The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae:Synotaxidae), a new species from Guyana, and notes on theridioid phylogeny

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Abstract.   The genus *Synotaxus* Simon, 1895 is reviewed. Modern systematic work has challenged the classical placement of *Synotaxus* as an argyrodine theridiid. Its placement is evaluated in a phylogenetic analysis containing a wide selection of theridiids, including all major argyrodine genera. For the analysis, two published matrices are fused to produce a dataset containing 83 orbicularian taxa and 302 morphological characters. Although the two matrices share only 10 taxa and 33 characters, a single most parsimonious tree is obtained. The results are congruent with results from each independent matrix, and unambiguously corroborate the placement of *Synotaxus* outside Theridiidae. Some superficial similarities, such as the elongate abdomen extending far beyond the spinnerets, are clearly convergent in the two taxa. *Synotaxus*, furthermore, lacks the suite of synapomorphies defining Theridiidae. Thus, its transfer out of Theridiidae is corroborated, and a sister relationship with *Chileotaxus* Platnick, 1990 is proposed, based on similarities in web and somatic morphology. A synapomorphy-based circumscription of the genus is given. *Synotaxus waiwai,* sp. nov. is described, *Synotaxus monoceros* (Caporiacco, 1947), previously only known from males, is redescribed and synonymised with *S. pupularum*, Exline & Levi, 1965, syn. nov., previously only known from females. A description of the webs of both species is given, as well as that of *Chileotaxus sans* Platnick, 1990. Many further *Synotaxus* species remain to be described.

Introduction

Simon (1895) described the genus *Synotaxus* and originally placed it in Theridiidae (Simon 1894: 494–7, 1895: 131). Exline and Levi (1965) revised *Synotaxus*, which then contained six species. No further species have been described to date. Traditionally *Synotaxus* was considered an argyrodine theridiid (e.g. Petrunkevitch 1928; Exline 1950). Lack of a rebordered labium, spineless long legs, few cheliceral teeth, and the presence of a tarsal comb associate it with Theridiidae, while similarities in general habitus, such as greatly elongated abdomen extending beyond spinnerets, low carapace and long, thin legs, and the relatively large colulus, are shared with Argyrodinae (e.g. Levi and Levi 1962). Forster *et al.* (1990), however, transferred *Synotaxus* to a revised Synotaxidae, a name based on Simon's (1895) tribal group Synotaxeae. They based the transfer on the following putative synotaxid synapomorphies: presence of a small, basally situated and dorsally excavated paracymbium, a longitudinal incision of the retrolateral cymbial margin, thickened dorsal macrosetae on the male palpal femur, patella, and/or tibia, and greatly elongated, spineless legs, with the first pair much longer than the rest and all femora basally thickened. Furthermore, they suggested that *Synotaxus* lacks typical theridiid synapomorphies, such a distal 'paracymbium', flattened aggregate spigots and cobweb. However, Forster *et al.* (1990) had only a single poorly preserved specimen of *Synotaxus* available to them, so they did not consider the evidence for the placement of *Synotaxus* to be conclusive. Griswold *et al.* (1998) included four synotaxid genera (*Synotaxus*, *Chileotaxus* Platnick, 1990, *Pahora* Forster, 1990 and *Meringa* Forster, 1990) in a family-level phylogeny of Orbiculariae, and supported the placement of *Synotaxus*, suggested by Forster *et al.* (1990), as well as the monophyly of Synotaxidae. However, only one of the putative synapomorphies of Synotaxidae suggested by Forster *et al.* was corroborated: the possession of a cymbium retrolateral groove. Two additional synotaxid synapomorphies were proposed by Griswold *et al.* (1998): the presence of a complex conductor and its terminal position.

The last species-level comparative taxonomic work on *Synotaxus* was done by Exline and Levi (1965). Subsequent

phylogenetic studies including *Synotaxus* (Coddington 1990; Forster *et al.* 1990; Griswold *et al.* 1998) were limited by specimen availability and thus relied, in part, on the descriptions of Exline and Levi (1965). These included a single *Synotaxus* species and did not test its placement in a matrix containing an argyrodine theridiid. Thus, the knowledge of *Synotaxus* morphology is relatively poor, an explicit synapomorphy-based generic circumscription is lacking, and its phylogenetic position remains to be empirically tested in a matrix containing both argyrodines and synotaxids. A spider diversity survey conducted in Guyana (J. Coddington, G. Hormiga, J. Miller, I. Agnarsson, M. Kuntner) in 1999 found numerous *Synotaxus* specimens. The availability of ample fresh material has allowed a more detailed morphological study than has been possible in recent phylogenetic works. Furthermore, phylogenetic hypotheses of the relationships among theridiid genera are now available for the first time (Agnarsson in press; Arnedo *et al.* in press), facilitating phylogenetic studies of related taxa.

The objective of this study is to provide morphological data to investigate the phylogenetic placement of *Synotaxus* based on a cladistic analysis. For that purpose, two available matrices are fused: Griswold *et al.*'s (1998) family-level orbicularian study, and Agnarsson's (in press) generic-level theridiid study, pooling all available morphological data in a simultaneous analysis. I discuss the circumscription and putative synapomorphies of the genus based on examination of six *Synotaxus* species. *Synotaxus waiwai*, sp. nov., is described, and *Synotaxus monoceros* (Caporiacco, 1947), previously only known from males, is redescribed and synonymised with *S. pupularum* Exline & Levi, 1965, syn. nov., previously only known from females. *Synotaxus turbinatus* Simon, 1895 and three undescribed *Synotaxus* species were also examined. Furthermore, illustrations of other described species (*S. ecuadorensis* Exline, 1950; *S. leticia* Exline & Levi, 1965; and *S. longicaudatus* (Keyserling, 1891)) were used to confirm the presence of diagnostic characters.

The main aim of this study is not to provide a novel phylogenetic hypothesis of orbicularians, but rather to summarise the available evidence on the placement of *Synotaxus*. A more comprehensive analysis will require scoring the character states for the majority of characters that are not shared between the two currently published phylogenies, a task much too large for this work. Nevertheless, combining all available data in a single analysis maximises the explanatory power of the resulting hypothesis and provides a more robust test than does each separate analysis (Nixon and Carpenter 1996; Kluge 1997).

Material and methods

Bold numbers in the text refer to character numbers in the fused matrix; up to character 242 these are the same as in Agnarsson (in press).

Data matrix

This study utilises two matrices: Griswold *et al.* (1998, hereafter labelled G98) from a family-level orbicularian study; and Agnarsson (in press, hereafter labelled A04) from a generic-level phylogeny of Theridiidae. The two matrices were maintained in NEXUS Data Editor (Page 2001), and transferred to Winclada (Nixon 2002) via Mesquite (Maddison and Maddison 2001), which allows the transfer of character information (names of characters and states), with the numerical data. The matrices were then fused in Winclada, using the 'new matrix merge' command, choosing not to match taxa or characters. Simple fusing in this way creates a single matrix composed of two non-overlapping boxes of data (taxa 1–62 and characters 1–242 from A04 and taxa 63–93 and characters 243–335 from G98). Taxa shared between the two matrices (*Argiope argentata* (Fabricius, 1775); *Tetragnatha extensa* (Linneus, 1758); *Linyphia triangularis* (Clerck, 1757); *Nesticus silvestrii* Fage, 1929; *Anelosimus studiosus* (Hentz, 1850); *Dipoena nigra* (Emerton, 1882); *Emertonella funebris* (Hentz, 1850); *Steatoda grossa* (C. L. Koch, 1838)) were then fused using the 'fuse terms' command. *Pimoa breviata* Chamberlin & Ivie, 1943 was, furthermore, fused with *P. rupicola* (Simon, 1884); as the monophyly of *Pimoa* is well supported (Hormiga 1994, 2003), the assumption is unlikely to introduce a topological error (see also Nixon and Carpenter 1996). The 'fuse terms' command appends the data from source terminals into a single new terminal. The two source terminals can then be deleted. This command does not identify identical characters from the two matrices and the fused terminals will thus initially have shared characters doubly scored, and those have to be manually fused. Note that since G98 had an undescribed *Synotaxus* species, it is here replaced with *S. monoceros* and *S. waiwai*, sp. nov. scored for all characters.

Thirty-three characters are shared between the two matrices and these were fused manually. Thus, for example, character 10 in A04 and character 26 in G98 are both 'spermathecal number' with the states '(0) two' or '(1) four'. In the original fused matrix, these are characters 10 and 268, describing the same condition, but scored for different taxa. To fuse them, the information was simply moved from character 268 to character 10 and then the former was deleted. In the fused matrix, character and state numbers (of shared characters) are as in A04; for example, 'PC: absent', is character 29, state 1 in A04, character 7, state 0 in G98, and character 29, state 1 here. When more states are present in G98, they are added, in their original order, after the states in A04, e.g. PC morphology (A04 character 30, G98 character 9) has states 0–5 as in A04, whereas G98 states 1 and 6, which are absent in A04, become states 6 and 7 respectively here. Where the two studies differ in coding for shared taxa, the entries from the more recent study were generally preferred (for justification see Agnarsson in press). In one case the difference is of crucial importance. Agnarsson (in press) suggests that the complex distal sclerite in *Synotaxus* is a homologue of the TTA, while a C is absent, whereas Griswold *et al.* (1998) presumed the opposite. As other synotaxids have a presumptively homologous, complex distal sclerite, following A04 for *Synotaxus* and G98 for other synotaxids (simple fusing) would be inconsistent (*a priory* denying the homology of similar sclerites in putative sister taxa). Therefore, the analyses were run with the two characters (**62** and **80**) either deactivated, scored as '?' for *Synotaxus*, or scored according to G98. In some other cases, character fusing was complicated, e.g. A04 character 122 is the presence or absence of a cheliceral boss. G98 does not include that character, but another character refers to the presence of striae (G98, character 39) on the boss, and indicates absence of boss with a '–' (inapplicable for striae). In this case, the information on the presence or absence of a boss was transferred, but no character was deleted. In G98 (Griswold's *et al.* (1998) character 65) the colulus is scored as large or small, and small includes absence, whereas A04 has two characters (172, 173), one

scoring presence/absence of a colulus, and the other size. Here the information from the single G98 character is transferred to both characters in A04.

