UNIVERSIDADE DE BRASÍLIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

Análise cladística de aranhas do gênero *Leucauge* White, 1841, com descrição de um novo gênero e novos grupos de espécies (Araneae: Tetragnathidae)

Leonardo Ferreira de Sousa

Brasília
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Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.
Orientador: Antonio José Camillo de Aguiar

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Banca Examinadora

Antonio José Camillo de Aguiar, Presidente – UnB

Veronica de Barros Slobodian Motta – UnB

Pedro de Souza Castanheira – MU

José Roberto Pujol Luz – UnB

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RESUMO

Análise cladística de aranhas do gênero *Leucauge* White, 1841, com descrição de um novo gênero e novos grupos de espécies (Araneae: Tetragnathidae)

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Antonio José Camillo de Aguiar

Resumo da Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.

A família de aranhas Tetragnathidae é composta por aproximadamente 1000 espécies de pequeno a médio porte, que ocupam preferencialmente ecossistemas florestais ou associados a cursos d'água. Suas espécies pertencem a 45 gêneros, sendo *Leucauge* White, 1841 o segundo gênero mais diverso e o foco desta dissertação, com 183 espécies distribuídas em regiões tropicais e subtropicais por todo o planeta. As relações filogenéticas em *Leucauge* e táxons relacionados foram investigadas através de análises de parcimônia com pesagem implícita por meio de dados morfológicos discretos. Codificamos 66 terminais no total, incluindo 36 espécies de *Leucauge* de todos as regiões biogeográficas nos quais o gênero ocorre. Nossos resultados corroboram o monofiletismo de *Leucauge*, que possivelmente se originou na Ásia ou na África, além da presença de duas linhagens Neotropicais distintas. Os dados sugerem múltiplos eventos de dispersão de longa distância. O dimorfismo sexual extremo também evoluiu independentemente duas vezes em *Leucauge*. Propomos cinco novos grupos de espécies, fornecendo uma estrutura classificatória mínima para este gênero diverso. Além disso, um novo gênero é proposto devido às suas características únicas que não se enquadram em nenhum dos gêneros atualmente delimitados para Leucauginae.

Palavras-chave: Leucauginae, sistemática filogenética, morfologia, taxonomia, análise de parcimônia.

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ABSTRACT

Cladistic analysis of the spider genus *Leucauge* White, 1841, with description of a new genus and new species groups (Araneae: Tetragnathidae)

Leonardo Ferreira de Sousa
Antonio José Camillo de Aguiar

Abstract da Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.

The spider family Tetragnathidae comprises approximately 1,000 species of small to medium-sized spiders, which occur primarily in forest ecosystems or associated to water courses. Its species belong to 45 genera, with *Leucauge* White, 1841 being the second most diverse genus and the focus of this dissertation, with 183 species distributed in tropical and subtropical regions across the planet. Phylogenetic relationships of *Leucauge* and closely related taxa were investigated through implied weighted parsimony analyses of discrete morphological data. We scored 66 terminals in total, including 36 species of *Leucauge* from all biogeographical regions in which it occurs. We found evidence of a monophyletic *Leucauge* with an Asian or African origin, and two distinct Neotropical lineages. Our data suggests multiple long-range dispersal events, as well as two independent origins of extreme sexual dimorphism within *Leucauge*. We propose five species groups, providing minimal classificatory structure for this specious genus. Additionally, a new monotypic genus is proposed due its unique characteristics that do not fit in any of the currently circumscribed Leucauginae genera.

Key-words: Leucauginae, phylogenetic systematics, morphology, taxonomy, parsimony analysis

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INTRODUCTION

The genus *Leucauge* White, 1841 (family Tetragnathidae), whose name was suggested by Darwin himself, is one of the most diverse spider genera, with 183 described species (World Spider Catalog, 2024). It has a pantropical distribution and its species are commonly found lying in their orb-webs in forest ecosystems or close to water bodies (Dimitrov & Hormiga, 2010). The genus has become a common subject of study for understanding varied biological aspects in the last few decades, such as web building (e.g.: Eberhard, 1987; 1990; Hénaut *et al*., 2006; Salomon *et al*., 2010; Tahir, *et al*., 2010); prey capture (e.g.: Briceño & Eberhard, 2011; Yoshida, 2000); parasitoid-prey interactions (e.g.: Gonzaga *et al*., 2015; Pádua *et al*., 2016), and reproductive biology (e.g.: Aisenberg, 2009; Aisenberg & Barrantes, 2011; Preston-Mafham *et al*., 2000). Some of these studies have been published with unidentified or even undescribed *Leucauge* species, due to the absence of modern taxonomic revisions for this taxon, exept for those of East Asia and the United States.

The genus *Leucauge* is recognized by the presence of two long rows of feathery thricobothria on femur IV (Levi, 1980; Ballesteros & Hormiga, 2021). Additional morphological characters include a soft and translucent sphermathecae; flagelliform embolus with wide base; conductor apically distened and sinuose sperm duct with many switchbacks (Alvarez-Padilla & Hormiga, 2011). However, none of these characters are exclusive to *Leucauge*, overlapping with other Leucauginae genera like *Tylorida* Simon, 1894 and *Mesida* Kulczynski, 1911, as seen in the revisionary work of Zhu *et al*. (2003, e.g.: figs. 144-145, 169-171).

The historical absence of a clearer diagnosis (Ballesteros & Hormiga, 2021) led the genus *Leucauge* to be poorly circumscribed and taxonomically unstable, becoming a dump genus for tetragnathids bearing femoral feathery thricobothria (Saaristo, 2003). On the other hand, numerous small genera have been described over the years to place species currently classified under *Leucauge*, but with colouration or body shape, different from those commonly associated to the genus by experts. For example, *Alcimosphenus* Simon, 1895 and *Opas* Pickard-Cambridge, 1896, were proposed to place species with abdominal tail-like projections, and red or dark coloration; *Mecynometa* Simon, 1894, contained species with small bodies and slender legs; while *Opadometa* Archer, 1951 had species with distinct pear-shaped abdomen and legs with tibial bristles.

Even before phylogenetic studies, Simon (1903) and Levi (1980) suggested that the genera above could not be separated from *Leucauge*. Álvarez-Padilla & Hormiga (2011) acknowledged the possible paraphyly of the group, partially corroborated on papers published in the following years (Álvarez-Padilla *et al*., 2020; Kallal and Hormiga, 2018). Finally, a molecular phylogeny focused on Leucauginae was published (Ballesteros & Hormiga, 2021), with a much more representative taxon sampling of *Leucauge*. This study revealed that all genera mentioned in the paragraph above are inner branches of *Leucauge*, being considered junior synonyms of the latter ever since. This study represented an important step towards the understanding of orchard spiders and their sister-taxa, but as said by authors themselves, still a first step in the "Herculean task that is the taxonomy and systematics of *Leucauge*".

With so many descibed species and several more awaiting descriptions (Dimitrov & Hormiga, 2010; Álvarez-Padilla & Hormiga, 2011), *Leucauge* still requires a deeper taxonomic classificatory structure to ease the work of arachnologists. Herein, we aim to further investigate the diagnostic features of *Leucauge*, testing its monophyly, as well as identifying diagnosable species groups within the genus based on morphological characters.

MATERIAL AND METHODS

Taxon sampling

Around 1,800 specimens were analyzed in the development of this study, with the final taxonomic sample consisting of 66 species: 65 of them are from the family Tetragnathidae, and the root species is a Mimetidae, *Gelanor zonatus* C. Koch, 1845. At least one species was sampled from each tetragnathid subfamily, as well as species not formally designated to subfamiliar taxa. More than half of the sampled taxa belong to *Leucauge*. Thrity-six species of the genus were sampled, including Neotropical, Afrotropical, Paleartic, Indomalayan and Australasian species, representing the most comprehensive taxon sampling of formaly described *Leucauge* species in a phylogenetic study to date.

