CSIRO PUBLISHING

Invertebrate Systematics, 2017, **31**, 8–36
http://dx.doi.org/10.1071/IS15062

Finding hot singles: matching males to females in dimorphic spiders (Araneidae : *Micrathena*) using phylogenetic placement and DNA barcoding

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Abstract. Many orb-weaving spiders exhibit remarkable sexual dimorphism, hampering the matching of males and females in taxonomic studies. This is the case for the spiny *Micrathena* spiders, a species-rich Neotropical genus with 27% of its species known from a single sex. In this paper we document several undescribed *Micrathena* specimens, and test whether they belong to some of those incompletely known species. In order to do so, we: (1) tested the phylogenetic position of males and their putative females using a previous morphological dataset; (2) calculated genetic distances among individuals based on a fragment of the mitochondrial gene cytochrome *c* oxidase subunit I; and (3) examined their geographical distributions. These approaches, isolated or in combination, allowed us to identify and describe the previously unknown males of *M. embira* Levi, *M. reimoseri* Mello-Leitão, *M. exlinae* Levi, *M. miles* Simon, *M. spinulata* F.O. Pickard-Cambridge, *M. yanomami* Magalhães & Santos and *M. cornuta* (Taczanowski), and the female of *M. beta* di Caporiacco. We found that the males previously associated with *M. bicolor* (Keyserling), *M. cornuta* and *M. lata* Chickering had been incorrectly matched with females. The latter actually belongs to a hitherto unnamed species, herein described as *Micrathena perfida*, sp. nov. New geographical data are given for these and other *Micrathena* species. Our study highlights the importance of using different sources of data for matching the sexes in diverse groups with strong sexual dimorphism.

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Additional keywords: Araneae, cladistics, taxonomy.

Received 18 December 2015, accepted 17 June 2016, published online 16 March 2017

Introduction

Orb-weaving spiders are known for their remarkable sexual dimorphism. The Araneidae family contains classical examples of extreme sexual size dimorphism, such as *Nephila* Leach, 1815 and *Argiope* Audouin, 1826, in which females can be more than 10 times larger than the males (Vollrath 1998). Sexual dimorphism may also include significant differences in body morphology and colouration patterns (Cheng and Kuntner 2015). Matching males to females, especially in diverse groups, is a challenging task for taxonomists (Edwards 2013), and the situation is particularly difficult in groups with pronounced sexual dimorphism (e.g. Przybyłowicz and Tarcz 2015). A good example of this situation is the araneid genus *Micrathena* Sundevall, 1833, which contains 116 species (World Spider Catalog 2016) occurring in forested habitats from the southern USA to northern Argentina. While females are a conspicuous element of Neotropical spider communities, with their spiny and colourful abdomens, males are usually much smaller and lightly built, with darker and unarmed abdomens (Figs 1–5). This makes males much harder to collect and, consequently, rarer in collections than females. For instance, in two recent inventories in the Brazilian Amazon, 134 and 1040 adult *Micrathena* individuals were collected, but of those only 18% and 12.8% were males (AAN, unpubl. data). Also, as of 2016, the spider collection at Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, housed 113 *Micrathena* males, as opposed to 579 females. This male–female disparity in specimen availability leads to two main

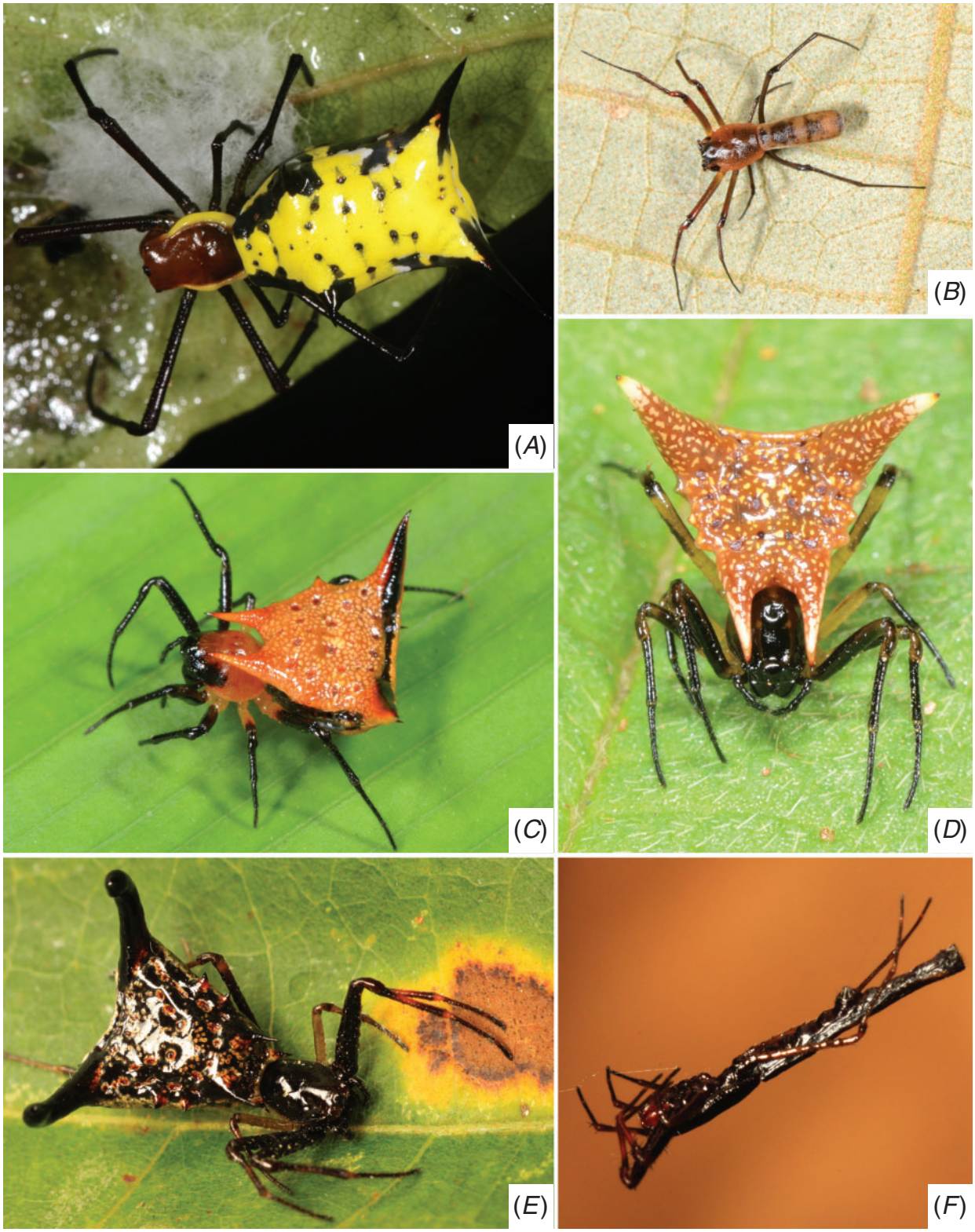

Fig. 1. Living *Micrathena* specimens. (*A*) *Micrathena miles*, female with egg-sac from Maynas, Loreto, Peru. (*B*) *Micrathena miles*, male from Maynas, Loreto, Peru (MUSM-ENT 510057). Approximately to scale regarding figure part *A*. (*C*) *Micrathena yanomami*, female from Tambopata, Madre de Dios, Peru (UFMG 19567). (*D*) *Micrathena yanomami*, female from Paucartambo, Cusco, Peru (MUSM-ENT 510056). (*E*) *Micrathena embira*, female from Porto Velho, Rondônia, Brazil. (*F*) *Micrathena embira*, male from the same locality. Photos *A–D* by A. Anker and P. H. Martins, *E*, *F* by F. U. Yamamoto.

consequences: (1) several species are known only from females (31 out of 116; only *Micrathena beta* di Caporiacco, 1947 is known only from the male); and (2) males are usually described subsequently, and their matching to existing females is often based on poor evidence.

The particularly difficult task of defining male–female associations in *Micrathena* has already been highlighted by Levi (1985) in his extensive revision of the genus. Prior to Levi's study, more than 77% of *Micrathena* species were known only from females, a proportion that decreased to 32% after his work. He also commented that matching males to females was the 'biggest problem of the genus' due to marked sexual dimorphism and high diversity. He overcame this matter by dividing the species (both males and females) into species-groups and associating them based on overlapping distributions (Levi 1985: 433). However, this geographic criterion can be difficult to apply as many species may occur in sympatry. For instance, an inventory in Porto Velho, in the Brazilian Amazon, revealed that as many as 26 species of *Micrathena* can be found in the same area (AAN, unpubl. data). Levi (1985) was aware of this problem, and admitted that the association between males and females was tentative in several cases.

Newly collected specimens are very important to complement the descriptions of species known from a single sex, and also to confirm the association of species known from both sexes. On recent field expeditions, we collected specimens of some poorly known *Micrathena* species: *M. beta*, *M. embira* Levi, 1985, *M. reimoseri* Mello-Leitão, 1935, *M. exlinae* Levi, 1985, *M. miles* Simon, 1895, *M. spinulata* F.O. Pickard-Cambridge, 1904 and *M. yanomami* Magalhães & Santos, 2011. All of these species have so far been known from a single sex, and most from only a few records (see Levi 1985; Magalhães and Santos 2011). In addition, several previously undescribed specimens, including males and females, were collected in these same areas (Table 1). It seemed clear that at least some of the undescribed specimens probably belonged to these species known from a single sex; however, matching them was not straightforward. For instance, our undescribed male #1 was collected in the same area as *M. miles* and *M. embira*, lacks a terminal apophysis, as would be expected for the male of *M. embira*, but has a hook on the coxa I, as expected for the male of *M. miles* (see Levi 1985). Additionally, in the recent inventory in Porto Velho several specimens of *M. bicolor* (Keyserling, 1864) and *M. cornuta* (Taczanowski, 1873) were collected. Although the two species are known from both sexes, the field sampling consistently yielded only males of the first species, and only females of the latter. Could the matching proposed by Levi (1985) for these species be wrong?

We considered that analysing males and females in a phylogenetic context would offer more robust evidence of association between the sexes than considering solely the geographic distribution and some morphological characteristics. *Micrathena* species can be sorted into species-groups, whose delimitation is reasonably clear for both sexes (Magalhães and Santos 2012). Although the use of morphological data to match dimorphic sexes may seem contradictory, we consider that the placement of both sexes in the same species-group along with their co-occurrence at collecting sites may represent strong evidence of conspecificity (see Edwards 2013; Barone *et al.* 2016). Another possibility is the use of molecular data, in which DNA sequences from both sexes can be compared (as opposed to morphological features, which more often than not are present in only one of the sexes). Molecular data have proven to be very useful in resolving taxonomic questions for groups in which the analysis of morphology alone is inconclusive. Examples include separating cryptic species in groups with low morphological variation (Clouse and Wheeler 2014), clarifying ecological interactions (Hulcr *et al.* 2007), associating different developmental stages of taxa with life cycles that exhibit remarkably different forms (e.g. cnidarians; Miranda *et al.* 2010) and, of course, associating males to females in sexually dimorphic species (Tanikawa 2011; Przybyłowicz and Tarcz 2015; Barone *et al.* 2016).

In this paper, we test male–female conspecificity hypotheses for *M. beta*, *M. embira*, *M. reimoseri*, *M. exlinae*, *M. miles*, *M. spinulata* and *M. yanomami* (all known from a single sex), and *M. cornuta*, *M. lata* and *M. bicolor* (known from both sexes, but with a dubious association between males and females). Specifically, we wanted to test whether some of the recently collected and yet undescribed specimens belong to the species known from a single sex, and whether the current male–female matching in *M. cornuta*, *M. lata* and *M. bicolor* could be wrong. We followed three approaches to verify our hypotheses: (1) determining the phylogenetic placement of each of the seven species and each of the undescribed specimens by including them in the morphological matrix of Magalhães and Santos (2012); (2) calculating genetic distances between males and females based on a fragment of the mitochondrial gene coding for the cytochrome *c* oxidase subunit I (COI); and (3) checking geographic distributions, with data from recent field surveys. After matching males to their females, we describe and illustrate them for the first time, and provide new records for these species.

We dedicate this paper to the recently deceased Herbert W. Levi, who devoted most of his life to studying the systematics of orb-weaving spiders, such as *Micrathena*. Although we herein suggest some modifications to combinations he proposed, it is needless to say that he got most of the species right, and that without his immense contribution, studies like our own would not be possible. We hope and believe that his fine work will continue to inspire generations of spider taxonomists.

Materials and methods

Phylogenetic inference based on morphology

To infer the phylogenetic position of the undescribed specimens and their candidate males or females, we included them in the discrete character matrix of Magalhães and Santos (2012). At first, we scored the undescribed specimens and their putative pairs (*M. beta*, *M. embira*, *M. reimoseri*, *M. exlinae*, *M. miles*, *M. spinulata*, *M. yanomami*, *M. cornuta*, *M. lata*, *M. bicolor*) as separate terminal taxa. Thus, at this phase each 'species' was represented by two terminal taxa, e.g. '*M. embira* female' (with all male characters coded as missing data) and 'Undescribed male #1' (with all female characters coded as missing data). This approach is similar to that employed by Platnick and Shadab (1978) and Barone *et al.* (2016), and the

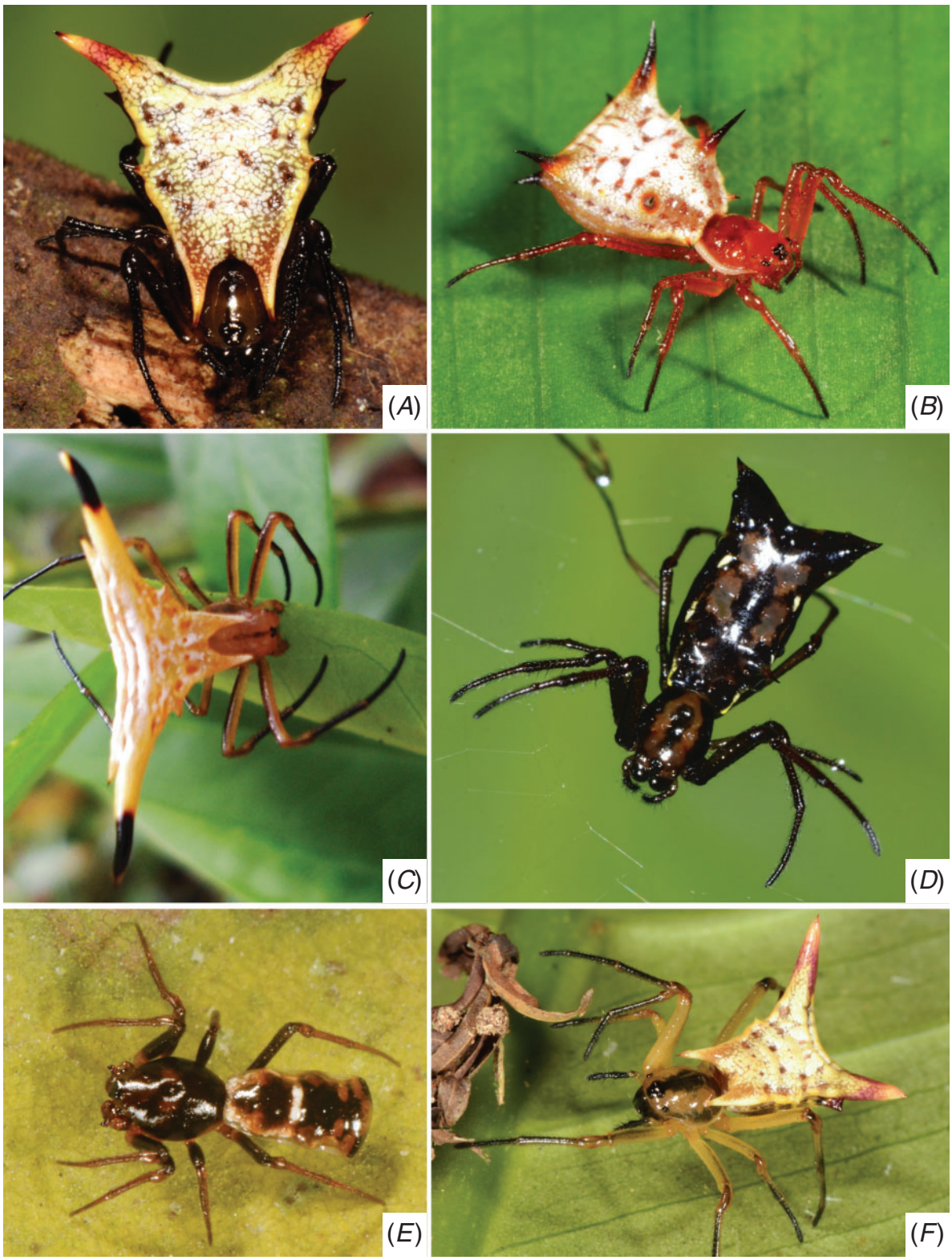

Fig. 2. Living *Micrathena* specimens. (*A*) *Micrathena beta*, female from Requena, Loreto, Peru (MUSM-ENT 510055). (*B*) *Micrathena cornuta*, female from Requena, Loreto, Peru (UFMG 19564). (*C*) *Micrathena reimoseri*, female from Miguel Calmon, Bahia, Brazil. (*D*) *Micrathena shealsi*, female from Paucartambo, Cusco, Peru (MUSM-ENT 510061). (*E*, *F*) *Micrathena perfida*, sp. nov., holotype male and paratype female from Duque de Caxias, Rio de Janeiro, Brazil (UFMG 19049, 19048). All photos by A. Anker and P. H. Martins, except for *C* by G. F. B. Pereira.

latter authors call this a 'split matrix'. *Micrathena cucharas* (Levi, 1985) and *M. woytkowskii* (Levi, 1985) have also been included in this analysis as both seem closely related to *M. cornuta* and the males and females of the three species could potentially be mixed up; we have found some specimens of them misidentified in collections, including a male of *M. cornuta* collected with a female *M. woytkowskii* in a MCZ vial. We took this approach of including sexes separately so we could check whether each would be found to belong in the same *Micrathena* species-groups. After this initial analysis and considering genetic and geographic evidence, males were matched to females. We then re-ran analyses joining males and females of each species into a single terminal taxon (this time coded for all characters) to infer their phylogenetic placement with fewer missing data (a 'merged matrix'; Barone *et al.* 2016). We also took this opportunity to test the monophyly of the *kirbyi* species-group as defined by Magalhães and Santos (2012) by including *Micrathena macfarlanei* Chickering, 1961 in the phylogeny. Laboratory procedures, coding schemes and characters are described in detail by Magalhães and Santos (2012). We searched for most-parsimonious trees under implied weight (Goloboff 1993) using TNT 1.1 (Goloboff *et al.* 2008), with heuristic searches starting with 10 000 random addition sequences, retaining 100 trees per replication, followed by tree-bisection-and-reconnection branch-swapping (TBR). Analyses were run with a k value of 5 (the preferred value over a wide range tested in Magalhães and Santos 2012). Results of analyses under equal weights and other values of k are not included here because preliminary runs yielded very similar results to the ones we present, and because the topologies and conclusions we take from them are robust to different search parameters (see also Magalhães and Santos 2012). We evaluated branch support using Bremer's decay index (estimated using the *bremer.run* script, which is part of the TNT package) and symmetric resampling (Goloboff *et al.* 2003). Symmetric resampling calculations were based on 100 pseudoreplicates with 500 random addition sequences, saving 100 trees per replication, followed by TBR.

