995

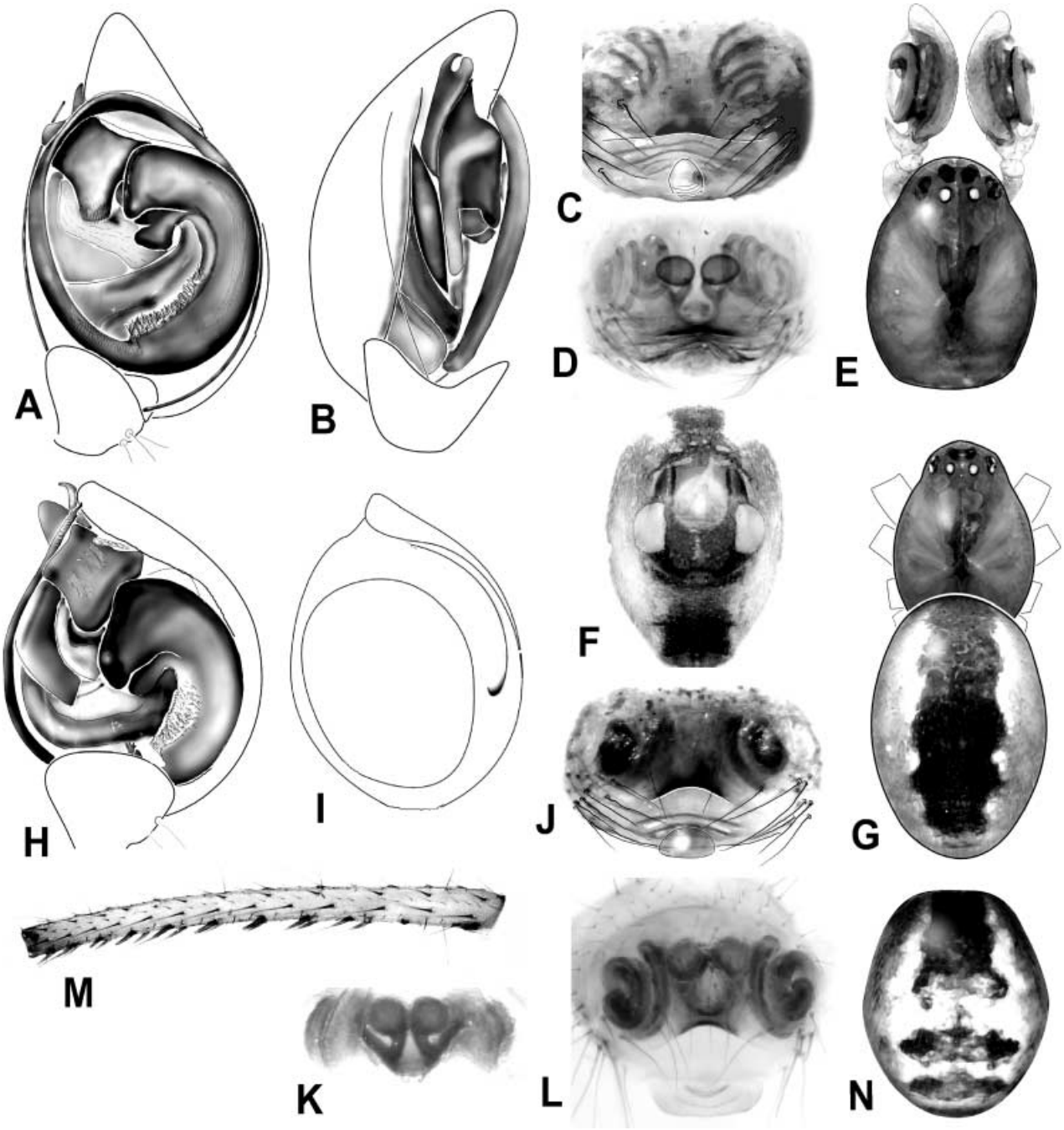

Fig. 1 A–G. *Anelosimus ethicus*. —A. Palp, ventral. —B. Palp, mesal. —C. Epigynum. —D. Digital photograph of internal epigynum. —E. Male prosoma. —F. Female abdomen, ventral. —G. Female habitus. H–N. *Anelosimus nigrescens*. —H. Palp, ventral. —I. Cymbium. —J. Epigynum. —K. Digital photograph of internal epigynum, caudal view. —L. Same, ventral view. —M. Male metatarsus I. —N. Female abdomen.

(2♀), [IA40964]; same data but 23.i.1996 (1♀), [IA40976]; same data but ii.1995, L. A. Chiaeadia (3♂, 13♀), [IA40948]; Xangrila, 24.ii.1993, A. A. Lise (1♀, MCP), [IA40956]. Santa Catarina: Bombinhas, Reserva Biologica Arvoredo, [27°7′0″S, 48°32′0″W], 5–6.x.1995, 0–5 m, A. A. Lise *et al*. (3♀, MCP), [IA40963]; Florianópolis, Lagoa do Peri [27°35′0″S, 48°32′0″W], 12.vi.2000, *c*. 30 m, A. L. T. Souza (2♂, 2♀, MCP), [IA40942]; Ilha do Arvoredo, [27°17′0″S, 48°21′0″W], 15–16.x.1993, A. A. Lise (1♂, 2♀, MCP), [IA40959]; Ilha Joao da Cunha, Porto Belo [27°10′0″S, 48°33′0″W], 7.xii.1992, *c*. 120 m,

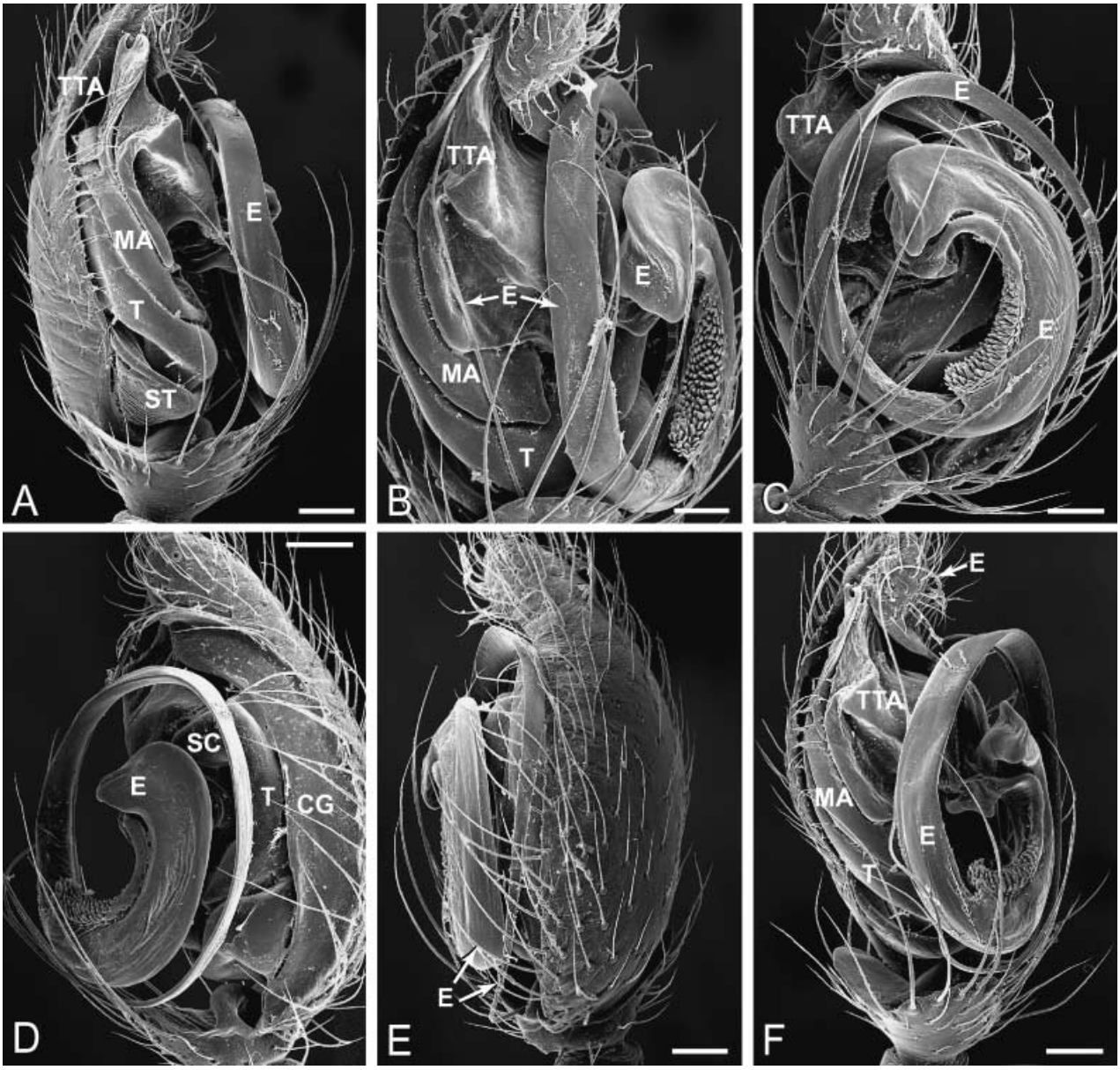

Fig. 2 A–F. *Anelosimus ethicus*, male palp. —A. Mesal. —B. Submesal. —C. Ventral. —D. Expanded subectal. —E. Ectal. —F. Expanded submesal. Scale bars: 100 μm.

R. G. Buss (1♂, 22♀, MCP), [IA40958]. São Paulo: São Paulo Botanical Garden [23°34′0″S, 46°37′0″W], 10.iv.1965, H. Levi & P. DeBiasi (1♂, MCZ), [IA071401]; same data but 1♀ [IA071601].

Etymology. Keyserling did not explain the species epithet, '*ethicus*' (Latin), meaning ethical.

Diagnosis. The male is readily distinguished from most other *Anelosimus* by the long embolus spiral, distinctly flattened medially (Figs 1B, 2A–F). Females are diagnosable by the numerous loops of the copulatory duct trajectory, readily seen through the cuticle (Fig. 1 C,D).

Redescription. Male (from Guaíba, Rio Grande do Sul, Brazil (30°06″S, 51°19″W), 3.vi.1994, A. A. Lise *et al.*). Total length 2.86. Prosoma 1.40 long, 1.11 wide, 0.78 high, dusky brown with cephalic region and border darker. Sternum 0.87 long, 0.74 wide, extending between coxae IV, brown. Abdomen 1.69 long, 1.19 wide, 1.40 high. Pattern as in female. Eyes subequal

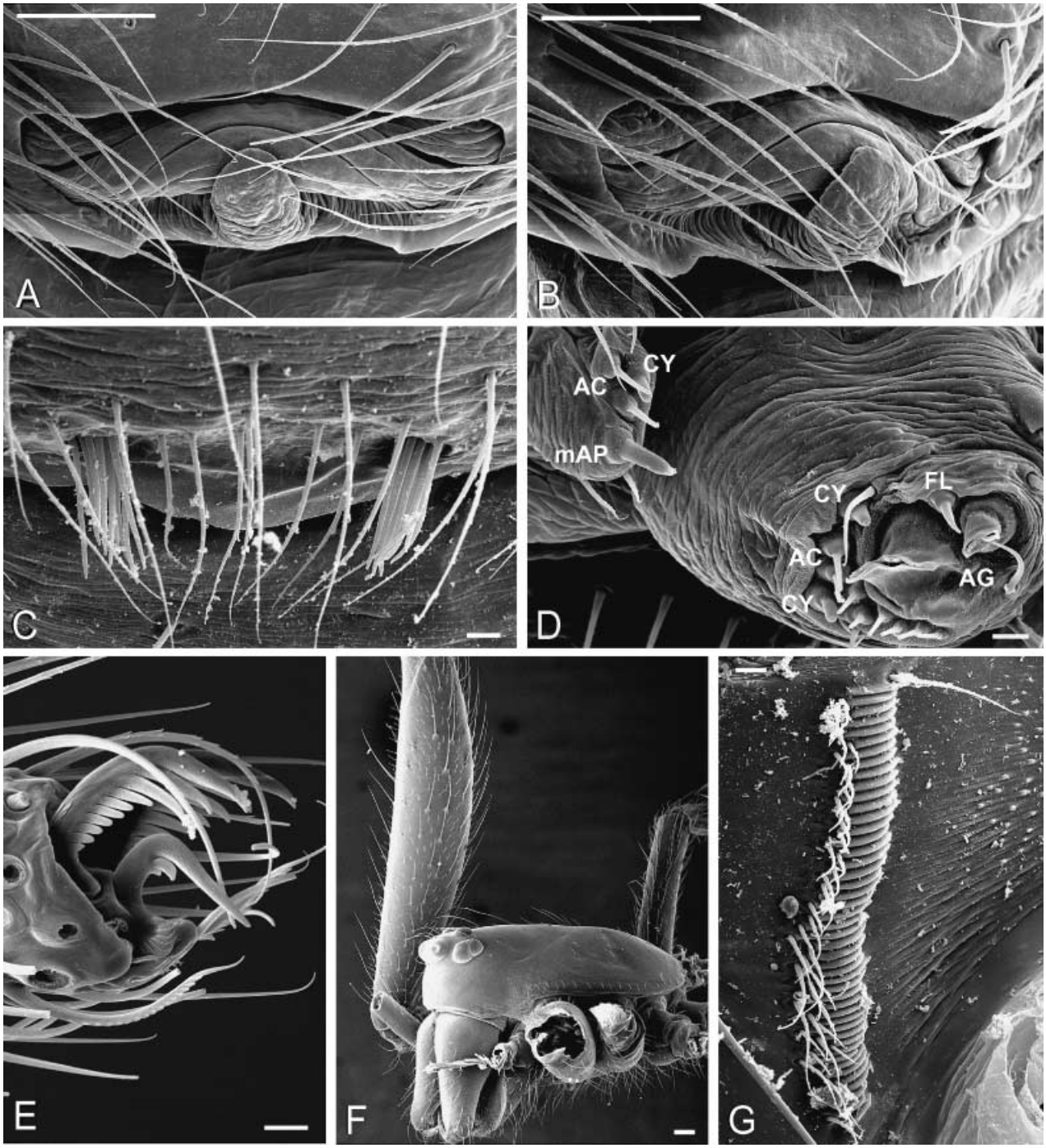

Fig. 3 A–G. *Anelosimus ethicus*. —A. Epigynum ventral. —B. Same ectal. —C. Epiandrous gland fusules. —D. Female PLS and PMS. —E. Male first tarsal claws. —F. Male prosoma and coxae I and IV. —G. Male stridulatory pick row. Scale bars: A, B, F = 100 μm, C–E, G = 10 μm.