The material examined belongs to the following collections (acronym and curators are between parenthesis): Coleção de Aracnídeos da Universidade de Brasília, Brasília, Brazil (DZUB, P. C. Motta); Coleção Zoológica Delta do Parnaíba, Universidade Federal do Piauí, Floriano, Brazil (CHNUFPI, L. S. Carvalho); Coleção de Aracnídeos do Museu Goeldi, Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG, A. B. Bonaldo); Coleção de Arachnida do Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG/ARA, A. J. Santos); Instituto Butantan, São Paulo, Brazil (IBSP, A. D. Brescovit); Museu de Ciências e Tecnologia da Pontífícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (MCTP, R. A. Teixeira); National Arachnida Collection, Plant Protection Research Institute, Pretoria, South Africa (NCA, AcAT, P. Marais); Senckenberg Museum Frankfurt, Frankfurt, Germany (SMF, P. Jäger); Queensland Museum, Queensland, Australia (QM, M. Rix).

The specimens were observed under a microscope stereoscope Leica M125. They were photographed by an external coupled camera AmScope M500 and the software AmScope version 3.7. The images were used as reference for both the measurements, made in comparison to a graph paper by the software ImageJ (Schneider *et al*., 2012), and the illustrations, which were drawn in the softwares Illustrator and Photoshop CC 2019 from the Adobe developer.

List of taxa used

MIMETIDAE Simon, 1881. *Gelanor* Thorell, 1869: *Gelanor zonatus* (C. L. Koch, 1845), Brasília, Brazil, DZUB 6203 (♂, ♀).

TETRAGNATHIDAE Menge, 1866. *Allende* Álvarez-Padilla, 2007: *Allende nigrohumeralis* (♀. O. Pickard-Cambridge, 1899), from literature (Álvarez-Padilla, 2007). ***Azilia* Keyserling, 1881**: *Azilia histrio* Simon, 1895, São Gonçalo do Rio Abaixo, Brazil, IBSP 263186 (♂), Conceição do Mato Dentro, Brazil, IBSP 261794 (♀). ***Baltleucauge* Wunderlich, 2008**: *Baltleucauge gillespiae* Wunderlich, 2008, from literature (original description). ***Chrysometa* Simon, 1894**: *Chrysometa* aff. *boraceia*, Jaborandi, Brazil, DZUB 9829 (♂, ♀); *Chrysometa opulenta* (Keyserling, 1881), São Gabriel da Cachoeira, Brazil, IBSP 278323 (♂, ♀); *Chrysometa zelotypa* (Keyserling, 1883), Cogua, Colombia, IBSP 225895 (♂, ♀). ***Cyrtognatha* Keyserling, 1881:** *Cyrtognatha atopica*, Dmitrov & Hormiga, 2009, Biritiba-Mirim, Brazil IBSP 93392 (♀) and IBSP 93610 (♂). ***Diphya* Nicolet, 1849**: *Diphya bicolor* Vellard, 1926, São Paulo, Brazil, IBSP 27325 (♂, ♀). ***Dolichognatha* O. Pickard-Cambridge, 1869**: *Dolichognatha pinheiral* Brescovit & Cunha, 2001, São Paulo, Brazil, IBSP 61310 (♂, ♀). ***Glenognatha* Simon, 1887**: *Glenognatha gaujoni* Simon, 1895, Porto Velho, Brazil, MZSP 54831 (♂, ♀). ***Harlanethis* Álvarez-Padilla, Kallal**

& Hormiga, 2020: *Harlanethis lipscombae* Álvarez-Padilla *et al*., 2020, from literature (original description). ***Homalometa*** **Simon, 1898**: *Homalometa* aff. *nossa*, Formosa, Brazil, DZUB 10918 (♀). ***Leucauge*** **White, 1841**: *Leucauge argyra* (Walckenaer, 1841), Brasília, Brazil, DZUB 3105 (♂, ♀); *Leucauge argyrobapta* (White, 1841), Angra dos Reis, Brazil, IBSP 26746 (♂, ♀); *Leucauge atrostricta* Badcock, 1932, Cornélio Procópio, Brazil, IBSP 274061 (♂, ♀); *Leucauge behemoth* Ferreira-Sousa *et al*., 2023, Manaus, Brazil, DZUB 97726 (♂, ♀); *Leucauge blanda* (L. Koch, 1878), Saga, Japan, SMF 3875-121 (♂, ♀); *Leucauge branicki* (Taczanowski, 1874), Senador Guiomard, Brazil, UFMG 18954 (♂, ♀); *Leucauge caudacuta* (Taczanowski, 1873), Fernandes Pinheiro, Brazil, CHNUFPI 1440 (♀); *Leucauge caudata* (Mello-Leitão, 1944), União, Brazil, CHNUFPI 4140 (♀); *Leucauge celebesiana* (Walckenaer, 1841), Malaysia, DZUB 10949 (♂, ♀); *Leucauge decorata* (Blackwall, 1864), Chumphon, Thailand, SMF 58166-121 (♂, ♀); *Leucauge dromedaria* (Thorell, 1881), Stradbroke, Australia, QM S55756 (♂, ♀); *Leucauge fastigata* (Simon, 1877), Sumatra, Indonesia, SMF 9901110-RII/1110-121 (♀), male scored from literature (Anju *et al*., 2021); *Leucauge festiva* (Blackwall, 1866), Mazzepa Bay, South Africa, AcAT 2007/146 (♂, ♀); *Leucauge funebris* Mello-Leitão, 1930, Novo Airão-Moura, Brazil, IBSP 37759 (♀); *Leucauge granulata* (Walckenaer, 1841), Kroombit tops, Australia, QM S121388 (♂, ♀); *Leucauge globosa* (O. Pickard-Cambridge, 1889), Cacoal, Brazil, ISBP 239248 (♂, ♀); *Leucauge grata* (Guérin, 1838), Champasak, Laos, SMF 63706-121 (♂) and SMF 60253-121 (♀); *Leucauge henryi* Mello-Leitão, 1940, Juriti, Brazil, MPEG 33069 (♂), Senador Guiomard, Brazil, UFMG 19192 (♀); *Leucauge idonea* (O. Pickard-Cambridge, 1889), San Andrés Tuxtla, Mexico, IBSP 226287; *Leucauge levanderi* (Kulczyński, 1901), St. Lucia, South Africa, AcAT 90/258 (♂, ♀); *Leucauge longimana* (Keyserling, 1881), Dourados, Brazil, IBSP 269054 (♂, ♀); *Leucauge mariana* (Taczanowski, 1881), Napo, Ecuador, UFMG 8915 (♂, ♀); *Leucauge medjensis* Lessert, 1930, South Africa, AcAT 2004/438 (♂, ♀); *Leucauge melanoleuca* (Mello-Leitão, 1944), Uma, Brazil, IBSP 46232 (♂) and 46230 (♀); *Leucauge paranensis* (Mello-Leitão, 1937), Belterra, Brazil, IBSP 234128 (♀); *Leucauge regnyi* (Simon, 1898), Santiago de Cuba, Cuba, UFMG 22200 (♂, ♀); *Leucauge roseosignata* Mello-Leitão, 1943, Teresópolis, Brazil, UFMG 10211 (♂, ♀); *Leucauge rubripleura* (Mello-Leitão, 1947), São Paulo, Brazil, IBSP 36153 (♂, ♀); *Leucauge severa* (Keyserling, 1893), Areia, Brazil, CHNUFPI 464 (♂, ♀); *Leucauge taczanowskii* (Marx, 1893), São Jorge, Brazil, DZUB 8262 (♂, ♀); *Leucauge tessellata* (Thorell, 1887), Louangphabang, Laos, SMF 60306-121 (♂, ♀); *Leucauge* cf. *thomeensis*, Lajuma, South Africa, AcAT 2008/489 (♂, ♀); *Leucauge trilineata* (Mello-Leitão, 1940), Caracaraí, Brazil, IBSP 252035 (♀); *Leucauge uberta* (Keyserling, 1893), Oriximiná, Brazil, UFMG 943 (♀); *Leucauge volupis* (Keyserling, 1893), Brasília, Brazil, UFMG 1715 (♂, ♀); *Leucauge xiuying* Zhu *et al*., 2003, Kampot, Cambodia, SMF 69753-121 (♂), Louangphabang, Laos, SMF 60765-121 (♀). ***Leucognatha* Wunderlich, 1992**: *Leucognatha acoreensis* Wunderlich, 1992, Azores, Portugal, SMF 60854-121 (♂, ♀). ***Gen.nov.***: *Gen.nov.sp.nov.* **new species**, Sabah, Malaysia, DZUB 10953 (♂, ♀). ***Mesida* Kulczyński, 1911**: *Mesida argentiopunctata* (Rainbow, 1916), Kinabalu, Malaysia, IBSP 16379 (♀), male scored from literature (Álvarez-Padilla & Hormiga, 2011); *Mesida pumila* (Thorell, 1877), Maluku, Indonesia, SMF 3913-121 (♀); *Mesida yangbi* Zhu *et al*., 2003, Kinabalu, Malaysia, IBSP 16336 (♂), F scored from literature (original description); *Mesida yini* Zhu *et al*., 2003, Louangphabang, Laos, SMF 60276-121 (♂, ♀). ***Meta* C. L. Koch, 1835**: *Meta menardi* (Latreille 1804), Nordrhein-Westfalen, Germany, SMF 9904315-RII/4315-122 (♂, ♀). ***Metabus* O. Pickard-Cambridge, 1899**: *Metabus debilis* (O. Pickard-Cambridge, 1889) Capão Bonito, Brazil, IBSP 48245 (♂), Miracatú, Brazil, IBSP 85959 (♀). ***Metellina* Chamberlin & Ivie, 1941**: *Metellina segmentata* (Clerck, 1757), Germany, Sassnitz, IBSP 215461 (♂, ♀). ***Nanometa* Simon, 1908**: *Nanometa dimitrovi* Álvarez-Padilla *et al*., 2020, Bartle Frere, Australia, QM S121390 (♂, ♀). ***Orsinome* Thorell, 1890**: *Orsinome vethi* (van Hasselt, 1882) Malaysia, DZUB 10954 (♂, ♀). ***Tetragnatha* Latreille, 1804**: *Tetragnatha bogotensis* Keyserling, 1865, São Desidério, Brazil, DZUB 11015 (♂, ♀). ***Tylorida* Simon, 1894**: *Tylorida flava* Sankaran *et al*., 2017; Sabah, Malaysia, DZUB 10956, (♀); *Tylorida striata* (Thorell, 1877), Raub, Malaysia, DZUB 10951 (♀), male scored from literature (Zhu *et al*., 2003); *Tylorida tianlin* Zhu *et al*., 2003, Bolikhamxai, Laos, SMF 60363-121 (♂, ♀); *Tylorida ventralis* (Thorell, 1877), Bangi, Malaysia, DZUB 10950.