Due to the inclusion of new taxa, we made some additions to the character list developed by Magalhães and Santos (2012). We added a fifth state to character 126 (palpal bulb, median apophysis, basal projection, shape): (4) pointed towards embolus tip. We also propose four new characters:

Ch. 137. Male carapace, *pars cephalica*, colouration: (0) same colour as the rest of the carapace; (1) with darker colouration around median eyes (scored 1 only for *M. kirbyi* (Perty, 1833), *M. macfarlanei* and *M. miles*).

Ch. 138. Palpal bulb, conductor, base shape: (0) small, not extending beyond tegulum; (1) enlarged, extending beyond tegulum.

Ch. 139. Carapace, tubercles, shape: (0) a swelling with projected setal bases; (1) spiniform. Only applicable to species with carapace tubercles.

Ch. 140. Abdomen, second pair of posterior spines, position in relation to first pair: (0) posterior/ventral; (1) anteriorly displaced.

Genetic distances

We used specimens collected by us or our colleagues in the field and stored in 96% ethanol at −20°C, or museum samples collected from no earlier than 2010 and stored in 75% ethanol at room temperature. We extracted DNA from muscle tissue of 1–4 legs of each individual using a Wizard Genomic DNA purification kit (Promega, Madison, WI, USA) following the manufacturer's instructions. We amplified a ~1200-bp fragment of the mitochondrial gene coding for COI using the primers LCOI1490 (5′-GGT-CAA-CAA-ATC-ATA-AAG-ATA-TTG-G-3′) (Folmer *et al.* 1994) and C1-N-2776 'SPID' (5′-GGA TAA TCA GAA TAT CGT CGA GG-3′) (Hedin and Maddison 2001). For specimens that failed to amplify for this fragment, we used the alternative pair C1-N-2568 (5′-GCT ACA ACA TAA TAA GTA TCA TG-3′) and C1-J-1751 'SPID' (5′-GAG CTC CTG ATA TAG CTT TTC C-3′) (Hedin 1997), which amplifies a ~720-bp fragment. We amplified the fragments using the following PCR conditions: 5 µL of 5× buffer (Promega Gotaq Flexi buffer), 2 µL of 25 mM $MgCl_2$, 2.5 µL of dNTP mix at 2 µM (Promega), 2.5 µL of each primer at 5 µM, 0.25 unit of Taq DNA polymerase (Promega Gotaq) and 1 µL of extracted DNA for a final volume of 25 µL (or 10 µL with proportional quantities). PCR cycles consisted of 10 min at 94°C, 35–40× (30 s at 95°C, 45 s at 48°C (primer pair 2568–1751) or 52°C (1490–2776), and 45 s to 1 min at 72°C) and 7–10 min at 72°C. An alternative PCR program (including five initial cycles at 46°C) was used when the first PCRs failed to succeed for museum samples. We checked PCR success on a 1% agarose gel stained with GelRed (Biotium, Fremont, CA, USA) and purified the products using a 20% 8000 polyethyleneglycol + NaCl solution followed by washes in 80% ethanol. Sequencing reactions consisted of 4 µL of PCR product, 1 µL of either forward or reverse primers, 1.6 µL of 5× sequencing buffer and 0.8 µL of BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster, CA, USA) for a 10 µL final volume. Automated sequencing was carried out on an ABI 3130xl Genetic Analyzer (Applied Biosystems) following the manufacturer's instructions. We checked chromatograms by eye in SeqScape 2.6.0 (Applied Biosystems). We aligned sequences using Muscle (Edgar 2004) as implemented in MEGA6 (Tamura *et al.* 2013). Additional *Micrathena* sequences from McHugh *et al.* (2014) were obtained from GenBank; newly generated sequences are deposited in the same database under accession numbers KX687305–KX687332. We used MEGA6 for inferring a neighbour-joining tree for the sequence set using a Kimura 2-parameter model of evolution. Branch support was evaluated using 100 bootstrap pseudoreplicates.

Specimen descriptions

The format of descriptions follows Magalhães and Santos (2011). Specimens were illustrated with the aid of a Leica M205C stereoscopic microscope with a camera lucida. Photographs were taken using a DFC295 digital camera attached to the same microscope and mounted as a single, multifocal image using Leica Application Suite 3.8. Measurements were taken on the left side of specimens, except when otherwise specified, and are expressed in millimetres.

Most new records were georeferenced *in situ* by the original collectors. Previously known and new records without coordinates were georeferenced *post hoc* using Google Earth and are approximate (and indicated between square brackets, rather than parentheses).

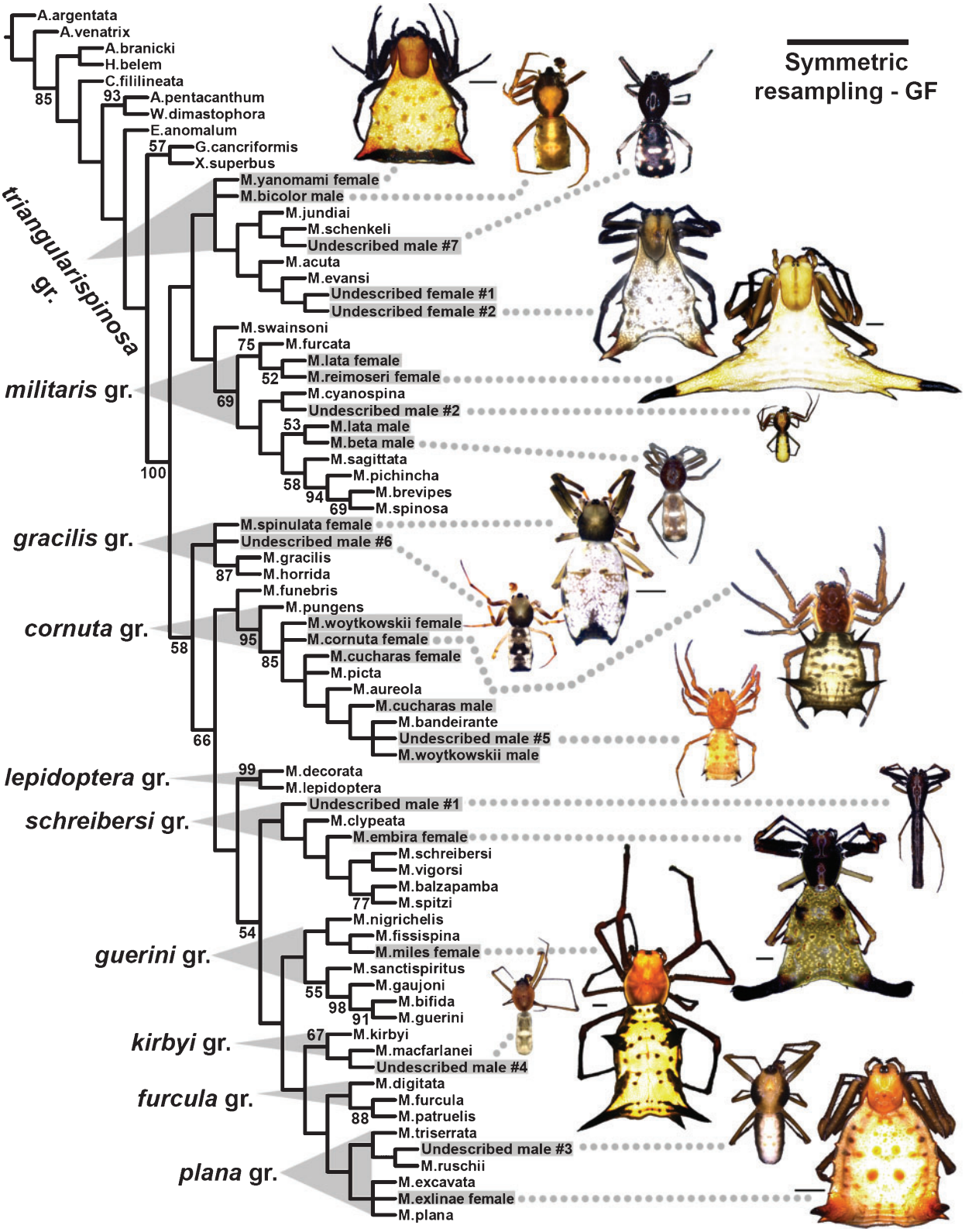

Fig. 3. Phylogeny obtained under implied weights analysis ($k = 5$) of morphological data, with newly described males and females coded as separate taxa ('split matrix'). Groups relevant to the pairings made here highlighted in grey, and codes for undescribed specimens follow Table 1; species are labelled with names that have been applied to them before the conclusions of our study. Values next to branches are group frequencies of symmetric resampling (only values higher than 50 are shown).

The material examined for this study is deposited in the following museum collections: CAS, California Academy of Sciences, San Francisco, USA; CHNUFPI, Coleção de História Natural da Universidade Federal do Piauí, Floriano, Brazil; IBSP, Instituto Butantan, São Paulo, Brazil; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Cambridge, USA; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MPEG, Museu Paraense Emílio Goeldi, Belém, Brazil; MUSM-ENT, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; and UFMG, Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. Specimens used for DNA extraction are listed together with collection and depository information and GenBank accession numbers in Supplemenary Table S1.

Results and discussion

Morphological phylogenetic inference with sexes coded separately (split matrix)

The analysis with sexes coded separately yielded two fittest trees differing only in the position of *M. exlinae* females, which were either sister to *M. plana* (C.L. Koch, 1836) or *M. excavata* (C. L. Koch, 1836), length = 599, fit = 95.64, CI = 0.275, RI = 0.714 (Fig. 3). Despite the addition of new taxa, the morphological topologies obtained in this analysis are very similar to those found by Magalhães and Santos (2012) (Fig. 3). The females of *M. embira*, *M. reimoseri*, *M. exlinae*, *M. miles*, *M. spinulata* and *M. yanomami* were recovered as members of the *schreibersi*, *militaris*, *plana*, *guerini*, *gracilis* and *triangularispinosa* species-groups, respectively, as anticipated by Levi (1985) and Magalhães and Santos (2012). The male of *M. beta* was recovered as sister to the male currently assigned to *M. lata*, both in the *militaris*-group (Fig. 3).

The undescribed specimens had contrasting behaviours. Most appeared in the same morphological groups as the females they had been collected with: this is true for undescribed males #1, 2, 3, 5 and 6 (Table 1; Fig. 3). Other males appeared in unexpected positions. For example, male #4 was collected with *M. miles* females (*guerini*-group), but was recovered as a member of the *kirbyi*-group (Fig. 3). Male #7 and *M. bicolor* males were collected in the same locality as *M. yanomami*, and all were recovered in the *triangularispinosa*-group. However, male #7 was recovered in a relatively apical position within this group, while *M. yanomami* females and *M. bicolor* males were recovered in a politomy at the base of the group (Fig. 3). Finally, the two undescribed females were recovered in the *triangularispinosa*-group; one of them had been collected along with males of *M. beta* (*militaris*-group) (Table 1; Fig. 3).

Genetic distances

The neighbour-joining dendrogram based on a COI fragment shows that undescribed male #1, collected in the same locality as *M. miles* and *M. embira* females, is genetically more similar to the latter (Fig. 4). Similarly, male #2 grouped with *M. reimoseri*, male #5 grouped with females of *M. cornuta*, and male #6 grouped with *M. spinulata* (Fig. 4) – each of these pairs coming respectively from the same localities. Undescribed male #7 is most similar to females identified as *M. triangularispinosa* (De Geer, 1778) (Fig. 4). Surprisingly, the females of *M. yanomami*, which we initially believed to be conspecific with this latter male, grouped with males of *M. bicolor* (Fig. 4). Undescribed female #1 and a *M. beta* male have almost identical COI sequences, as do undescribed female #2 and the male currently assigned to *M. lata*; these two pairs form a cluster, although with more than 4% COI sequence divergence between them (Fig. 4).

Matching sexes using different sources of data

Associating males to females in spider groups with several sympatric species is always challenging. Levi (1985) stated that the chances of successfully matching couples are higher in the context of a revision, but that does not prevent association mistakes. Fortunately, most of Levi's pairings have proved to be correct over the years. Nowadays we are lucky to obtain data that were not available to him, such as additional specimens deposited in museums, data from recent field expeditions, a robust phylogeny of the genus and DNA sequences. With these, we can review some of the old pairings and propose new ones.

The utility of DNA sequences for matching sexes (or different developmental stages) in spiders had already been anticipated by Barrett and Hebert (2005). It is now routinely used in taxonomic papers (e.g. Faynel *et al*. 2012; Trivinho-Strixino *et al*. 2012; Przybyłowicz and Tarcz 2015; Barone *et al*. 2016). Our study shows that DNA barcoding can be successfully used for matching sexes in organisms with marked sexual dimorphism. Even in cases where a single male and a single female of a particular species could be sequenced (such as *M. reimoseri* or *M. embira*; Fig. 4), the information was useful and concordant with other sources of data. This is in part because, at least in *Micrathena*, divergences in COI correlate well with morphology-based identification (McHugh *et al*. 2014; this study, Fig. 4). On the other hand, coding different life stages (or sexes) as separate terminal taxa (= semaphoront coding) in a phylogenetic analysis is controversial, although it may be useful in some situations (e.g. Steyer 2000; Gilbert *et al*. 2009; Meier and Lim 2009; Wolfe and Hegna 2014). At least two studies have successfully used this approach to associate the males with females in anyphaenids (Barone *et al*. 2016) and anapids (Platnick and Shadab 1978), although in the latter case the authors noted some conflicts between male and female characters. Sharma *et al*. (in press) argue against semaphoront coding. We do agree with them that it violates several assumptions of cladistic analysis and should not be used to infer phylogenies in the strict sense. On the other hand, it might be useful in situations such as the present one, to infer if different stages present synapomorphies of a particular group, which might represent evidence of conspecificity. Needless to say, after matching the sexes it is fundamental to abandon semaphoront coding and re-analyse the data, and that is why we present the tree in Fig. 5. Here, we demonstrate that semaphoront coding, in combination with DNA sequences and geographic information, allowed us to either confirm existing or propose new matches for seven species of *Micrathena*. Details of each particular case are given in the 'Taxonomy' section.

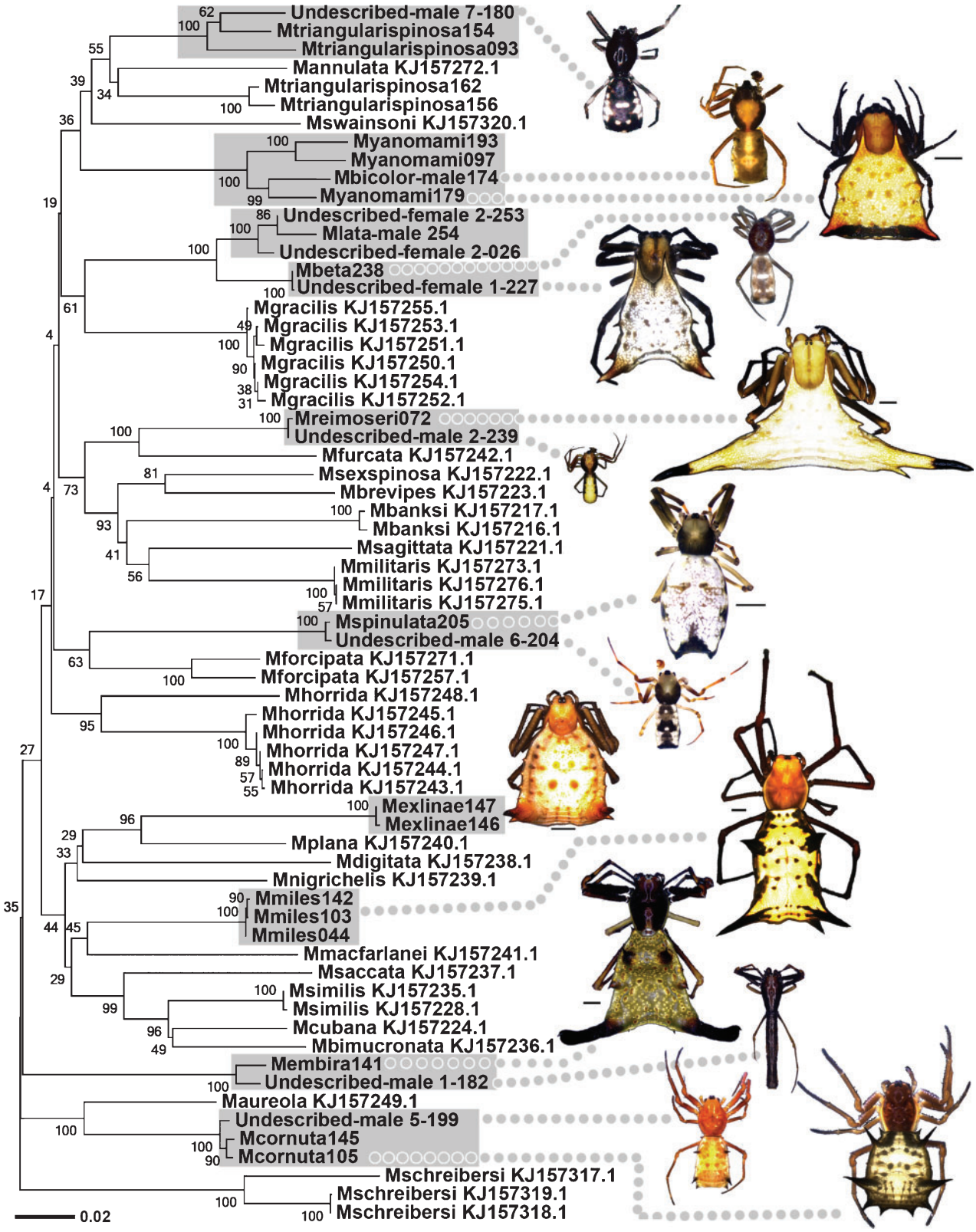

Fig. 4. Neighbour-joining dendrogram based on Kimura 2-parameter distances. Numbers next to nodes represent bootstrap supports (based on 1000 pseudoreplications). Codes for undescribed specimens follow Table 1; species are labelled with names that have been applied to them before the conclusions of our study.