in size, about 0.08 in diameter. Clypeus height about 2.8× one 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 1.33, tarsus 0.65. Femur I thick, about 4× longer than wide, about 1.75× thicker centrally than at base, metatarsus I about 14× longer than wide. Leg formula 1243. Leg base colour yellowish with distal tip of all segments darkened, most notably on leg I. Tarsal organs

central (0.50) on tarsi I, proximal (0.40–0.45) on II–IV. Three to six small trichobothria dorsally on all tibia, 3–5 on tibia I, five on tibia III. Trichobothria on metatarsi I–II slightly proximal (about 0.45), central (0.50) on III, absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palpal organ as in Figs 1A,B and 2A–F, conductor seemingly absent.

Female (locality data as male). Total length 3.58. Prosoma 1.43 long, 1.07 wide, 0.91 high, coloration as in male. Sternum 0.86 long, 0.69 wide, extending between coxae IV, brown. Abdomen 2.47 long, 1.90 wide, 2.06 high. Pattern as in Fig. 1G. Eyes subequal in size, about 0.09 in diameter. Clypeus height about 2.4× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.63, patella 0.59, tibia 1.37, metatarsus 1.24, tarsus 0.59. Femur I thick, but less so than in male, about 5× longer than wide, metatarsus I about 14× longer than wide. Leg formula 1243. Leg base colour yellowish with distal tip of all segments darkened, most notably on leg I, coloration less distinct than in male. Tarsal organs central proximal (0.40–0.45) on all tarsi. Four to six small trichobothria dorsally on all tibia, 5–6 on tibia I, five on tibia III. Trichobothria on metatarsi I–II central (0.5), slightly distal (0.50–0.55) on III, absent on metatarsus IV, distal (0.85) on palpal tarsus. Three dorsal trichobothria on palpal tibia. Epigynum as in Figs 1C,D and 3A,B.

Variation. Male total length 2.50–2.90, prosoma 1.17–1.43, femur I 1.63–1.95, female total length 3.19–3.58, prosoma 1.43–1.56, femur I 1.60–1.75. Abdomen pattern is quite variable; the dorsal band ranges from uniformly dark, as in Fig. 1G, to having a white rim forming horizontal bands through it as in Fig. 1N.

Distribution. Only known from southern Brazil (Fig. 15), and possibly Venezuela (Stejskal 1976).

Taxonomic history. Keyserling (1884: 44–45, fig. 24) described *Theridion ethicum* based on a male from Rio de Janeiro, Brazil. In the same publication he described *T. gymnasticum* (Keyserling 1884: 43–44, fig. 23) based on a female, also from Rio de Janeiro, and *T. nigrescens* (Keyserling 1884: 42–43, fig. 22) based on a female from Minas Gerais, Brazil. Levi (1956: 416, figs 25, 28–30) synonymized all three species and transferred them to *Anelosimus*. Levi used the name *A. ethicus*, arguing '[s]ince the determination of the male is most certain, the name *ethicus* is used rather than the names of females which have page priority' (Levi 1956: 416). Preference for a name based on a male is clearly desirable in *Anelosimus*. However, Levi did not draw the palp of the male type, but rather unfortunately a misidentified male belonging to *A. nigriscens* (Levi 1956, fig. 25). Levi illustrated both females; his figs 28 and 29 are *A. nigriscens*, and his fig. 30 is *A. ethicus*.

Natural history. Anelosimus ethicus has been described as subsocial (Stejskal 1976), but serious doubts remain about the identification of several of the species by Stejskal (see Agnarsson 2005). Other data (Gonzaga & Vasconcellos-Neto 2001; L. Avilés, pers. Comm.) suggest solitary behaviour.

Anelosimus nigrescens (Keyserling, 1884) (Figs 1H–N, 4A–F, 5A–F, 6A–F)

Theridion nigrescens. Keyserling, 1884a: 42, pl. 2, fig. 22, ♀; Simon 1894, 1: 540; Petrunkevitch 1911, 29: 201; Roewer 1942 1: 495; Mello-Leitão 1943, 37: 170.

A. ethicus. Levi, 1956 (in part), figs 25 and 28–29, ♂, ♀, misidentified (see taxonomic history).

Theridion gymnasticum. Keyserling, 1884: 43, pl. 2, fig. 23, ♀; Simon 1894, 1: 540; Petrunkevitch 1911, 29: 201; Roewer 1942, 1: 493. Synonymized by Levi 1956: 416–417.

Material examined. Female holotype from BRAZIL, Minas Gerais (HDO). Epigynum previously partially detached, removed and placed in a microvial. Female holotype of *Theridium gymnasticum* from BRAZIL, Rio de Janeiro (NMV, coll. Musei Vindobonensis, Inv. no. 722, Koelbel's Nachlass/1896.VIII.530./1). As pointed out by Levi (1963) the type specimen has been completely dried out and is shriveled. The epigynum is, nonetheless, faintly visible and recognizable. Other specimens: BRAZIL. Minas Gerais: Lavras, [21°14′0″N, 45°0′0″W], 8.xi.1978, W. Dan Frank (1♂, MCZ), [IA070601]; Minas de Serrinha, Diamantina, [18°14′0″S, 43°36′0″W], i–ii.1945, E. Cohn (1♀, AMNH), [IA40996]; same data but xii.1944 (1♀), [IA40526]; Ouro Prêto, [20°23′0″S, 43°30′0″W], iv.1954, 1160 m, N. L. H. Krauss (1♀, AMNH), [IA40991]. Rio de Janeiro: Leblon (Rio de Janeiro), [22°59′0″S, 43°13′0″W], 6.vi.1946, *c.* 0–5 m, H. Sick (1♀, AMNH), [IA40995]; Petrópolis, [22°31′0″S, 43°11′0″W], 2–5.xi.1945, 850 m, H. Sick (2♂, 3♀, AMNH), [IA40990]; Rio de Janeiro, [23°54′0″S, 43°11′0″W], ii.1946, 2–300 m, H. Sick (1♂, AMNH), [IA40989]; Teresópolis [22°24′0″S, 42°58′0″W], iii.1946, 900–1000 m, H. Sick (2♀, MCZ), [IA071101]; same data but iii.1946 (2♂, 4♀), [IA40992]. Rio Grande do Sul: Alto dos Casemiros, Cachoeira do Sul, [30°2′0″S, 52°53′0″W], 3.i.1994, *c.* 60 m, R. G. Buss (2♂, MCP), [IA40953]; same data but 26.xi.1992 (1♀), [IA40967]; same data but 14.xi.1992 (2♀), [IA40972]; same data but 25.iv.1993 (3♂, 3♀), [IA40961]; same data but 13.xii.1996 (3♂, 1♀), [IA40977]; Mariana Pimentel, [30°19′0″S, 51°35′0″W], 21.viii.1993, *c.* 150 m, A. Braui (1♂, MCP), [IA40983]; Pelotas, [31°46′0″S, 52°19′0″W], iii.1959, 0–5 m, C. Blezanko (1♀, AMNH), [IA40988]; Santo

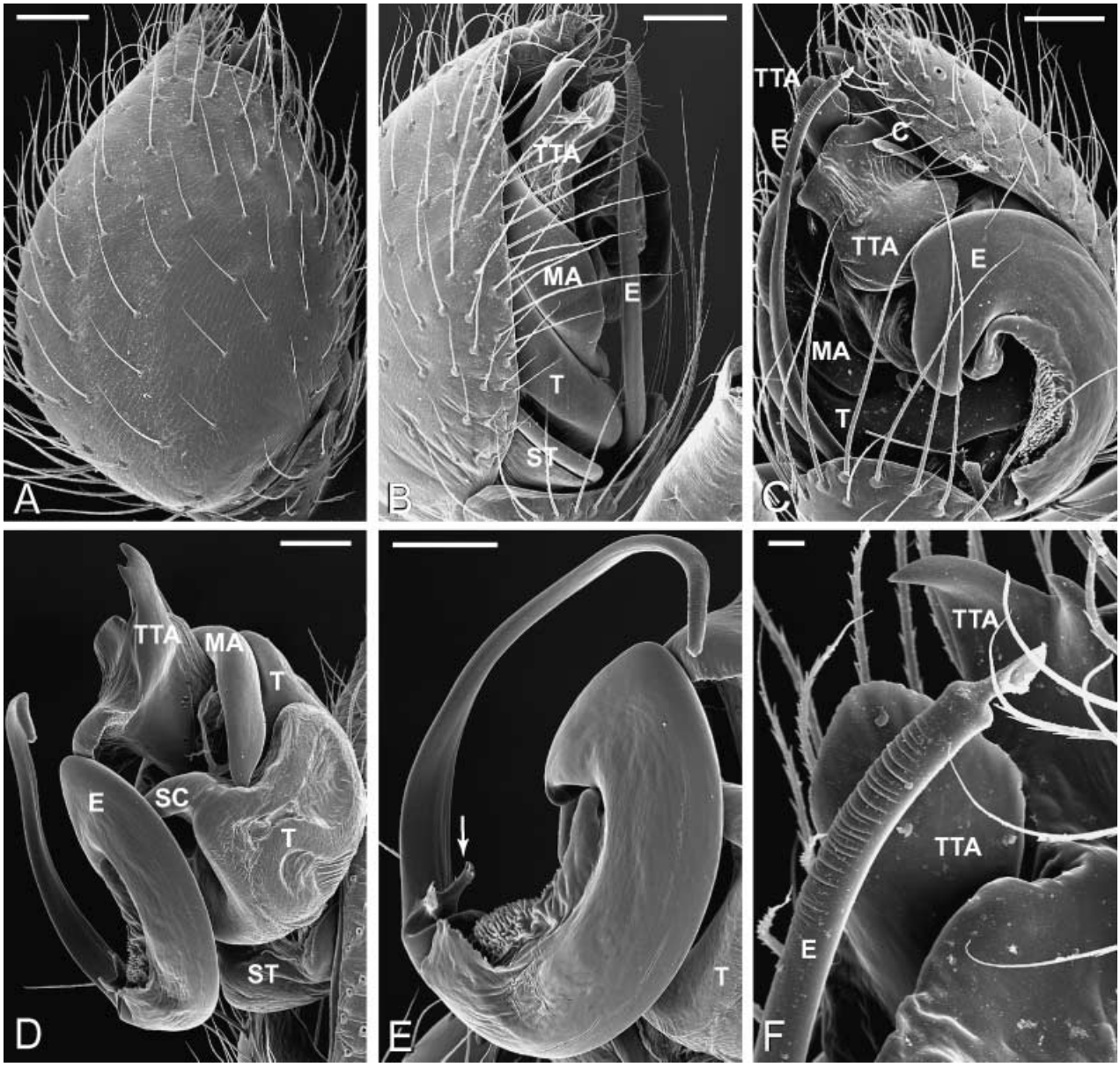

Fig. 4 A–F. *Anelosimus nigrescens*, male palp. —A. Dorsal. —B. Mesal. —C. Ventral. —D. Sclerites of the expanded palp; the view of the tegulum is as if looking through the ectal side of the cymbium. —E. Details of the embolus; note a conspicuous fork (arrow) located just after the spiral narrows abruptly. —F, embolus tip. Scale bars: A–E = 100 μm, F = 10 μm.