The fused data matrix contains 302 morphological characters and 83 taxa, including several synotaxids, and a wide array of theridiid genera, with all major argyrodine genera represented. The data were analysed with the NONA ratchet (Goloboff 1993) using mult*1000 command and the ratchet 'island hopper' (Nixon 1999) with 1000 replications, holding 10 trees and selecting 25 characters for each, using both amb = and amb – settings, and PAUP* (Swofford 2002) with 1000 random stepwise additions, and the subtree-pruning and regrafting branch swapping algorithm, searching for minimal length trees under the criterion of parsimony. Successive weighting (Farris 1969) was conducted in NONA (command line: run swt.run hold100000 hold/1000 mult*100 jump 10), reweighting characters using the consistency index. All multistate characters were treated as non-additive (Fitch 1971).

The fused matrix used here contains large blocks of '?', i.e. unknown entries, as well as inapplicable entries '–'. Although fundamentally different, both unknowns and inapplicable entries are treated identically by available software, and both can cause problems for phylogenetic analyses (e.g. Coddington and Scharff 1994; Nixon and Carpenter 1996; Strong and Lipscomb 1999). Emphasizing possible loss in resolution owing to multiple equally parsimonious optimisations of missing entries, Nixon and Carpenter (1996) warned against uncritical fusion of matrices. However, as all analyses here resulted in a single most parsimonious tree, missing entries are clearly not causing resolution-loss problems in this specific case. Other problems of '?' and '–' may include a 'false' increase in resolution owing to character state optimisations not supported by the underlying data. Inapplicable entries may furthermore result in illogical character state optimisations. Thus, every node of the tree was examined to ascertain that it was supported by character data.

Unfortunately, the data available for the type species of *Synotaxus* (*S. turbinatus*), was not sufficient for the inclusion of it in the matrix, as dissection, or scanning electron microscopy (SEM), were not feasible. In principle, this adds uncertainty regarding the phylogenetic placement of the genus. However, a large amount of missing data would, in my opinion, be more likely to lead to misplacement than does following the assumption that *S. monoceros* and *S. waiwai*, sp. nov. well represent this striking genus. Furthermore, even scoring *S. turbinatus* fully would not remove this uncertainty as many other genera, both in Griswold *et al*. (1998) and Agnarsson (in press), are not represented by their type.

New data presented here on the web structure, and coloration of live specimens of *Chileotaxus* suggests affinity with *Synotaxus*. Therefore, the effect of adding this information (characters: **143**, abdomen colour pattern (uniform light green coloration); **201**, spinneret insertion (abdomen extending beyond spinnerets); **134**, labium distal margin (not rebordered); **225**, web (uniform sheet w/o knock-down lines)) was tested. The scores for these traits were added to the fused matrix, and then the data reanalyzed, using the same search strategies as before. Both matrices are available from http://www.gwu.edu/~spiders/cladograms.htm and from the *Invertebrate Systematics* website as Accessory Material.

For details of data collection, analyses and results of each study see Griswold *et al*. (1998) and Agnarsson (in press).

Specimen preparation

Specimens were collected as part of a structured species diversity study (following a protocol) (e.g. Coddington *et al*. 1991; Colwell and Coddington 1994; Coddington *et al*. 1996; Silva and Coddington 1996; Scharff *et al*. in press), near Gunn's landing, southern Guyana; and in general sampling near Bartica, northern Guyana. Specimens were

obtained using 'looking up' (aerial search) and beating methods, as described in Coddington *et al*. (1991). Specimens were examined under a Wild M-5A dissecting microscope. For expansion, male palps were originally immersed in concentrated KOH (~1 g mL^{-1}) for one minute and then transferred to distilled water (method modified from Shear 1967). Full expansion required more than one immersion cycle. 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 the same results and is more convenient; the latter method was thus used after its discovery. Sketches of expanded palps were made using a camera lucida. Other genitalia drawings were made using a Leica compound microscope with a camera lucida. For the latter, specimens were temporarily mounted as described by Coddington (1983). Palps were made transparent by immersion in methyl salicylate (Holm 1979). For SEM examination, specimens were cleaned ultrasonically for one minute and then transferred to 100% ethanol overnight. The specimens were then dissected and critical point dried. Five preparations were made for each species: abdomen of both sexes, prosoma of both sexes with all legs but 4th removed, and male palp. Specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin, and then sputter coated for examination with a LEO 1410 VP SEM. Digital images were made of the habitus and cleared epigyna using a Nikon digital camera attached to both dissecting and compound microscopes. All drawings were rendered in Adobe Photoshop, and plates were composed and labelled, in Adobe Illustrator. All artwork and photos are by the author, unless otherwise indicated.

Interpretation of palpal sclerites

Exline and Levi (1965) found it straightforward to interpret *Synotaxus* palpal sclerites and proposed homologies with those of theridiids. They indicate the presence of both conductor and median apophysis in *Synotaxus*, at least in *S. turbinatus*. The conductor was indicated at the back of the theridioid tegular apophysis, a small sclerotised part of the TTA surrounded by less sclerotised region, and a process of the TTA was presumed to be the MA. I find this interpretation of the *Synotaxus* palpal sclerites to be problematic, but have not been able to solve this problem adequately. It appears to me that only a single large sclerite, the TTA, is present. It is complex, bears several processes, and is not uniformly sclerotised. During dissection, however, it separates from the palp as a single unit. This may represent the partial, or complete, fusion of the MA and C with the TTA. Alternatively, however, and more consistent with outgroup comparison, and (the admittedly meager) ontogenetic evidence (Bhatnagar and Rempel 1962; Coddington 1990) such fusion appears a less plausible explanation than a transformation of the TTA and loss of the C and MA. The related nesticids also have a large, complex, TTA, while retaining both the C, and a large MA. The MA and C of both nesticids and theridiids are well separated from the TTA, both topologically, and at least in the latter, ontogenetically (Bhatnagar and Rempel 1962). I thus presume the C to be lost in *Synotaxus* and the MA to be lost in at least some species (Fig. 2*I*). However, in *S. monoceros* a small outgrowth is present ventrally on the tegulum which may be the MA (Fig. 2*C*, *G*; 3*C*). As discussed above, Griswold *et al*. (1998) likewise consider only a single sclerite (in addition to the embolus) to be present in *Synotaxus*, but label it as C, as they do the same sclerite in other synotaxids. Further work is clearly needed to solve palpal sclerite homologies in these taxa; in general, the crucial problem of sclerite homologies is far from solved (Coddington 1990).

Abbreviations

Fig. (upper case F) refers to a figure in this publication, fig. (lower case f) to figures in other publications. All measurements are given in millimetres (mm).

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinnerets
AMNH	American Museum of Natural History, New York, USA
AS	accessory sac
C	conductor
CD	copulatory ducts
CY	cylindrical gland spigot(s)
E	embolus
FD	fertilisation ducts
Fr	frame thread
MA	median apophysis
mAP	minor ampullate gland spigot(s)
MAP	major ampullate gland spigot(s)
MCN	Museu de Ciencias Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil
MCZ	Museum of Comparative Zoology, Harvard, Cambridge Massachusetts, USA
NMNH	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
Mpt	most parsimonious tree
NS	non-sticky silk
PC	paracymbium
PI	piriform gland spigot(s)
PLS	posterior lateral spinnerets
PMS	posterior median spinnerets
S	spermathecae
SS	sticky silk
ST	subtegulum
T	tegulum
TTA	theridioid tegular apophysis