It is clear that male–female matching requires a good deal of logical reasoning and 'detective work'. This is especially true in cases like *Micrathena*, in which data are incomplete or ambiguous for some of the species. For example, male #1 was collected with *M. embira* females, and both DNA sequences and the morphological phylogeny indicate that it belongs to this species (Table 1). The decision was unequivocal in this case. However, male #4 was collected with *M. miles*, but we could not obtain sequences from the male, and males and females were placed apart in the morphological phylogeny (Fig. 3). In this case, we had to rely solely on geography to make a decision. In the cases of the *cornuta* and *triangularispinosa* species-groups, species are morphologically homogeneous and morphological phylogenetic placement was not of great help; having sequence data was crucial to identify the correct males of *M. cornuta* and *M. yanomami*. A similar case occurred with *M. miles* and *M. beta*, in which females and males were not placed in the same groups in the morphological analysis. This suggests that sometimes using only female characters for estimating the position of a species may be misleading, and that sequence data should be used whenever possible. Finally, it is interesting that having data on closely related species can help decision-making for a poorly known taxon. This is the case of *M. beta* and *M. perfida*, sp. nov.: recognising the female of *M. beta* allowed us to notice that the male considered to belong with *M. lata* by Levi (1985) was actually wrongly matched, and that it belongs to a so far undescribed species (see details in the 'Taxonomy' section below).

Based on the results and arguments presented in the 'Taxonomy' section, we were able to match six of the seven undescribed males to the females of *M. embira*, *M. reimoseri*, *M. exlinae*, *M. miles*, *M. spinulata* and *M. cornuta*, respectively. The male previously assigned to *M. cornuta* belongs to *M. woytkowskii* instead. Unidentified male #7, which we initially suspected to be conspecific with *M. yanomami* females, was placed within a complex formed by specimens identified by us as *M. triangularispinosa*. On the other hand, females of *M. yanomami* were associated with males previously matched by Levi (1985) to the females of another species, *M. bicolor*. One of the undescribed females is matched to *M. beta*. Finally, the male previously described as *M. lata* does not belong with this species and is here described as *Micrathena perfida*, along with its true female. For a detailed justification of the matching of each species, diagnoses, descriptions and new geographical records, see the 'Taxonomy' section.

Phylogenetic analysis with both sexes coded (merged matrix)

The phylogenetic analysis with both male and female characters coded for every species known from both sexes had similar results (Fig. 5) (length = 605, fit = 83.16, CI = 0.273, RI = 0.710) to the previous analysis (Fig. 3). In the cases in which males and females of the same species were placed in different groups in the previous analysis, the species retained the position previously found for the male (*M. miles* in the *schreibersi*-group; *M. lata* and *M. perfida* in the *militaris*-group) (Fig. 5). In this dataset, there are fewer male characters than female characters (see Magalhães and Santos 2012), but they seem to be especially important to correctly estimate the phylogenetic position of *Micrathena* species. This highlights the importance of describing unknown males. One of the unexpected results of our analyses is the position of *M. beta* and *M. perfida*, which share male characters with the *militaris*-group, but whose females definitely resemble those of the *triangularispinosa*-group. This means that the limits and relationships of this group might change upon the addition of more data.

Pending taxonomic issues in Micrathena

Micrathena is arguably one of the best-known Neotropical spider genera with regard to its systematics: it has been thoroughly reviewed, a phylogeny is available and few taxonomic novelties have appeared over the years (reviewed in Magalhães and Santos 2011; Argañaraz and Rubio 2011; this study). Nevertheless, some problems remain to be solved. The most obvious one, which we partially tackled with this contribution, is the lack of knowledge on the males of many species. Another major issue is the taxonomy of the *triangularispinosa*-group, which currently includes 11 small species. Some species are difficult to distinguish from others, such as *M. annulata* Reimoser, 1917 and *M. jundiai* Levi, 1985. On the other hand, many of the nominal species, as currently recognised, have a variable morphology and may represent species complexes; examples include *M. evansi* Chickering, 1960 and *M. flaveola* (Perty, 1839). To address this, we believe it is necessary to carry out a comprehensive revision of this species-group based on exhaustive examination of museum specimens (including types of junior synonyms). As these issues are gradually solved, an even more solid base will be erected for the taxonomy of *Micrathena* – an excellent outcome, as these spiders are as much conspicuous and charismatic as they are excellent models for studies in ecology, evolution and biogeography.

Taxonomy

Family **ARANEIDAE** Clerck

Genus ***Micrathena*** Sundevall

Micrathena perfida, sp. nov.

(Figs 2*E*, *F*, 6, 7*A–C*, 15)

http://zoobank.org/urn:lsid:zoobank.org:act:3A9E9EB7-3534-4A07-BBBD-1535AF51C5FA

Micrathena lata Chickering: Levi, 1985: 565, figs 608–615 (in part, misidentified male); Magalhães & Santos, 2012: 51 (in part, misidentified male).

Material examined

Holotype. Brazil: Rio de Janeiro: ♂, Duque de Caxias, Parque Natural Municipal da Taquara (22°35′35.3″S, 43°14′17.8″W, 36 m), 6–7.i.2016, A. Anker, P. H. Martins and R. Brito (UFMG 19409).

Paratypes. Same data as the holotype, 1 ♀ (UFMG 19408). **Brazil:** Espírito Santo: Santa Teresa [19°55′S, 40°36′W], 29.ix.1942, B. A. Soares, 1 ♂ (MZSP 7982); Linhares, Reserva Natural Vale [19°8′15.6″S, 40°3′36″W], 5–12.i.1998, A. D. Brescovit *et al.*, 1 ♂ (IBSP 16749). São Paulo: Iguapé, Serra de Itimirim, divisa com Miracatu [24°22′30″S, 47°31′8″W], 20.xii.1998, R. Pinto-da-Rocha and S. Bérnils, 1 ♂ (MZUSP 17212);

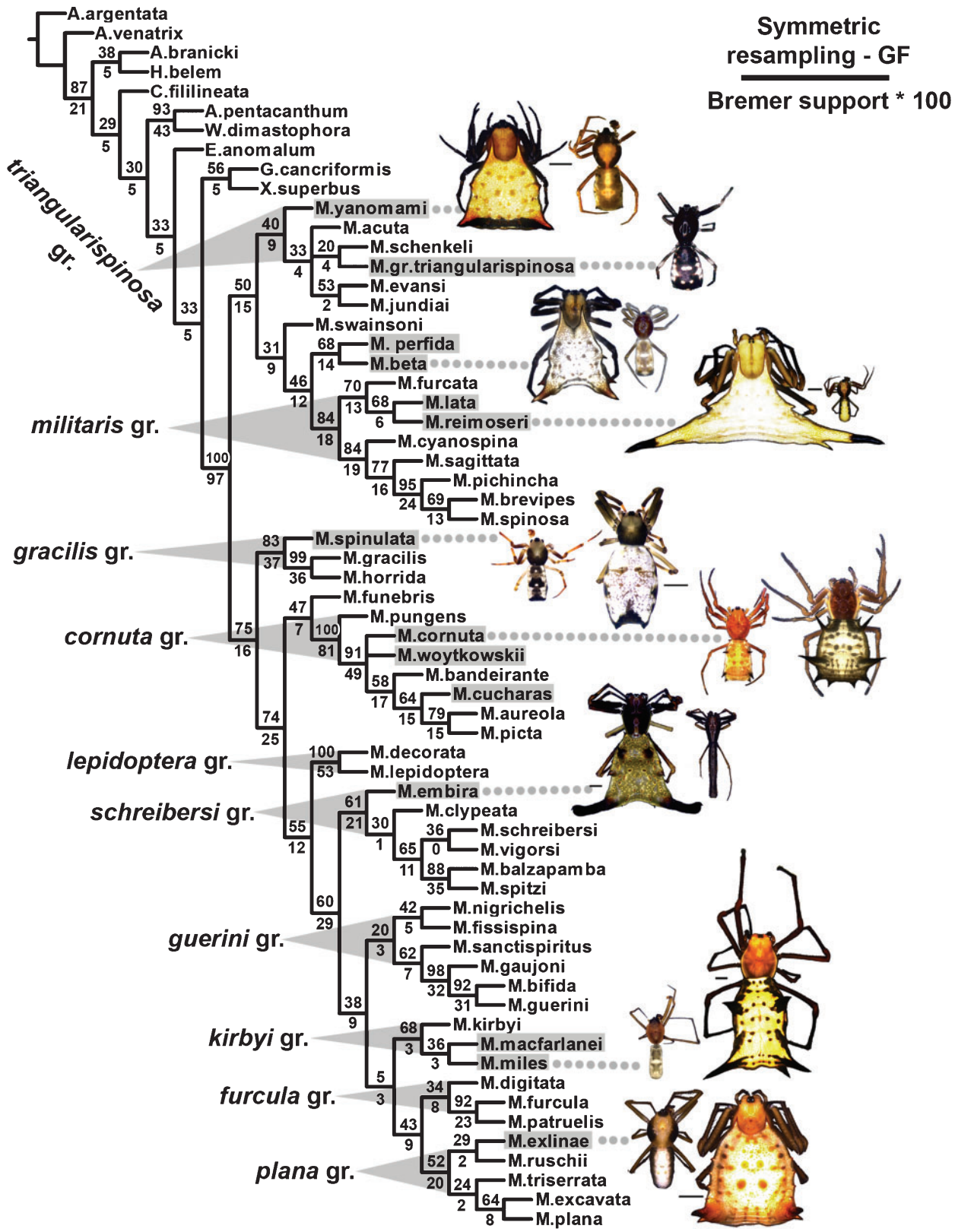

Fig. 5. Phylogeny obtained under implied weights analysis ($k = 5$) of morphological data with all characters coded for each species ('merged matrix'). Values below branches represent Bremer support values multiplied by 100, values above branches represent group frequency values for symmetric resampling. Males and females to scale with each other, but not among different species. Codes for undescribed specimens follow Table 1. Species are labelled with the names that should be applied to them after the conclusions of our study.

Table 1. Data on the new *Micrathena* specimens described here and the new pairings proposed for males and females, which had been incorrectly matched in the past

'Collected with' refers to which specimens have been collected in the same localities as the specimens of dubious assignment; 'final assignment' refers to our final taxonomic decision; and 'evidence' to the reasons why we propose the new pairings (*P* = phylogenetic position, L = locality data, B = DNA barcoding); all localities in Brazil except where noted

Dubious specimens	Collected with	Localities	Final assignment	Evidence
Undescribed female #1 (Fig. 6)	*M. lata* ♂	Bahia; Minas Gerais; São Paulo; Rio de Janeiro	*M. perfida*, sp. nov.	LB
Micrathena lata male (Fig. 7*A–C*)	Undescribed female #1	Santa Teresa (Espírito Santo); Rio de Janeiro	*M. perfida*, sp. nov.	LB
Undescribed female #2 (Fig. 8)	*M. beta* ♂	Pará; Porto Velho (Rondônia); Requena (Loreto, Peru)	*M. beta*	LB
Undescribed male #1 (Fig. 9)	*M. embira* ♀	Porto Velho (Rondônia)	*M. embira*	LBP
Undescribed male #2 (Fig. 10)	*M. reimoseri* ♀	Castro Alves (Bahia); Miguel Calmon (Bahia)	*M. reimoseri*	LBP
Undescribed male #3 (Fig. 11)	*M. exlinae* ♀	Caracaraí (Roraima)	*M. exlinae*	LP
Undescribed male #4 (Fig. 12)	*M. miles* ♀	Senador Guiomard (Acre); Maynas (Loreto, Peru)	*M. miles*	L
Undescribed male #5 (Fig. 13)	*M. cornuta* ♀	Porto Velho (Rondônia); Tambopata (Madre de Dios, Peru)	*M. cornuta*	LB
M. cornuta male (Levi 1985: figs 809–811)	*M. woytkowskii* ♀	Puerto Asis (Putumayo, Colombia)	*M. woytkowskii*	L
Undescribed male #6 (Fig. 14)	*M. spinulata* ♀	Pico de Orizaba (Veracruz, Mexico)	*M. spinulata*	LBP
Undescribed male #7	*M. yanomami* ♀	Porto Velho (Rondônia)	*triangularispinosa* group	LBP
M. bicolor male (Levi 1985: figs 453–455)	*M. yanomami* ♀	Juruti (Pará); Porto Velho (Rondônia)	*M. yanomami*	LBP

Iporanga, Parque Estadual Turístico do Alto Ribeira [24°29′9.33″S, 48°38′47.11″W], 12–18.x.2001, Biota team, 1 ♂ (IBSP 97016); Peruíbe, Estação Ecológica de Juréia-Itatins, Núcleo Arpoador (24°23′13.6″S, 41°1′3.3″W, 13 m), 21–26.iv.2012, G. H. F. Azevedo and J. P. P. Pena-Barbosa, 1 ♀ (UFMG 12666).

Additional material (*not types*). **BRAZIL:** Bahia: Ilhéus, 1 ♀ (IBSP 19025); Una, Reserva Biológica do Una, 1 ♀ (IBSP 46447), 1 ♀ (IBSP 47029), 1 ♀ (IBSP 46946). Minas Gerais: Marliéria, Parque Estadual do Rio Doce, 2 ♀ (IBSP 94984), 1 ♀ (IBSP 94903), 1 ♀ (IBSP 94956).

Diagnosis

Micrathena perfida males differ from all other *Micrathena* species, except for *M. beta*, by the elaborate shape of the palpal tibia, the folded paracymbium, the large hook-shaped conductor and by the spine-shaped digitiform projection of the median apophysis (Fig. 7*B*, *C*; DP). It can be distinguished from *M. beta* by the truncate embolus (Fig. 7*B*) (pointed and curved in *M. beta*; Fig. 7*D*) and by the apex of the terminal apophysis surpassing the tegulum edge (Fig. 7*B*, *C*; see also Levi and Santos 2013: fig. 3). Females differ from all species of the *triangularispinosa*-group, except *M. beta*, by the second pair of posterior spines being anteriorly displaced (Fig. 6*A*; ps). They differ from *M. beta* by the narrower and more pointed epigynal lobe (Fig. 6*F*).

Description

Holotype male from Duque de Caxias, Rio de Janeiro (UFMG 19049) (Fig. 2*E*). Prosoma dark brown, light brown in the ocular area and with two light brown markings in the *pars thoracica*; clypeus pale yellow, chelicerae light brown and sternum dark brown. Endites, labium and coxae yellow, femora proximally yellow and distally dark brown; distal articles pale yellow. Abdomen brown with a white band medially, and posteriorly with dark patches on each side; venter dark brown with white patches. Posterior median eyes the largest. Carapace glabrous with rounded *pars thoracica*, and an elongated depression as a fovea, without dimples, slightly flattened dorsoventrally in lateral view. First coxae without hooks, and legs without macrosetae. Abdomen rectangular, widest posteriorly, without spines. Total length 3.7; carapace 1.78 long, 1.27 wide at its widest point; abdomen 2.23 long; length of femur I 1.17, patella 0.41, tibia 0.81, metatarsus 0.61, tarsus 0.46; femur II 0.91, patella 0.46, tibia 0.76; femur III 0.86, patella 0.30, tibia 0.51; femur IV 1.47, patella 0.36, tibia 0.81, metatarsus 0.81, tarsus 0.51. Palp (Fig. 7*B*) with membranous, apically flattened, spoon-like terminal apophysis. Embolus thick and truncate in apex. Conductor with large sclerotised hook, and a membranous bifid lobe close to apex. Paramedian apophysis absent. Median apophysis fused to radix, basal projection of the median apophysis well developed, rhomboid and slightly sclerotised, with a proximal spine posteriorly directed. Paracymbium enlarged and folded onto itself, tibia modified, with three projections, one rounded, one conical and another digitiform (Fig. 7*C*).