Antônio da Patrulha, [29°49′0″S, 50°32′0″W], 27.viii.1994, L. Koch (1♀, MCP), [IA40973]; Santo Antônio da Patrulha, [29°49′0″S, 50°32′0″W], 27.viii.1994, L. Koch (5♂, 2♀, MCP), [IA40979]; Taquari, [29°48′0″S, 51°51′0″W], 18.ix.1985, *c.* 50 m, D. Lorenaato (1♀, MCP), [IA40981]; Viamão, [30°5′0″S, 50°58′0″W], 17.x.1995, *c.* 50 m, A. A. Lise *et al.* (1♀, MCP), [IA40944]; same data but 23.i.1996, A. A. Lise *et al.* (1♀, MCP), [IA40974]; same data but 7.x.1994 (1♀), [IA40982]. São Paulo: Jabaquara, Cidade São Paulo, [23°38′0″S, 46°37′0″W], 21.xii.1945, H. Sick (1♀, AMNH), [IA40578]; São Paulo Botanical Garden, [23°34′0″S, 46°37′0″W], 9.iii.1985, H. & L. Levi (1♀, MCZ), [IA071801]. [Label states only 'Brazil'] (1♂, NMNH), [IA40415]. French Guiana. Cheyenne Province: Near Camp Caimans, Monagnes Kaw, [4°33′0″N, 52°9′0″W], 8.viii.1988, 100–300 m, S. Marshall (1♀, NMNH), [IA1110]. TRINIDAD. St. George Co. Arima Ward, Blanchisseuse Road, Radio Station (10°43′0″N, 61°18′0″W), 6.ii.1984, 600 m, J. Coddington (1♀, NMNH), [IA40412].

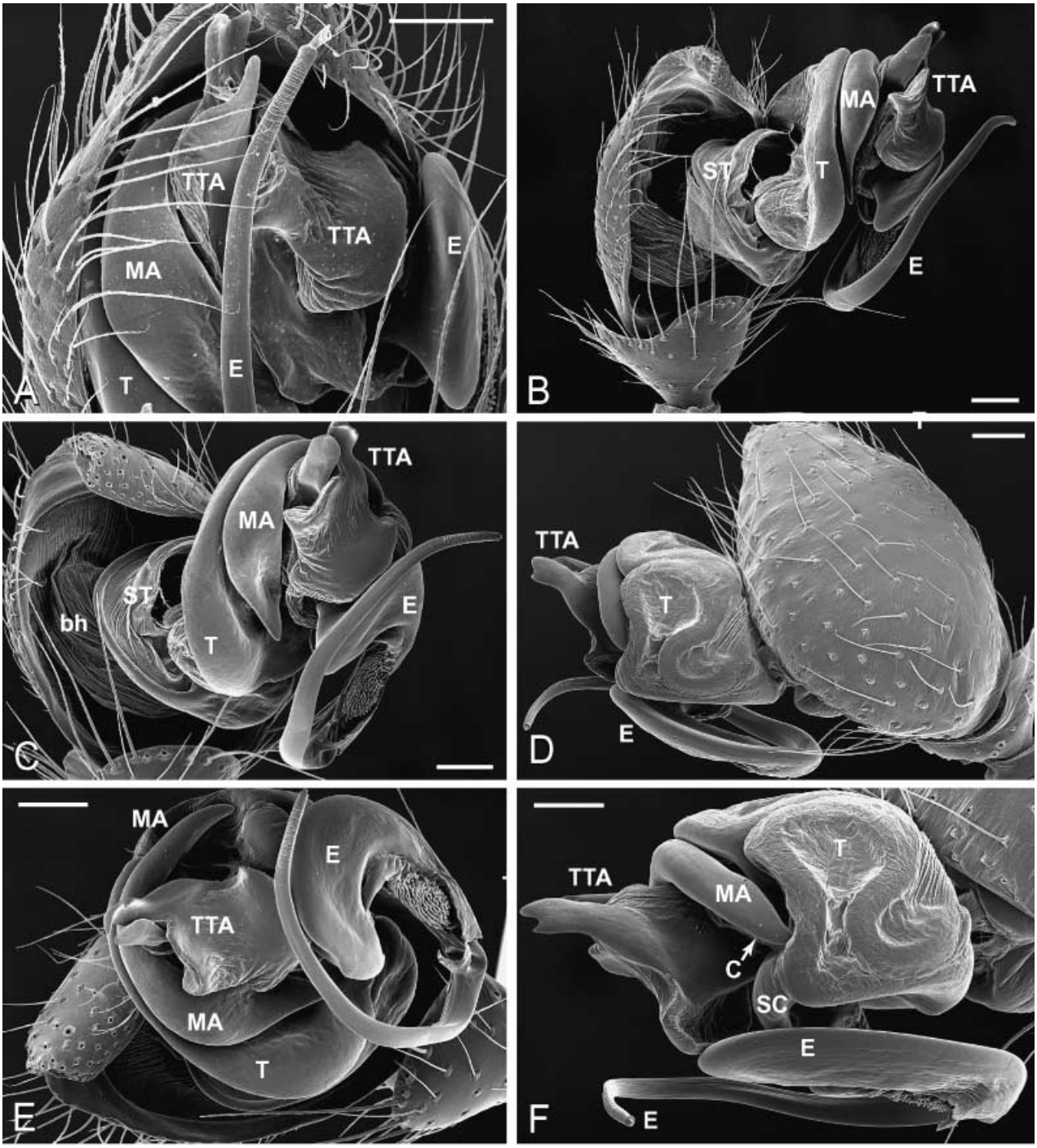

Fig. 5 A–F. *Anelosimus nigrescens*, male palp II. —A. Details of sclerites in the unexpanded palp. B–F. Expanded palp, orientation given with respect to the cymbium. —B. Ventral. —C. Apical. —D. Dorsal. —E. Ectal. —F. Details of sclerites, the conspicuous ridges on the tegulum show a part of the trajectory of the sperm duct. Scale bars = 100 μm.

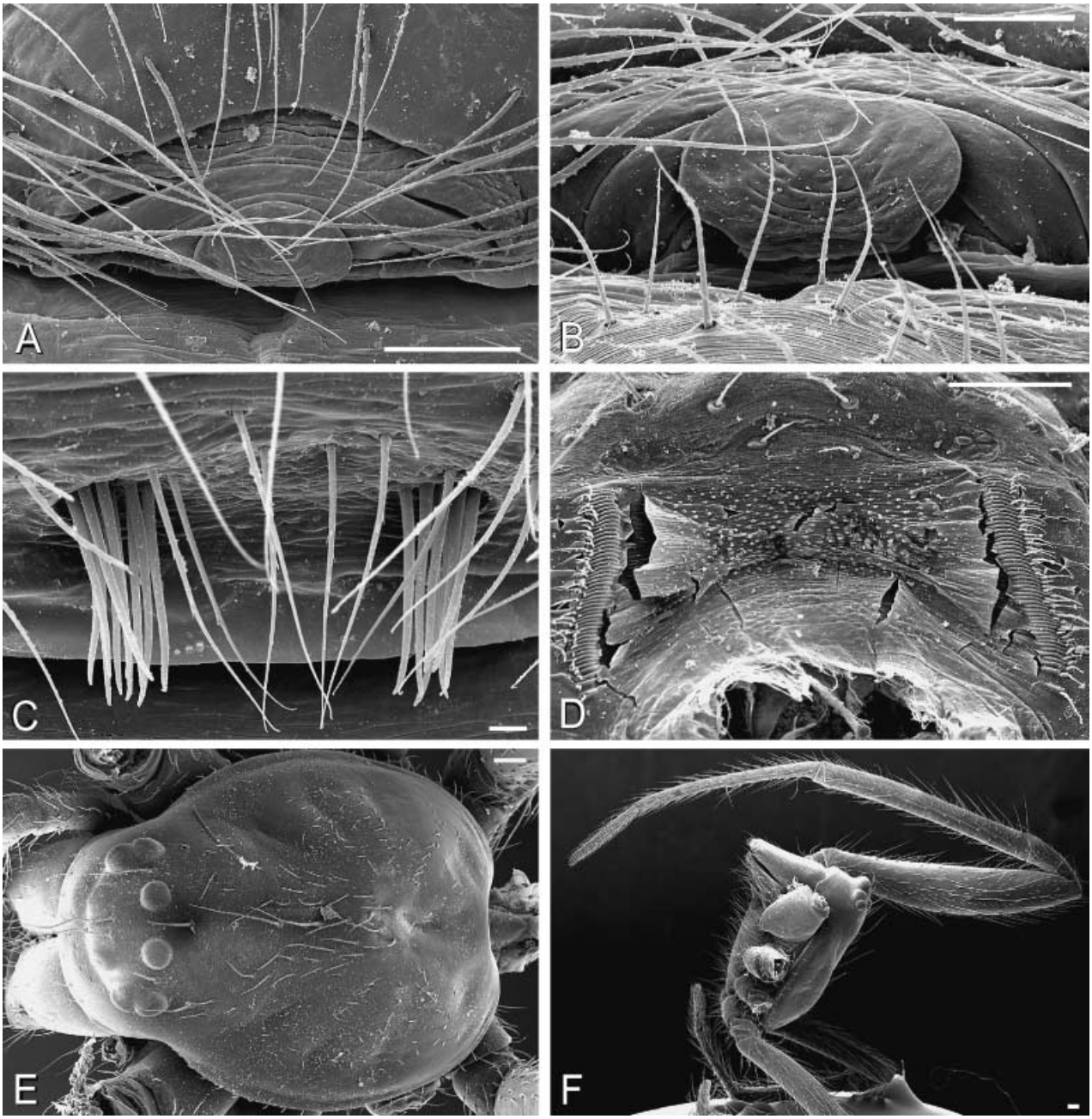

Fig. 6 A–F. *Anelosimus nigrescens*, III. —A. Epigynum ventral. —B. Same caudal, note the broad ventral scape. —C. Epiandrous gland fusules. —D. Male SPR. —E. Female prosoma dorsal. —F. Male prosoma with legs I and IV. Scale bars: A, D–F = 100 µm, B = 50 µm, C = 10 µm.

Etymology. Keyserling (1884) did not explain the species epithet; '*nigrescens*' (Latin) means blackish, and *A. nigrescens* is darker in appearance than most *Anelosimus* species.

Diagnosis. Males are readily diagnosable by a round embolus spiral, distinctly ridged distally (Figs 1H, 4E). Females can be diagnosed by the trajectory of the copulatory ducts, and their width, which is greater than in other species of the *ethicus* group (Fig. 1J–L). Females also differ from the similar *A. ethicus* by a broader scape (Fig. 6A).

Redescription. Male (From: Alto dos Cosemiras, Cachoeira do Sul, Rio Grande do Sul, Brazil (approx. 30°02′S, 52°53′W), 8.viii.1992, R.G. Buss). Total length 2.80. Prosoma 1.43

long, 1.19 wide, 0.92 high, orange. Sternum 0.91 long, 0.79 wide, extending between coxae IV, yellow to orange. Abdomen 1.76 long, 1.20 wide, 1.29 high. Pattern as in Fig. 1N. Eyes subequal in size, about 0.11 in diameter, AME slightly smaller than others. Clypeus height about 3× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.08, patella 0.65, tibia 1.98, metatarsus 1.56, tarsus 0.68. Femur about 5× longer than wide, distinctly thickened centrally, about 1.75× wider than basally, over 1.5× wider than femur II, metatarsus I about 16× longer than wide. Leg formula 1243. Leg base colour yellowish with distal half of femur I distinctly darkened, and tip of tibia I darker than base. Tarsal organs central or slightly distal (around 0.50–0.55) on tarsi I, proximal (0.40–0.45) on II–IV. Four to six small trichobothria dorsally on all tibia, 4–5 on tibia I, 4 on tibia III. Trichobothria on metatarsi I–II slightly proximal (about 0.45), central (0.50) on III, absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palpal organ as in Figs 1H,I, 4A–F, 5A–F.

Female (from Teresópolis, Rio de Janeiro, Brazil (22°24′S, 42°58′W), 900–1000 m, iii.1946, H. Sick). Total length 3.38. Prosoma 1.50 long, 1.17 wide, 0.96 high, brown, cephalic region dark brown. Sternum 1.01 long, 0.84 wide, extending between coxae IV, brown. Abdomen 2.02 long, 1.73 wide, 1.82 high. Pattern as in male. Eyes subequal in size, about 0.09 in diameter. Clypeus height about 2.7× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.85, patella 0.68, tibia 1.56, metatarsus 1.40, tarsus 0.65. Femur about 5× longer than wide, metatarsus I about 13× longer than wide. Leg formula 1243. Leg base colour yellowish, distal tip of all segments darkened, most notably on leg I, which like the male has distal half of femur I distinctly darkened. Tarsal organs central or slightly distal (around 0.50–0.55) on tarsi I, proximal (0.40–0.45) on II–IV. Numerous (3–6) small trichobothria dorsally on all tibia, 3–6 on tibia I, five 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 Figs 1K,L and 6A,B.