Results and discussion

The analysis of the combined matrices resulted in a single most parsimonious cladogram (L = 889 CI = 40, RI = 76) (Fig. 1). The same trees resulted from the three different treatments of characters **62** and **80** (the trees are, of course, shorter when the two are deactivated). Tree statistics reported here are based on the analysis that treats them as '?' for *Synotaxus*. The results are the same whether using amb = or amb –. Successive weighting results in a single tree, differing only in that *Pholcomma* Thorell, 1869 and *Carniella* Thaler & Steinberger, 1988 swap places (the same happens when A04 is analysed alone). The large number of unknown and inapplicable entries seemingly did not cause problems, either in loss of resolution or in spurious results—all nodes are supported by character data. The results are congruent with those obtained with each dataset analysed separately. The most parsimonious tree conflicts with Griswold *et al*. (1998) only in the position of Hadrotarsinae as sister to remaining theridiids (hadrotarsines also nest within the Theridiidae in Arnedo *et al*. (in press), see discussion in Agnarsson in press). The recent transfer of *Synotaxus* out of Theridiidae (Forster *et al*. 1990) is thus again strongly corroborated (see also Griswold *et al*. 1998). Placing *Synotaxus* inside Theridiidae adds minimally 20 extra steps (five if placed sister to Theridiidae), and placement as sister to Argyrodinae (32 extra steps) or inside it (up to ~50 extra steps) is clearly an inferior explanation of the data. Similarities shared with argyrodine theridiids, such as abdomen elongated and extended beyond the spinnerets (Fig. 2*F*, *J*) are clearly convergent. *Synotaxus* lacks several theridiid synapomorphies. Thus unlike in theridiids, *Synotaxus* male palpal tibia is not distally broadened (**14**, Figs 3*A*, 4*A*; compare with fig. 4E), paracymbium is present (**29**, Fig. 3*A–B*, *E*), bulb-to-cymbium lock mechanism (**31**, fig. 31F) is absent, alveolus is central rather than mesal on the cymbial margin (**41**, fig. 92D–I, M), MA lacks a loop of sperm duct (**72**, figs 90F, 91A) and a distal hood on MA (**78**, fig. 31F), anterior and posterior PLS AG spigots are not flattened (**215** and **216**, Fig. 5*B–C*; compare with Fig. 11*B*), PMS mAP nubbins are present (**220**, Fig. 5*B–C*), and more than two PMS AC spigots are present (**222**, Fig. 5*B–C*; compare with fig. 18G). *Synotaxus* furthermore lacks synapomorphies of theridioids (Nesticidae plus Theridiidae) having, for example, more than two colular setae (**175**, Fig. 5*E–F*; compare with fig. 9D), a rectangular orb web rather than a cobweb (**225**, Fig. 6*A–C*; compare with figs 96D–F, 99A–B, 100A–F, 101A–F), and sticky silk in the sheet rather than on gumfoot lines (**227**, Fig. 3*C*; compare with figs 96F, 97B–D, 101B, D). Also *Synotaxus* lacks a regular row of long serrated setae on the male palpal tibial rim (**16**, Fig. 3*C*; compare with fig. 13C), abdominal stridulatory picks (**150**, fig. 18B–D), and dorsal supra-pedicellate proprioreceptors (**163**, fig. 43A–B).

Unsurprisingly, some of the features classically linking *Synotaxus* to theridiids reflect superficial similarities that break down under further scrutiny. The presence of a tarsal comb has been one of the primary pieces of evidence in this erroneous placement. However, despite some serrated setae on the fourth tarsus of *Synotaxus* (Fig. 5*I*), these share little similarity with the theridiid comb, as exemplified, for example, by the argyrodine *Ariamnes* Thorell, 1869 (Fig. 5*J*).

The web of *Synotaxus* (Fig. 6*A–C*), and the method of its construction, have been relatively well documented (including for *S. turbinatus*, *S. ecuadorensis* and an undescribed species). It seems to share more point similarities with orbs than with the cobwebs of theridiids (Eberhard 1977, 1995). Similarities with araneoid orbs include: a planar vertical web, frame threads, highly stereotyped construction of both dry and sticky lines, and frequent web destruction and renewal. Most theridiid webs are three dimensional, without typical frame threads, their construction is less stereotyped and the web is typically mended by patching, rather than being destroyed and renewed (see Benjamin and Zschokke 2003, and references therein). The webs of all *Synotaxus* species hitherto observed are nearly identical (the unique web of *S. ecuadorensis* is an exception): a planar, vertical sheet, with long vertical lines of dry silk on the sides and in the centre of the web (frame threads), forming usually three to several modules, or 'unit webs' (Fig. 6*A–C*, nomenclature from Eberhard 1977). In each module there are straight horizontal dry silk lines, and typically one to three jagged vertical lines
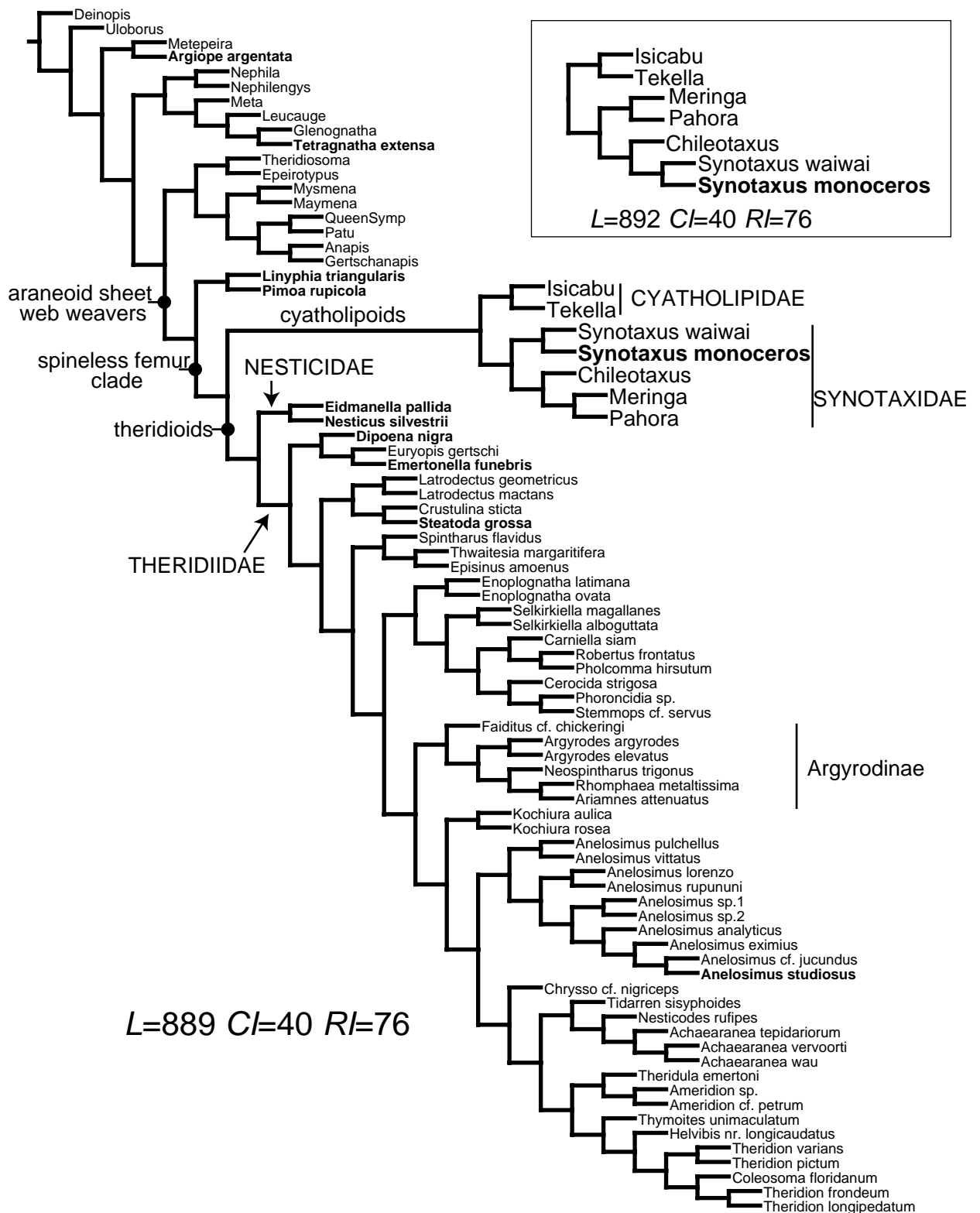
Fig. 1. The single most parsimonious cladogram of the fused matrices (L = 889, CI = 40, RI = 76). Taxa with genus names only are from Griswold *et al*. (1998), taxa with species epithets spelled out are from Agnarsson (in press), 'bold' taxa are shared. The results mirror those of Griswold *et al*. (1998) and Agnarsson (in press); habitus similarities of *Synotaxus* and Argyrodines are clearly convergent. The detached clade shows the changes in the position of *Synotaxus* and *Chileotaxus* in the single most parsimonious cladogram obtained when new data are added (see Methods), indicating sister relationships of these taxa.

(one- to three-stranded unit webs) with sticky globules (Fig. 6*C*). Three-stranded modules are most common, while narrower modules are often formed at the webs exterior; some units are, furthermore, vertically asymmetrical. The webs of *S. waiwai,* sp. nov. and *S. monoceros* are here described for the first time, and are identical to those of *S. turbinatus*; this chicken-wire like web or 'rectangular orb' (see Eberhard 1977) thus seems synapomorphic for the genus.

Some aspects of the web of the synotaxid *Chileotaxus sans* Platnick, 1990 (Fig. 6*F*) are shared with *Synotaxus*. As in *Synotaxus*, *C. sans* web cells are relatively large and the web is built from a horizontal leaf, under which the spider resides (Fig. 6*F*). *Chileotaxus sans* webs also have relatively long and uninterrupted exterior non-sticky frame threads (the last is also shared with many cyatholipoids, e.g. *Wanzia fako* Griswold, 1998 (Griswold 1998, Figs 18–19, but note how dense its sheet is). However, instead of being planar like *Synotaxus* webs, the *C. sans* web is dome-shaped around the centre of the leaf and does not have a regular *Synotaxus* 'chicken-wire like' pattern to it (Fig. 6*F*). The resemblance is close to that of *S. ecuadorensis* (see Eberhard 1995, Fig. 1), with only a single module and sticky silk spread throughout the sheet. The webs of other synotaxids are little known, but at least some build sheet webs with knock-down threads, resembling those of linyphiids (Forster *et al.* 1990; Griswold *et al*. 1998). As *C. sans* also shares morphological similarities with *Synotaxus*, beyond those shared by all synotaxids, the genera may closely related. Characters that may unite them include: pale green colouration, abdomen extending beyond the spinnerets, labium not rebordered, web structure, retreat locus and posture in web. If these characters (see methods) are coded accordingly for all taxa in the fused matrix, a single most parsimonious cladogram is obtained (*L* = 892, *CI* = 40, *RI* = 76), where the two do indeed become sister taxa (Fig. 1; note, however, that simply cherry-picking putative synapomorphies of the two genera is biased; a cladistic review of all synotaxid genera is necessary for a strong test). Unlike other synotaxids the two also have cheliceral grooves without teeth, the femora are not basally thickened, the tibial spur is usually absent (but a patellar one present in *Synotaxus*), and the male abdomen is not modified anteriorly.