Female paratype from Estação Ecológica da Juréia, Peruíbe, São Paulo (UFMG 12666). Carapace light brown, with median dark brown line and dark brown sides. Chelicerae black, and light brown proximally. Endites and labium pale yellow. Sternum dark brown with yellowish blots. Coxae yellowish, distal articles of legs dark brown, femora yellowish on the bases and with a longitudinal dark brown band. Dorsum of abdomen white, sides white with dark line following the apodemes; venter white, with a black sclerotised ring around the spinnerets. The four pairs of spines yellowish. Carapace dome-shaped, glabrous and without dimples; thoracic fovea circular. Abdomen triangular, widest posteriorly. Four pairs of spines on the abdomen, the first and the third the longest; the second pair of posterior spines directed posterolaterally (Fig. 6*A*, *B*). Total length 6.14; carapace 2.05 long, 1.91 wide at its widest point; abdomen 4.9 long. The specimen lacks the first and second legs on the left side, and all the legs on the right side. Length of femur III 1.53, patella

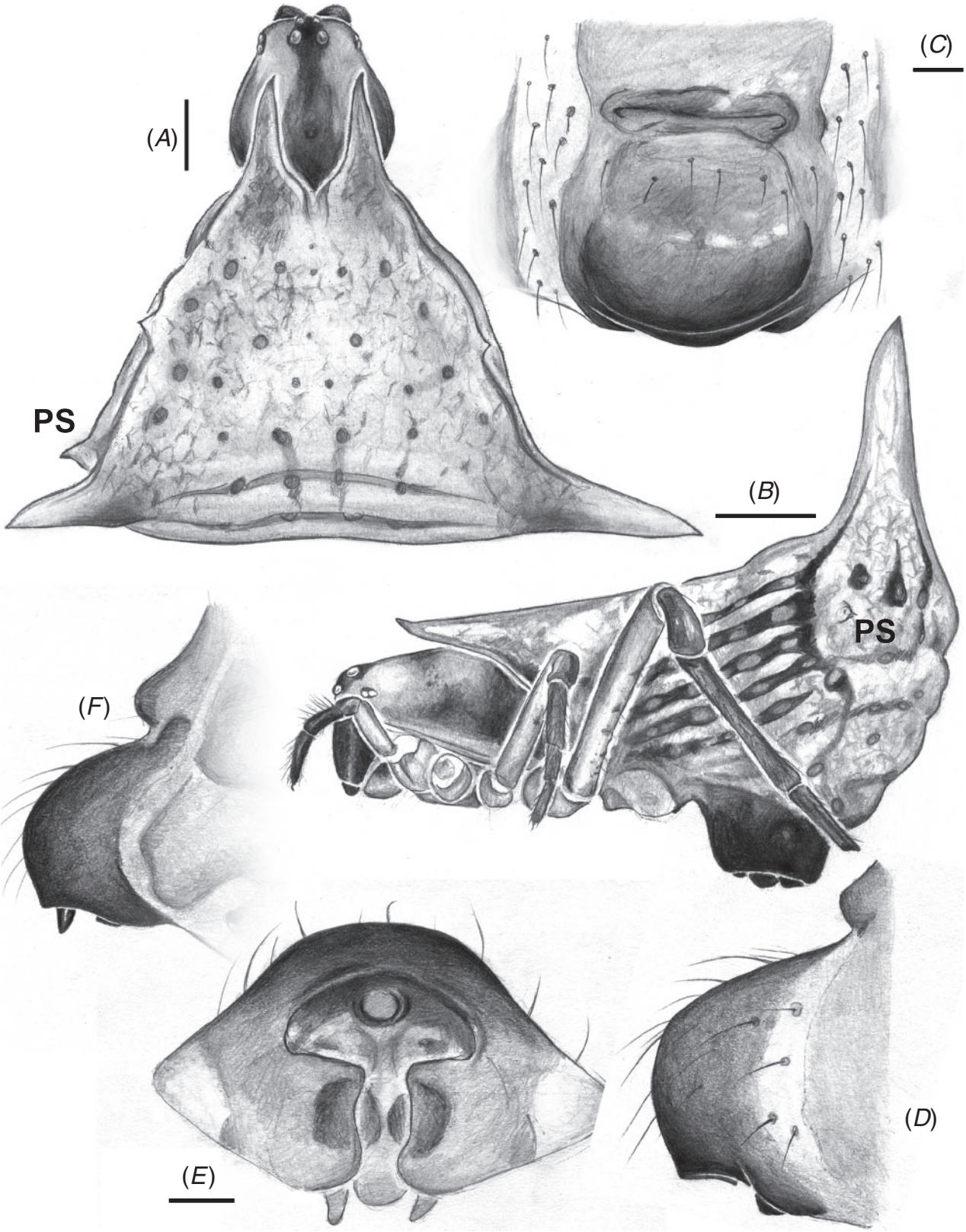

Fig. 6. *Micrathena perfida*, sp. nov. (*A–E*) Female paratype from Peruíbe, São Paulo, Brazil (UFMG 12666): (*A*) habitus, dorsal; (*B*) lateral view. (*C–E*) Epigynum: (*C*) ventral; (*D*) lateral; (*E*) posterior. (*F*) Female from Una, Bahia, Brazil (IBSP 46447), epigynum lateral view. Scale bars = 1 mm (*A*, *B*) and 0.1 mm (*C–F*). Abbreviation: PS, second posterior spine.

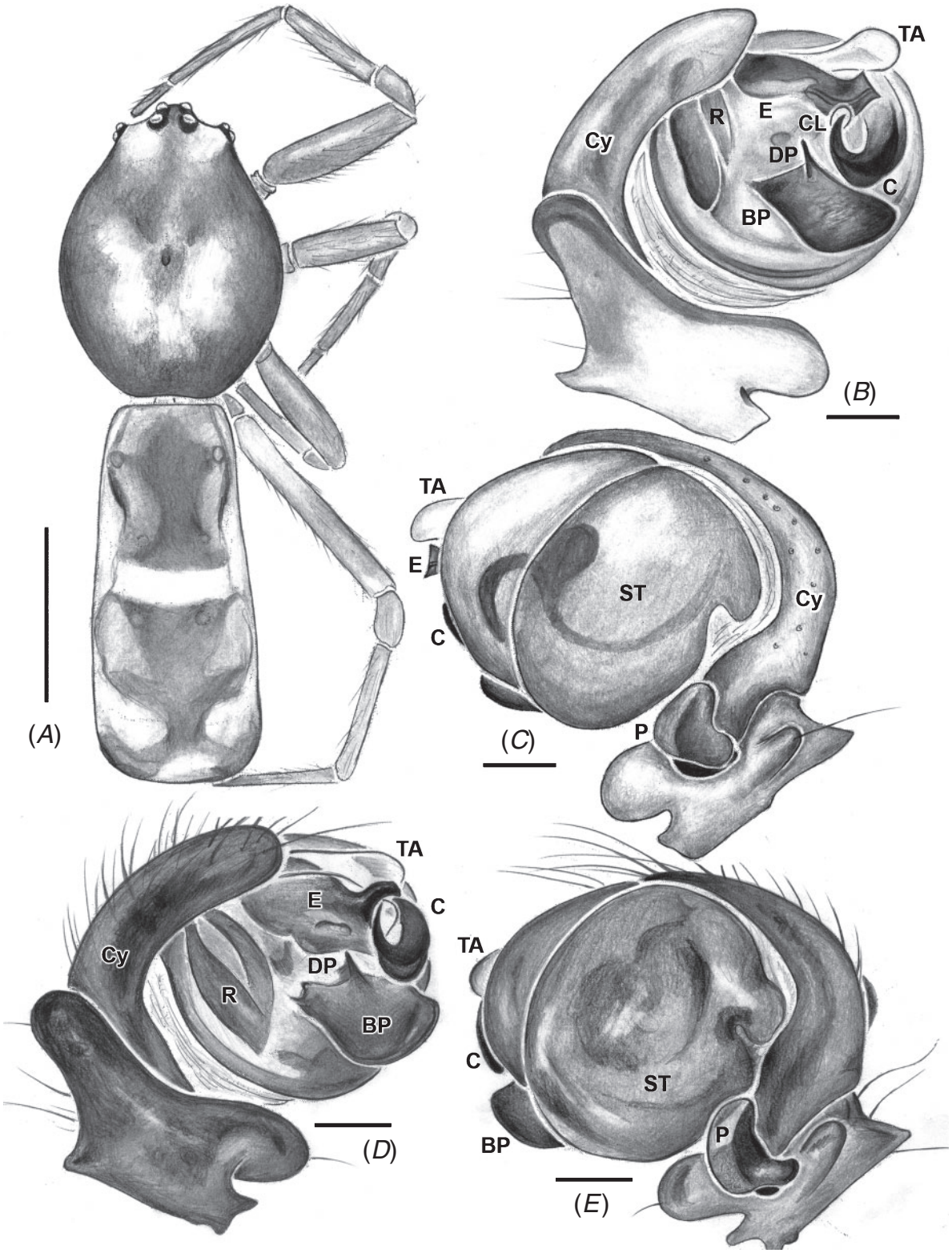

Fig. 7. (*A–C*) *Micrathena perfida*, sp. nov., male paratype from Santa Teresa, Espírito Santo, Brazil (MZSP 7982): (*A*) habitus, dorsal; (*B*) palpal bulb, prolateral; (*C*) palpal bulb, retrolateral. (*D*, *E*) *Micrathena beta*, male from Requena, Loreto, Peru (MUSM-ENT 510054): (*D*) palpal bulb (right, mirrored), prolateral; (*E*) palpal bulb, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B–E*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; CL, conductor lobe; Cy, cymbium; DP, digitiform projection; E, embolus; P, paracymbium; R, radix; ST, subtegulum; TA, terminal apophysis.

0.51, tibia 1.02, metatarsus 0.78, tarsus 0.51; femur IV 2.81, patella 0.75, tibia 1.73, other articles missing. Epigynum with a domed bulge, lacking posterior lobe (Fig. 6*E*, *D*). Posterior median plate a little wider than long, mushroom-shaped and with two well-separated, inflated black marks corresponding to the region where the copulatory openings lie (Fig. 6*C–E*).

Female paratype from Duque de Caxias, Rio de Janeiro (UFMG 19048). Colouration and abdomen shape as described above. Length of femur I 2.59, patella 0.82, tibia 1.64, metatarsus 1.57, tarsus 1.02; femur II 2.23, patella 0.61, tibia 0.86; femur III 1.75, patella 0.61, tibia 1.01; femur IV 3.04, patella 0.76, tibia 1.78, metatarsus 1.62, tarsus 0.86.

Intraspecific variation

Males ($n = 2$) vary in total body length from 3.6 to 3.7 and carapace length from 1.62 to 1.78. The male from Santa Teresa is lighter than the male from Duque de Caxias, probably because of the better conservation state of the latter. In the paratype female from Juréia (UFMG 12666), the right second posterior spine was much smaller than the left one. This female lacks the epigynum lobe, which is present on the other analysed specimens (Fig. 6*F*). Total length varies from 5.59 to 6.14, carapace length from 2.05 to 2.52.

Distribution

This species is known from the Atlantic Forest in eastern Brazil, from Bahia to São Paulo states (Fig. 15).

Remarks

The male of *M. perfida* was described by Levi (1985) under the name *M. lata*. The only evidence he used for matching this male to the female of *M. lata* was that both presented characteristics of his *militaris*-group, and he admitted that the association was uncertain. We here present evidence that the male identified by Levi (1985) as *M. lata* actually should be matched to undescribed female #2: they have similar COI sequences (Fig. 4) and have been collected in the same locality at Duque de Caxias, Rio de Janeiro. Also, the male is similar to *M. beta* and the female is similar to undescribed female #1 (Figs 3, 6–8), which are another pair for which we have good evidence of a correct match (see notes under *M. beta* below). As the holotype of *M. lata* is a female, it is this sex that retains Chickering's (1960) name. We could not find any name that has been applied to the Atlantic Forest specimens here described as *M. perfida*, and thus name it for the first time.

Etymology

The specific name is a Latin adjective meaning 'perfidious' or 'treacherous' and refers to the fact that males of this species were incorrectly matched to females of *Micrathena lata* for a long period of time.

Micrathena beta di Caporiacco

(Figs 2*A*, 3, 5, 7*D*, *E*, 8*A–E*, 15)

Micrathena beta di Caporiacco, 1947: 26 (holotype male from Two Mouths, Essequibo River, Guyana, deposited in Museo di Storia Naturale dell'Univerisità di Firenze, not examined); di Caporiacco, 1948: 668–669, fig. 81; Levi, 1985: 446 (transferred to Linyphiidae *incertae sedis*); Levi & Santos, 2013: 223–224, figs 2–4 (returned to Araneidae).

Micrathena triangularispinosa (De Geer): Levi, 1985: fig. 472 (misidentified in part, only some females).

Micrathena lata Chickering: Dierkens, 2011: figs 36, 44 (misidentified).

Material examined

BRAZIL: Acre: Cruzeiro do Sul, Parque Nacional da Serra do Divisor, 6 ♀ (IBSP 12180, 12345, 12432, 20294, 20295); Senador Guiomard, Estação Experimental Catuaba, 1 ♀ (UFMG 19038). Amazonas: Manaus, 1 ♂ (MZSP 7687), 1 ♀ (IBSP 80052); Porto Urucu, 1 ♂ (MPEG 20065). Pará: Bagre 1 ♂ (MPEG 31656), 7 ♀ (MPEG); Belterra, 1 ♂ (MPEG 30309); Transgarimpeiro, 1 ♂ (MPEG 25000); Fazenda Euclides Gallo, 1 ♂ (MPEG 30301); Juruti, 1 ♂ (MPEG 31666), 1 ♀ (MPEG 31667). Rondônia: Porto Velho, Abunã, 1 ♀ (MZSP 39760), 1 ♀ (MZSP 35008), 1 ♀ (MZSP 35441), 1 ♀ (MZSP 35490), 1 ♀ (MZSP 41399); Porto Velho, Caiçara, 1 ♀ (MZSP 40267), 1 ♀ (MZSP 40407), 1 ♀ (MZSP 37867), 1 ♀ (MZSP); Porto Velho, Mutum, 1 ♀ (MZSP 35153); Porto Velho, 5 ♂ (MZSP 40277, 40434, 40525, 44146, 50567), 3 ♀ (MZSP 33907, 33911). **ECUADOR:** Napo: Napo-Galeras, 1 ♂ (UFMG 3356). **PERU:** Loreto: Requena, Saquena, 1 ♂ (MUSM-ENT 510054), 1 ♀ (MUSM-ENT 510055), 1 ♀ (UFMG 19560); Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera, 1 ♂ (IBSP 165538).

Diagnosis

Male diagnosed by Levi and Santos (2013: 223): 'This is an unusual species of *Micrathena*, with the palpus having an enlarged and modified paracymbium and a strangely modified tibia (fig. 4). It closely resembles *M. lata* Chickering, 1960 (Levi 1985: 567, figs 614–615), but differs by having a narrower hook as a conductor (fig. 3), a more elaborate paracymbium and a slightly differently shaped tibia (Fig. 7*D*, *E*)'. Females resemble *M. perfida* in having the second pair of posterior spines displaced anteriorly (Fig. 8*A*; ps); they differ from it by the shape of the epigynal lobe, which is thicker and more rounded in lateral view in *M. beta* (Fig. 8*D*).

Description

For the male description, see Levi and Santos (2013).

Female from Requena, Loreto, Peru (UFMG 19560). Carapace light grey, with median dark line and dark sides. Chelicerae black. Endites black and labium dark brown. Sternum yellowish with white and black blots. Coxae pale yellow, remaining leg segments dark brown, yellowish on the basis of femora. Dorsum of abdomen white, sides dark with white spots, venter white with black blots and two dark red blots on the sides of the sclerotised ring of the spinnerets, and with black stripes in posterior view; sclerotised ring around spinnerets black. Anterior spines pale yellow, lateral spines black, the first pair of posterior spines orange-brown and reddish, and the second posterior pair dark red. Carapace dome-shaped, glabrous, without dimples; thoracic fovea an indistinct circular marking. Abdomen trapezoidal, widest posteriorly. Four pairs of spines on the abdomen, the first and the third the longest; fourth pair directed posterolaterally (Fig. 8*A*, *B*). Total length 5.32; carapace 2.18 long, 1.63 wide at its widest point; abdomen 3.0 long; length of femur I 2.11, patella 0.75, tibia 1.36, metatarsus 1.16, tarsus 0.55; femur II 1.91, patella 0.68, tibia 1.30; femur III 1.36, patella 0.55, tibia 0.82; femur IV 2.52, patella 0.68, tibia 1.50, metatarsus 1.43, tarsus

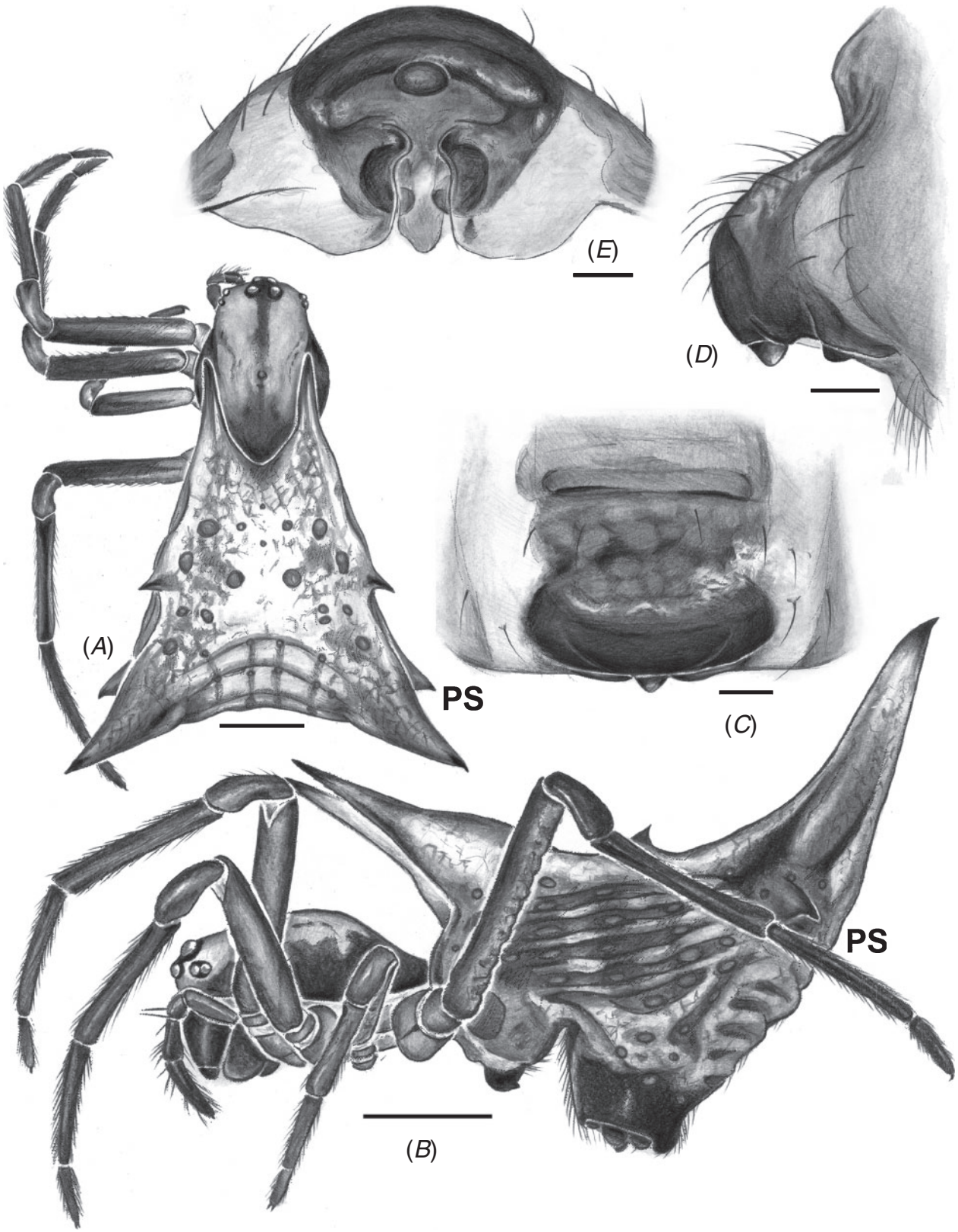

Fig. 8. *Micrathena beta* di Caporiacco, 1947, female from Requena, Loreto, Peru (MUSM-ENT 510054). (*A*) Habitus, dorsal; (*B*) lateral. (*C–E*) Epigynum: (*C*) ventral; (*D*) lateral; (*E*) posterior. Scale bars = 1 mm (*A*, *B*) and 0.1 mm (*C–E*). Abbreviation: PS, second posterior spine.