Variation. Male total length 2.60–3.25, prosoma 1.24–1.75, femur I 1.69–2.15. Female total length 2.73–3.95, prosoma 1.29–1.53, femur I 1.65–1.90. Often darker in appearance than many other *Anelosimus* (and darker than the sympatric *A. ethicus*), but prosoma coloration varies from dark brown to yellow. Abdomen pattern is quite variable; the dorsal band ranges from uniformly dark as in Fig. 1G, to the white rim forming horizontal bands through it as in Fig. 1N. The shape of the embolus base is variable, sometimes broader than in Fig. 1A. Males from Petrópolis, Brazil (850 m elevation) [IA40990] differ subtly from others (n = 2). The embolus base is placed slightly more distally, the embolic division b is slightly shorter, and the theridiid tegular apophysis is narrower. The females collected with those males (n = 3) are fairly typical *nigrescens*. The males may therefore belong to a different species, or possibly belong to *A. sumisolena*, known only from females in the same area (see below). However, more data are necessary to resolve this issue.

Distribution. Brazil, Guyana (Fig. 15), and possibly Venezuela (Stejskal 1976).

Taxonomic history. Keyserling (1884) described *Theridion nigrescens* based on a female from Minas Gerais, Brazil. Levi (1956: 416) synonymized it with *A. ethicus* based on a misidentified male (see Taxonomic history under *A. ethicus*). His figs 25 (male) and 28 and 29 (female) of '*A. ethicus*' are in fact of *A. nigrescens*.

Natural history. Unknown.

Anelosimus misiones* sp. nov. *(Fig. 7A–D)

Holotype. Male holotype from Argentina, 'Misiones e Corrientes' [approx. 28°3′S, 55°44′W], 11–21.iv.1989 (collected on the 'Garabi project') (MCP). The holotype is lacking metatarsus and tarsus I on the left side, left palp has been removed and placed in a microvial.

Paratype. Same data as for holotype, 1♀ (MCP). Female allotype lacks tibia, metatarsus and tarsus I on left side; abdomen has been separated from the prosoma and the epigynum removed and placed in a microvial.

Other material. Only known from type series.

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

Diagnosis. Differs from other *Anelosimus* of the *ethicus* group in having an embolus intermediate in length between that of *A. nigrescens* and *A. ethicus*, and an embolus base located relatively more distally on the tegulum than in other species (Fig. 7A,B). Females differ in having copulatory ducts intermediate in length between those of *A. nigrescens* and *A. ethicus*, and distinctly narrower than those of *A. sumisolena* (Fig. 7C,D).

Description. Male (holotype). Total length 2.60. Cephalothorax 1.37 long, 1.11 wide, 0.78 high, yellowish-brown, slightly darker in centre. Sternum 0.83 long, 0.69 wide, extending between coxae IV, light yellowish-brown. Abdomen 1.50 long, 1.20 wide, 1.19 high. Pattern as in other species of the *ethicus* group. Eyes subequal in size, about 0.07 in diameter. Clypeus height about 2.5× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I

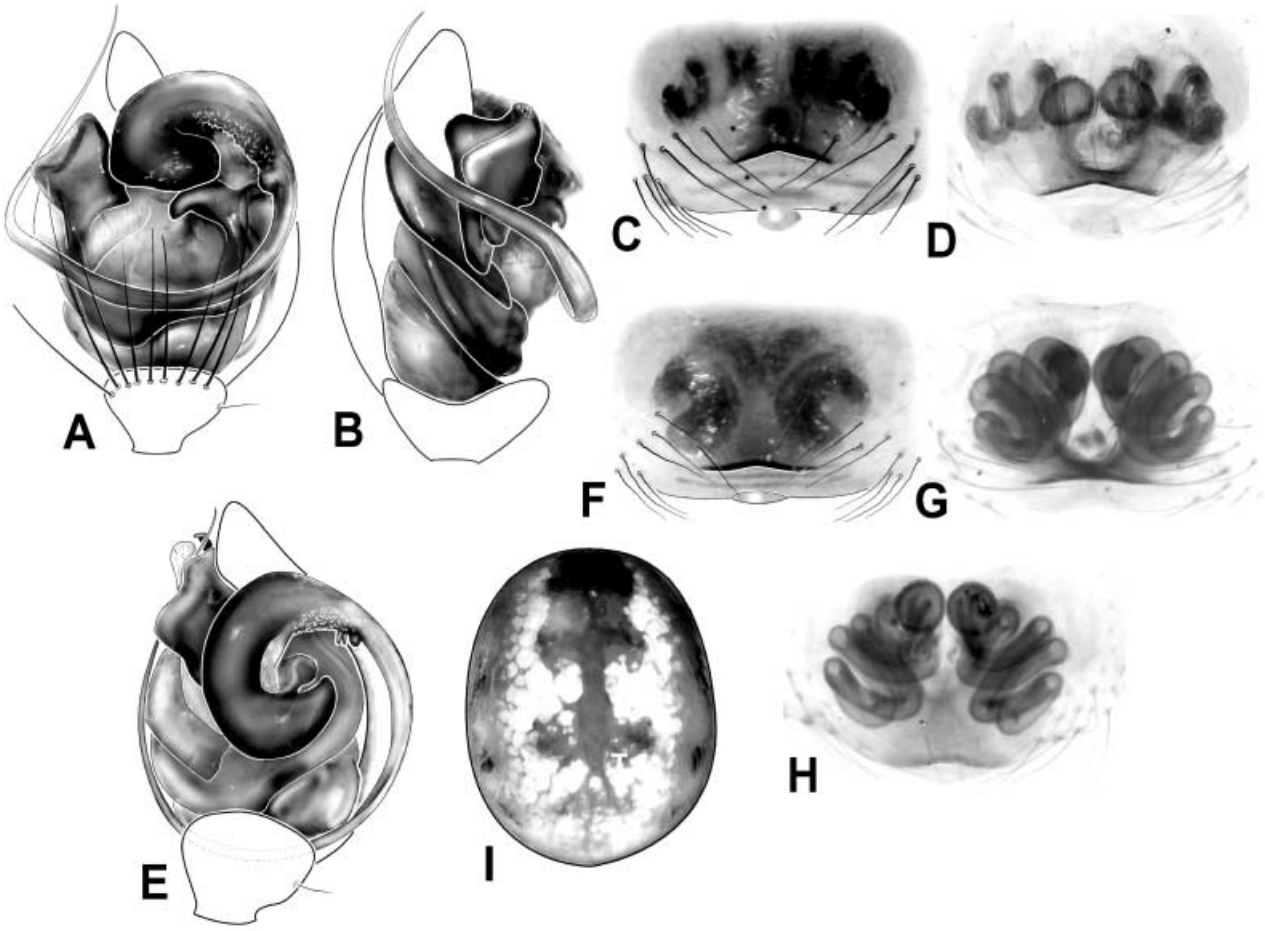

Fig. 7 A–D. *Anelosimus misiones*. —A. Palp, ventral. —B. Palp, mesal. —C. Epigynum. —D. Digital photograph of internal epigynum. —E. *Anelosimus inhandava* palp, ventral. F–I. *Anelosimus sumisolena*. —F. Epigynum. G, H. Digital photographs of internal epigynum. —G. Caudal. —H. ventral. —I. Female abdomen, dorsal.

femur 1.79, patella 0.59, tibia 1.53, metatarsus 1.37, tarsus 0.68. Femur I robust compared to femur II, about 5× longer than wide, metatarsus I about 8× longer than wide. Leg formula 1243. Leg base colour yellowish with distal half of femur I slightly darkened. Tarsal organs central distal (0.50) on tarsi I, proximal (0.40–0.45) on II–IV. Five small trichobothria dorsally on all tibia. Trichobothria on metatarsi I–II slightly proximal (about 0.45), near central (0.45–0.50) on III, absent on metatarsus IV. Two prolateral and one retrolateral trichobotrhia on palpal tibia. Palpal organ as in Fig. 7A,B.

Female (paratype). Total length 4.16. Cephalothorax 1.50 long, 1.29 wide, 0.96 high, yellowish-brown, cephalic area darker. Sternum 0.96 long, 0.86 wide, extending between coxae IV, yellowish-brown. Abdomen 2.73 long, 2.26 wide, 2.15 high. Pattern as in others of the *ethicus* group. Eyes subequal in size, about 0.08 in diameter. Clypeus height about 2× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.72, patella 0.65, tibia 1.46, metatarsus 1.30, tarsus 0.65. Femur I robust compared to femur II, about 5× longer than wide, metatarsus I about 7× longer than wide. Leg formula 1423. Leg base colour yellowish, distal portion of femur and tibia I darker. Tarsal organs proximal on all tarsi (0.40–0.45 on I–II, 0.35 on III–IV). Five to six small trichobothria dorsally on all tibia, six on tibia I, five on tibia III. Trichobothria on metatarsi I (0.35–0.40) and II (0.45) proximal, central on III, absent on metatarsus IV. Three trichobothria dorsally on palpal tibia. Epigynum as in Fig. 7C,D.

Variation. Only known from type material.

Distribution. Only known from type locality, which is very approximate (Fig. 15).

Natural history. Unknown.

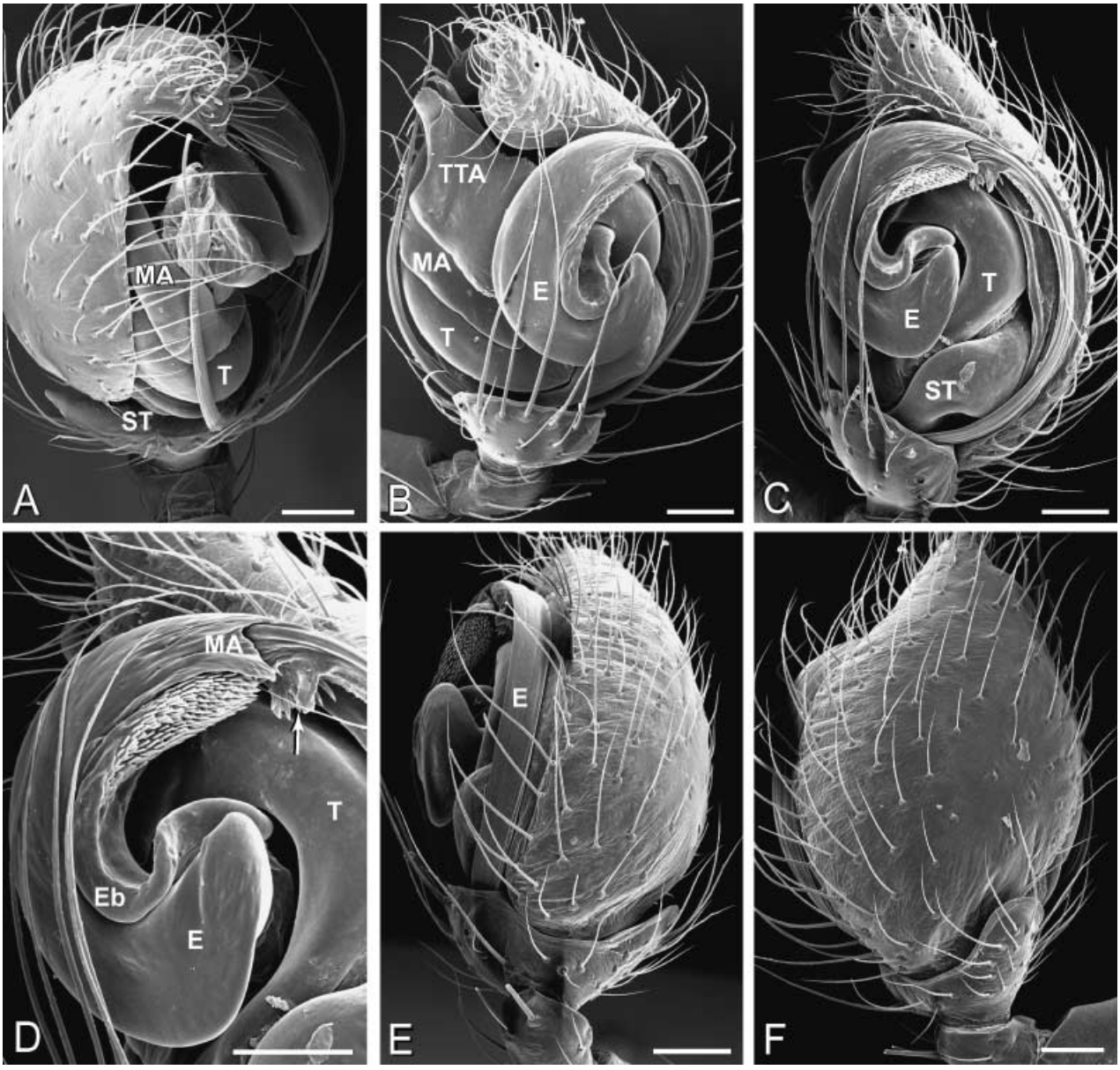

Fig. 8 A–F. *Anelosimus inhandava*, male palp. —A. Caudomesal. —B. Ventral. —C. Subectal. —D. Details of embolus. —E. Ectal. —F. Dorsal. Scale bars = 100 μm.

Anelosimus inhandava* sp. nov. *(Figs 7E, 8A–F)

Holotype. Male holotype from Brazil, Rio Grande do Sul: Rio Inhandava [approx. 27°35′0″S, 51°44′0″W], ii.1989 (MCP), [IA40957]. The left palp has been removed and placed in a microvial, and the abdomen is separated from the prosoma.