The monophyly of Synotaxidae rests on three characters (the same as in Griswold *et al*. 1998): incised retrolateral cymbial margin (Fig. 3*D*), and complex and terminally situated palpal sclerite (be it homologous to the TTA, as presumed here, following Exline and Levi (1965), Coddington (1990) and Agnarsson (in press) or to the C, as presumed by Griswold *et al*. 1998). As the latter two characters are shared e.g. with Nesticidae, further work is clearly needed to adequately circumscribe and analyse the intergeneric relationships of the Synotaxidae.

Interestingly, with the change in topology of *Synotaxus* and *Chileotaxus* resulting from the addition of new data (see

above), the presence of a single PLS CY spigot becomes an additional unambiguous synapomorphy of the cyatholipoids (reversed in *Synotaxus*).

Taxonomy

Family **Synotaxidae** Simon

Synotaxeae Simon, 1894: 494.
Synotaxidae Forster, Platnick & Coddington, 1990: 110.

Diagnosis

Synotaxids can be diagnosed by an incised retrolateral cymbial margin (Fig. 3*D*), and an excavate paracymbium. Many other synotaxid features (e.g. Forster *et al*. 1990), such as complex, and terminally situated palpal sclerite, femora basally thickened, tibial and patellar spurs, and male abdomen modified anteriorly are either shared with other related taxa, or occur only sporadically in the family.

Description

For a description of this highly variable family, see Griswold *et al*. (1998: 12–13).

Genus *Synotaxus* Simon

Synotaxus Simon, 1894: 495, fig. 495–497 (*nomen nudum*).
Synotaxus Simon, 1895: 131.
Type species by original designation: *Synotaxus turbinatus* Simon 1895 (indicated in Simon 1894; see also Exline and Levi, 1965).

Diagnosis

The highly regular 'rectangular orb' web (Fig. 6*A–C*) separates *Synotaxus* from all other synotaxids. *Synotaxus* differs from synotaxids other than *Chileotaxus* by: cheliceral grooves without teeth, femora not basally thickened, tibial spur usually absent (Figs 2*A–B*, *G–H*; 3*A–B*; 4*A–B*), and male abdomen not modified anteriorly. Males of *Synotaxus* differ from all synotaxids by having a stout patellar spur (**20**, Figs 3*A–B*, *H*; 4*A–B*).

Description

Pale green (white in alcohol) spiders with long abdomen (up to 4–5× prosoma length), extending beyond spinnerets. Legs long and thin, especially in males (leg I up to 4–5× body length) (Figs 2*F*, *J*; 6*D–E*). Body and legs covered with long, fine, semi-erect setae, often lost in preserved specimens. Several (~5–8) stouter setae in row parallel to pedicel on abdomen, presumably proprioreceptors (see Agnarsson in press). Carapace wide and flat. Anterior median eyes slightly the largest, others subequal (Figs 3*F–G*, 4*I*), both eye rows recurved. Sternum as wide as or wider than long, convex, extending between coxae IV, which are far apart. Labium separated by seam, not rebordered. Chelicerae weak, with three teeth and sometimes a denticle prolaterally, 2–5 denticles retrolaterally. Colulus fairly large, usually bearing
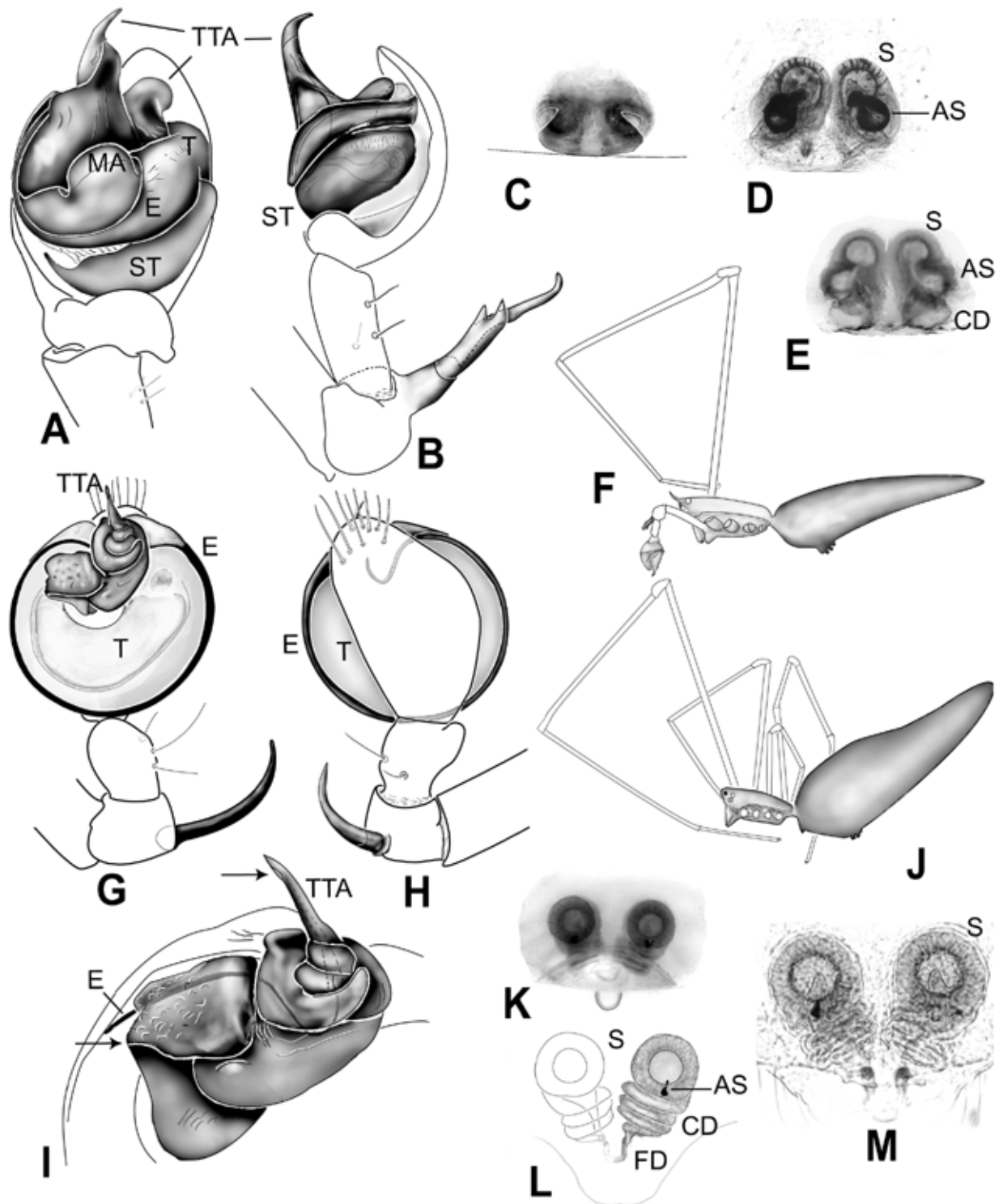
Fig. 2. *A–F Synotaxus monoceros*. *A*, palp ventral; *B*, palp ectal; *C*, epigynum ventral; *D*, cleared epigynum dorsal, note large sclerotised accessory sacs (AS), whose function is unknown; *E*, ditto, ventral, exact paths of fertilisation and copulatory ducts remain ambiguous; *F*, male habitus. *G–M*, *Synotaxus waiwai*, sp. nov. *G*, palp ventral; *H*, palp dorsal; *I*, details of the TTA. This complex sclerite comes off in one piece, but may represent fusion of palpal sclerites, the folded part (lower arrow) may be the MA, the TTA is excavate and the E enters it basally and exits through an opening at its tip (upper arrow); *J*, female habitus; *K*, epigynum ventral; *L*, details of spermathecae and ducts, note small AS; *M*, cleared epigynum ventral.

3–4 setae (Fig. 5*E–F*). Suprapedicellate stridulatory nubbins present, but no stridulatory picks (see Agnarsson in press). Posterior tip of abdomen ridged (Fig. 4*G*), with modified setal bases (Fig. 5*H*). Araneoid PLS triplet not functional in adult males (Fig. 4*H*). Spinnerets with all araneoid spigot types present (Fig. 5*A–D*), PLS AG larger than other spigots (Fig. 5*B–C*), CY round, smooth and without a distinct base (Fig. 5*B*), FL small (Fig. 5*B*); three AC on PMS, PMS mAP nubbin distinct (Fig. 5*B*). ALS with a stout, strongly serrate seta (Fig. 5*D*) and piriform field with 40–50 spigots.

Some serrated bristles on tarsi IV present in some species (Fig. 5*I*). Female palpal tarsus with row of serrated seta, and 'sustentaculum-like' bent tipped setae anteriorly (Fig. 3*I*). Tarsal organs small (Fig. 4*D*). Legs thin and very long, relative leg and segment length similar in all species (see leg measurements Tables 1 and 2 for *S. monoceros*).

Males with grossly enlarged macrosetae, or spurs, on palpal patella; sometimes also on palpal femur or tibia (Figs 2*B*, *G–H*; 3*A–B*, H; 4*A–B*). Male palpus with characteristic embolus (Figs 2 *A*, *G*; 3*C*; 4*A*) and terminally situated, large and complex, excavate tegular apophysis (Figs 2*A*, *I*; 3*C*; 4*C*). This apophysis is presumably homologous to the theridioid tegular apophysis, see Exline & Levi 1965; Agnarsson in press). Both C and MA presumably absent (see methods), albeit in *S. monoceros* a small outgrowth is present ventrally on the tegulum which may be a vestigial MA (Fig. 2*C*, *G*; 3*C*).