0.68. Epigynum with a domed bulge, from which a rounded lobe projects posteriorly. Posterior median plate as wide as long, mushroom-shaped and with two well-separated, inflated, black, kidney-shaped spots corresponding to the region where the copulatory openings lie (Fig. 8*C–E*).

Intraspecific variation

The lobe of the epigynum is broken in a female from Requena. Females ($n = 5$) vary in total length from 5.32 to 6.2; carapace length varies from 2.11 to 2.50. The populations found in Porto Velho have the half-distal part of the first pair of posterior spines black, and they lack the red colour in the abdomen observed in the population from Peru; individuals of these two colour variants have been collected in the same locality in Juruti, Pará.

Distribution

This species is known from the western Amazon, from French Guiana to Peru (Fig. 15).

Natural history

At Porto Velho, Rondônia, specimens were captured in the understorey of dense ombrophilous forest at 50, 1050 and 2050 m from the Madeira River. In Requena, specimens were collected in floodpain forest next to the Cumaceba River, with sparse understorey; the webs were connected to shrubs.

Remarks

Females of this species have been misidentified as *M. triangularispinosa* in collections, mainly because Levi (1985) depicted a female *M. beta* as a variation of the first species (see his figs 472, 473). We have checked the original description of *M. triangularispinosa* and some of its synonyms and none mention the anteriorly displaced posterior spine; so it seems that di Caporiacco's name has indeed been the first to be applied to this species. Males and females of *M. beta* are here matched because they have been collected in the same localities (Bagres and Juruti, Pará; Porto Velho, Rondônia; Manaus, Amazonas, Brazil; Requena, Loreto, Peru): at one of them the male was hanging from a long thread connected to a female's web. Also, males and females share almost identical COI sequences (Fig. 4).

Micrathena embira Levi

(Figs 1*E*, *F*, 3–5, 9, 15)

Micrathena embira Levi, 1985: 552, figs 551–555 'holotype female from 'Mouth of rio Embira, Rio Jurura, N. Amazonia' (sic), Western Amazon, Brazil, deposited in the American Museum of Natural History, not examined).

Material examined

BRAZIL: Amazonas: Coari, Base de Operações Geólogo Pedro de Moura, Porto Urucu, 1 ♀ (MPEG 20061); São Gabriel da Cachoeira, Pico da Neblina, 1 ♀ (INPA 6290). Rondônia: Porto Velho, Abunã, 1 ♂ (MZSP 39156), 1 ♀ (MZSP 39942), 1 ♀ (MZSP 45587), 1 ♀ (MZSP 39155); Porto Velho, Caiçara, 1 ♂ (MZSP 40691), 1 ♀ (MZSP 34455), 1 ♂ (MZSP 46089). Roraima: Caracaraí, Arquipélago Mariuá, 1 ♀ (IBSP 165519).

Diagnosis

Males of *M. embira* share with other species in the *schreibersi*-group the lack of a terminal apophysis (Fig. 9*B*) and a flattened paracymbium (Fig. 9*C*, *D*). It can be distinguished from other *Micrathena* species in this group by the rectangular abdomen, much longer than wide and without a median constriction (Fig. 9*A*); by the long and thin embolus held by the large and membranous conductor (Fig. 9*B*); and by the large basal projection of the median apophysis, which is divided into two parts (Fig. 9*B*; BP). Female diagnosed by Levi (1985: 552): 'The fourteen spines of the abdomen (figs 551, 552) and the epigynum, with its small projecting lobe on the anterior face of the globular bulge (figs 553–555), separate *M. embira* from others of the *schreibersi*-group'.

Description

Male from Abunã, Porto Velho, Rondônia, Brazil (MZSP 39156). Carapace, sternum, labium, endites, chelicerae and abdomen dark brown. Legs light brown, except for dark brown first and second femora. Carapace coffin-shaped, wider at the anterior third. Thoracic groove round and shallow. First coxa with a hook and second femur with a corresponding prolateral groove. First and second femora and tibiae ornamented with strong macrosetae; second femora with single ventral row of macrosetae. Abdomen rectangular, with two tiny tubercles at the posterior end (Fig. 9*A*). Total length 6.58; carapace 2.29 long, 1.25 wide at its widest point; abdomen 4.41 long; length of femur I 1.73, patella 0.48, tibia 1.19, metatarsus 0.97, tarsus 0.46; femur II 1.5, patella 0.41, tibia 0.94; femur III 1.02, patella 0.31, tibia 0.53; femur IV 2.03, patella 0.36, tibia 1.22, metatarsus 1.02, tarsus 0.53. Palp (Fig. 9*B*) lacking terminal apophysis. Embolus thin, long, ending near tip of conductor. Conductor long, narrow, membranous, extending beyond tegulum margin. Paramedian apophysis present, digitiform. Conductor lobe present, digitiform. Median apophysis with lobe, bent triangular rim, and basal projection divided in two parts. Paracymbium enlarged and folded, with flat retrolateral lobe (Fig. 9*C*, *D*).

For female description, see Levi (1985).

Intraspecific variation

Males ($n = 3$) vary in total length from 5.92 to 6.58, carapace length from 2.26 to 2.29 and femur I length from 1.73 to 1.75. Females ($n = 6$) vary in carapace length from 3.0 to 3.5 and femur I length from 3.07 to 3.5.

Distribution

This species is known from the western Amazon, in the states of Roraima, Rondônia and Amazonas, Brazil (Fig. 15).

Natural history

A single female was captured at the base (100 m above sea level) of Pico da Neblina, São Gabriel da Cachoeira, Amazonas (see Nogueira *et al*. 2014). At Porto Velho, Rondônia, 11 individuals were collected, of which 10 were found in the sampling plots located 50 m from the Madeira River, and one was found in a sampling plot situated 1050 m away from the river. In both

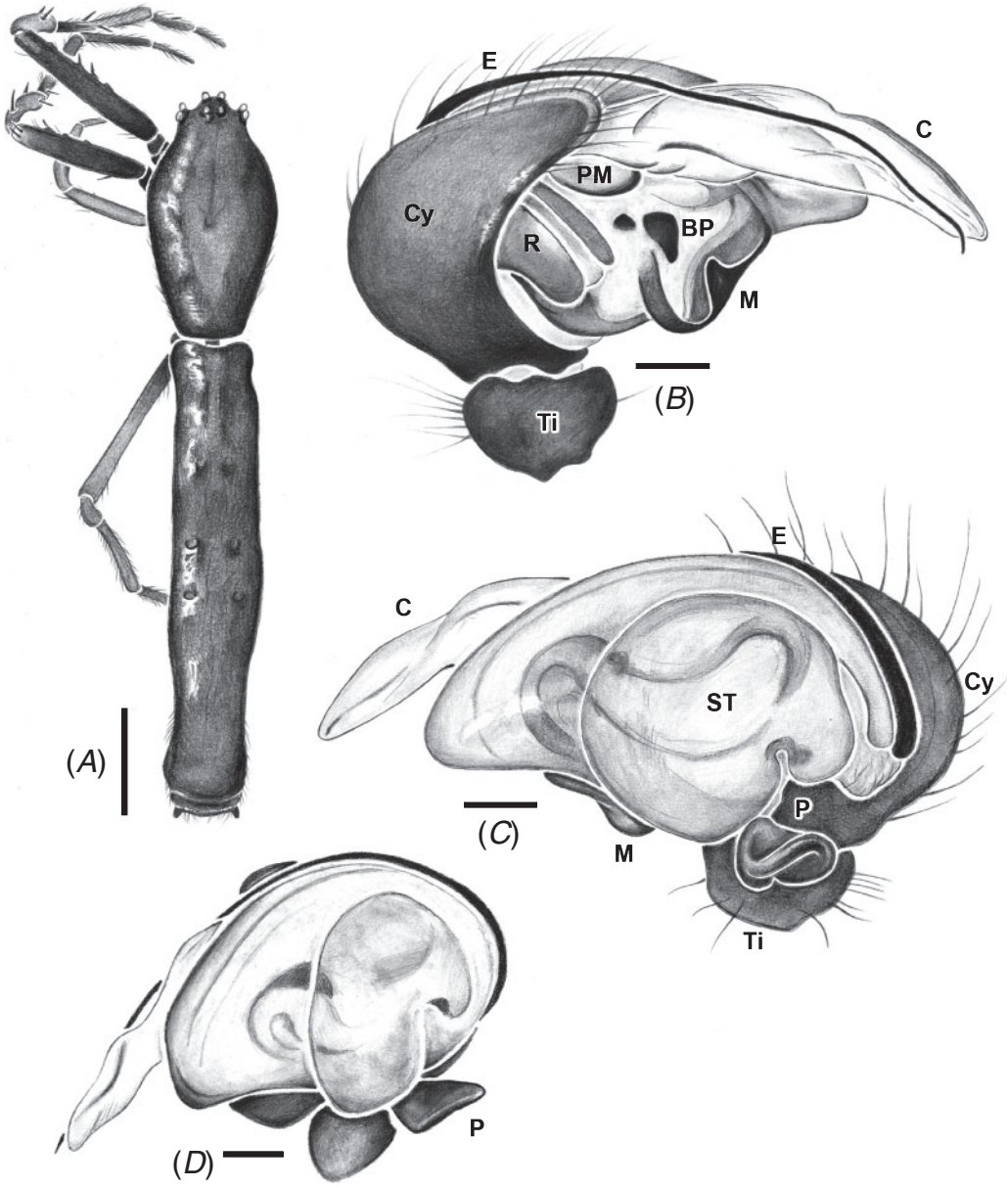

Fig. 9. *Micrathena embira* Levi, 1985, male from Porto Velho, Rondônia, Brazil (MZSP 39156). (*A*) Habitus, dorsal; (*B*) palpal bulb, prolateral; (*C*) palpal bulb, retrolateral; (*D*) palpal bulb, subapical. Scale bars = 1 mm (*A*) and 0.1 mm (*B–D*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; Cy, cymbium; E, embolus; M, median apophysis; P, paracymbium; PM, paramedian apophysis; R, radix; ST, subtegulum; Ti, palpal tibia.

localities, all individuals were captured in areas of *terra firme* old-growth forest.

Remarks

The association of *M. embira* with its putative male seems unequivocal. Both sexes were repeatedly collected in the same area, and one male was found hanging from a female's web (S. Outeda-Jorge, pers. obs.). The morphological phylogeny shows both males and females at a relatively basal position in the *schreibersi*-group (Fig. 3). Finally, males and females have similar COI sequences (Fig. 4). This is corroborated by some morphological features present in both sexes, such as the coffin-shaped, shiny and dark carapace and the colouration of the legs. Interestingly enough, both sexes present features synapomorphic for the *schreibersi*-group (such as epigynal keels and lacking a terminal apophysis), but also plesiomorphic features not shared by the higher members of this group (such as a rounded tegulum, a coxal hook and straight spermathecae). The original type locality is somewhat confusing; we interpret it as the confluence between the Juruá and Envira rivers, approximately at 7°30′S 70°06′W.

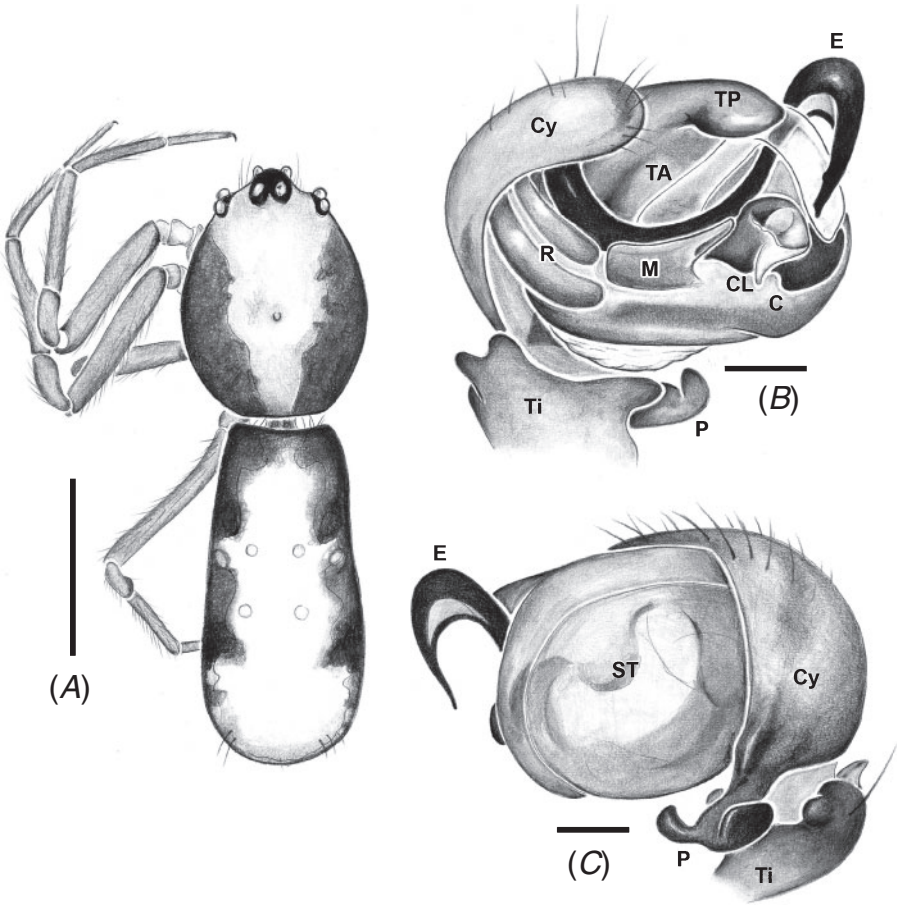

Fig. 10. *Micrathena reimoseri* Mello-Leitão, 1935, male from Miguel Calmon, Bahia, Brazil (IBSP 162301). (*A*) Habitus, dorsal; (*B*) palpal bulb, prolateral; (*C*) palpal bulb, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B*, *C*). Abbreviations: C, conductor; CL, conductor lobe; Cy, cymbium; E, embolus; M, median apophysis; P, paracymbium; R, radix; ST, subtegulum; TA, terminal apophysis; Ti, palpal tibia; TP, tegular projection.

Micrathena reimoseri Mello-Leitão

(Figs 2*C*, 3–5, 10, 15)

Micrathena reimoseri Mello-Leitão, 1935: 97, fig. 14 (female lectotype and one female paralectotype designated by Levi (1985) from Petrópolis, Rio de Janeiro, Brazil, deposited in Museu Nacional do Rio de Janeiro (MNRJ 41999), not examined); Levi, 1985: 565, 566, figs 616–619.

Material examined

BRAZIL: Bahia: Castro Alves, Serra da Jibóia, 1 ♂ (UFMG 19676) 1 ♀ (CHNUFPI 1601); Miguel Calmon, Parque Estadual das Sete Passagens, 1 ♂ (IBSP 162301), 3 ♀ (UFMG 11031), 5 ♀ (IBSP 162302); Serra Bonita, 1 ♀ (MZSP). Espírito Santo: Santa Teresa, Reserva Biológica Augusto Ruschi, 1 ♀ (MZSP).

Diagnosis

Males of *M. reimoseri* are unique among *Micrathena* due to the large tegular projection inserted near the base of the embolus (Fig. 10*B*; TP) and the folded and complex conductor lobe (Fig. 10*B*; CL). Female diagnosed by Levi (1985: 566): 'This species differs from *M. lata* by having the fourth pair of spines minute (fig. 616, in *M. lata* they are half the length of the third spine) and in having small knob on the tip on the epigynum (fig. 617–619). They differ from others of the species-group by the wide abdomen (fig. 616)'.