Other material. ARGENTINA. misiones: San Javier, [27°52′0″S, 55°7′0″W], 3–12.i.1989, *c.* 75 m, Garabi project (1♂, MCP), [IA40946]. BRAZIL. Rio Grande do Sul: Machadinho, [27°34′0″S, 51°39′0″W], ix.1988, *c.* 650 m (1♂, MCP), [IA40947].

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

Diagnosis. Can be diagnosed from other *Anelosimus* of the *ethicus* group by the shape and orientation of the embolus base (Fig. 7E).

Description. Male (holotype). Total length 2.80. Cephalothorax 1.43 long, 1.11 wide, 0.83 high, pale yellowish-brown. Sternum 0.83 long, 0.78 wide, extending between coxae IV, brown.

Abdomen 1.50 long, 1.17 wide, 1.34 high. Pattern as in others of the *ethicus* group. Eyes subequal in size, about 0.08 in diameter. Clypeus height about 2.6× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.95, patella 0.39, tibia 1.50, metatarsus 1.20, tarsus 0.46. Femur about 5× longer than wide, metatarsus I about 12× longer than wide. Leg formula 1243. Leg base colour pale yellowish with distal half of femur I slightly darkened. Tarsal organs proximal on all tarsi (0.45–50 on I) (0.40–0.45 on II) (0.34–40 on III–IV). Four to five small trichobothria dorsally on tibia, four on tibia III, five on I. Trichobothria on metatarsi I–II proximal (about 0.45), near central (0.45–0.50) on III, absent on metatarsus IV. Two prolateral and one retrolateral trichobotrhia on palpal tibia. Palpal organ as in Figs 7E and 8A–F.

Female. Unknown.

Variation. Male total length 2.60–2.93, prosoma 1.37–1.50, femur I 1.72–1.95. The holotype is very pale coloured, probably from having been stored in alcohol. The other specimens are slightly darker; the tips of the tibia and metatarsus I are darkened.

Distribution. Argentina and Brazil (misiones region and surrounding areas).

Natural history. Unknown.

Anelosimus sumisolena* sp. nov. *(Fig. 7F–I)
Holotype. Female holotype from Brazil, Rio de Janeiro, Petrópolis, [22°31′0″S, 43°11′0″W], 2–5.xi.1945, 850 m, H. Sick (MCP) [IA40985].

Paratypes. Same data as for holotype, 3♀ (MCP) [IA40985].

Other material. Only known from type series.

Etymology. The species epithet is an arbitrary combination of letters.

Diagnosis. Differs from *A. ethicus* and *A. misiones* by thicker copulatory ducts and broader scape, and from *A. nigrescens* by longer copulatory ducts (Fig. 7F–H).

Description. Male. Unknown.

Female (holotype). Total length 3.06. Cephalothorax 1.43 long, 1.11 wide, 0.83 high, yellowish-brown with centre and rim darker. Sternum 0.84 long, 0.71 wide, extending between coxae IV, pale yellowish-brown, slightly darker around rim. Abdomen 1.76 long, 1.53 wide, 1.65 high. Pattern as in Fig. 7I. Eyes subequal in size, about 0.08 in diameter. Clypeus height about 2.5× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.53, patella 0.59, tibia 1.33, metatarsus 1.24, tarsus 0.62. Femur about 5× longer than wide, metatarsus I about 9× longer than wide. Leg formula 1423. Leg base colour pale yellowish-brown, distal half of femora I and II darker (more pronounced on I) and tip of tibia and metatarsus I darker. Tarsal organs slightly distal on tarsus I (0.50–55), proximal on II (0.45–50), III (0.40–0.45) and IV (0.35–0.40). Four to seven small trichobothria dorsally on all tibia, five on tibia I, four on tibia III. Trichobothria on metatarsi I–III slightly distal (0.50–0.55), absent on metatarsus IV. Three trichobothria dorsally on palpal tibia. Epigynum as in Fig. 7F–H.

Variation. Female total length 2.47–3.10, prosoma 1.37–1.56, femur I 1.43–1.65.

Distribution. Only known from type locality (Fig. 15).

Natural history. Unknown.

Anelosimus rabus Levi, 1963 (Fig. 9A–D)
Anelosimus rabus. Levi, 1963f: 35, figs 66–68, ♂♀.

Material examined. Male holotype and three female paratypes from BRAZIL, Santa Catrína, Nova Teutonia, 27°11S, 52°23W, xi.1957, F. Plaumann (KBIN, examined).

Etymology. The species epithet is an arbitrary combination of letters (Levi 1963).

Diagnosis. Separated from all other *Anelosimus* by the embolus tip spiraling towards the cymbium, around the TTA distally (Fig. 9A). Females diagnosable by the shape of the epigynal plate (Fig. 9B) and the pathway of the copulatory ducts (Fig. 9C).

Redescription. Male (holotype). Total length 2.67. Prosoma 1.37 long, 0.91 wide, 0.87 high, pale brown with centre and narrow rim darker. Sternum 0.83 long, 0.71 wide, extending between coxae IV, dusky grey markings on pale brown. Abdomen 1.30 long, 1.12 wide, 1.16 high. Pattern as in Fig. 9D. Eyes subequal in size, about 0.08 in diameter. Clypeus height about 3.0× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.45, patella 0.46, tibia 1.20, metatarsus 1.01, tarsus 0.55. Femur about 4× longer than wide, metatarsus I about 11× longer than wide. Leg formula 1423. Legs pale brown, with distal part of tibia I dark, and narrow dark rings around other joints (except coxa-trochanter). Tarsal organs proximal on all tarsi (0.4–45) most proximal on IV (0.35). Numerous (4–6) small trichobothria dorsally on all tibia, six on tibia I, 4–5 on tibia III. Trichobothria on metatarsi I–III slightly

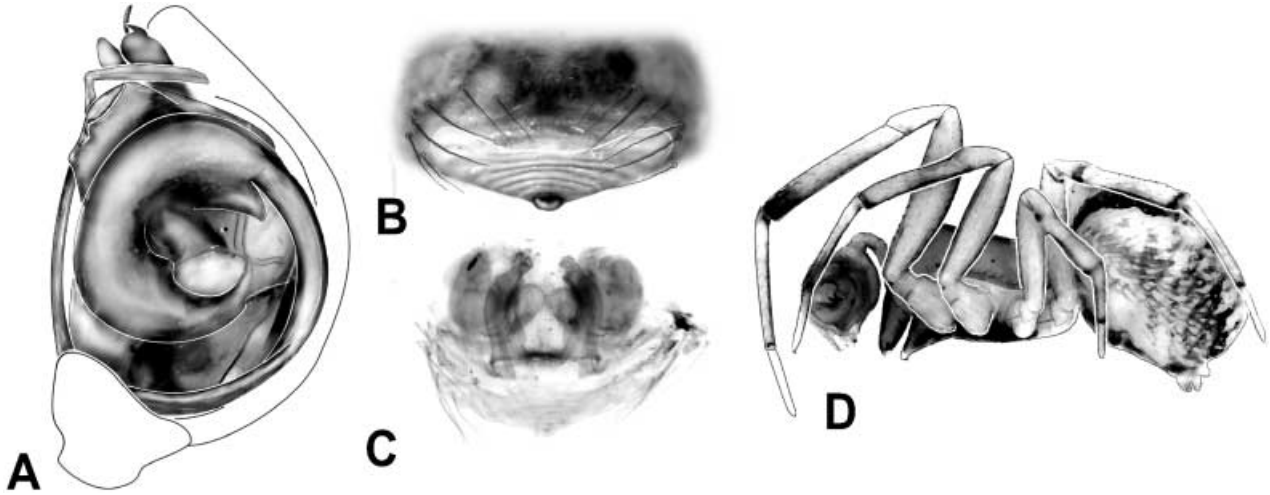

Fig. 9 A–D. *Anelosimus rabus*. —A. Palp ventral. —B. Epigynum. —C. Digital photograph of internal epigynum. —D. Male habitus.

proximal, or central (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palpal organ as in Fig. 9A.

Female (paratype). Total length 3.45. Prosoma 1.30 long, 1.09 wide, 0.99 high, pale brown with centre and narrow rim darker. Sternum 0.86 long, 0.73 wide, extending between coxae IV, dusky brown markings. Abdomen 2.28 long, 1.82 wide, 2.06 high. Pattern as in male. Eyes subequal in size, about 0.09 in diameter. Clypeus height about 3.0× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 1.30, patella 0.52, tibia 1.07, metatarsus 0.91, tarsus 0.59. Femur about 4× longer than wide, metatarsus I about 12× longer than wide. Leg formula 1423. Legs pale brown, with distal part of tibia I dark, and narrow dark rings around other joints (except coxa-trochanter). Tarsal organs proximal on all tarsi (0.35–45) most proximal on I and IV (0.35). Numerous (5–6) small trichobothria dorsally on all tibia, wsix on tibia I, five on tibia III. Trichobothria on metatarsi I–III slightly proximal, or central (about 0.45–0.50), absent on metatarsus IV. Three trichobothria dorsally on palpal tibia. Epigynum as in Fig. 9B,C.

Variation. Male only known from holotype. Female total length 2.80–3.45, prosoma 1.26–1.30, femur I 1.17–1.30.

Distribution. Only known from type locality (Fig. 15).

Natural history. Unknown.

The rupununi group

Diagnosis. The *rupununi* group can be distinguished from all other *Anelosimus* by their unusual genitalia: the huge, folded, embolus of the male palp (Fig. 10B,E), a medially acute copulatory bursa margin in the female epigyna (Fig. 10F,H), and by leg coloration, dark spots surrounding setal bases, especially on femora (Fig. 10J).

Description. Small to medium sized (1.70–2.70) *Anelosimus* spiders with characteristic *Anelosimus* abdomen pattern coloration, a dark (red in live specimens) dorsal longitudinal band edged with white. Males with a characteristic, large, flat and folded embolus. Female epigyna with a medially acute copulatory bursa. Legs typically with conspicuous dark spots around setal bases (Fig. 10J).

Phylogenetics. Synapomorphies of the *rupununi* group (see Agnarsson 2005; character numbers follow those of sister publication) 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).

Composition. Two species, *A. rupununi* and *A. lorenzo*.

Distribution. Caribbean and tropical South America, in lowland rainforest and plantations.

Natural history. Both species are quasisocial, forming extensive colonies containing up to thousands of individuals.

Anelosimus rupununi Levi, 1956 (Figs 10A–E, 11A–G, 12A–F)

Anelosimus rupununi. Levi, 1956b: 414, figs 24, 46, 47, ♂, ♀; Stejskal 1976: 344, figs 4.1 and 6.1, ♂, ♀.

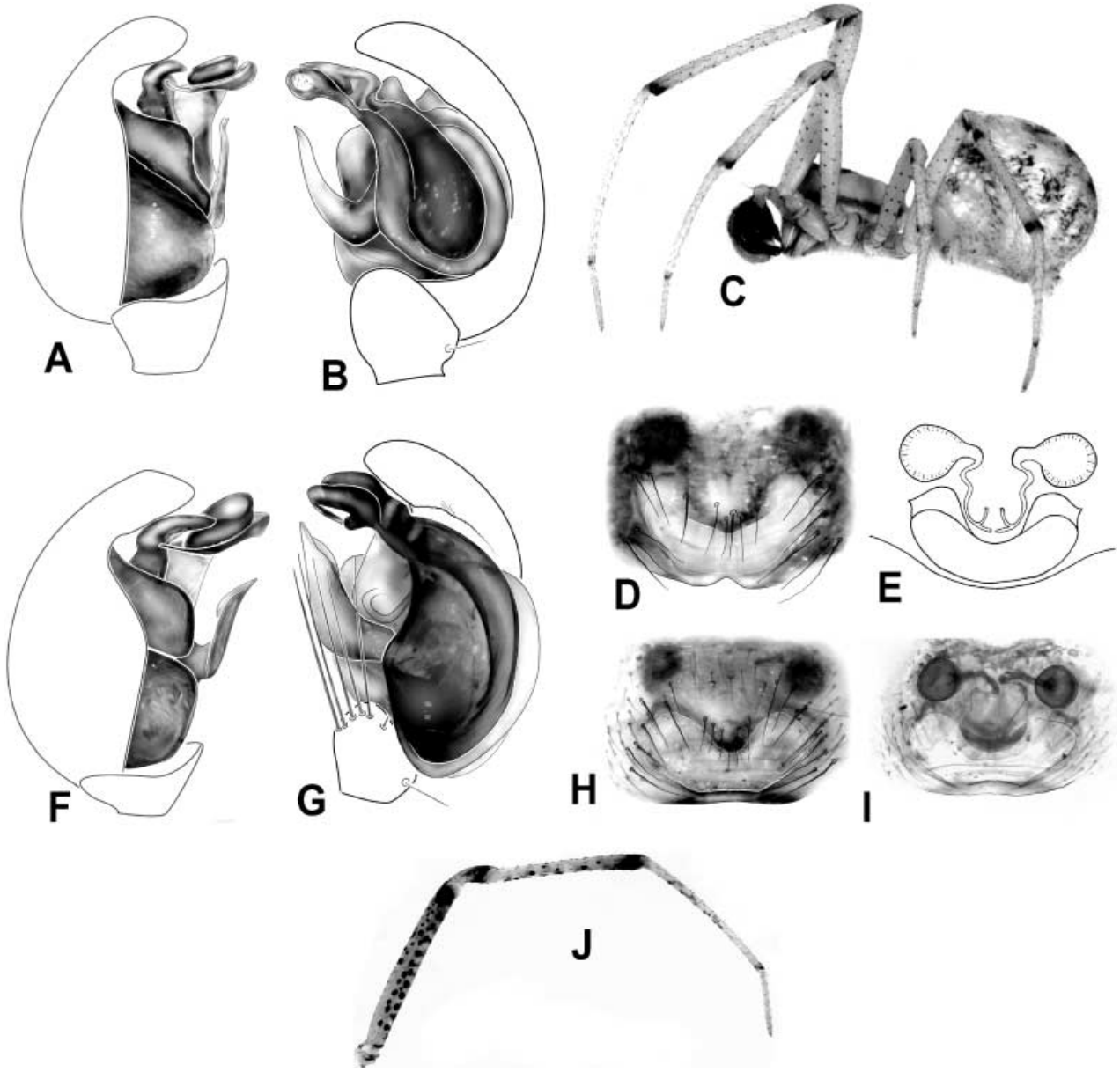

Fig. 10 A–E. *Anelosimus rupununi*. —A. Palp, mesal. —B. Palp, ventral. —C. Male habitus. —D. Epigynum. —E. internal epigynum. F–J. *Anelosimus lorenzo*. —F. Palp, mesal. —G. Palp, ventral. —H. Epigynum. —I. Digital photograph of internal epigynum. —J. Male leg I.