Characters and Codification

In this study we define characters as structures hypothetically independent on the semaphoronts. Character states are the interpretation of how a given trait (character) is expressed in different comparable semaphoronts of the study sample. We prioritized discrete characters of binary and contingent codification (Brazeau, 2011;

Strong & Lipscomb 1999). In the contigent coding scheme, characters of higher hierarchy indicate the existence of a structure (present), and a subordinate character describes the variation of this structure within the sample. The terminals lacking the structure (absent) are coded as "inapplicable" (-) in the subordinate character. We did not include characters with autapomorphic states (unique to a single terminal).

The matrix was built in the software Mesquite 3.81 (Maddison & Maddison, 2023), and the characters were written according to Sereno (2007), following the example: "Male chelicerae" (secondary locator, L2), "modfied setae" (primary locator, L1), distribution (variable, V): (0) concentred in a diagonal section; (1) sparse (character states, v0 and v1). Due to the predominance of females in the collection specimens in a ratio of more than 4:1 to males, and with seven of the 66 species with males unavailable, we opted to base our character coding from female specimens. The exceptions are those characters that are exclusive to males, such as dimorphic pedipalp and cheliceral characters. In our study, most of the explored characters include the male and female genitalia, used in Arachnology not only to differentiate closely related species, but also valuable to diagnose higher rank taxa such as genera and families (Huber, 2003); but also the chelicerae, which are diverse in shape within Tetragnathidae and sometimes play a direct role in courtship and copula (Eberhard & Huber, 1998; Danielson-François & Sullivan, 2021); the carapace and eyes; the sternum; the legs, which might have modified setae and macrosetae, commonly used in diagnosing genera; the different abdominal shapes and ornamentation patterns, which according to our observations in the specimens identification stage, has species specificities. Several characters used here come from a pool of published phylogenetic inferences on Tetragnathidae and related taxa (Álvarez Padilla, 2007; Álvarez-Padilla *et al.*, 2009; Alvarez-Padilla & Hormiga, 2011; Cabra-García & Brescovit, 2016; Dmitrov & Hormiga, 2009; Griswold *et al.*, 1998; Hormiga *et al.*, 1995; Kuntner, 2005, 2006; Kuntner *et al.*, 2008; Levi, 1980; Tanikawa, 2001; Zhu, Song & Zhong *et al.*, 2003). If a character originates from this study, it will be explicitly stated in the results section. Morphological abbreviations were used as follows: AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes; EBA, embolic basal apophysis.

Phylogenetic analyses

We conducted the parsimony analyses for equal-weights and implied-weights in the software TNT 1.6 (Goloboff & Morales, 2023). Both searches used new technology algorithms (Goloboff, 1999; Nixon, 1999), which are adequate for matrices when traditional searches fail to find the best score successively, normally with more than 100 terminals and/or containing a high number of incongruences. All four algorithms were implemented; the parameters were set to perform 20 interactions of ratchet, 20 cycles of tree drifting and five rounds of tree-fusing. The remaining boxes were kept in the default state. Starting from a random seed equaling zero, algorithms were set to stop operating once the best score was hit 250 times.

To explore the effects of homoplasy downweight, we performed a sensitivity analysis (Wheeler, 1995; Giribet, 2003), using the different values of *K* (concavity constant) obtained through the scripts provided by Mirande (2009), which use equal-weigths searches to find at which values of *K* the average characters would have fit percentages corresponding to 50, 54, 58, 62, 66, 70, 74, 78, 82, 86 and 90% of a non-homoplastic character. By using this script, we avoid arbitrarily choosing regular values of *K*. The 11 resultant values of *K* were used in implied-weigthing searches with the parameter configurations detailed above. Subsequentely, the frequencies of clade recuperation in the most optimal tree obtained under each value of *K* were compared (rfrequs command). The tree that was chosen as reference was the one with the highest average frequency of topological similarity. The remaining frequencies were plotted in navajo rugs for each clade of this tree. Thereafter, character optimizations, clade supports, values of fit and retention and consistency indices are given for the reference tree.

Relative Bremer supports (Goloboff & Farris, 2001) were calculated based on a pool of suboptimal trees obtained through TBR searching. First, 5,000 trees with 1 extra step were retained, then 5,000 trees with 2 extra steps and finally more 10,000 trees with up to 10 extra steps, totalizing a sample of 20,000 suboptimal trees. The symmetric resampling (Goloboff *et al*., 2003) was calculated with 5,000 replications with default settings for change probabilities (= 33) and the values are given in frequency differences (GC). Indices of consistency (CI), retention (RI) and Fit were given by the script *statsall.run*. Character optimizations (unambiguous, fast and slow) were visualized in the software Winclada 1.00.08 (Nixon, 2002).

RESULTS

Characters

The matrix consisted of a total of 139 binary characters derived from the external morphology of males and females, distributed as follows: 44 characters for male pedipalp; 15 for male chelicerae; 12 for female carapace; two for male legs and seven for female legs; 37 for female genitalia; only one for female sternum; 20 for female abdominal features, and one for sexual dimorphism. Forty one of these characters were proposed for the first time in this study. The characters are described in the sections below.

Male pedipalp (Ch. 1 to 44)

Male pedipalps are highly valued in Aracnology due their usefulness in studies of reproductive biology, and by being used as a species-specific diagnostic character. Specifically, within the Araneomorphae, there are normally numerous sclerites on the male pedipalp, each one of them bearing potential information. Investigating homologies and roles of these sclerites is a common subject of research (e.g.: Coddington, 1990). Additionally, the existence of multiple cymbial projections appears to be an evolutionary trend within Tetragnathidae, and provide strong phylogenetic signal (Álvarez-Padilla & Hormiga, 2011). Pedipalp characters have been widely used in reconstructing cladograms, and this study is no exception.