Paracymbium cup shaped, situated proximally on cymbial margin, which is strongly incised (Fig. 3*D*, 4*E*). Epiandrous gland fusules irregularly (not in a clear row, or groups) arranged on plate just above genital furrow (Fig. 4*F*). Epigynum simple plate with two roundish openings caudally (Figs 2*C–E*, *K–M*; 5*G*). Spermathecae and ducts sclerotised, usually visible through integument. A strongly sclerotised sac, or sclerite (here termed accessory sac), associated with spermathecae (Fig. 2*D–E*, *L*), its function (if any) is unknown.

Web highly regular, chicken-wire like vertical sheet, in two to several modules (Fig. 6*A–C*, see below), although only a single module in *S. ecuadorensis* (Eberhard 1995).

Composition

Synotaxus currently contains six species: S. *ecuadorensis* Exline, 1950, *S. leticia* Exline & Levi, 1965, *S. longicaudatus* (Keyserling, 1891, *S. monoceros* (Caporiacco, 1947), *S. pupularum* Exline & Levi, 1965, *S. turbinatus* Simon, 1895, and *S. waiwai*, sp. nov.

These, however, only represent a portion of *Synotaxus* diversity. Numerous other new species remain to be described, e.g. from Bolivia, Peru and Venezuela, (personal observations), and Brazil (A. Santos, personal communication). Furthermore, Exline and Levi (1965) reported considerable geographical variation in some species (see

e.g. their figs 1–15) and at the least *S. turbinatus sensu* Exline & Levi (1965) is most likely a species complex.

Phylogenetics

Putative *Synotaxus* synapomorphies include: patellar spur (Figs 2*B*, *G–H*; 3*A–B*, *H*; 4*A–B*), TTA excavate, forming a tunnel for embolus (Fig. 2*I*), strongly sclerotised accessory sac associated with spermathecae (Fig. 2*D–E*), female palpal tarsus with 'sustentaculum-like' setae (Fig. 3*I*), posterior tip of abdomen ridged (Fig. 4*G*), modified setal bases on abdomen (Fig. 5*H*), 'chicken-wire' or 'stranded' web type (Fig. 6*A–C*), web in two or more independent modules (only one in *S. ecuadorensis*); sticky silk-dry silk construction interspersed (data lacking for other synotaxids); formation of drag line 'rung' (see Eberhard 1995: 28). This list is based on observations on *Synotaxus* (see introduction), further morphological studies on other synotaxids may show some of these characters are shared with other genera.

Distribution

Synotaxus is widely distributed in tropical America, from Central America and the Caribbean to Argentina (Fig. 7). Some species, e.g. *S. turbinatus* Exline & Levi, and *S. longicaudatus* appear widespread (but see above). Most *Synotaxus* appear to be rare, or are at least rarely collected. *Synotaxus waiwai*, sp. nov. was encountered several times nightly in a survey in Guyana (personal observation); at least locally, it is thus fairly common. The distribution of all described *Synotaxus* is shown on Fig. 7.

Synotaxus monoceros (Caporiacco)

(Figs 2*A–F*, 3*A–I*, 5*F*, 6*B*, *D*; Tables 1–2)

Argyrodina monoceros Caporiacco, 1947: 24. Male holotype from Two Mouths, Essequibo River, Guyana. In The Natural History Museum, London; not examined.
Conopistha monoceros Caporiacco, 1948: 649, figs 57–59 (male).
Synotaxus pupularum Exline & Levi, 1965: 183, figs 28–29 (female). Female holotype from vicinity of Port of Spain, Trinidad, Lesser Antilles, 1913 (R. Thaxter) (MCZ); examined. **Syn. nov.**

Material examined

Other material examined. **Guyana**: 1♀, lowland blackwater-rainforest, near Essequibo River just south of Gunns Landing, 1°36′45.7″N, 58°38′14.6″W, *c.* 50 m, 06–15.vii.1999, coll. J. Coddington, G. Hormiga, J. Miller, I. Agnarsson, M. Kuntner (NMNH); 1♀, 4♂, forest and plantations on bank of Essequibo River just north of Bartica, 6°28′03.4″N 58°37′10.7″W, coll. I. Agnarsson, M. Kuntner (NMNH); 2♀, Vicinity of Port of Spain, Trinidad, Lesser Antilles, 10°40′N, 61°30′W, 1913, coll. R. Thaxter (MCZ).

Additional records

1♂, Two Mouths, Essequibo River, Guyana; 1♂ Ishear-tun (on label, other spellings: Ishelton, Isherton), ~20 km east of Rupununi River, 2°19′N 59°22′W (AMNH).
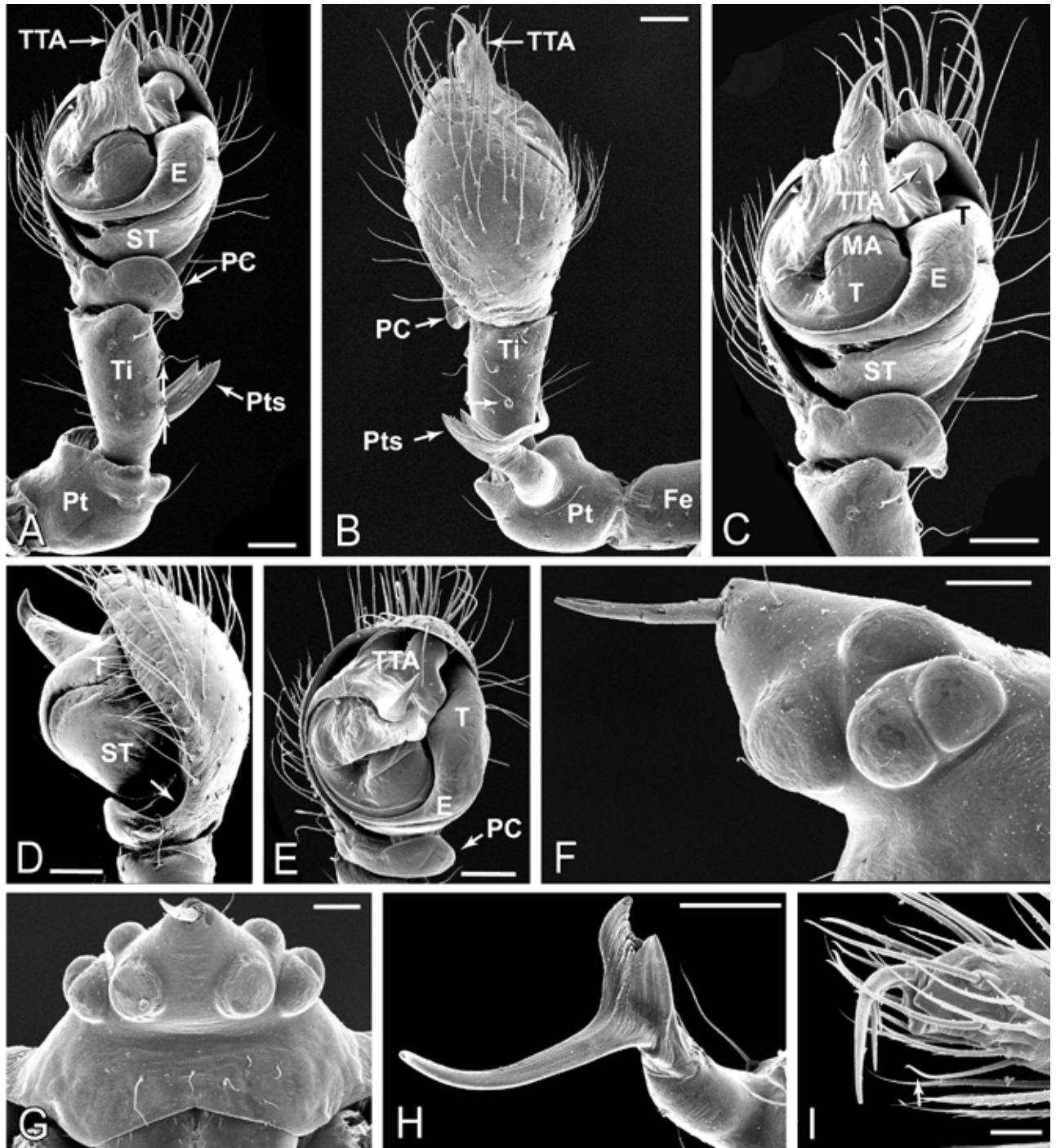
Fig. 3. *Synotaxus monoceros*. *A–H*, male. *A–D*, palp. *A*, ventral; *B*, dorsal; *C*, ventral bulb; *D*, ectal, note incised cymbium (arrow) a synotaxid synapomorphy; *E*, apical; *F*, ocular area from side, the horn is diagnostic for the species, but a similar horn is present in some undescribed species (personal observation); *G*, ocular area front view; *H*, patellar spur of the male palpus, the three pronged condition is diagnostic for *S. monoceros*; *I*, female fourth tarsal claw, note a sustentaculum-like setae (arrow). Scale bars: *A–H* 100 µm; *I*, 20 µm.
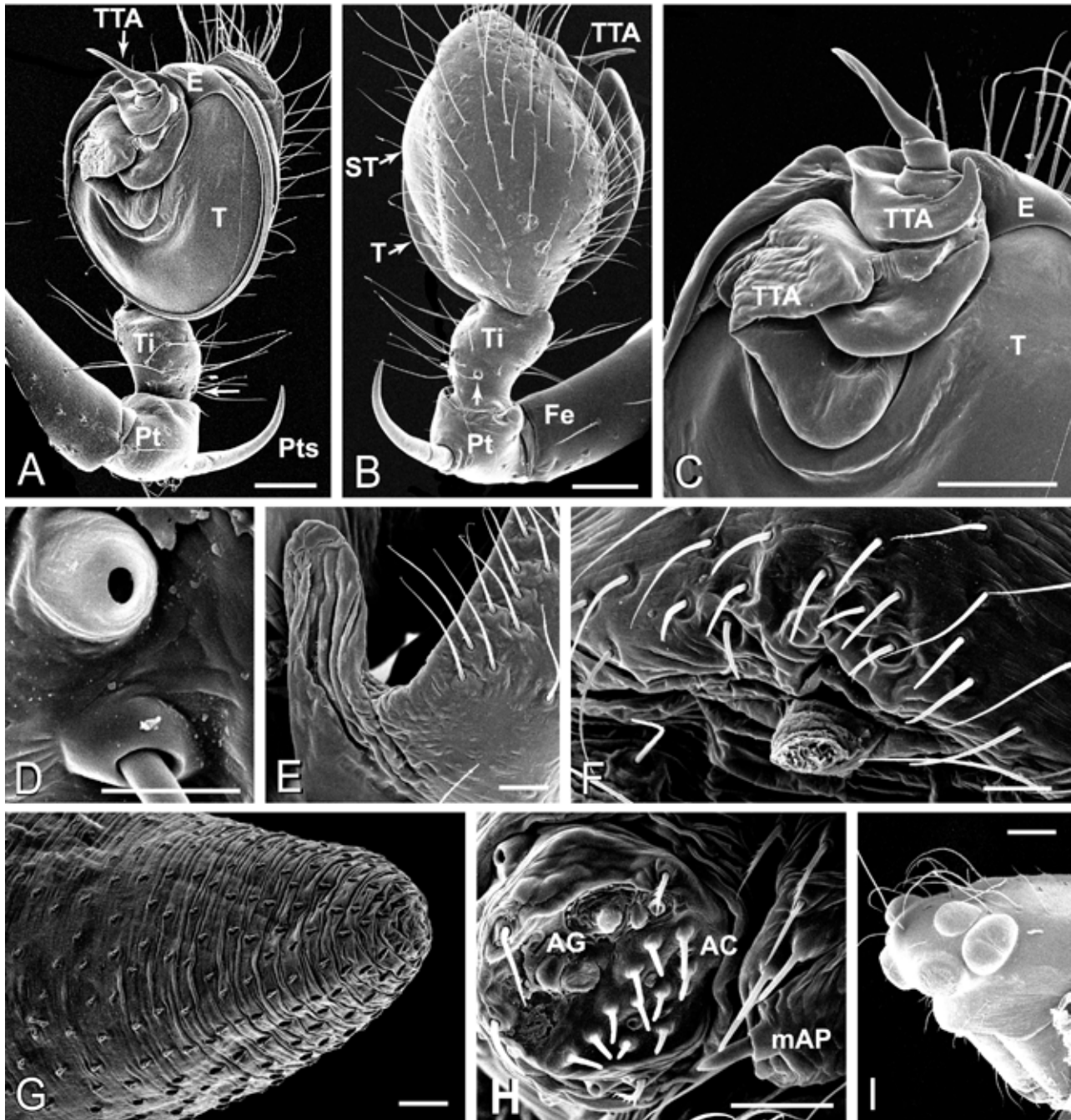
Fig. 4.   A, *Synotaxus waiwai*, sp. nov. *A–H*, male. *A–D*, palp. *A*, ventral; *B*, dorsal; *C*, details of sclerites; *D*, tarsal organ; *E*, paracymbium; *F*, epiandrous gland spigots. *G*, posterior tip of abdomen; *H*, PLS and PMS; *I*, ocular area. Scale bars: *A–C*, *G*, *I*, 100 µm; *E–F*, *H*, 20 µm; *D,* 10 µm.