Material examined. Female holotype from GUYANA, Rupununi river between Dadanawa and Isherton [also spelled Ishelton], 5.xi.1937 WG. Hassler (AMNH). The detached abdomen is ruptured and in poor condition, but the epigynum is intact. Other specimens: BRAZIL. Mato Grosso: 260 km N of Xavantina (12°49′0″S, 51°46′0″W), ii–iv.1969, 400 m, Xavant-Cachimbo Expedition (1♂, MCZ), [IA030801]; Chapada dos Guimaraes (15°26′0″S, 55°45′0″W), 5.xii.1990 (1♂, NMNH), [IA1103]. Mato Grosso do Sul: Cuiabá, on campus of the Universidade Federal Do Mato Grosso, [15°36′0″S, 56°5′0″W], 27.xi.1990 (1♂, 4♀, NMNH), [IA40629]; Corumbá, [19°0′0″S, 57°38′0″W], 7.i.1959, A. M. Nadler (1♂, AMNH), [IA40907]. ECUADOR. Napo: Alinahui, 20 km E of Puerto Napo (1°0′0″S, 77°25′0″W), i.1994, 450 m, V. D. & B. Roth (1♂, 1♀, CAS), [IALA12]; same data but 4.i.1994 (10♂, 50♀), [IA40891]. PERU. Departamento de Piura: Pariñas Valley, [4°30′0″S, 81°8′0″W], 9.x.1938, *c.* 130 m, D. & H. Frizzell (1♂, 6♀, CAS), [IA40859]; same data but 19.x.1938 (1♂, 1♀), [IA40860]; same data but 16.x.1938 (2♂, 27♀), [IA40878]; same data but 16.x.1938,

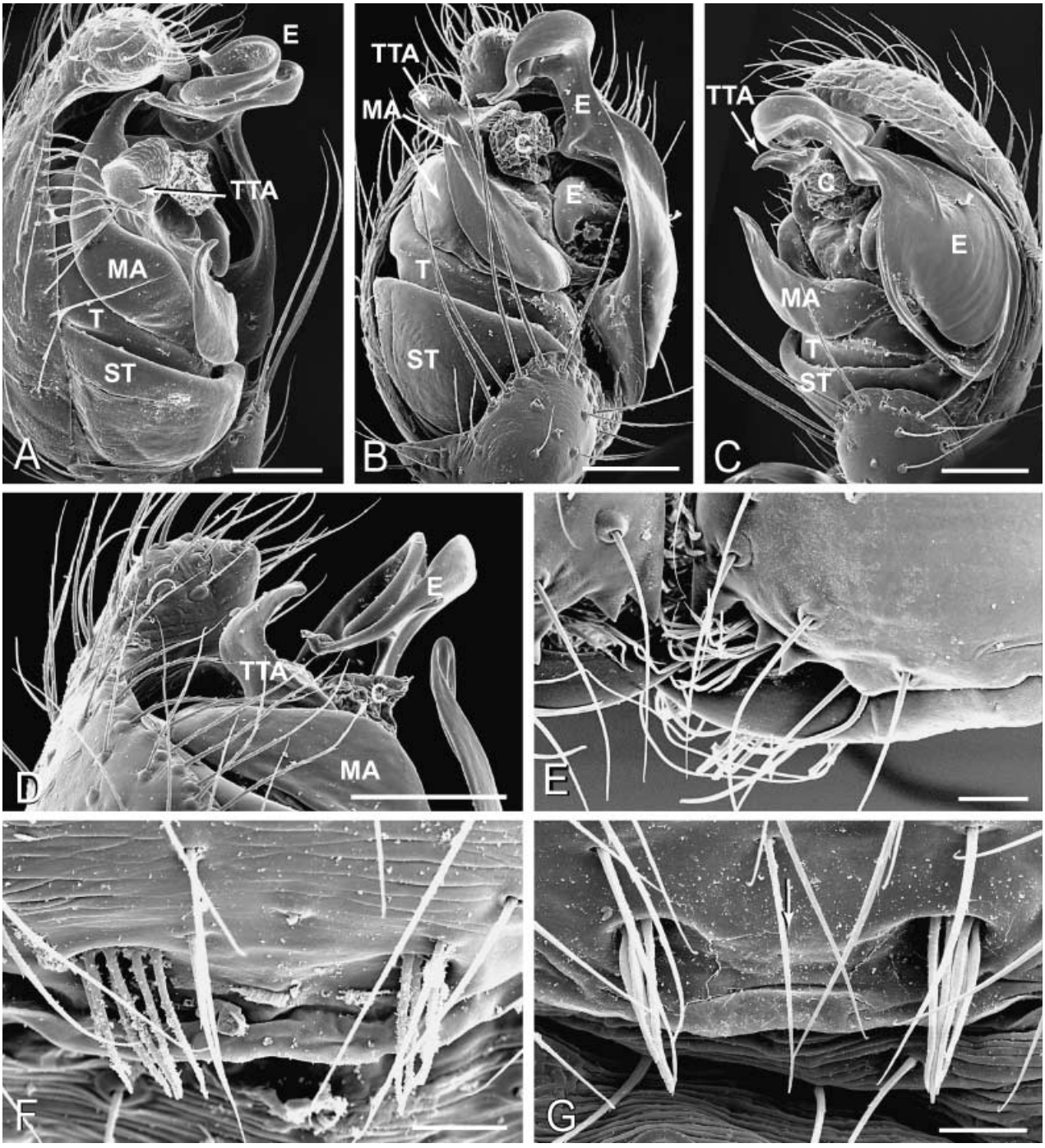

Fig. 11 A–G. *Anelosimus rupununi* A–D. Male palp. —A. Mesal, note bifurcated MA. —B. Ventral. —C. Ectal. —D. Distal tip. —E. Cheliceral promarginal teeth. —F. Epiandrous gland spigots. —G. Same, different specimen. Scale bars: A–D = 100 μm, F, G = 20 μm.

D. L. Frizzell (1♂, 2♀, MCZ), [IA033301]. Madre de Dios: Madre de Dios, Zona Reservada Tambopata, lagoon Cococha [12°50′0″S, 69°17′0″W], 27.vii.1986, A. L. Rypstra (20♀, NMNH), [IA40628]. SURINAM. Geyersvlijt-N. [5°49′0″N, 55°10′0″W], 25.viii.1959, P. H. van Doesburg jr. (8♂, AMNH), [IA40906]. [Surinam, no detailed locality], viii.1968, USDA (2♂, 2♀, MCZ), [IA031601]. VENEZUELA. Lara: 5 km W of Barquisimeta, [10°4′0″N, 69°23′0″W], 8.iv.1975, Y. Lubin

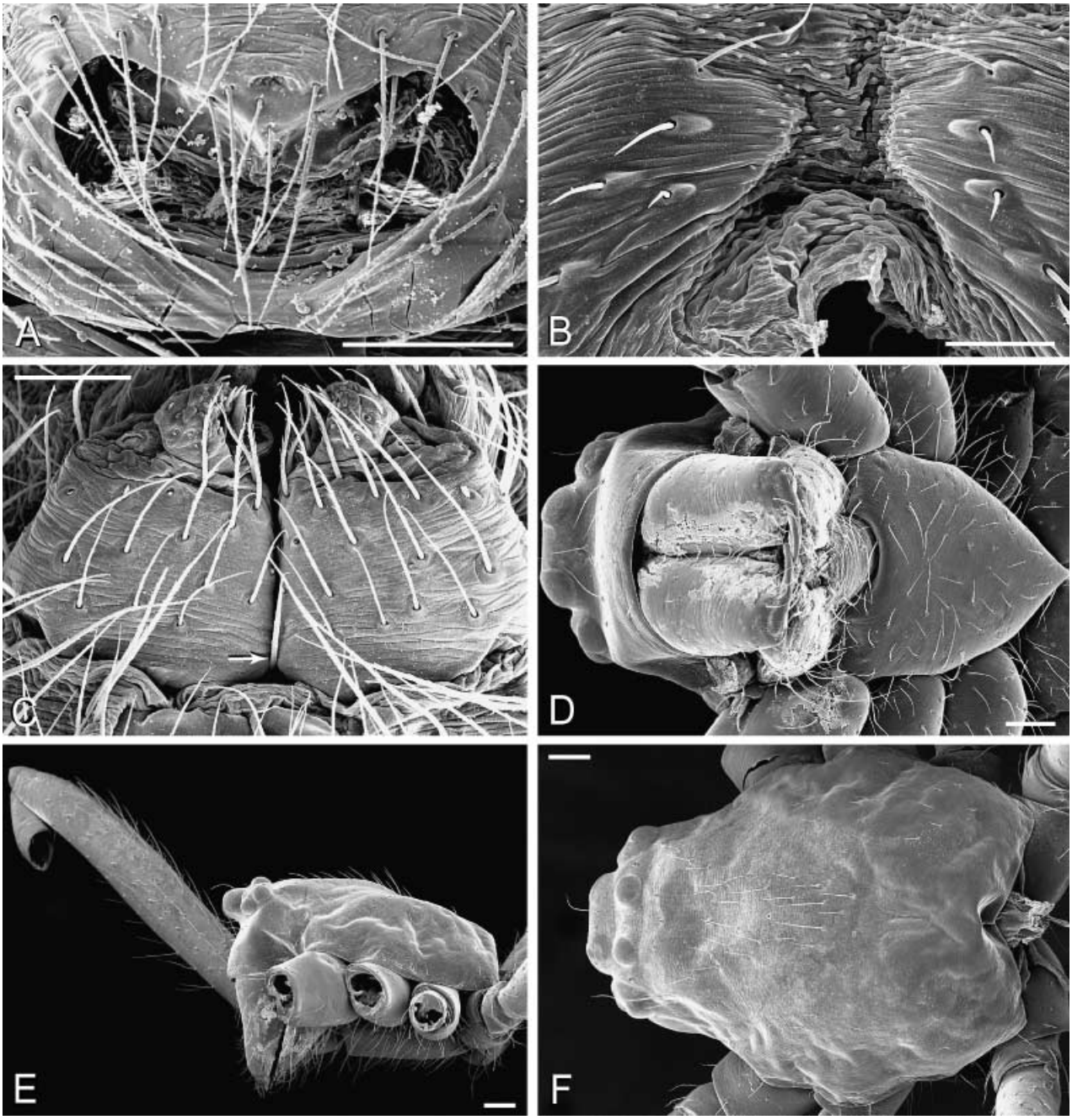

Fig. 12 A–F. *Anelosimus rupununi* female. —A. Epigynum; note acute upper wall of bursa. —B. Male stridulatory pick row. —C. Colular setae (arrow). —D. Male prosoma ventral. —E. Same ectal. —F. Same dorsal. Scale bars: A, B = 50 μm, C, D = 20 μm, E, F = 100 μm.

(2♂, 12♀, MCZ), [IA032701]. Monagas: Jusepín [9°45′0″N, 63°31′0″W] (1♂, MCZ), [IA031501]; same data but 15.xii.1976, H. Stejskal (22♀, 7 juveniles), [IA032101].

Etymology. The species epithet is presumably a noun in apposition referring to the Rupununi river, the type locality.