Description

Male from Parque Estadual Sete Passagens, Miguel Calmon, Bahia, Brazil (IBSP 162301). Carapace yellowish orange, with dark brown sides. Sternum, labium, endites and chelicerae yellow. Legs orange, except for light yellow coxae and trochanters. Abdomen dorsum light yellow with dark brown lateral margins, venter orange. Carapace oval, with shallow and round thoracic groove. Abdomen rectangular, slightly wider in the posterior end. No coxal hook, femoral groove, or strong macrosetae on any of the legs or tubercles at the posterior end of the abdomen (Fig. 10*A*). Total length 3.29; carapace 1.4 long, 1.04 wide at its widest point; abdomen 1.88 long; length of femur I 1.04, patella 0.38, tibia 0.79, metatarsus 0.64, tarsus 0.43; femur II 1.04, patella 0.36, tibia 0.74; femur III 0.69, patella 0.2, tibia 0.38; femur IV 1.12, patella 0.31, tibia 0.66, metatarsus 0.58, tarsus 0.38. Palp (Fig. 10*B*) with a flat, sinuous terminal apophysis

ending in a rounded tip. Embolus thick, long, S-shaped with accompanying membrane and distal knob. Conductor short, hook-shaped, heavily sclerotised. Conductor lobe present, complex, cup-shaped with posteriorly directed tip. Paramedian apophysis absent. Median apophysis reduced to basal projection, which bears a short projection pointing towards the embolus. Paracymbium enlarged, laterally directed (Fig. 10*C*). Palpal tibia with bifid prolateral projection.

For the female description, see Levi (1985).

Intraspecific variation

Females ($n = 9$) vary in carapace length from 3.1 to 3.5 and femur I length from 3.5 to 4.05. The genitalic variation mentioned by Levi (1985) has not been observed by us in specimens from Miguel Calmon, Bahia.

Distribution

This species is known from the Atlantic rainforests of southern and eastern Brazil, from Rio de Janeiro to Bahia states.

Natural history

Individuals from Castro Alves and Miguel Calmon, Bahia, were collected in rainforest enclaves located in the Brazilian Caatinga, a dry tropical forest not suitable for most *Micrathena* species. Most females were found in webs in low (30–50 cm) plants with a bromeliad-like architecture.

Remarks

Males and females have been collected in two areas in Bahia, Brazil. The only other *Micrathena* collected in one of those areas was *M. digitata* (C.L. Koch), an unrelated and very common species whose male–female association is unequivocal. Both sexes of *M. reimoseri* possess synapomorphic features of the *militaris*-group (such as a reduced median apophysis, palpal tibia with projections, and abdomen apodemes arranged in a single line) and are therein placed (Fig. 3). Furthermore, the COI sequences of males and females are nearly identical (Fig. 4).

Micrathena yanomami Magalhães & Santos

(Figs 1*C*, *D*, 3, 5, 15)

Micrathena bicolor Keyserling: Levi, 1985 (partially misidentified, males only).

Micrathena triangularispinosa (De Geer): Dierkens, 2011: figs 8, 23 (misidentified).

Micrathena yanomami Magalhães & Santos, 2011: 43, figs 9–13 (holotype female from Bebedouro Novo, Pico da Neblina, São Gabriel da Cachoeira, Amazonas, Brazil, deposited in INPA 6286, examined).

Material examined

BRAZIL: Acre: Senador Guiomard, Fazenda Experimental Catuaba, 2 ♀ (UFMG 10623, 15518). Amazonas: Coari, Porto Urucu, 1 ♀ (MPEG 20062); São Gabriel da Cachoeira, Pico da Neblina, 2 ♀ (INPA 6286, holotype; INPA 6287, paratype). Pará: Fazenda Euclides Gallo, 1 ♀ (MPEG 24944); Juruti, 1 ♀ (MPEG 31673), 1 ♂ (MPEG 31674); ParNa da Amazônia, 1 ♀ (MPEG 30300). Rondônia: Porto Velho, Abunã, 1 ♀ (MZSP 34041), 7 ♂ (MZSP 43160, 50839, 51345, 51601, 53727, 55224, 55266), 1 ♀ (MZSP 34042), 1 ♀ (MZSP 34515), 1 ♀ (MZSP 37715), 1 ♀ (MZSP 46381), 1 ♀ (MZSP 38718), 1 ♀ (MZSP 34933); Porto Velho, Mutum, 1 ♀ (MZSP 38142). **PERU:** Cusco: Paucartambo, Kosñipata, 1 ♀, 1 juvenile (MUSM-ENT 510056), 1 ♀, 1 juvenile (MUSM-ENT 510060), 1 ♀ (UFMG 15502), 1 ♀ (UFMG 19566). Madre de Dios: Tambopata, Inotawa Lodge, La Torre, 1 ♀ (MUSM-ENT 510059), 1 ♀ (UFMG 19567). Loreto: Iquitos, San Juan Bautista, Zungarococha, 1 ♂ (IBSP 165534).

Diagnosis

Males differ from all other species by having a black band on the carapace, starting in the ocular region, passing in the lateral edges of the *pars cephalica* and nearly touching each other near the pedicel insertion (Fig. 4). They also differ from the other species of the *triangularispinosa*-group by the wide and weakly sclerotised lobe of the conductor (Levi 1985: fig. 454) and by the shape of the paracymbium, which is divided into two lobes, the dorsal one with an indentation (Levi 1985: fig. 455). Females diagnosed by Magalhães and Santos (2011: 43): '*Micrathena yanomami* females differ from the other species of the *triangularispinosa*-group by the colouration pattern of the carapace, with a black band along its entire edge, by the granulation in the carapace edges and by the setal bases of the femora, which are more projected and domed (figs 9, 10). The epigynum is similar to that of *M. triangularispinosa* (De Geer) (Levi 1985: figs 474–476), but differs by the more robust lobe, which is also more detached from the bulge (figs 11, 12), and by the median plate of the epigynum in posterior view, which is wider than long and has a mushroom-shaped clear area embracing two dark spots (fig. 13)'.

Description

Male described by Levi (1985) under the name *Micrathena bicolor*. Female described by Magalhães and Santos (2011).

Intraspecific variation

Females vary in total length from 5.92 to 6.58 ($n = 3$), carapace length from 2 to 2.5 and femur I length from 1.14 to 1.86 ($n = 9$). The females collected in Cusco, Peru, have a rather deviant somatic morphology: the carapace is uniformly dark, they have three pairs of lateral spines (a characteristic not found in the entire *swainsoni* clade; Magalhães and Santos 2012), and the abdomen and legs do not have the colouration pattern typical of this species (Fig. 1*C*; compare with Fig. 1*B*). These were initially thought to represent a different species, but genital morphology and COI sequences (Fig. 4; Myanomami193) suggest they are a morphological variant of *M. yanomami*.

Distribution

This species is known from the Amazon, in French Guiana (see Dierkens 2011; under *M. triangularispinosa*; these records have not been included in the map because we could not verify their exact placement), Amazonas, Acre and Rondônia states, Brazil, and Cusco, Loreto and Madre de Dios states, Peru.

Natural history

At Pico da Neblina, 17 individuals were collected. Four were found at the first altitude sampled, at the base of the mountain (100 m above sea level), two were located at 400 m, and the remaining 11 were captured at 860 m. At Porto Velho, specimens

were captured throughout the entire year. Of the 111 individuals captured, most of them (86) were found in the sampling plots 50 m from the Madeira River, while 12 were located at 1050 m and 13 were captured 2050 m from the river. In both localities, all individuals were captured in areas of *terra firme* old-growth forest.

Remarks

We here present evidence that the male previously assigned to *M. bicolor* by Levi (1985) is actually the male of *M. yanomami.* We had initially thought that undescribed male #7 belonged with *M. yanomami*; however, both phylogenetic placement (Fig. 3) and COI sequences (Fig. 4) show that *M. yanomami* females are closer to *M. bicolor* males than to male #7. Moreover, we also have evidence for a *M. yanomami* female–*M. bicolor* male association based on a 4-year spider inventory conducted in Porto Velho, Rondônia (AAN, unpubl. data). During this period, we collected 13 male specimens of *M. bicolor* and not a single female, which is very unusual given that females are more conspicuous and easier to collect than males. On the other hand, 121 female individuals of *M. yanomami* were obtained in this inventory. *Micrathena bicolor* males and *M. yanomami* females have also been collected in Juruti, Pará. Levi (1985: 536) observed that 'the placement of the male with *M. bicolor* is uncertain'. Although we do not have genetic data for *M. bicolor* females (currently known from two localities in Colombia), current evidence is stronger in favour of the association of this male with *M. yanomami* than it is with *M. bicolor*. The true male of *Micrathena bicolor* is thus unknown and remains to be found. On the other hand, we could not confidently associate male #7 with any species, and its placement must await a revision of the *triangularispinosa*-group.

Micrathena exlinae Levi

(Figs 3–5, 11, 15)

Micrathena exlinae Levi, 1985: 514, 516, figs 342–346 (female holotype and female paratype from Cucharas, Huallaga Valley, Huánuco, Peru, deposited at the MCZ, not examined).

Material examined

BRAZIL: Amazonas: São Gabriel da Cachoeira, Pico da Neblina, 1 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (INPA), 2 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (INPA), 1 ♀ (IBSP), 1 ♀ (IBSP), 2 ♀ (IBSP), 1 ♀ (IBSP). Roraima: Caracaraí, Arquipélago Mariuá, 1 ♂ (IBSP 165527), 4 ♀ (IBSP 165521); Tatocuara, 1 ♀ (IBSP 165522).

Diagnosis

Males of *M. exlinae* resemble the unrelated *M. patruelis* (C. L. Koch, 1839) due to the shape of the terminal apophysis, which is anteriorly rounded and acuminate distally (Fig. 11*B*; TA). They differ from *M. patruelis* and all other *Micrathena* with similar palpi by the combination of a smoothly rounded edge of the median apophysis rim (Fig. 11*B*; M) and by a large and distally widened paramedian apophysis (Fig. 11*B*; PM). Female diagnosed by Levi (1985: 514, 516): 'This species differs from *M. huanuco* by having a bottle-shaped septum on the posterior face of the epigynum (fig. 345). It differs from *M. triangularis* by having only two posterodorsal spines (figs 342, 343)'.

Description

Male from Comunidade Caicubi, Caracaraí, Roraima, Brazil (IBSP 165527). Carapace yellow, with lateral dark brown bands. Sternum whitish yellow, labium, endites and chelicerae yellow. Legs yellow at the base, gradually becoming brown in the three apical articles. Abdomen whitish yellow, with lateral dark brown bands ventrally and dorsally. Carapace rounded, with round thoracic groove. Abdomen rectangular. First coxa with a hook and second femur with a corresponding prolateral groove. First femur with a row of dorsal macrosetae and first and second tibiae ornamented with ventral macrosetae. No tubercles in the abdomen (Fig. 11*A*). Total length 3.43; carapace 1.73 long, 1.37 wide at its widest point; abdomen 2.19 long; length of femur I 1.55, patella 0.48, tibia 1.17, metatarsus 0.99, tarsus 0.43; femur II 1.27, patella 0.41, tibia 0.89; femur III 0.79, patella 0.28, tibia 0.48; femur IV 1.53, patella 0.38, tibia 0.94, metatarsus 0.97, tarsus 0.41. Palp (Fig. 11*B*) with short terminal apophysis, with rounded apex that acuminates distally. Embolus thick, sclerotised, partially fused to terminal apophysis. Radix drop-shaped. Conductor short, folded near tip of embolus. Conductor lobe present, digitiform. Paramedian apophysis present, large and wide, with subsquarish tip. Median apophysis with small lobe, gently rounded and bent rim, and large but lightly sclerotised basal projection. Tegular projection small. Paracymbium enlarged, but simple (Fig. 11*C*).

For the female description, see Levi (1985).

Intraspecific variation

Females ($n = 3$) vary in carapace length from 2.0 to 2.1 and femur I length from 2.3 to 2.4.

Distribution

This species is known from the western Amazon, in Brazil and Peru.

Natural history

At Pico da Neblina, São Gabriel da Cachoeira, Amazonas, all the 15 females collected were found at the base of the mountain (100 m above sea level) in an area covered by *terra firme* old-growth forest.

Remarks

The single putative male (undescribed male #3) did not amplify for the COI fragment we used. It was collected in the same area as five adult females of *M. exlinae.* Both sexes present features synapomorphic with the *plana*-group (e.g. a folded conductor and four pairs of lateral abdominal spines). This male–female association must be taken with caution, as there are several species of the *plana*-group known only from females (notably *M. marta* Levi, 1985; *M. bananal* Levi, 1985; *M. alvarengai* Levi, 1985; and *M. huanuco* Levi, 1985). Although none has been recorded from the particular region where this male was collected, it is possible that some of them have wider distributions than those reported by Levi (1985). However, the fact that *M. exlinae* females are common in the region suggests that our association is correct.

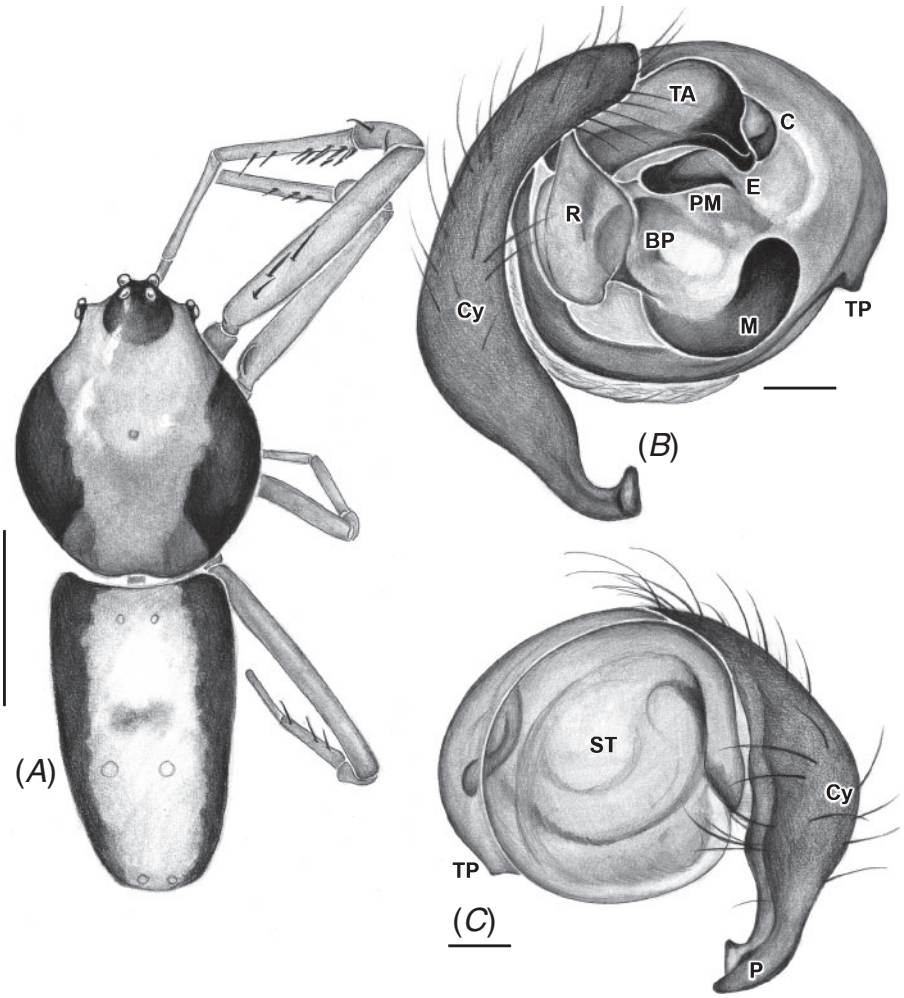

Fig. 11. *Micrathena exlinae* Mello-Leitão, 1935, male from Caracaraí, Roraima, Brazil (IBSP 165527). (*A*) Habitus, dorsal; (*B*) palpal bulb, prolateral; (*C*) palpal bulb, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B*, *C*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; Cy, cymbium; E, embolus; M, median apophysis; P, paracymbium; PM, paramedian apophysis; R, radix; ST, subtegulum; TA, terminal apophysis.

Micrathena miles Simon

(Figs 1*A*, *B*, 3–5, 12, 15)

Micrathena miles Simon, 1895: 852, fig. 907 (female syntypes from Fonte Boa and Tefé, Amazonas, Brazil, deposited at the Museum National d'Histoire Naturelle, Paris (catalogue 1172), not examined); Simon, 1897: 468; Levi, 1985: 482–483, figs 164–168.

Micrathena cuminamensis Mello-Leitão, 1930: 62, fig. 16. Synonymised by Levi, 1985;

Micrathena miles nigra di Caporiacco, 1948: 667. Synonymised by Levi, 1985.

Material examined

BRAZIL: Acre: Senador Guiomard, Estação Experimental Catuaba 2 ♀ (UFMG 15648), 5 ♀ (UFMG 15611), 1 ♂ (UFMG 15612). Rondônia: Porto Velho, Caiçara, 1 ♀ (MZSP 35448), 1 ♀ (MZSP 33394). **PERU:** Loreto: Maynas, Indiana, near San Rafael, 1 ♂ (MUSM-ENT 510057), 1 ♀ (MUSM-ENT 510062); Iquitos, San Juan Bautista, Zungarococha, 1 ♀ (IBSP 165530).

Diagnosis

Males of *M. miles* are most similar to those of *M. macfarlanei* and *M. kirbyi* due to the black pigmentation around the eyes, the presence of a retrolateral membrane on the conductor, and the basal projection of the median apophysis, which is distally detached and points towards the embolus. It differs from these two species by the shorter, more rounded terminal apophysis (Fig. 12*B*; TA) and by the median apophysis rim, whose apex is more acuminate (Fig. 12*B*; M). Female diagnosed by Levi (1985: 483): 'This species differs from *Micrathena raimondi* by lacking a frame on each side of the transverse bar and lobe of the epigynum (fig. 166). It differs from *M. kirbyi* by lacking anterior spines overhanging the carapace (fig. 165)'.