Diagnosis

The male can be easily distinguished from other described species of *Synotaxus* by the unique unicorn like projection in the eye region (Figs 2*F*; 3*F–G*), the unique three-pronged patellar spur (Fig. 3*H*) and by details of the palp, such as the large, bulky, and distally bent TTA (Figs 2*A–B*; 3*A–E*). Females may be separated by the depth of the groove under the anterior median eyes that is greater than in other *Synotaxus*, and by the shape of the genital plate and internal genitalia (Fig. 2*C–E*).

Description

Male (Guyana, Essequibo River (NMNH)).

Total length 4.90. Prosoma 1.50 long, 1.10 wide, 0.60 high. Ocular area protruded, narrowing to blunt tip that bears large spur (Fig. 3*F–G*). Carapace flat, 0.10 mesally. Sternum 0.70 long, 0.70 wide. Abdomen 3.50 long, 0.90 wide, 1.45 high. Eyes subequal in size ~0.10 across, round (Fig. 3*F–G*). AME conspicuously dark, others white. PME separation more than 2× PME diameter, AME separation about equal to AME diameter. Lateral eyes juxtaposed (Fig. 3*F*), PLE close to PME. Clypeus slightly more than 2× AME diameter (Fig. 3*G*). Chelicera with 2–3 prolateral teeth and 3–5 small retrolateral denticles. Colulus with prominent distal protrusion (Fig. 5*F*). Legs very long and thin, e.g. leg I over 3× longer than total length of the animal (Fig. 2*F*).

Femur I ~35–40× longer than wide, tibia I about over 45× longer than wide, thickening slightly at the distal tip (Table 1). Patella, distal tip of tibia, and metatarsus slightly darkened. Leg setae numerous, macrosetae absent. Trichobothria distal on metatarsi I (0.90), II (0.90), and III (0.75), absent on IV. Bristles ventrally on tarsus IV unmodified, with no marks of serrations. Tarsal organs small, barely visible using light microscopy. Pedipalp as in Figs 2*A–B*; 3*A–E*.

Female (Guyana, Essequibo (NMHN))

Total length 6.30. Prosoma 1.65 long, 1.05 wide, 0.60 high, light green (white in alcohol), interocular area with protruding long, thin setae. Carapace flat. Sternum whitish, 0.70 long, 0.70 wide. Abdomen 4.65 long, 1.75 wide, 1.55 high, broadest anterior to middle, narrows evenly to posterior end. Colulus fairly large, bearing three colular setae. Eyes subequal in size ~0.08, oval. AME dark, others white. PME separation 2× PME width, AME separation 1.3× AME diameter, PME touching PLE and lateral eyes juxtaposed. Clypeus height ~2.0× AME diameter. Chelicerae with three prolateral teeth, 4–5 denticles retrolaterally. Legs long and thin, shorter than in male, whitish, with patella, distal tip of tibia, and metatarsus darker.

Femur I over 30× longer than wide, tibia I over 45× longer than wide, thickening slightly at the distal tip (Table 2). Numerous setae on legs but, no stout macrosetae. Trichobothrium distal on metatarsi I (0.90), II (0.90), and III (0.75), probably absent on IV. Tarsus IV with a few serrated bristles, not theridiid like (see Fig. 5*I–J*). Epigynum as in Fig. 2*C–E*, lightly sclerotised externally.

Variation

The size and shape of the abdomen varies somewhat: as for most spiders, the abdomen can increase greatly in size after a meal and in particular in a gravid female; the posterior tip of the abdomen may be either straight or bent upwards in preserved specimens.

Natural history

Females make typical *Synotaxus* chicken-wire-like webs, as those described for *S. turbinatus* and *Synotaxus* sp. (Fig. 6*B*, see Eberhard 1977, 1995). The webs (two examined) are spun between two parallel vertical branches, 10–60 cm apart. Adult males appear not to make webs and are found under leaves, holding on to a few silk threads. A female was found guarding an egg sac in a small, non-typical web. The egg sacs are whitish, round and loosely woven. Habitat includes rainforest and plantations. Almost all specimens were collected 'looking up at night'. Therefore, as other *Synotaxus*, these seem to take down their webs daily and rebuild at night; generally placing their webs at least 50 cm above ground level.

Etymology

The species epithet, *monoceros* is a noun in apposition meaning unicorn, presumably referring to the ocular projection of the male.

Distribution

This species is so far known only from Trinidad and Guyana. It is the only species known from northern Guyana, but is much rarer than *S. waiwai*, sp. nov. in the south (Fig. 7).

Table 1. Measurements of male *Synotaxus monoceros* (NMNH).

	I	II	III	IV	Pdp
Femur	6.20	3.85	2.00	3.60	0.85
Patella	0.55	0.50	0.35	0.35	0.25
Tibia	5.30	3.05	1.20	2.55	0.30
Metatarsus	5.90	3.30	1.40	2.80	–
Tarsus	2.00	1.30	0.75	1.05	0.55
Total	19.95	12.00	5.70	10.35	1.95

Table 2. Measurements of female *Synotaxus monoceros* (NMNH).