Character 1 (original). Male pedipalp, cymbium, shape: (0) elliptical (Fig. 1A); (1) cup-shaped (CI = 1.000; RI = 1.000).

In most spiders, including the tetragnathids, the cymbium has somewhat elliptical shapes, with its middle region wider than the base and the acuminate apex. Herein, the cymbium was considered cup-shaped when the widest part is at its apex. This character is one of the grouping characteristics for a clade containing *Diphya bicolor*, *Chrysometa*, and *Allende nigrohumeralis*. In the reference tree, this clade contains *Homalometa* aff. *nossa*, although this placement is unstable throughout different values of *K*. Looking in congeneric species, since the male is unknown for this terminal, the cymbium is thin and elliptical rather than cup-shaped (Levi, 1986: figs. 736, 739).

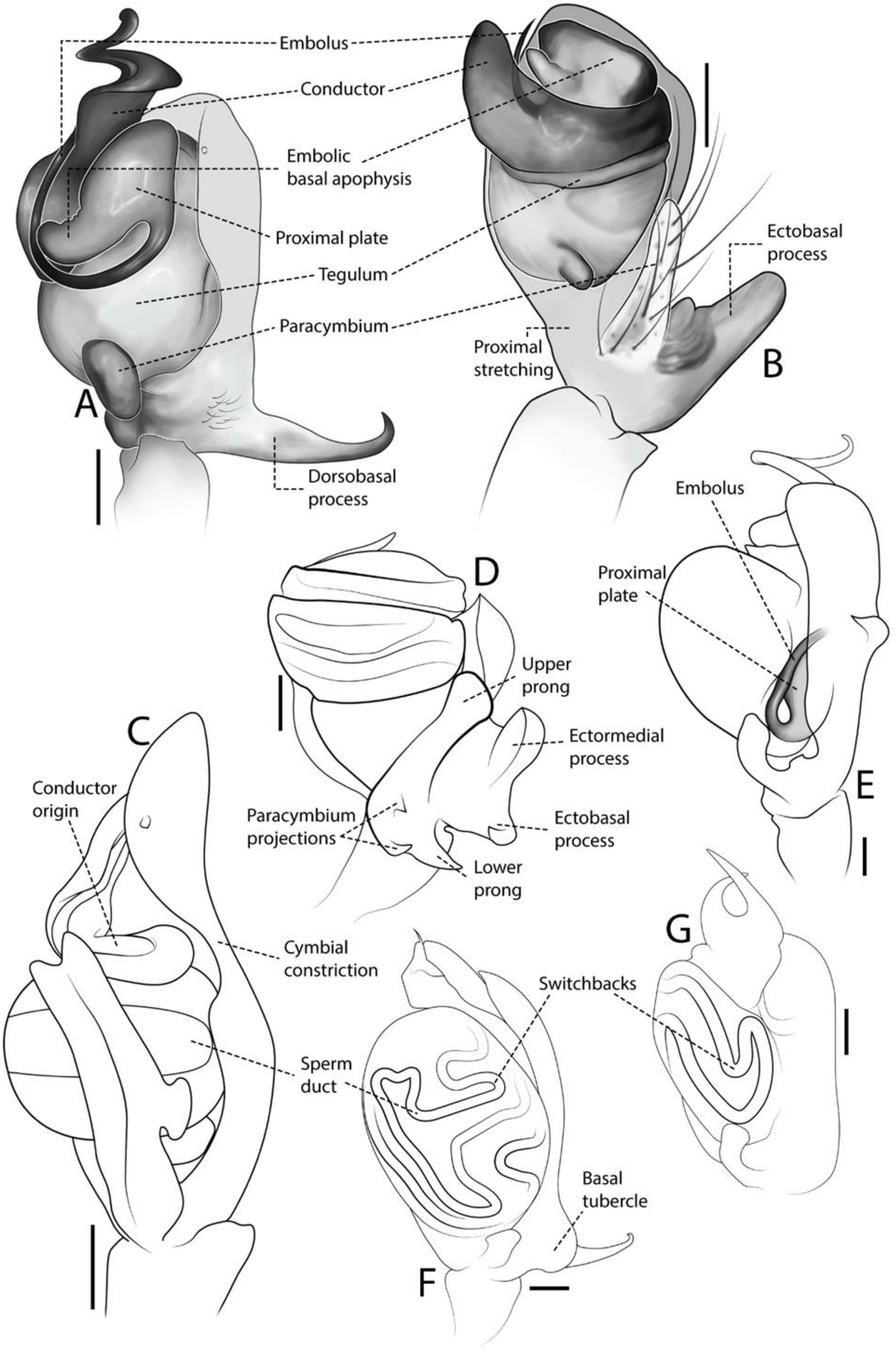

Embolus
Conductor
Embolic basal apophysis
Proximal plate
Tegulum
Paracymbium
A
Dorsobasal process
Ectobasal process
Proximal stretching
B
D
Upper prong
Ectormedial process
Paracymbium projections
Ectobasal process
Lower prong
Embolus
Proximal plate
E
C
Conductor origin
Cymbial constriction
Sperm duct
G
Switchbacks
Basal tubercle
F

Figure 1. Pedipalp illustrations and structures of some species from our sample. A, *Leucauge longimana*, lateral. B, *Metellina segmentata*, ventral. C, *Tetragnatha bogotensis*, lateral. D. *Chrysometa* aff. *boraceia*, ventral. E, *Orsinome vethi*, lateral. F, *Tylorida ventralis*, lateral. E. *Leucauge argyrobapta*, lateral. Scale bars = 0.1 mm.

Character 2. Male pedipalp, cymbium, medial width: (0) entire (Fig. 1B); (1) constricted (Fig. 1C) (CI = 0.500; RI = 0.667).

Cymbium with the middle region narrower than or as narrow as the base and the apex are coded here as constricted. This condition is synapomorphic for Tetragnathinae. In *Chrysometa cambara*, the narrow lateroapical part of the cymbium is also interpreted as constriction rather than a projection because it bears the tarsal organ, present in the apex of the tetragnathid pedipalps.

Character 3. Male pedipalp, cymbium, dorsobasal process, occurrence: (0) absent (Fig. 1C); (1) present (Fig. 1A) (CI = 0.143; RI = 0.727).

The dorsobasal process differs from other cymbial processes by its position and its distinct spine-like shape. This character is synapomorphic for Leucauginae, but was lost at least three times: in *Metabus debilis*, although still present in the congeneric *Metabus ocellatus* (Keyserling, 1864); in **Gen.nov.** and in the *Leucauge* clades C and D, containing mostly Neotropical species. Using fast optimization, the presence of a dorsobasal process has three different origins in clade D after its loss: in *L. longimana*; in *L. argyra*; and in the *L. globosa* group. Using slow optimization, the dorsobasal process is lost in clade C, in *L. behemoth* and in the remaining species of clade D, but originates independently in the *globosa* group. The projections present in *Orsinome vethi* and *L. branicki* were coded as dorsobasal processes because of their shapes, despite having different positions.

Character 4. Male pedipalp, cymbium, dorsobasal process, orientation in relation to the cymbial longitudinal axis: (0) perpendicular (Fig. 1A); (1) parallel (CI = 0.500; RI = 0.667). Inapplicable for taxa without the dorsobasal process (Ch. 3; state 0).

Parallel orientation is present in dorsobasal processes of the *globosa* group, *L. agyra* and *Orsinome vethi*. In the remaining species, this process is perpendicular.

Character 5. Male pedipalp, cymbium, ectobasal process, occurrence: (0) absent (Fig. 1C); (1) present (Fig. 1B) (CI = 0.333; RI = 0.778).

This projection differs from the dorsobasal process by its position, adjacent with the ectal margin of the cymbium. The ectobasal process is recovered as synapomorphic for Metainae and the '*Diphya*/*Chrysometa*' clade. In one analysis (*K* = 6.42) *Leucognatha acoreensis* and *Nanometa dimitrovi* were also recovered at the base of the later clade, which implies in less steps for this character.

Character 6. Male pedipalp, cymbium, ectobasal process, denticles, occurrence: (0) absent; (1) present (CI = 0.333; RI = 0.333). Inapplicable for taxa without the dorsobasal process (Ch. 5; state 0).