Description

Male from Senador Guiomard, Acre, Brazil (UFMG 15612). Carapace orange, suffused with black, ocular area black.

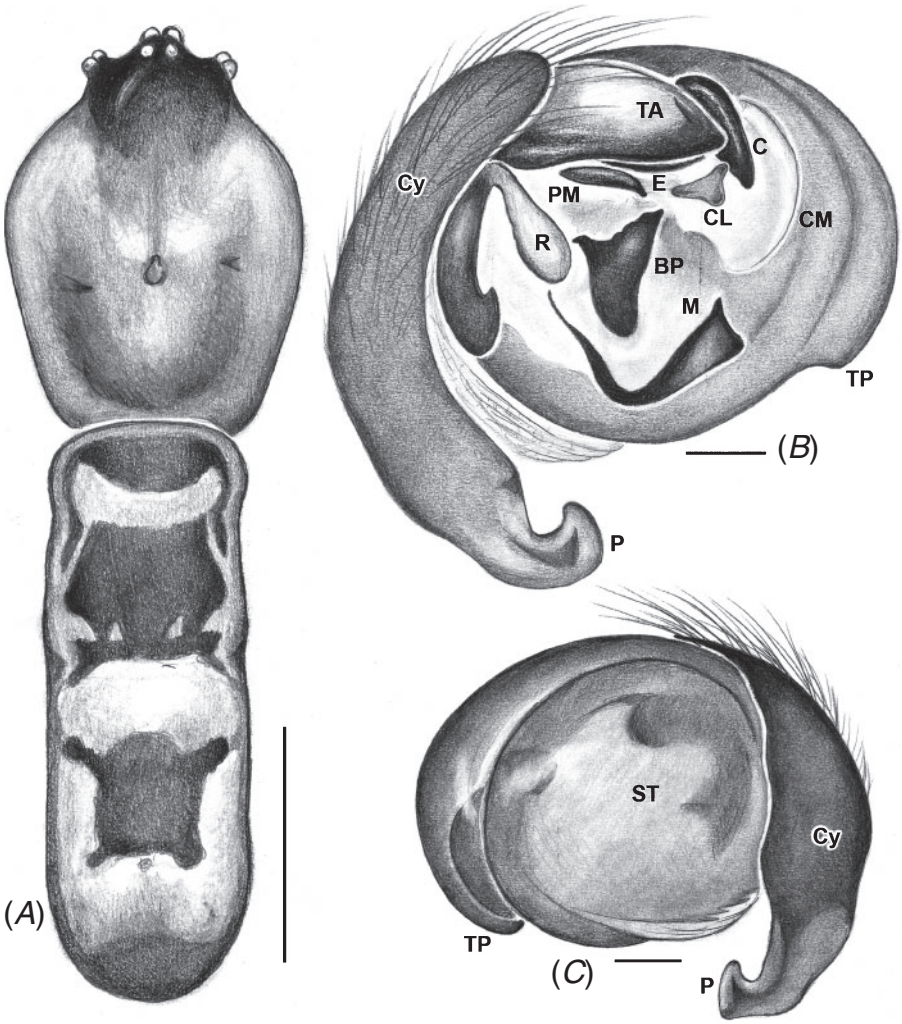

Fig. 12. *Micrathena miles* Simon, 1895, male from Maynas, Loreto, Peru (MUSM-ENT 510057). (*A*) Habitus, dorsal; (*B*) palpal bulb, prolateral; (*C*) palpal bulb, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B*, *C*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; CL, conductor lobe; CM, conductor retrolateral membrane; Cy, cymbium; E, embolus; M, median apophysis; P, paracymbium; PM, paramedian apophysis; R, radix; ST, subtegulum; TA, terminal apophysis.

Chelicerae, endites, labium and sternum black. Legs I and II light brown, III and IV dark brown. Abdomen dark brown ventrally, dorsally beige with four median dark-brown spots. Carapace coffin-shaped, wider at the anterior third. Carapace with a shallow, round thoracic groove. First coxa with a hook and second trochanter with a corresponding prolateral groove. First femur with two ventral rows of macrosetae, stouter on the apical quarter. First and second tibiae with two ventral rows of stout macrosetae. Abdomen subrectangular, truncated anteriorly, gently rounded posteriorly, without tubercles (Fig. 12*A*). Total length 5.12; carapace 2.23 long, 1.52 wide at its widest point; abdomen 2.89 long; length of femur I 2.23, patella 0.51, tibia 1.37, metatarsus 1.57, tarsus 0.61; femur II 1.83, patella 0.41, tibia 1.01; femur III 1.02, patella 0.34, tibia 0.54; femur IV 2.99, patella 0.46, tibia 1.78, metatarsus 2.28, tarsus missing. Palp (Fig. 12*B*) with short, mango-shaped terminal apophysis. Embolus partially fused to terminal apophysis. Conductor large, sclerotised with a pointed apex. Conductor lobe present, digitiform, slightly truncate on the apex. Paramedian apophysis present, narrow, digitiform. Median apophysis with large lobe, pointed and bent rim, and large and heavily sclerotised basal projection, which points towards embolus. Tegular projection small. Paracymbium enlarged but simple (Fig. 12*C*).

For the female description, see Levi (1985).

Intraspecific variation

Males ($n = 2$) vary in total length from 4.09 to 5.12 and in carapace length from 1.74 to 2.23.

Distribution

Known from the Amazon, in Brazil, Guyana and Peru.

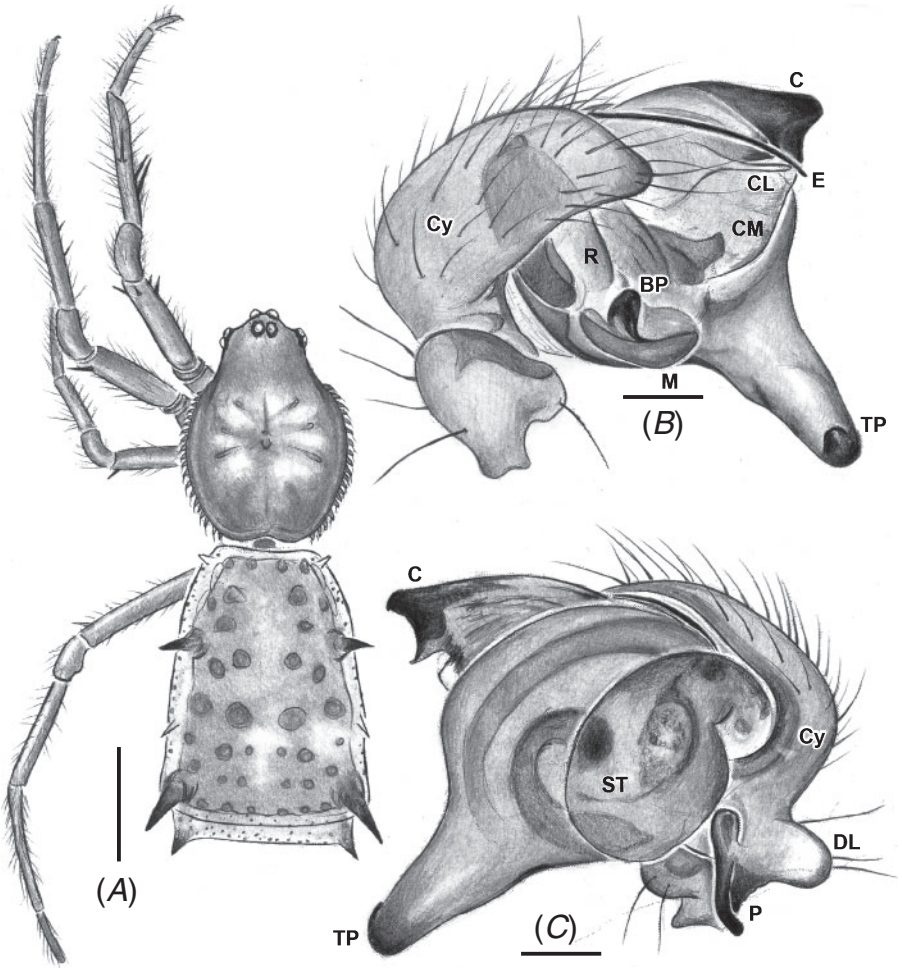

Fig. 13. *Micrathena cornuta* (Taczanowski, 1873), male from Requena, Loreto, Peru (UFMG 19561). (*A*) Habitus, dorsal; (*B*) palpal bulb (right, mirrored), prolateral; (*C*) same, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B*, *C*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; CL, conductor lobe; CM, conductor retrolateral membrane; Cy, cymbium; DL, dorsal lobe of the paracymbium; E, embolus; M, median apophysis; P, paracymbium; R, radix; ST, subtegulum; TP, tegular projection.

Natural history

A female from Maynas has been observed with a white, disc-like egg sac attached to the underside of a leaf (Fig. 1*A*). At Porto Velho, Rondônia, 30 individuals were captured throughout the year. Most of them (26) were found at sampling plots located 50 and 1050 m from river banks.

Remarks

We were unable to extract DNA from the putative males (undescribed male #4), which came from two areas (one in Peru and another in Brazil) where several females of this species were collected. Regarding the morphological phylogeny, females were inferred as members of the *guerini*-group, while males were members of the *kirbyi*-group (Fig. 3). However, females are genetically similar to *M. macfarlanei* Chickering, which belongs in this latter group (Fig. 5), and a preliminary phylogeny based on three molecular markers strongly suggests the placement of *M. miles* females in the *kirbyi*-group (ILFM, unpubl. data). It seems to us that the morphological placing of *M. miles* females in the *guerini*-group we observed (Fig. 3) is an artefact caused by missing data, particularly of the key characters associated with the male genitalia. With this in mind, it seems likely that this undescribed male does indeed belong with *M. miles*. Due to an unfortunate laboratory incident, the male specimen from Peru has been lost; the only part remaining is its left palp, which was being kept in a separate vial.

Micrathena cornuta (Taczanowski)

(Figs 2*B*, 3–5, 13, 15)

Acrosoma cornuta Taczanowski, 1873: 268, pl. 5, fig. 22 (female holotype from Cayenne, French Guiana (Polska Akademia Nauk, Warszawa), not examined).

Chaetacis cornuta (Taczanowski): Simon, 1895: 854, figs 920, 921; Soares & Camargo, 1948: 379, fig. 36; Levi, 1985: 604, figs

803–808 (in part, only females); Dierkens, 2011: 102, figs 17, 38, 47, 50.

Micrathena cornuta (Taczanowski): Magalhães & Santos, 2012: 31.

Material examined

BRAZIL: Acre: Cruzeiro do Sul, Parque Nacional da Serra do Divisor, 1 ♀ (IBSP 12404); Sena Madureira, Rio Purus, 1 ♀ (MCZ 91711); Rio Branco, Reserva Extrativista Humaitá, 2 ♀ (IBSP 15716); Senador Guiomard, Estação Experimental Catuaba, 3 ♀ (UFMG 15608, 15644). Pará: Bagre, 1 ♂ (MPEG 31655); Paragominas, Aldeia Araw, 1 ♂, 1 ♀ (MZSP 3273); Cachoeira, 1 ♀ (IBSP 42). Rondônia: Porto Velho, 2 ♂, 2 ♀ (MZSP 33864, 38362, 41312, 42432). Roraima: Alto Alegre, Aldeia Yanomami Palimi-U, 1 ♀ (IBSP 55482). **PERU:** Madre de Dios: Tambopata, Tambopata, La Torre, Inotawa Lodge, 1 ♂ (UFMG 19562), 2 ♀ (UFMG 19563); Manu, Madre de Dios, Reserva Particular Bonanza, 1 ♂ 1 ♀ (MUSM-ENT 510058), 1 ♂ (UFMG 19561), 1 ♀ (UFMG 19564). Loreto: Requena, Saquena, Río Cumaceba, 1 ♀ (UFMG 19565); Requena, Jenaro Herrera, Centro de Investigaciones Jenaro Herrera, 1 juvenile (IBSP 165539).

Diagnosis

Males are most similar to those of *M. cucharas* (Levi, 1985) and *M. woytkowskii* (Levi, 1985), due to the very long tegular projection, slightly bent at the apex, and by the shape of the paracymbium (Fig. 13*B*, *C*). They can be differentiated from them by the shape of the basal projection of the median apophysis: undetached in *M. cucharas* (see Levi 1985: fig. 819), hook-shaped in *M. woytkowskii* (see Levi 1985: fig. 810), and round and tooth-shaped in *M. cornuta* (Fig. 13*B*; BP). Also, the sclerotised tip of the conductor is thick and bifid, with a hook-shaped apical projection in *M. cornuta* (visible in mesal view; Fig. 13*B*) (thinner and simple in *M. cucharas* and *M. woytkowskii*). Finally, *M. cornuta* also can be differentiated from *M. cucharas* and *M. woytkoskii* by the more triangular, tapering shape of the retrolateral lobe of the paracymbium (Fig. 13*C*). Female diagnosed by Levi (1985: 604): 'Females differ from most other species by having a spine on each side of the head and by having only twelve spines on the abdomen (figs 803, 804). It differs from *M. woytkowskii* by having the abdomen squarish and the truncate eqigynum [*sic*] (figs 804, 808)'.

Description

Male from Reserva Particular Bonanza, Manu, Madre de Dios, Peru (UFMG 19561). Carapace, chelicerae, legs, abdomen, endites, labium and sternum orange-brown. Carapace with a round thoracic groove, one pair of dimples, two pairs of sulci and tiny denticles on the edge and dorsum of the *pars thoracica* (Fig. 13*A*). First coxa without hook; fourth coxa with denticles. First pair of tibiae straight, not modified; first and second pairs of tibiae with a few strong macrosetae, only on the ventral side on the second pair; other legs without strong macrosetae in the tibiae; femora with strong macrosetae in the distal extremity (Fig. 13*A*). Abdomen rectangular, widest posteriorly, with six pairs of spines. First, third and sixth pairs of spines orange-brown, the remaining black (Fig. 13*A*). Total length 3.2; carapace 1.29 long, 0.95 wide at its widest point; abdomen 1.66 long; length of femur I 0.95, patella 0.37, tibia 0.81, metatarsus 0.75, tarsus 0.41; femur II 0.95, patella 0.34, tibia 0.68; femur III 0.61, patella 0.24, tibia 0.37; femur IV 1.08, patella 0.31, tibia 0.68, metatarsus 0.71, tarsus 0.37. Palp without terminal or paramedian apophyses. Embolus long, sclerotised, slightly and proximally curved. Conductor with sclerotised apex bifurcated, apical projection hook-shaped, membranous and spiniform lobe parallel to embolus, and membranous basal projection. Median apophysis lightly sclerotised, except for dark and tooth-shaped basal projection. Tegular projection long and strongly bent in apex (Fig. 13*B*). Paracymbium with rounded, lightly sclerotised dorsal lobe and tapering retrolateral lobe, which is highly sclerotised (Fig. 13*C*).

For female description, see Levi (1985).

Intraspecific variation

Males ($n = 6$) vary in total length from 2.81 to 3.32; carapace length varies from 1.22 to 1.39. The orange colouration of the specimen in Fig. 2*B* is very unusual; most females have dark-brown carapace and legs.

Natural history

At Porto Velho, Rondônia, specimens were captured in the understorey of dense ombrophilous forest at 50, 1050 and 2050 m from the Madeira River. In Peru, specimens were collected in primary and secondary floodplain forests, in webs in the understorey next to rivers (100–200 m). In Tambopata, a male was found in a female's web.

Distribution

This species is known from the Amazon, from French Guiana and Pará, Brazil, to Peru. The records from Colombia by Levi (1985) were misidentified and are of *M. woytkowskii* (see below).

Comparative M. cucharas *material examined* (all identified by Levi 1985)

PERU: Huánuco: Cucharas, Huallaga Valley, 2 ♂, 2 ♀ (CAS 9058771); Santa Tereza, Huallaga Valley, 1 ♂ (CAS 9058775); Tingo Maria, 3 ♂, 6 ♀ (CAS 9058772, 9058773, 9058774, 9058776, 9058777, 9058778).

Remarks

We have re-examined a male Levi (1985) apparently used for his description of *M. cornuta*, but it was stored in the same vial as a female of *M. woytkowskii* (MCZ 91700). On the other hand, females of *M. cornuta* are frequently collected in the same areas as undescribed male #5 (Porto Velho, Rondônia, Brazil; Tambopata, Madre de Dios, Peru; French Guiana: see Dierkens 2011). In the above-referenced 4-year inventory at Porto Velho, four specimens of undescribed male #5 and 64 females of *M. cornuta* were collected, and on two occasions both were collected in the same sampling unit (one hour of nocturnal hand searching). However, not a single male of *M. cornuta* (*sensu* Levi 1985) was collected in the same area. Furthermore, the genetic distance between undescribed male #5 and *M. cornuta* females is among the smallest of the genus – only 0.8% (Fig. 4). These findings strongly suggest undescribed male #5 is, in fact, that of *M. cornuta*. As a consequence, the male described as *M. cornuta* by Levi (1985) is, in fact, *M. woytkowskii* (see below). The true male of *M. cornuta* was first illustrated by Dierkens (2011: figs 38, 47).