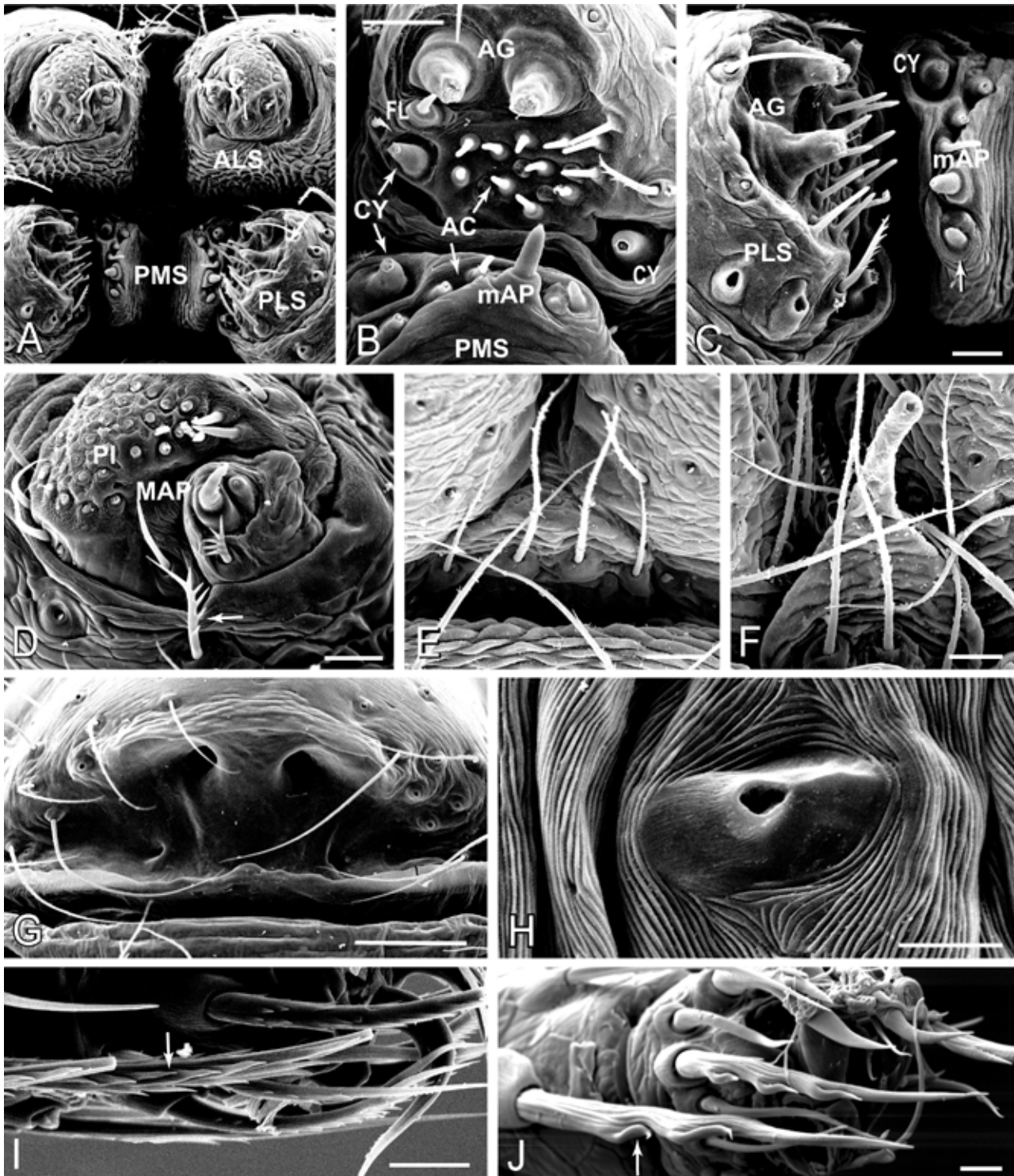|	I	II	III	IV	Pdp
Femur	5.15	3.25	1.60	3.35	0.65
Patella	0.55	0.50	0.30	0.40	0.20
Tibia	4.25	2.50	1.05	2.20	0.30
Metatarsus	4.65	2.65	1.15	2.40	–
Tarsus	1.55	1.15	0.65	0.95	0.55
Total	16.15	10.05	4.75	9.30	1.60

Fig. 5.   *A–H, Synotaxus waiwai*, sp. nov. *A–E, G–H* female. *A*, spinnerets; *B*, PMS and PLS; *C*, ditto, note round shape of AG's and the conspicuous PMS mAP nubbin (arrow); *D*, PLS; *E*, colulus; *F*, male colulus; *G*, epigynum, apical; *H*, spine base on abdomen. *I, Synotaxus monoceros* female fourth tarsus, showing the serrated setae (arrow), part of the synotaxid tarsal comb; *J, Ariamnes* sp. female fourth tarsus, an argyrodine with a typical theridiid tarsal comb setae (arrow). Scale bars: *A*, 100 µm; *B–J*, 10 µm.

Taxonomic remarks

Synotaxus monoceros (Caporiacco, 1947) was described based on a single male from British Guiana (now Guyana). Another male was reported by Exline and Levi (1965) also from Guyana and to date these are the only specimens of the species reported. *Synotaxus pupularum* Exline & Levi 1965 was described from two females from Trinidad (the male was unknown). No further specimens have been reported. Here, four males and two females, corresponding to these two nominal species, are reported from Guyana. A male was found within two metres of the females' web, north of Bartica, Guyana. Females from Guyana are identical to those from Trinidad, and it therefore seems simplest to conclude that these are conspecific.

Synotaxus waiwai, sp. nov.
(Figs 2*G–M*; 4*A–I*; 5*A–E*, *G–H*; 6*A*, *C–D*)

Material examined

Holotype.   1♂, Guyana, lowland blackwater-rainforest, near Essequibo River just south of Gunns Landing, 1°36′45.7″N, 58°38′14.6″W, *c*. 50 m, 06–15.vii.1999, coll. J. Coddington, G. Hormiga, J. Miller, I. Agnarsson, M. Kuntner (NMNH).
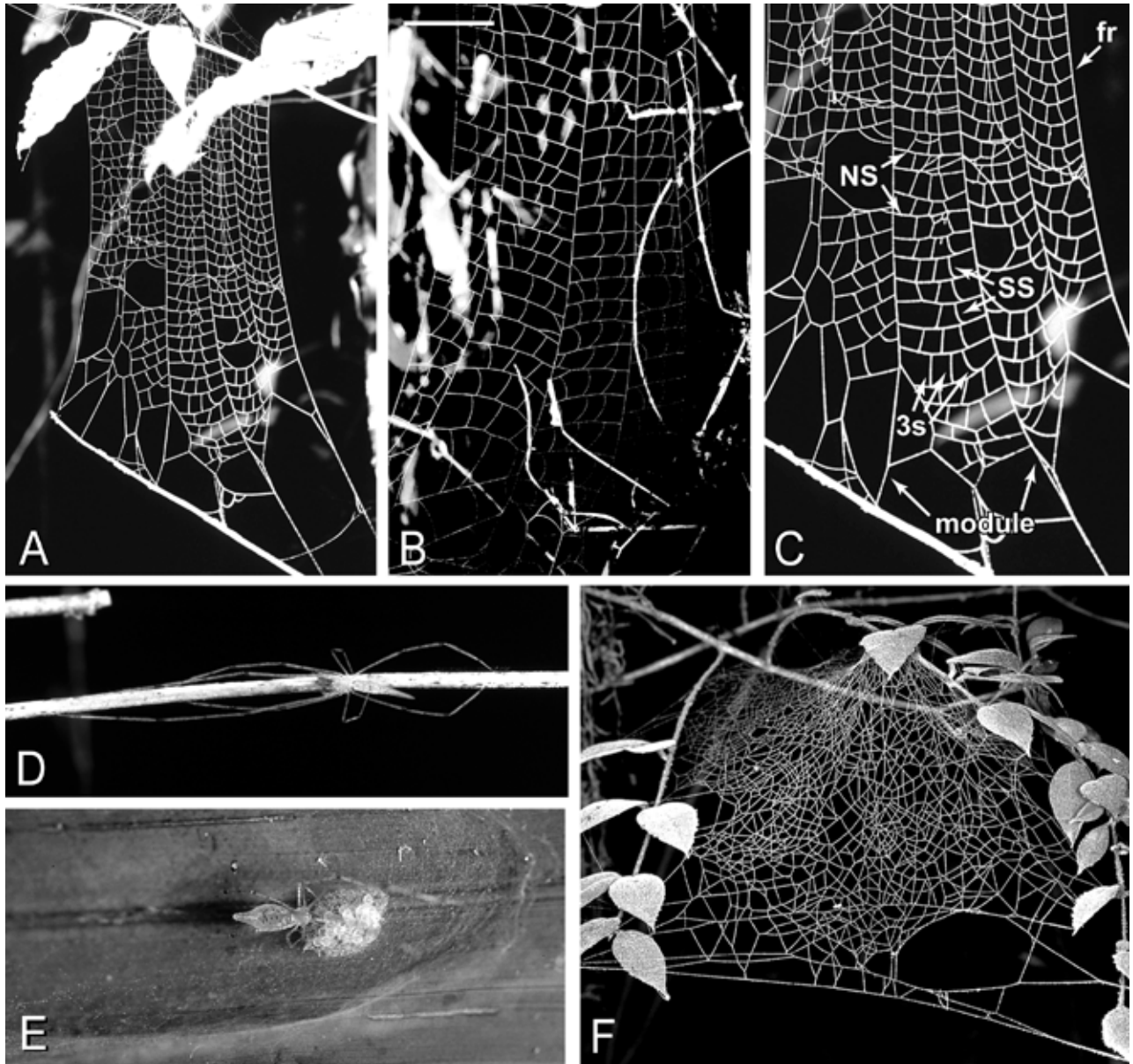
Fig. 6.   *A*, *Synotaxus waiwai*, sp. nov. female web, size ~45 × 20 cm (photo by M. Kuntner); *B*, *S. monoceros* female web, size ~55 × 25 cm; *C*, details of the *Synotaxus* web, made of three to several modules, each edged by a frame thread (fr), and containing non sticky (NS) horizontal threads and sticky (SS) vertical threads. Typically each module has three SS, a 'three stranded module' (3s). *D*, *S. monoceros* male habitus (photo by M. Kuntner); *E*, *S. monoceros* female guarding egg sac; *F*, *Chileotaxus sans* female web, size ~25 × 20 cm (photo by J. Coddington).