The denticles are short and thick macrosetae, variable in number, that cover part of the ectobasal process. In the present analysis, the optimization reveals three different origins for these denticles, and they were synapomorphic for *Allende nigrohumeralis* plus *Chrysometa cambara*.

Character 7. Male pedipalp, cymbium, ectomedial process, occurrence: (0) absent (Fig. 1C); (1) present (Fig. 1D) (CI = 0.333; RI = 0.667).

The ectomedial process has at least two different origins and is found mostly in Nanometinae, *Chrysometa* and closely related taxa (Álvarez-Padilla *et al*., 2020). In Leucauginae, this is one of the characters that separates **Gen.nov.** from relatives like *Tylorida* and *Harlanethis*.

Character 8 (orginal). Male pedipalp, cymbium, proximal stretching, occurrence: (0) absent (Fig. 1A); (1) present (Fig. 1B) (CI = 1.000; RI = 1.000).

The bulb typically connects to the cymbium at its base. However, in certain Metainae species, the base of the cymbium is stretched to accommodate the particularly large ectobasal process and the paracymbium. As a result, the bulb occupies only the distal two-thirds of the cymbium. This character was recovered as synapomorphic for *Meta menardi* + *Metellina segmentata*, but is also present in Metainae not included in the present study, such as some *Dolichognatha* species (Dimitrov *et al*., 2010) and *Zhinu* Kallal and Hormiga, 2018.

Character 9 (original). Male pedipalp, cymbium, basal tubercle, occurrence: (0) absent (Fig. 1C); (1) present (Fig. 1F) (CI = 0.083; RI = 0.476).

A swollen region at the base of the cymbium, present in some Leucauginae and in *Meta menardi*, but highly homoplastic. This character is commonly found in *Tylorida* and species from clades A and B of *Leucauge*, whereas its absence was recovered for *argyra* group and clade C, excluding *L. xiuying*.

Character 10 (original). Male pedipalp, cymbium, basal tubercle, distribution: (0) close to ectal margin (Fig. 1F); (1) covering the whole dorsum (Fig. 1G) (CI = 0.250; RI = 0.400). Inapplicable for taxa lacking the basal tubercle (Ch. 9; state 0).

The basal tubercle can either be a small swelling positioned next to the ectal margin and close to the dorsobasal process (when it is present) or a wider hump covering almost the entire base of the cymbium. This last condition is found mostly within an inner portion of the *argyrobapta* group, in the branch that is sister to *L. atrostricta*.

Character 11 (original). Male pedipalp, cymbium, cymbial hook, occurrence: (0) absent (Fig. 1A); (1) present (CI = 1.000; RI = 1.000).

This projection is only found in the *argyra* group. It is one of the most readily recognazible palpal characters, differing from the remaining cymbial apophyses by its dorsomedial position and the presence of a massive modified macrosetae on its apex. The terminology was proposed by Barrantes *et al*. (2013), which discussed the signficance of this character for reproduction.

Character 12. Male pedipalp, paracymbium, cuticle, aspect: (0) soft (Fig. 1A); (1) sclerotized (Fig. 1B) (CI = 0.500; RI = 0.667).

Soft paracymbium is present in some smaller species like *Nanometa dimitrovi* and *L. globosa*, where the sclerotization is generally low. In Metainae, the soft cuticle of the paracymbium was optimized as synapomorphic and unlike the previous examples, seems unrelated to size and degree of sclerotization from the rest of the pedipalp.

Character 13. Male pedipalp, paracymbium, degree of sclerotization in comparison to cymbium: (0) equal; (1) more sclerotized (CI = 0.077; RI = 0.454). Inapplicable for taxa with soft paracymbium (Ch. 12; state 0).

The character is optimized as very homoplastic regardless of the value of *K* or the optimization choice. Nevertheless, it still can be useful in diagnosing some clades since the state 0 is consistent through Afrotropical species (clade A) and the state 1 is synapomorphic for *Chrysometa* plus *Allende*; for *argyra* group and an inner portion of the *argyrobapta* group.

Character 14. Male pedipalp, paracymbium, apex, shape: (0) swollen (Fig. 1A); (1) acuminate (Fig. 1B) (CI = 0.500; RI = 0.667).

Paracymbium with swollen apex exhibits a spatuliform shape and is narrower in the middle. This is the most common shape within Tetragnathidae. The acuminate apex, otherwise, is present only in Metainae and in some *Tetragnatha* species. Coding the shape of the paracymbium apex in *Tetragnatha* can be tricky due to the presence of a marginal flat projection (Castanheira *et al*., 2019) that changes the silhouette of this sclerite.

Character 15. Male pedipalp, cymbium, dorsoapical macrosetae, occurrence: (0) absent; (1) present (CI = 0.250; RI = 0.000).

This character did not recover any clade in most analysis, except for the highest values of *K* (29.67 and 42.98), in which it was optimized as synapomorphic for *Azilia histrio* plus **Gen.nov.**

Character 16 (original). Male pedipalp, paracymbium, apex: (0) single (Fig. 1A); (1) double (Fig. 1D) (CI = 0.500; RI = 0.500).

The paracymbium is typically connected to the bulb at its base. However, in most *Chrysometa* species, the connection occurs at the midpoint, creating a c-shaped structure with two apices pointing in opposite directions. Levi (1986) introduced the terms "upper prong" and "lower prong" for these apices.

Character 17. Male pedipalp, parabymcium, orientation in relation to the palpal axis; (0) parallel; (1) perpendicular (CI = 0.071; RI = 0.480).

Similar to Character 13, the orientation of the paracymbium is very homoplastic, but its optimization was still useful in diagnosing smaller clades for the reference tree. While parallel in most tetragnathids, the perpendicular state is present in *Mesida*, *Leucauge* clade A (excluding *L. levanderi*), clade C and in *argyra* group.

Character 18. Male pedipalp, paracymbium, projections, occurrence: (0) absent (Fig. 1A); (1) present (Fig. 1D) (CI = 0.167; RI = 0.167).
This character is difficult to optimize since it is present in taxa with inconsistent placements through different *K* values, such as *Azilia histrio* and *Leucognatha acooresnsis*. Paracymbial projections originated at least twice within Tetragnathidae. In most genera, they are present as a single marginal knob. When present in *Chrysometa*, these projections can vary in number, size and position, suggesting a potential utility in diagnosing species. The projections in *Chrysometa* might not be homologous to the ones present in other genera.

Character 19. Male pedipalp, paracymbium, setae, occurrence: (0) absent; (1) present (Fig. 1B) (CI = 0.020; RI = 0.000).
The absence of this trait did not recover clades in any analyses, as almost all species of Tetragnathidae bear setae on the paracymbium.

Character 20. Male pedipalp, paracymbium, setae, coverage: (0) evenly; (1) unequal (CI = 0.500; RI = 0.667). Inapplicable for taxa with naked paracymbium (Ch. 19; state 0)
In most species of the present study, the setae occupy a subapical or marginal position on the paracymbium. In Metainae, however, the setae are uniformly distributed all over the weakly sclerotized paracymbium. This condition is also present in various *Tetragnatha* species (Castanheira *et al*., 2019).

Character 21. Male pedipalp, paracymbium, setae cluster next to the base, occurrence: (0) absent; (1) present (CI = 0.090; RI = 0.523).
A group of short and dense setae may be present either on the base of the paracymbium or on the ectal margin of the cymbium. The presence of a setae cluster is very homoplastic within Leucauginae, but still useful in grouping for some clades, which include *Mesida*, *Leucauge* clade A, *L. granulata* plus *L. dromedaria* and *argyra* group. Regardless of topology and optimization scheme, this character is consistently given as plesiomorphic for *Leucauge*.

Character 22 (original). Male pedipalp, paracymbium, insertion: (0) close to cymbial margin (Fig. 1A); (1) close to the tibial apex (Fig. 1C) (CI = 0.500; RI = 0.667).
The paracymbium originating close to the tibial apex is synapomorphic for Tetragnathinae, where it superficially appears to be dettached from the cymbium. In *Chrysometa opulenta*, a similar attachment point exists, although the paracymbium does not exhibit the same appearance of disconnection from the cymbium.