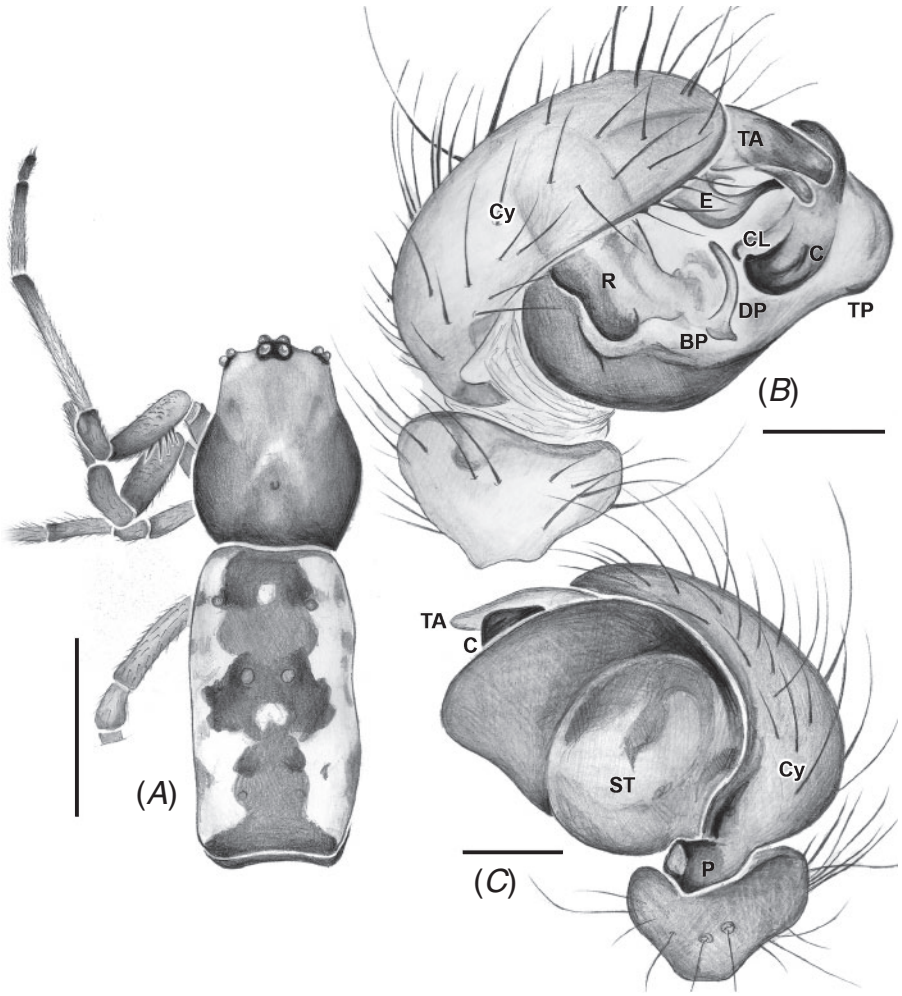

Fig. 14. *Micrathena spinulata* F.O. Pickard-Cambridge, 1904, male from Pico de Orizaba, Veracruz, Mexico (IBSP). (*A*) Habitus, dorsal; (*B*) palpal bulb (right, mirrored), prolateral; (*C*) same, retrolateral. Scale bars = 1 mm (*A*) and 0.1 mm (*B*, *C*). Abbreviations: BP, basal projection of the median apophysis; C, conductor; CL, conductor lobe; Cy, cymbium; DP, digitiform projection of the median apophysis; E, embolus; P, paracymbium; R, radix; ST, subtegulum; TA, terminal apophysis.

Micrathena woytkowskii (Levi)

Chaetacis woytkowskii Levi, 1985: 608, figs 821–826 (female holotype and 10 female paratypes from Cucharas, Huallaga Valley, Huánuco, Peru (MCZ), not examined).
Chaetacis cornuta: Levi, 1985: 608, figs 809–811 (misidentified in part, only males).
Micrathena woytkowskii: Magalhães & Santos, 2012: 31.

Material examined

COLOMBIA: Putumayo: Puerto Asis, Río Putumayo, 1 ♂, 2 ♀ (MCZ 91700, 91725).

Diagnosis

Male diagnosed by Levi (1985: 604) under the name *Chaetacis cornuta*: 'The paracymbium of the male has a diagnostic hook (fig. 811)'. Female diagnosed by Levi (1985: 608): '*Chaetacis woytkowskii* differs from *C. cornuta* by having a longer abdomen, the second and fourth spines subequal in size (figs 821, 822), and by having the epigynum more cone-shaped in profile (figs 825, 826); it differs from *M. cucharas* by having spines rather than tubercles behind the eyes (figs 821, 822)'.

Description

Male described by Levi (1985) under the name *Chaetacis cornuta* (see his figs 809–811). Female described by Levi (1985).

Distribution

This species is known from Peru and Colombia.

Remarks

Levi (1985) examined males and females of this species from Colombia and misidentified them as *M. cornuta*. We have re-examined some of these specimens seen by him, and the females fit with his diagnosis of *M. woytkowskii*, while the males fit his diagnosis of *M. cornuta*. We here describe the true male of

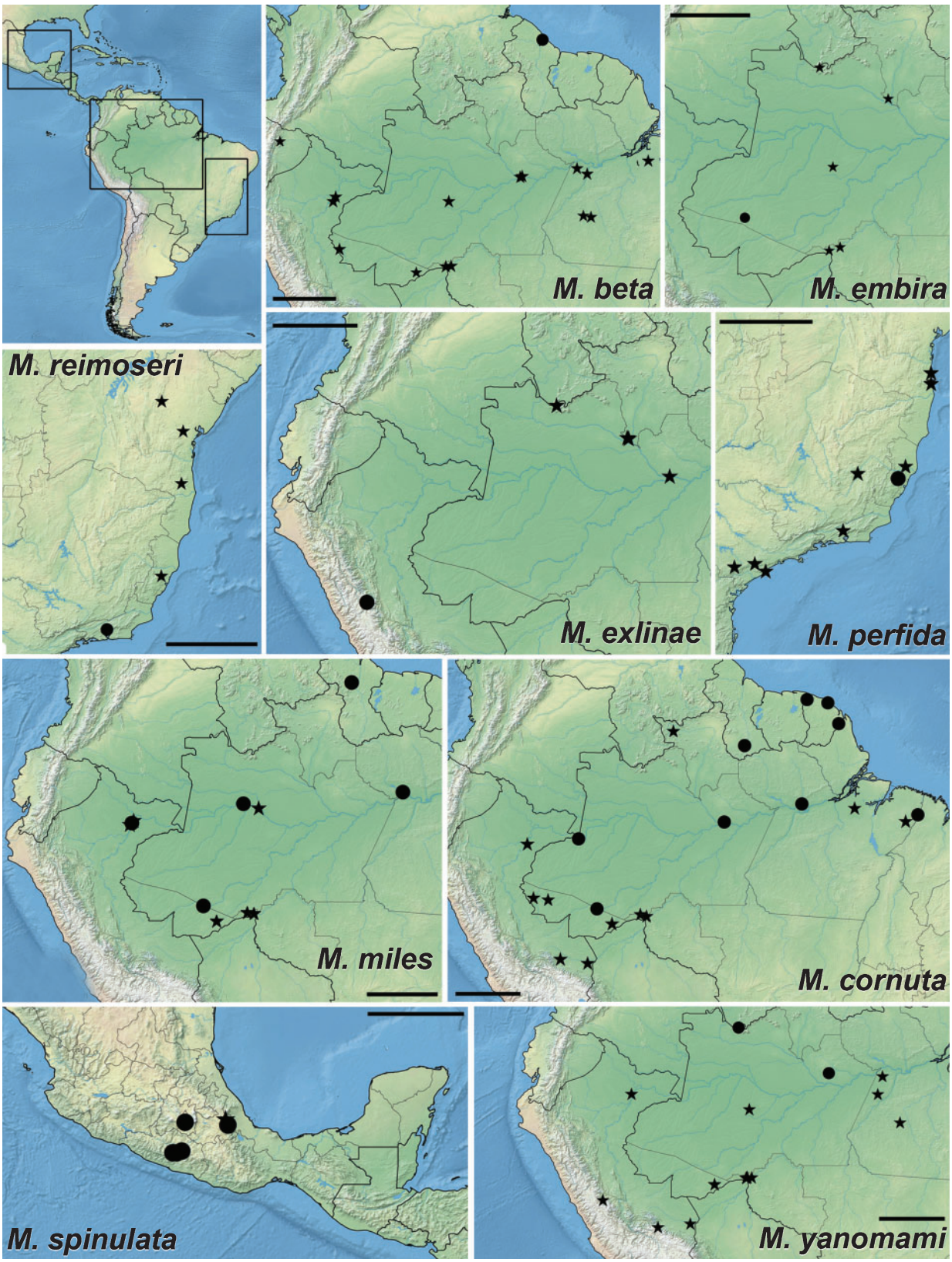

Fig. 15. Geographic distribution records of the species with newly matched males and females. Circles represent previously known records and stars represent new records. Scale bars = 500 km.

M. cornuta (see above), thus the male described by Levi as *M. cornuta* becomes unpaired. As it has been collected with females of *M. woytkowskii*, it seems more parsimonious that it belongs with the latter species.

Micrathena spinulata F.O. Pickard-Cambridge

(Figs 3–5, 14, 15)

Micrathena spinulata F.O. Pickard-Cambridge, 1904: 530, pl. 50, fig. 7 (four female syntypes from Amula, Guerrero, Mexico, and one syntype from Omilteme, Guerrero, WSW of Chilpancingo, 2400 m alt., deposited at the British Museum of Natural History, not examined); Chickering, 1961: 459, figs 181–184; Levi, 1985: 592, 594, figs 751–755.

Material examined

MEXICO: Veracruz: Pico de Orizaba Volcano, Atotonilco de Calcahuaco, 2 ♂, 2 ♀ (IBSP 166385–166388).

Diagnosis

Males differ from those of *M. gracilis* (Walckenaer, 1805) and *M. horrida* (Taczanowski, 1873) by having the posterior end of the abdomen entire (Fig. 14*A*), rather than pseudosegmented. They are most similar to those of *M. forcipata* (Thorell, 1859) due to the enlarged and curved conductor and the broad and blunt paracymbium; they can be distinguished by the strongly curved embolus, visible just below the terminal apophysis (Fig. 14*B*; E), and by the more curved digitiform projection of the median apophysis (Fig. 14*B*; D*P*). Female diagnosed by Levi (1985: 594): '*Micrathena spinulata* differs from *M. striata* and *M. margerita* by having all six spines the same size (figs 751, 752)'.

Description

Male from Pico de Orizaba Volcano, Veracruz, Mexico (IBSP 166386). Carapace light brown, with yellowish white *pars cephalica*. Sternum and labium dark brown. Endites light brown. Chelicerae light brown, darker at apex. Legs yellowish brown. Abdomen white, with light-brown median markings. Carapace suboval, widest at *pars thoracica*, with subsquarish *pars cephalica* and round thoracic groove. First coxa without hook and second femur without groove. Legs without macrosetae, except for a line of 3 or 4 macrosetae on the dorsum of femora I and II. Abdomen rectangular, with posterior end not pseudosegmented and with a pair of tiny tubercles at the posterior end (Fig. 14*A*). Total length 2.81; carapace 1.3 long, 0.94 wide at its widest point; abdomen 1.7 long; length of femur I 1.3, patella 0.43, tibia 0.99, metatarsus 0.86, tarsus 0.48; femur II 1.17, patella 0.38, tibia 0.79; femur III 0.71, patella 0.23, tibia 0.43; femur IV 1.17, patella 0.33, tibia 0.76, metatarsus 0.79, tarsus 0.38. Palp (Fig. 14*B*) with short, bifid terminal apophysis with subsquarish apex. Embolus sinuous, thicker near base, partially fused to terminal apophysis. Conductor projecting anteriorly and with sclerotised apex pointing posteriorly. Conductor lobe present, subsquarish and pointing dorsally. Paramedian apophysis absent. Median apophysis reduced to basal projection, which bears a long, curved and unsclerotised digitiform projection. Tegular projection wide, subsquarish. Paracymbium enlarged, but simple (Fig. 14*C*).

For the female description, see Levi (1985).

Intraspecific variation

Females ($n = 2$) vary in carapace length from 1.78 to 1.88. Males ($n = 2$) vary in total length from 2.81 to 2.90 and in carapace length from 1.27 to 1.30.

Distribution

This species is known from Central Mexico.

Natural history

Label data state that specimens were collected in *Quercus* forest 2300 m above sea level using the 'looking-up' method.

Remarks

We first became aware that the undescribed male had been collected through the Araneomorphae of Mexico Digital Images Catalogue (Alvarez-Padilla Laboratory 2014), which reports males and females repeatedly collected together in the same inventory in Veracruz, Mexico. The morphological phylogeny suggests that both the putative male and the female fall within the *gracilis*-group (Fig. 3). Also, they do bear some morphological resemblance to each other, especially regarding the shape and colour of carapace and legs. Finally, COI sequences are almost identical in males and females (Fig. 4).

New records

During the course of this study, we found some specimens representing new species records for Argentina and Peru. They are detailed below.

Micrathena bandeirante (Magalhães & Santos)

Chaetacis bandeirante Magalhães & Santos, 2011: 49–53, figs 20–40 (holotype male from Usina Hidrelétrica Engenheiro Sérgio Motta, Presidente Epitácio [21°45′S 52°05′W, 310 m], São Paulo, Brazil, Equipe IBSP, 16.i–13.ii.1999, deposited in IBSP 23255. Paratypes: female from the same locality (IBSP 160897); two males and four females from the same locality (IBSP 160898); one male and two females from Base de Pesquisa do Instituto Brasileiro de Desenvolvimento Florestal, Poconé [16°15′S 56°37′W, 142 m], Mato Grosso, Brazil, U. A. Drumond, 16.ii.1984 (MZSP 11443); two males and two females from Passo do Lontra, Corumbá [19°0′S 57°39′W, 118 m], Mato Grosso do Sul, Brazil, J. Raizer *et al.* iv.1998 (UFMG 4889); one female from Nhecolândia [19°14′S 57°02′S, 86 m], S. Haris, 11.xi.1987 (MNRJ 14587); all examined).

Material examined

ARGENTINA: Formosa: Pirané, 2 ♀ (MACN 32539).

Micrathena annulata Reimoser

Micrathena annulata Reimoser, 1917: 149, 150, pl. 9, fig. 31 (nine females and one juvenile syntypes from Santa Catarina, Brazil, deposited in Naturhistorisches Museum, Wien, not examined; see World Spider Catalog (2016) for complete taxonomic citation history).

Material examined

ARGENTINA: Misiones: Cainguás, Parque Provincial Salto Encantado, 1 ♀ (MACN 32548).

Micrathena lata Chickering

Micrathena lata Chickering, 1960: 6, figs 8–12 (female holotype from Teresópolis, Rio de Janeiro, Brazil, deposited in MCZ, not examined; see World Spider Catalog (2016) for complete taxonomic citation history).

Material examined

ARGENTINA: Misiones: San Javier, 1 ♀ (MACN 33832).

Micrathena sanctispiritus Brignoli

Micrathena sanctispiritus Brignoli, 1983: 249 (new name for *M. parallela* Mello-Leitão, 1940 preoccupied by *Micrathena parallela* O. Pickard-Cambridge, 1890) (male holotype from Colatina, Espírito Santo, Brazil, M. Rosa, 1936–1937, in MNRJ, not examined; see World Spider Catalog (2016) for complete taxonomic citation history).

Material examined

ARGENTINA: Misiones: San Pedro, Parque Provincial Cruce Caballero, 1 ♀ (MACN 32552).

Micrathena shealsi Chickering

(Fig. 2*D*)

Micrathena shealsi Chickering, 1960: 8, figs 13–17 (female holotype from Sunchal, Argentina, deposited in MCZ, not examined; see World Spider Catalog (2016) for complete taxonomic citation history).

Material examined

PERU: Cusco: Paucartambo, Kosñipat, road to Manu, 1 ♀ (MUSM-ENT 510061).

Acknowledgements

We would like to thank C. Griswold and A. Carmichael (CAS), L. S. Carvalho (CHNUFPI), A. D. Brescovit (IBSP), M. Oliveira (INPA), M. J. Ramírez and C. Scioscia (MACN), G. Giribet and L. Leibensperger (MCZ), A. B. Kury (MNRJ), A. B. Bonaldo (MPEG), D. Silva (MUSM-ENT), and R. Pinto-da-Rocha and S. Outeda-Jorge (MZSP) for making specimens available. Many thanks are due to A. Anker, F. U. Yamamoto and G. F. B. Pereira, who collected specimens essential for this study and allowed publication of their gorgeous photos of living specimens. We are very much indebted to M. Servin-Pastor and F. Álvarez-Padilla for sorting and lending specimens of *M. spinulata* collected within the research project funded by the Program UNAM-DGAPA-PAPIIT code IN213612. L. S. Carvalho provided some specimens, and he and L. M. Moras helped with some of the sequence data acquisition. R. Ott provided information on some specimens deposited at the Museo de Ciências Naturais spider collection in Porto Alegre, Brazil. The permission for collecting at Parque Estadual Sete Passagens has been issued by SEMA-Bahia, and fieldwork there was kindly supported by the reserve staff. AAN thanks PPGEco-INPA, IBAMA/ICMBio and PARNA Pico da Neblina for collecting permits, FUNAI and the Ayrca, a local Yanomami association, for their reception at the Yanomami Indigenous Land, and several colleagues for their help with the fieldwork. Molecular work has been carried out in the Laboratório de Malacologia e Sistemática Molecular and Laboratório de Biodiversidade e Evolução Molecular at the Universidade Federal de Minas Gerais. We thank the Willi Hennig Society for sponsoring and allowing free use of TNT. Earlier versions of the manuscript were improved by critical readings by R. Botero-Trujillo and by a thorough review by M. Harvey, M. G. Rix and an anonymous referee. This study was supported by grants from CNPq and CONICET to ILFM (372279/2013–9), from CNPq, BECA-IEB/Moore Foundation (B/2007/01/BDP/01) and Wildlife Conservation Society (WCS) to AAN, from Programa Pronoturno (FUMP/UFMG) to PHM and from FAPEMIG (APQ-01991–09; PPM-00553–11, PPM-00335–13), CNPq (474680/2010–0; 475179/2012–9, 407288/2013–9, 308072/2012–0), FAPESP (2011/50689–0) and Instituto Nacional de Ciência e Tecnologia dos Hymenoptera Parasitóides da Região Sudeste Brasileira (http:/www.hympar.ufscar.br/) to AJS.

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Handling editor: Mark Harvey