Diagnosis. Anelosimus rupununi is among the smallest of the *Anelosimus* species. It is easily separated from most *Anelosimus* by the broad and folded embolus rim, and complex embolus tip (Figs 10A,B, 11A–C) in the male and the acute upper margin of the epigynal wall in the female (Figs 10D, 12A). It differs from the closely related *A. lorenzo* in being considerably

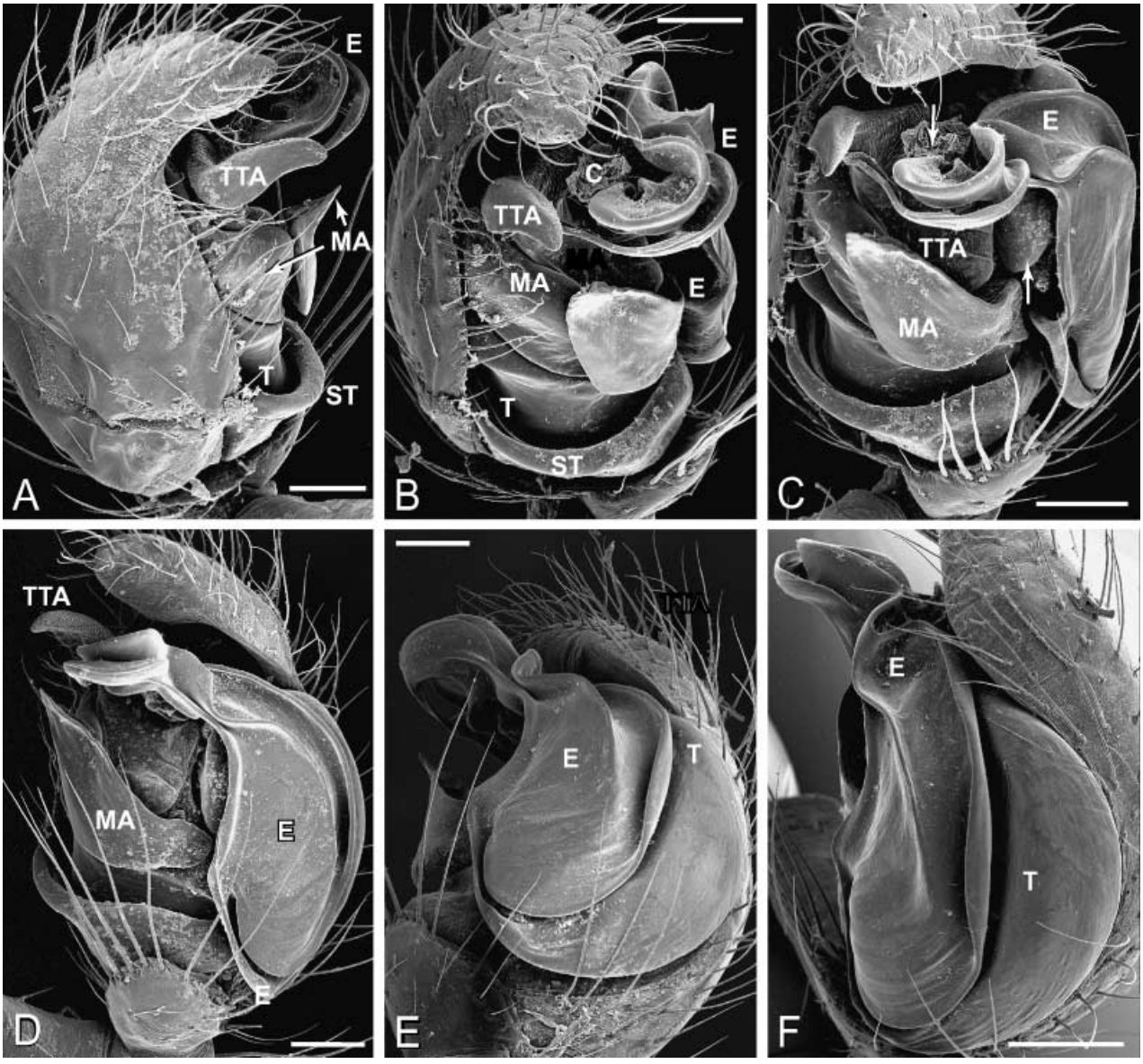

Fig. 13 A–F. *Anelosimus lorenzo*, male palp. —A. Mesal. —B. Mesoapical. —C. Ventral. —D. Subectal. —E. Caudoectal. —F. Ectal. Scale bars = 100 μm.

smaller, by having a narrower MA branch 2 in the male palp (Fig. 10B), and by details of the internal genitalia in the female (Fig. 10E).

Redescription. Male (from Ecuador, Napo, 20 km E. Puerto Napo, Alinahui, 1°0′S, 77°25′W, 450 m, i.1994, V.D. & B. Roth). Total length 1.82. Prosoma 0.85 long, 0.69 wide, 0.53 high, yellowish-brown, dusky markings in centre and around rim. Sternum 0.51 long, 0.50 wide, broadly extending between coxae IV, yellowish-brown, dusky markings in centre and around rim. Abdomen 1.04 long, 0.83 wide, 0.96 high. Pattern as in Fig. 10C. Eyes subequal in size, about 0.07 in diameter. Clypeus height about 2.3× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 0.85, patella 0.26, tibia 0.68, metatarsus 0.59, tarsus 0.39. Femur about 5× longer than wide, metatarsus I about 9× longer than wide. Leg formula 1423 with legs 4 and 2 subequal. Leg base colour yellowish-brown, distal tip of femora sometimes slightly darkened, patella, tibia, and metatarsus with a narrow dark ring distally, femora and tibia

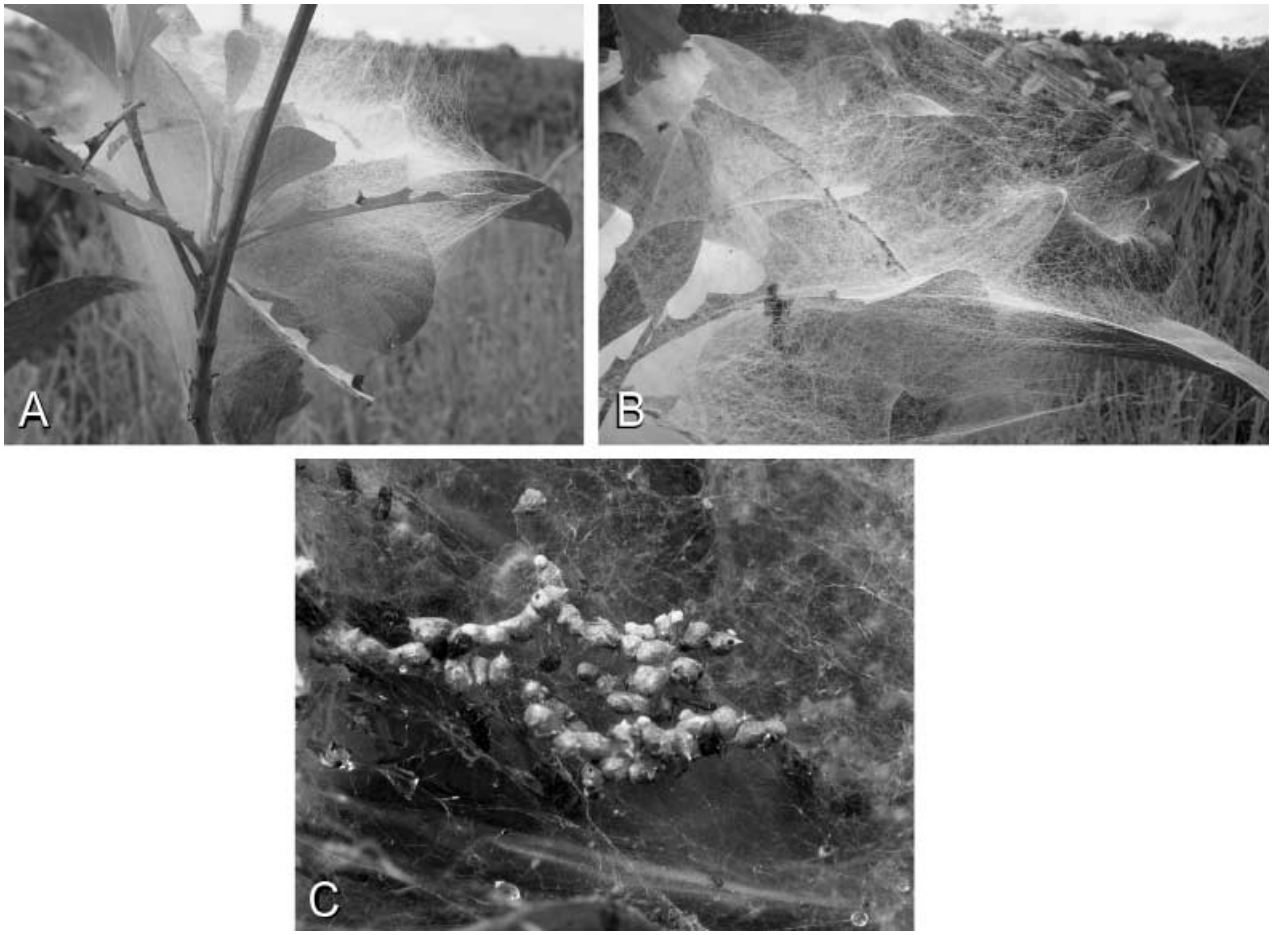

Fig. 14 A–C. —A, B. Photographs of a small *A. rupununi* colony. —C. Hoarded egg sacs within the colony.

sometimes with dark stripes. Tarsal organs proximal (0.30–0.40) on all tarsi. Numerous (3–5) small trichobothria dorsally on all tibia, 4–5 on tibia I, three on tibia III. Trichobothria on metatarsi I–II proximal (0.35–4), nearly central on III (about 0.45–0.50), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palpal organ as in Figs 10A,B and 11A–D.

Female (locality data as male). Total length 2.60. Prosoma 0.98 long, 0.74 wide, 0.53 high, yellowish-brown, dusky markings in centre and around rim. Sternum 0.63 long, 0.56 wide, extending between coxae IV, yellowish-brown, dusky markings in centre and around rim. Abdomen 1.63 long, 1.35 wide, 1.24 high. Pattern as in male. Eyes subequal in size, about 0.07 in diameter. Clypeus height about 2.2× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 0.91, patella 0.29, tibia 0.65, metatarsus 0.62, tarsus 0.46. Femur about 6× longer than wide, metatarsus I about 8× longer than wide. Leg formula 1423. Leg base colour yellowish-brown, distal tip of femora sometimes slightly darkened, patella, tibia, and metatarsus with a narrow dark ring distally, femora and tibia sometimes with dark stripes. Tarsal organs proximal (0.40–0.50) on all tarsi, nearly central on I. Numerous (5–6) small trichobothria dorsally on all tibia, 4–5 on tibia I, four on tibia III. Trichobothria on metatarsi I–III proximal (0.35–4), absent on metatarsus IV, distal on palp (0.80). Two prolateral and one retrolateral trichobothria on palpal tibia. Epigynum as in Figs 10D,E and 12A.

Variation. Size varies little in available material, apart from that of the female abdomen. Total length of male 1.70–1.85, leg I femur 0.80–0.88. Female total length 1.90–2.7, prosoma 0.95–1.05. Coloration, on the other hand, is very variable, from dark to very pale, and from a fairly typical *Anelosimus* dark longitudinal abdominal band, edged by white, to a small dark patch anteriorly on the dorsum. Some specimens in alcohol nearly colourless. Legs range from pale yellow with narrow

Fig. 15 Distribution of species of the *ethicus* and *rupununi* groups.

dark bands at tips of segments, to brown with longitudinal stripes and dark tips. Males from Tombopata, Peru are darkly coloured and differ subtly in the palp, by a shorter median apophysis branch 2, and a longer, more gently curving tip of the theridiid tegular apophysis. Given that these are the only specimens at my disposal that show this variation, it seems unwarranted to describe them as a new species.

Distribution. Caribbean (Trinidad) to South America, including Brazil, Ecuador, Venezuela, Peru (Fig. 15).

Natural history. *Anelosimus rupununi* is a quasisocial species with nests containing up to several thousand individuals (Levi 1972). According to Stejskal (1976), the spiders cause damage to citrus and coffee orchards; their dense webbing may cover entire canopies of trees and eventually kill them. Typically, smaller nests occur in the vicinity of larger ones, indicating colony formation by 'budding' (Avilés 1997). The nests differ from those of the *eximius* lineage in being made of silk of a whiter and lighter appearance, containing almost no dry leaves and no definite top–bottom polarity (Fig. 14A,B, see also Avilés & Salazar 1999). Furthermore, they rarely contain knock-down lines, but rather the spiders forage below the main sheet. *Anelosimus rupununi* has a more synchronous life cycle than, say, *A. eximius*. The sex ratio, both at embryo and at maturity, is a strongly biased towards females, with about 8% males (Avilés *et al*. 2001). More than one egg sac is usually generated by each female. An unusual characteristic of this species (and possibly *A. lorenzo*) is that the egg sacs are hoarded (Fig. 14C) and guarded mutually. Typically, each bundle has a single guardian, or a few colony members may take turns as guardian.