Character 23. Male pedipalp, subtegulum, position relative to tegulum: (0) under (Fig. 1B); (1) mesal (Fig. 7A) (CI = 0.333; RI = 0.882).
The subtegulum can be positioned either mesally, aligning side by side with the tegulum along the longitudinal axis of the pedipalp, or completely underneath it. This feature is synapomophic to Leucauginae plus *Azilia histrio*, but suffers reversion in species of the *grata* group and in *Harlanethis*.

Character 24. Male pedipalp, tegulum, shape: (0) ovoid (Fig. 1A); (1) disk-shaped (Fig. 1B) (CI = 0.250; RI = 0.571).
The tegulum exhibits an ellipsoid shape in most species we studied. In certain taxa, its length can be approximately three times larger than its width. These species were coded as having a disk-shaped tegulum. The last state is shared among Metainae, but it also present in some species from the *Diphya*/*Chrysometa* complex, *Nanometa dimitrovi* and *L. tacznowskii*.

Character 25 (original). Male pedipalp, tegulum, orientation: (0) longitudinal (Fig. 7A); (1) transversal (Fig. 1C) (CI = 0.333; RI = 0.846).
The orientation is determined by comparing the longer axis of the tegulum with the longitudinal axis of the cymbium. If the longer axis runs parallel to the cymbium, it is coded as longitudinal. If perpendicular, it is coded as transversal. Longitudinal tegulum is synapomorphic for *Azilia histrio* plus Leucauginae, with only one reversion in *Harlanethis*.

Character 26. Male pedipalp, tegulum, ectal surface height compared to mesal surface: (0) same (Fig. 1C); (1) higher (Fig. 7A) (CI = 0.250; RI = 0.800).
In *Azilia histrio*, *Leucognatha acoreensis* and Leucauginae, the exposed portion of the tegulum is swollen in comparison with its opposite side that remains covered by

the cymbium. This is one of the diagnosing characters for Leucauginae, although reversed in *Leucauge taczanowskii* and *Leucauge decorata*.

Character 27. Male pedipalp, conductor, morphology: (0) folded (Fig. 1A); (1) open (Fig. 1B) (CI = 0.250; RI = 0.750). All conductor characters are inapplicable for *Azilia histrio* because it lacks this sclerite.

The conductor is classified as folded when at least one portion coils upon itself to create a sheath-like structure. This folded configuration is observed in Tetragnathinae, most Leucauginae and *Allende nigrohumeralis*.

Character 28. Male pedipalp, conductor and embolus, interface: (0) conductor covering one side (Fig. 1B); (1) conductor enclosing the distal portion (Fig. 1A) (CI = 0.333; RI = 0.867).

The conductor in tetragnathids is always associated to the embolus, covering at least one side of it. In *Tetragnatha* and Leucauginae (except for *Harlanethis* and *L. taczanowskii*) the conductor encloses totally at least the distal portion of the embolus.

Character 29. Male pedipalp, conductor apophysis, occurrence: (0) absent (Fig. 1A); (1) present (Fig. 1G) (CI = 0.142; RI = 0.000).

This character did not support monophyletic groups in any of the analyses. However, it still holds potential for future studies on *Leucauge*. State 1 is observed in undescribed species resembling taxa from the *argyrobapta* group, which includes two terminals bearing apophyses on the conductor: *L. argyrobapta* and *L. roseosignata*.

Character 30. Male pedipalp, conductor, tegular origin: (0) central (Fig. 1C); (1) ventral (Fig. 7A) (CI = 0.200; RI = 0.600).

In Tetragnathidae, the tegular sclerites are inserted at the apex. The embolus originates from the dorsal margin, with one side shielded by the cymbium. The conductor may originate either from the center of the tegular apex, or from the opposite side of the embolus, at the ventral margin. State 1 is synapomorphic to Metainae, Leucauginae (excluding *Harlanethis*), and is also present in *Diphya bicolor* and *Chrysometa zelotypa*. A reversal of this state occurs in *L. dromedaria*.

Character 31. Male pedipalp, conductor, path in relation to tegular margin: (0) following the margin (Fig. 1B); (1) apically distended (Fig. 7A) (CI = 0.333; RI = 0.800). Innaplicable for *Azilia histrio*.

The conductor is coded with state 0 when its path forms a semicircle around the tegular margin. Otherwise, the conductor just points apically parallel to the pedipalp longitudinal axis, which corresponds to the state 1. Apically distended conductors were recovered as synapomorphic for *Leucognatha acoreensis* plus Tetragnathinae and Leucauginae, with one independent origin in *Dolichognatha pinheiral* and a reversion in *Leucauge branicki*.

Character 32. Male pedipalp, embolus, shape: (0) tubular (Fig. 1A); (1) lamelliform (Fig. 1D) (CI = 0.250; RI = 0.625).

In Álvarez-Padilla and Hormiga (2011) this character had a third state, the flagelliform shape, that was coded for Leucauginae and Nephilinae. Essentially, this state indicates a tubular embolus that abruptly widens at its base. In this study, we opted to threat these particularities as independent characters (see Character 37). Lamelliform embolus is synapomorphic for Metainae and the '*Diphya*/*Chrysometa'*, with a reversion in *Chrysometa cambara* and two different origins in *Azilia histrio* and *Cyrtognatha atopica* respectively.

Character 33. Male pedipalp, embolus, basal apophysis, occurrence: (0) absent (Fig. 7A); (1) present (Fig. 1A) (CI = 0.200; RI = 0.600).

The embolic basal apophysis or EBA is a projection contiguous with the embolus, but not crossed by the sperm duct. Originally referred to as "metainae embolic apophysis" due to being a putative synapomorphy for this subfamily, this terminology was later revised after phylogenetic analyses demonstrated the homoplastic nature of this character. The apophyses are found in species topologically unrelated, a conclusion further supported by our study, which identified three to four independent origins of this trait, varying with optimization scheme choice. Among the Leucauginae sampled, only *L. longimana* bears the EBA.

Character 34 (original). Male pedipalp, embolic basal apophysis, length compared to embolus: (0) as long as the embolus; (1) short (Fig. 1A) (CI = 0.500; RI = 0.500). Inapplicable for taxa lacking EBA (Ch. 33; state 0).

The EBA can either be as long as the embolus or much smaller. Although state 1 is not shared by any clade, state 0 was synapomorphic for Metainae plus *Diphya*/*Chrysometa* clade, with the only exception being *Chrysometa cambara*.

Character 35 (original). Male pedipalp, embolic basal apophysis, shape compared to embolus: (0) similar to the embolus; (1) broad plate (Fig. 1B) (CI = 0.500; RI = 0.500). Inapplicable for taxa lacking EBA (Ch. 33; state 0).

In species where the EBA is coded with state 0 for both Characters 34 and 35, the apophysis is barely distinguished from the embolus, only being identified by the absence of a sperm duct. However, this is not the scenario for *Meta menardi* and *Metellina segmentata*, as they possess very broad EBA that covers the side of the embolus unprotected by the conductor. The EBA in *L. longimana* is also broad, but very short, and do not cover the embolus.

Character 36 (original). Male pedipalp, embolous, position in relation to tegular apex: (0) above (Fig. 7A); (1) side to side (Fig. 1E) (CI = 0.333; RI = 0.714).

All Tetragnathidae embolus originate from the tegular apex. However, in certain Leucauginae species, it takes a turn towards the lateral face of the ectal portion of the tegulum. This condition has three different origins across all analysis: in *Orsinome* plus *Tylorida*; in the *globosa* group and in *L. longimana*.

Character 37. Male pedipalp, embolus base-apex, narrowing: (0) abrupt (Fig. 1E); (1) gradual (Fig. 1C) (CI = 1.000; RI = 1.000).

Embolic apices in Tetragnathidae are typically thin, while the embolus itself is wider at the base. This widening of the sclerite can occur either gradually along its length or abruptly. In the latter, the proximal portion of the embolus is notably wider than its apex, forming what we opted to call as “proximal plate”. The presence of a proximal plate is synapomorphic to Leucauginae.