Paratypes.   13♂, 20♀, **Guyana**: lowland blackwater-rainforest, near Essequibo River just south of Gunns Landing, 1°36′45.7″N, 58°38′14.6″W, *c.* 50 m, 06–15.vii.1999, coll. J. Coddington, G. Hormiga, J. Miller, I. Agnarsson, M. Kuntner (NMNH).

Additional records

Brazil, Amazonas, Manaus, 3°06′07″S, 60°01′30″W, iv.1988–vi.1990, coll. E. Morato, 3 (MCN 23747); 1♂ (MCN 23748); Brazil, Manaus, Reserva Florestal Adolpho Ducke, 02°55′S, 59°59′W, 4.vii.1987, coll. J. Vidal, 1♀ (MCN 32563); Paraguay, Boquerón, Colonia Filadélfia, 22°21′0″S 60°1′60″W, 1.xi.1981, coll. I. Unger Peters, 1♂ (MCN 22597).

Diagnosis

The male can be easily distinguished from other species of *Synotaxus* by the large palpal tegulum extending beyond the cymbial cavity, very long embolus spiraling along the entire rim of the tegulum (Figs 2*G–H*, 4*A–B*), and a complex, folded TTA (Figs 2*I*, 4*C*). The simple patellar spur is also diagnostic (Figs 2*G–H*, 4*A–B*). Females may be identified by the copulatory duct with several (~4–5) loops, encircling the fertilisation duct (Fig. 2*L–M*).

Description

Male (holotype)

Total length 2.5. Prosoma 1.0 long, 0.9 wide, 0.40 high. Ocular area slightly protruded (Fig. 4*I*), with numerous long erect thin setae (easily lost in preserved specimens). Carapace flat, ~0.1 mesally. Sternum slightly wider (0.6) than long (0.55). Abdomen 1.50 long (range 1.4–1.8), 0.50 wide, 0.5 high. Colulus fairly large, with single pair of setae present. Eyes round, subequal in size, AME slightly enlarged. PME separation about 2× PME diameter, AME separation equal to AME diameter, laterals juxtaposed, PLE close to PME. Clypeus about equal to AME diameter.
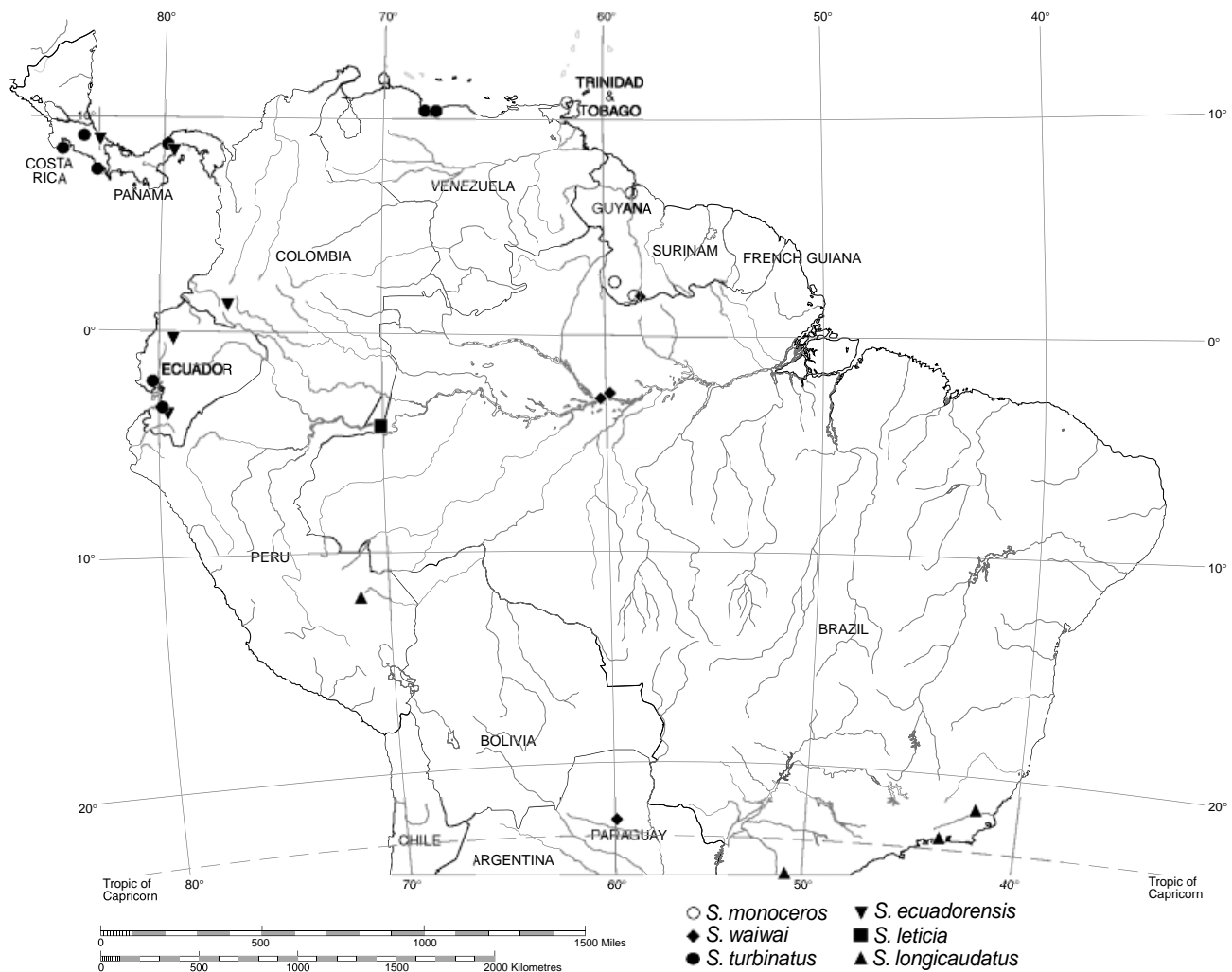

Fig. 7.   Known distribution of all described *Synotaxus* species. Record of *S. longicaudatus* from Peru probably represents an undescribed species (personal observation), '*S. turbinatus*' found in Costa Rica, Ecuador and Venezuela most likely represents a species complex (see Exline & Levi, 1965, figs 1–15). Undescribed species have been seen from French Guiana, Bolivia, and Peru (personal observations), and several occur in Brazil (A. Santos, personal communication).

Chelicera with 2–3 prolateral teeth, 3–5 retrolateral denticles. All legs very long and thin, 1st legs especially long, ~5× total body length; Leg I: femur 3.95, patella 0.30, tibia 3.40, metatarsus 3.60, tarsus 1.50. Relative leg and segment length as in other *Synotaxus*. Femur I over 30× longer than wide, not basally thickened, tibia I over 40× longer than wide, thickening slightly at the distal tip. Pedipalp as in Figs 2*G–I*, 4*A–D*.

Female *(paratype)*

Total length 3.9 (range 2.5–4.0). Prosoma 1.1 long, 0.90 wide, 0.50 high, interocular with a protruding long thin setae. Carapace flat, 0.1 mesally. Abdomen 2.7 long, 1.4 wide at widest point, 1.2 high, broadest just anterior to middle, then narrows evenly to posterior end. Colulus fairly large bearing three to four setae. Spinnerets anteriorly, ~3/4 of abdomen extending beyond them (Fig. 2*J*). Eyes subequal in size ~0.07 diameter, round. AME conspicuously dark, others white. PME separation 2× PME diameter, AME separation 1.4× AME diameter. Lateral eyes touching, PLE close to PME. Clypeus about 2× AME diameter. Chelicera with 2–3 prolateral teeth and 3–5 small retrolateral denticles. Legs very long and thin, leg I total length 11.65: femur 3.80, patella 0.40, tibia 3.10, metatarsus 3.10, Tarsus 1.20, relative leg length as in other *Synotaxus*.. Femur I ~35× longer than wide, tibia I over 50× longer than wide, thickening slightly at the distal tip. Numerous fragile (easily lost in preserved specimens) small setae on legs but macrosetae absent. Trichobothrium distal on metatarsi I–III, absent on IV. Tarsus IV with few serrated bristles, not theridiid like.

Epigynum as in Figs 2*K–M*, 5*G*, lightly sclerotised externally.

Variation

Male total length ranges from 2.2–2.8 mm, female total length from 2.5–4.0 mm (based on type series). The size and shape of the abdomen varies somewhat: the posterior tip of the abdomen can be either straight or bent upwards in preserved specimens.

Natural history

Web as in other *Synotaxus* (Fig. 6*A*, *C*), typically with four or more modules (*c.* 10 webs examined). Two females found guarding egg sacs in a small, non-typical web (Fig. 5*E*). The egg sacs are whitish, round and loosely woven. The preferred habitat seems to be rainforests. All specimens were collected 'looking up at night', or beating vegetation. Therefore, as other *Synotaxus*, these seem to take down their webs daily and rebuild at night; generally placing their webs at least 50 cm above ground level.

Distribution

Known from type locality near Essequibo River southern Guyana, the northern Brazilian Amazon, and one record from Paraguay (Fig. 7, records other than type locality are specimens identified by Adalberto Santos). An additional record of this species exists (one male and one female) collected by Jonathan Coddington, but the date and locality information are uncertain; probably collected in Brazil.

Etymology

The species epithet is a noun in apposition, in recognition of the hospitality, friendliness and help of the WaiWai people of Gunn's landing, Guyana.

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