***Anelosimus lorenzo* Fowler & Levi, 1979 (Figs 10F–J, 13A–F)**
Anelosimus lorenzo. Fowler & Levi, 1979: 11, figs 1–4 ♂, ♀.

Anelosimus rupununi. Levi, 1963: 34, map p. 31, specimens from Paraguay later presumed to be *A. lorenzo* (see Fowler & Levi 1979: 12).

Material examined. Male holotype and female paratype from PARAGUAY, San Lorenzo, [25°21′0″S, 57°30′0″W], 25.vii.1976, *c.* 130 m, H. Fowler (MCZ). The types are in very poor condition, having been desiccated. Three female paratypes from same locality, H. Fowler '25.7.76 1980.3.20.1–3' (BMNH). Three female paratypes from same locality, H. Fowler 25.7.76 (AMNH), [IA40581]. Other specimens: ARGENTINA. Catamarca: Andalgalá, [27°35′0″S, 66°18′0″W], 8.i.1974, *c.* 1000 m, F. A. Enders (2♂, NMNH), [IA40558]; same data but 16.iii.1974 (1♀), [IA40404]. BRAZIL. Amazonas: Paraquequara, Manaus, [1°45′0″S, 57°7′1″W], 21.vii.1991, *c.* 30 m, K Rotke (7♀, MCP), [MCP10]. Mato Grosso: km. 11 Transpanteneira, Poconé [16°19′0″S, 56°38′0″W], 16.ix.1986, A. Varredura (2♂, 1♀, MCZ), [IA030601]; Fazenda santa Ines, Poconé (20°34′0″S, 47°49′0″W), 4–10.viii.1992, *c.* 50 m, A. A. Lise (1♂, MCP), [MCP06]; Santo Antonio do Leverger (15°51′0″S, 56°5′0″W), 29.vii.1992, *c.* 150 m, A. A. Lise (2♂, 4♀, MCP), [MCP07]; same data but 29.viii.1992, A. A. Lise & A. Braoul Jr. (1♂), [MCP09]. São Paulo: Campinas [22°54′0″S, 47°4′0″W], iv–v.1989, E. S. A. Marques (1♂, 1♀, MCZ), [IA032301]. PARAGUAY. Alto Paraná: Jaguararapa, [25°33′0″S, 55°7′0″W], *c.* 400 m (1♂, 1♀, AMNH), [IA40902], same data but (1♀), [IA40905].

Etymology. The species epithet is presumably a noun in apposition, referring to the type locality.

Diagnosis. *Anelosimus lorenzo* is easily separated from most *Anelosimus* by the broad and folded embolus rim and complex embolus tip in the male (Figs 10D–G, 13A–D) and the acute upper margin of the epigynal wall in the female (Fig. 10H,I). It differs from the closely related *A. rupununi* in being considerably larger, by having a thicker MA branch 2 in the male palp (Figs 10G, 13D), basal portion of the embolus much thicker in ectal view (Fig. 13F) and embolus base extending further towards the palpal tibia (Fig. 10G). Females differ from *A. rupununi* by more rounded spermathecae (Fig. 10I).

Description. Male (holotype) (holotype in bad condition; description is limited to undamaged parts). Total length 2.28. Prosoma 1.24 long, 1.11 wide, pale brown with a dark rim and centre. Sternum extending between coxae IV, brown. Abdomen 1.17 long, 0.99 wide. Pattern as in *A. rupununi*. Eyes subequal in size, about 0.08 in diameter. Clypeus height about 3.4× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 2.10, patella 0.49, tibia 1.92, metatarsus 1.85, tarsus 0.65. Femur about 8× longer than wide, metatarsus I about 15× longer than wide. Leg formula 1423 with legs 4 and 2 subequal. Leg base colour yellowish, femur I darkest, tips of segments slightly darkened. Conspicuous dark rings around setal bases, most prominently on leg I. Tarsal organs central (0.50) on tarsus I, nearly central (0.45–50) on II, proximal (0.40–0.45) on III–IV. Numerous (3–6) small trichobothria dorsally on all tibia, very hard to see under light microscopy. Probably 3–4 on tibia I, three on tibia III. Trichobothria on metatarsi I–III distinctly proximal (*c.* 0.25–0.35), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palpal organ as in Figs 10F,G and 13A–F.

Female (paratype). Total length 2.21. Prosoma 1.04 long, 0.91 wide, 0.66 high, brown, with a dark narrow band around rim. Sternum 0.74 long, 0.54 wide, extending between coxae IV, brown, with a dark narrow band around rim. Abdomen 1.43 long, 1.07 wide. Pattern as in *A. rupununi*. Eyes subequal in size, about 0.05 in diameter. Clypeus height about 1.9× one AME diameter. Chelicerae with one large and two small prolateral teeth, 4–5 denticles retrolaterally. Leg I femur 0.98, patella 0.39, tibia 0.81, metatarsus 0.72, tarsus 0.46. Femur about 6× longer than wide, metatarsus I about 10× longer than wide. Leg formula 1243 with legs 2 and 4 subequal. Leg base colour brown, tips of segments slightly darkened. Conspicuous dark rings around setal bases, most prominently on leg I. Tarsal organs proximal (0.40–0.45) on I and III–IV, leg II lacking. Tibial trichobothria could not be counted using light microscopy. Trichobothria on metatarsi I distinctly proximal (about 0.35), proximal

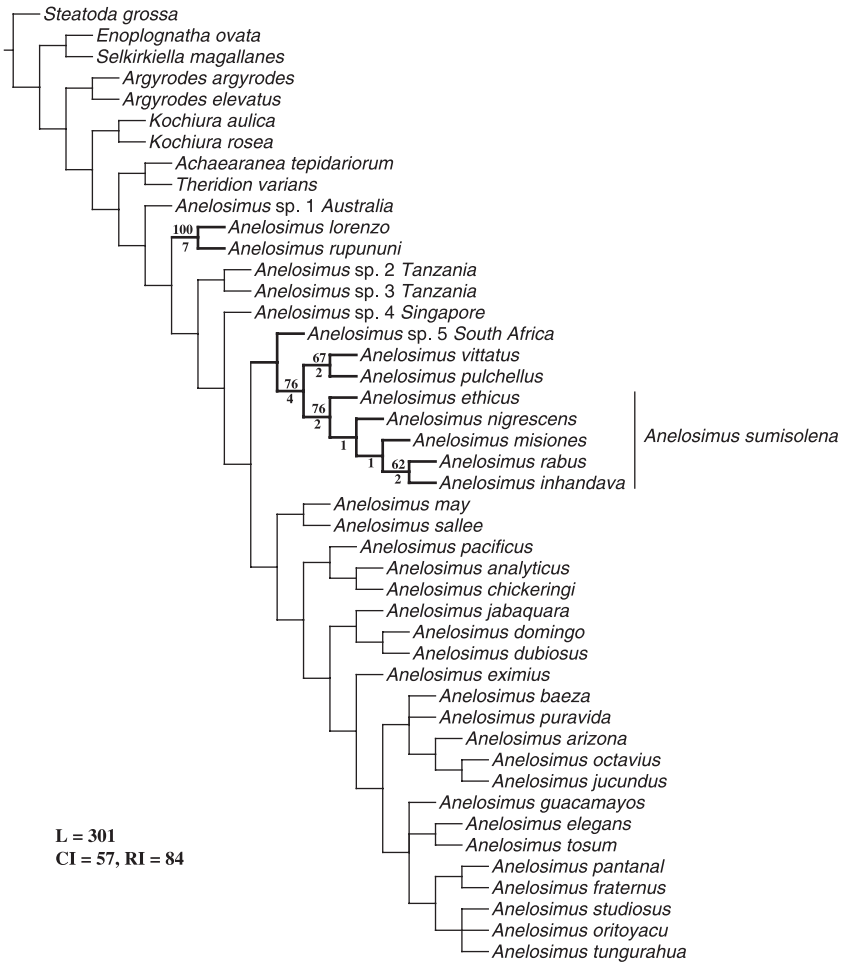

Fig. 16 A summary cladogram, based on the strict consensus of the two most parsimonious trees when *A. sumisolena*, a redundant taxonomic equivalent of *A. nigriscens*, has been removed from the analysis (see Results and discussion). The *rupununi* (above) and *ethicus* (below) groups are indicated in bold. Bremer support (numbers below nodes) and Bootstrap percentages (numbers above nodes) are given for relevant clades. For further detail on other clades see Agnarsson (2005). The possible placements of *Anelosimus sumisolena* are here indicated as described in Kearney & Clark (2003). When *A. sumisolena* is included, all resolution within the *ethicus* group is lost, and both Bremer and Bootstrap values for the group are lower (1 and 48, respectively).

on III (0.45), absent on metatarsus IV (leg II lacking). Two trichobothria on palpal tibia. Epigynum as in Fig. 10H,I.

Variation. Male total length 2.20–2.32, prosoma 1.24–1.30, femur I 2.10–2.31. Female total length 2.21–2.30, prosoma 1.04–1.10, femur I 0.98–1.2.

Distribution. Paraguay, Brazil, Argentina (Fig. 15). Fowler & Levi (1979) assumed that all southern records of Levi's (1963) '*A. rupununi*' were indeed *A. lorenzo*. However, the ranges of these species overlap, at least in Brazil.

Natural history. *Anelosimus lorenzo* is a quasisocial species with nests with up to at least 1.4 m^3 in size with 550 individuals (Fowler & Levi 1979). The web periphery is covered with loosely spun silk, while densely spun platforms form the interior. The web is spun communally, mostly at night, and can be located in between, or at the tips of, branches. Curled up leaves form retreats, sheathed with silk. The most common prey items appear to be large beetles (Cerambycidae, Carabidae, Scarabaeidae). As in *A. rupununi*, colony foundation is via budding, or sociotomy.

Fowler & Levi (1979) introduced *A. lorenzo* to non-natal colonies; they were not encountered aggressively. By contrast, other introduced theridiids did not spur immediate reactions, but were attacked when accidentally encountered by resident *A. lorenzo*. This suggests at least two types of tolerance mechanism in *A. lorenzo*: (1) a general suppression of aggression to vibrations caused by (similarly sized) spiders walking around, and (2) a specific recognition mechanism via touch that allows the distinction between con- and heterospecifics. *Anelosimus lorenzo* has an adult female-biased sex ratio similar to that of *A. rupununi*, most likely due to primary bias, as in several other *Anelosimus* (e.g. Avilés & Maddison 1991).

Phylogenetics

The parsimony analysis resulted in 54 most parsimonious trees (L = 301, CI = 57, RI = 84). The results are congruent with the phylogeny of Agnarsson (in press), with identical topology outside the groups revised here (Fig. 16). The phylogeny

provides robust support for the monophyly of the *rupununi* group (Bremer support = 7, Bootstrapping = 100), but weak support for the enlarged *ethicus* group (Bremer support = 1, Bootstrapping = 65).

The strict consensus leaves the interrelationships of the *ethicus* group species unresolved. This may be due to the amount of missing data in the two species known only from one sex (*A. inhandava* and *A. sumisolena*). Fragmentary taxa are problematic when alternative optimizations of question marks affect their placement (a 'wildcard' phenomenon). However, lack of resolution can also be due to character conflict where fragmentary taxa pose no special problems (Kearney 2002; Kearney & Clark 2003). The computer program TAXEQ3 (Wilkinson 2001) is designed to flag fragmentary taxa in a matrix that have no unique character combinations (their character coding has no conflict with some other, more complete, taxon). These 'redundant taxonomic equivalents' are potential wildcard taxa (see Wilkinson 1995; Kearny 2002; Kearny & Clark 2003) and can thus be 'safely' removed, without sacrificing character information. Here, *A. sumisolena* is the taxonomic equivalent of *A. nigrescens*; removing *A. sumisolena* results in a fully resolved *ethicus* group, and support for the group and clades within it increases (see Fig. 16). The ambiguity in placing *A. sumisolena* is thus, at least in part, a result of missing entries.

Although the natural history of most of the species of the *ethicus* group is unknown, their behaviour can be predicted based on their phylogenetic position. Subsocial behaviour optimizes unambiguously to the base of *Anelosimus* (see Agnarsson 2004, in press, fig. 55) and is primitively present in the node leading to the *ethicus* group. The *ethicus* group species can thus all be predicted to be subsocial, unless sociality has been secondarily lost.

A similar phylogenetic prediction recently led to the discovery of numerous subsocial *Anelosimus* species in Madagascar (Agnarsson & Kuntner 2005). Recent studies all conclude that quasisociality evolves from intermediate subsociality (Avilés 1997; Bukowski & Avilés 2002; Powers & Avilés 2003; Agnarsson 2002, 2004, in press). Understanding the evolution of quasisociality thus requires the study of subsocial (or even secondarily solitary) species, and the *ethicus* group is a promising source of case studies worthy of attention from ethologists. Quasisociality arose *de novo* in the *rupununi* group, representing one of 6–7 independent origins in theridiid spiders. Within *Anelosimus* each of the 4–5 origins of quasisociality occurs on a subsocial branch, congruent with the maternal care pathway hypothesis to sociality (see also Agnarsson 2002, 2004, in press).

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