Character 38. Male pedipalp, embolus, proximal plate, position in relation to cymbium: (0) hidden (Fig. 1F); (1) exposed (Fig. 1A) (CI = 0.153; RI = 0.533). Inapplicable for taxa without the basal plate (Ch. 37; state 1).

The basal plate may not always be visible when present. In some cases, it is positioned between the tegular wall and the cymbium, requiring the pedipalp to be expanded or the cymbium to be moved aside to see the plate. This condition (state 0) is synapomorphic for *Tylorida* and *Leucauge* clade B, while a exposed basal plate is synapomorphic for *Leucauge* clades A and C. For the clade D, this caracter was optimized as homoplastic with at least three transformation events.

Character 39. Male pedipalp, embolus, proximal plate, position: (0) ectal (Fig. 1E); (1) mesal (CI = 0.500; RI = 0.500). Inapplicable for taxa without the basal plate (Ch. 37; state 1).

Whether hidden or exposed, the proximal plate typically remains close to the ectal margin. In a state that arose independently twice, observed in *Leucauge dromedaria* and the *grata* group, the narrowing of the basal plate occurs much closer to its base, next to the mesal margin of the cymbium.

Character 40. Male pedipalp, embolus, basal plate, path to embolus body: (0) forming a switchback (Fig. 1E); (1) forming a right angle (CI = 0.500; RI = 0.500). Inapplicable for taxa without the basal plate (Ch. 37; state 1).

The narrowing between the the proximal plate and the embolic apex has two different aspects: either forming a loop due the apex pointing in the opposite direction; or forming a right angle due the apex pointing in about 90°. The later condition (state 1) originates in in a clade containing *grata* group plus *L. tesselata,* but also in *L. xiyuing*.

Character 41. Male pedipalp, sperm duct, path: (0) spiral (Fig. 1ED); (1) with switchbacks (Fig. 1F). (CI = 0.250; RI = 0.727).

Sperm ducts with sinuose path are synapomorphic for *Azilia* plus *Leucauginae*, and present in some Metainae as well as *Chrysometa cambara* through independent origins. The main distinction between the switchbacks in Leucauginae and those in the latter taxa lies in their placement. In Leucauginae, the loops are much closer to the tegular wall or may even touch it.

Character 42. Male pedipalp, sperm duct, number of switchbacks visible on the ventral face of the tegular wall: (0) four (Fig. 1G); (1) six (Fig. 1F) (CI = 1.000; RI = 1.000). Inapplicable for terminals lacking switchbacks (Ch. 41; state 0) or with switchbacks not touching the tegular wall.

State 1 was recovered as synapomorphic for *Tylorida*. In these species, the ventral swollen wall of the tegulum is much larger than in other Leucauginae species, and the path of the sperm duct is more sinuous. The tegulum of *Leucauge festiva* is similar in size and shape to those of *Tylorida* but still has four switchbacks like its congeners.

Character 43. Male pedipalp, sperm duct, reservoir, diameter: (0) gradual with sperm duct (Fig. 7A); (1) widened (Fig. 1C) (CI = 1.000; RI = 1.000).
One of the prominent features in the Tetragnathinae subfamily is the very wide reservoir that occupies most of the wide and wheel-shaped tegulum. This condition is especially pronounced in *Glenognatha* species (Cabra-García & Brescovit, 2016).

Character 44. Male pedipalp, patella, macrosetae, occurrence: (0) absent; (1) present (CI = 0.111; RI = 0.333).
The absence of patellar macrosetae was optmized as synapomorphic for Tetragnathinae. In contrast, its presence was synapomorphic for two distinct clades: *Azilia* plus Leucauginae and Metainae plus *Diphya*/*Chrysometa* clade. The macrosetae is lost in *Chrysometa opulenta* and in at least five different species within Leucauginae.

Male chelicerae, (Ch. 45 to 59)
The chelicerae are among the most prominent structure of tetragnathids, giving rise to the names of many genera (suffix "gnatha") and even the family itself. They are particularly significant for Tetragnathinae and Leucauginae by their role in the reproduction of certain genera (e.g.: Aisenberg *et al.*, 2015). The variation and characters of interest are primarily observed in male chelicerae.

Character 45. Male chelicerae, cheliceral boss, occurrence: (0) absent; (1) present (CI = 0.076; RI = 0.250).
The cheliceral boss is found in the females of all species of Tetragnathidae observed within our sample. In males, however, the boss has been lost multiple times, being absent in half of the species from the *Leucauge* clade D, including *globosa* group and *argyra* group.

Character 46. Male chelicerae, proximal swelling, occurrence: (0) absent (Fig. 2A); (1) present (Fig. 2C) (CI = 0.111; RI = 0.272).
A prominent hump or tubercle present at the base of the paturon. This character helped to recover smaller clades across various branches of the reference tree: *Meta menardi* plus *Metellina segmentata*, *L. festiva* plus *L. medjensis* and *globosa* group.

Character 47. Male chelicerae, cuticle, texture in comparison to female chelicerae: (0) similar; (1) more rugose (CI = 0.167; RI = 0.583).
Rough chelicerae exhibit variations in surface relief, often organized around small setae, with “valleys” closer to the setae insertions and “peaks” in their interdistances. Increased roughness in male chelicerae is synapomorphic for *Mesida* and the *Diphya*/*Chrysometa* clade. Female chelicerae, in contrast, consistently display a smooth texture across all analyzed taxa.

Character 48. Male chelicerae, lateral view, silhoutte compared to female’s chelicerae: (0) similar (Fig. 2D); (1) more slender (CI = 0.500; RI = 0.000).
State 1 was not optimized as synapomorphic for any clade in most trees, except when using a *K* value of 6.42, where *Chrysometa zelotypa* was found to be the sister species to *Chrysometa* aff. *boraceia* plus *Chrysometa opulenta*.

Character 49. Male chelicerae, frontal spur, occurrence: (0) absent; (1) present (CI = 0.500; RI = 0.000).
The presence of a frontal spur is one of the traditional diagnostic features for *Mesida* (Álvarez-Padilla & Hormiga, 2011). There is photographic evidence showing the influence of this character in copulation. Females enfold their fangs around the spur, while males flex their pedipalps to reach the copulatory openings. This spur serves as one of the mechanisms for male-female cheliceral interlocking, which evolved independently in various lineages of Leucauginae and Tetragnathinae

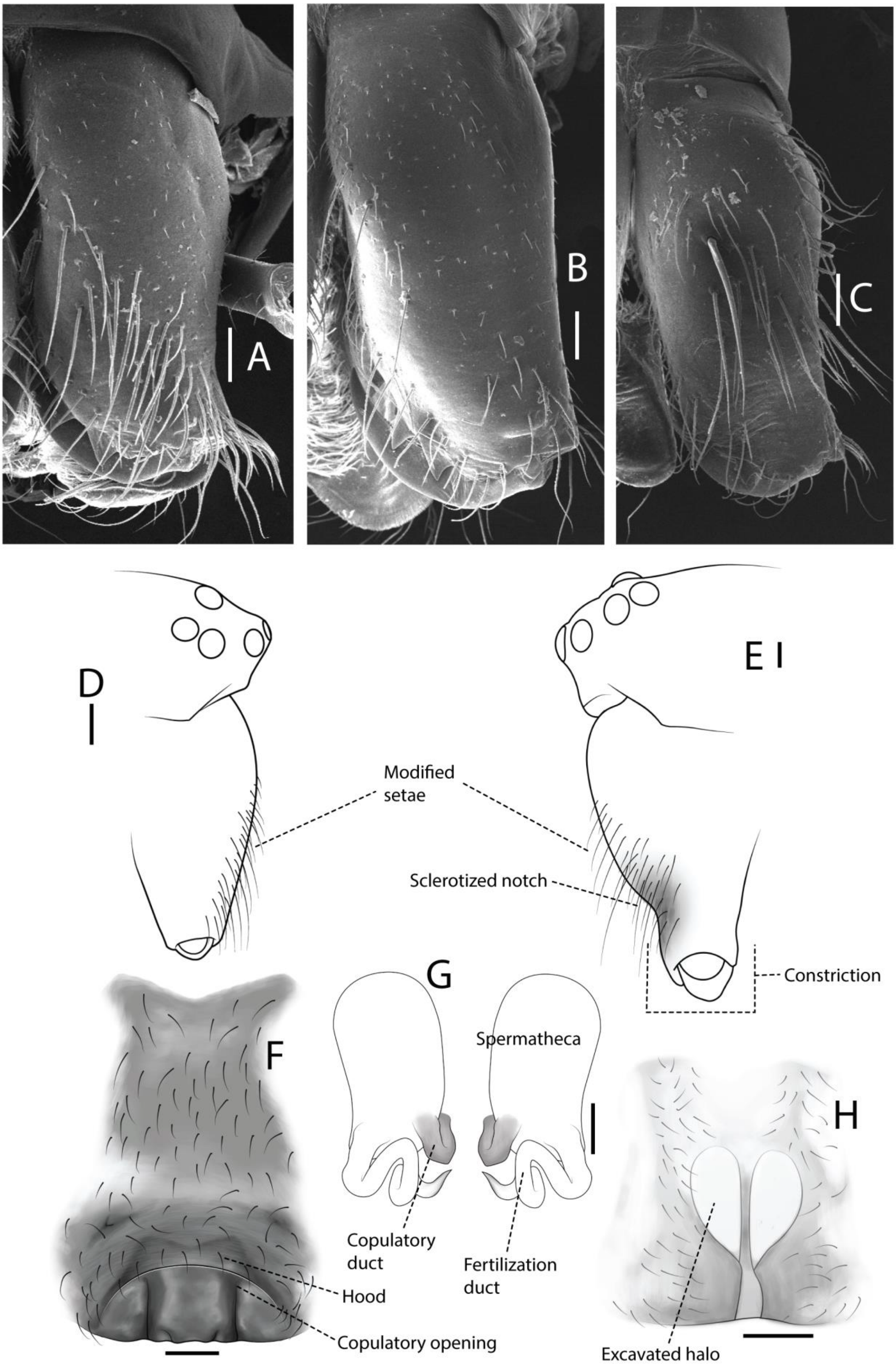

A
B
C
D
E
Modified setae
Sclerotized notch
Constriction
F
G
Spermatheca
Copulatory duct
Fertilization duct
Hood
Copulatory opening
H
Excavated halo

Figure 2. A-C: Electron micrographs showing cheliceral setae variation of Leucauge males. A, *Leucauge roseosignata*, modified setae distributed in a diagonal section. B, *Leucauge rubripleura*, without modified setae. C, *Leucauge branicki*, modified setae heterogenous in width and occupying beyond the diagonal section. D-E, illustrations of the difference between the chelicerae of males of *Leucauge roseosignata* and *Leucauge behemoth*. F-H Epigynum of Leucauginae species. F, *Leucauge argyrobapta*, ventral view. G, same, dorsal view. H, *Mesida argentiopuncata*, ventral view. Scale bars = 0.1 mm.

Character 50. Male chelicerae, setae, morphology: (0) as in females (Fig. 2B); (1) modified (Fig. 2A) (CI = 0.250; RI = 0.850).

Similar to the spur in *Mesida* and the elongated teeth in *Tetragnatha*, the sexually dimorphic setae present in the chelicerae of *Leucauge* males play a role in the adhesion between males and females during copulation. Aisenberg et al. (2014) observed an interaction between these setae on male chelicerae and the setae present on endites and sternum of females. In the reference tree, this character had three different origins: in the clade A (except *L.* cf. *thomeensis*); in the *grata* species group plus *L. tessellata*; and in clade D, being lost only in *L. severa*. In analyses with higher values of *K* (from 17.55 and above), species from clades A and D are recovered together and the state 1 of this character is optimized as one of its synapomorphies.

Character 51 (original). Male chelicerae, modfied setae, morphology: (0) heterogenous (Fig. 2C); (1) homogeneous (Fig. 2A) (CI = 1.000; RI = 1.000). Inapplicable for taxa without dimorphic cheliceral setae (Ch. 50; state 1).

Male chelicerae from *globosa* group and *L. henryi* have a mix of setae and macrosetae with different sizes and thicknesses. In the remaining species, the setae are more homogenous, with differences in size being subtle and gradual.

Character 52. Male chelicerae, modfied setae, distribution: (0) concentred in a diagonal section (Fig. 2A); (1) sparse (Fig. 2C) (CI = 0.250; RI = 0.500). Inapplicable for taxa without dimorphic setae in the chelicerae (Ch. 50; state 1).

The setae are organized in a diagonal stripe (state 0) close to the promargin of the chelicerae in clade D (except *L. longimana)* with a reversion in *globosa* group. A state also present in *L. festiva* and *L. medjensis*. For the remaining species, the setae ocuppy other regions of the chelicerae, being very homogeneous in distribution within the species of *grata* group.

Character 53 (original). Male chelicerae, distal region, narrowing: (0) absent (Fig. 2D); (1) present (Fig. 2E) (CI = 0.333; RI = 0.750).
This narrowing is shared by species from clade D but is lost in *L. regnyi* and in the *argyrobapta* group. Aisenberg *et al*. (2014) observed that the constriction intersects with the female endites during copulation in *L. mariana*. This behavior might be present in other species bearing this morphological condition. Additionally. to the narrow area, a deep concavity can be found in *L. globosa*.

Character 54 (original). Male chelicerae, distal region, sclerotized notch, occurrence: (0) absent (Fig. 2D); (1) present (Fig. 2E) (CI = 0.200; RI = 0.500).
A rigid spot present in the paturon next to the fang. The notch is one of the many modifications in the male chelicerae associated with reproductive behavior, and is present mostly in clade D. It presumably acts as a receptor for the distal margin of the female chelicerae (Eberhard & Huber, 1998). The notch is very homoplastic, being lost in *L. idonea*, *L. branicki* and in *argyrobapta* species group. It also originates independently in the clade containing *L. blanda* plus *L. levanderi*, which in other analyses (*K* = 17.55 or higher) are recovered at the base of clade D.

Character 55. Male chelicerae, distal end, paturon-paturon relation: (0) parallel; (1) divergent (CI = 0.333; RI = 0.714).
Divergent alignment in the chelicerae is typically associated with Tetragnathinae. In the present study, this was optimized as synapomorphical not only for this subfamily, but for *Tylorida* plus *Orsinome* as well as *L. festiva* plus *L. medjensis*.

Character 56. Male chelicerae, distal apophysis, occurrence: (0) absent (Fig. 2A); (1) present (CI = 0.333; RI = 0.000).
Typical of Tetragnathinae, the homology of such cheliceral projections needs to be reassessed, as different terminologies are used in each genus (Cabra-García & Brescovit, 2016; Castanheira et al., 2019; Dimitrov & Hormiga, 2009) for structures that can be homologyzed. Our hypotesis is that neither the distal apophysis nor the

spur in *Mesida* are homologous to the pormarginal teeth or to each other. The presence of this apophysis (state 1) has two different origins, one in Tetragnathinae (being lost in *Glenognatha gaujoni*) and other in *L. festiva*.

Character 57. Male chelicerae, promarginal teeth, arrangement: (0) subequal (Fig. 2B); (1) with modified teeth (CI = 0.250; RI = 0.500).
Each cheliceral promargin usually bears three teeth in most species. Therefore, modfied structures found in the promarginal region like those of *Orsinome vethi* can be homologyzed to one the teeths by their topological position and order. Exceptions occur in *Tetragnatha* and *Cyrtognatha*, which have a high number of marginal teeth, variable from species to species, making it harder to infer their homologies. In *Orsinome* and many *Tylorida*, the third tooth is enlarged, playing a role in the chelicerae clasping during copulation (Sankaran *et al*., 2017). Modfied teeth are also present in *L. festiva*.

Character 58. Male chelicerae, fang, outgrowth, occurrence: (0) absent (Fig. 2B); (1) present (CI = 0.500; RI = 0.500).
The outgrowth refers to a bifurcation in the cheliceral fang. These modifications in the fangs shape and size are characteristic of Tetragnathinae. Notably, those characters (Ch. 55 to 58) probably evolved independently in *L. festiva*, which has the most distinct male chelicerae within known *Leucauge* species by far.

Character 59. Male chelicerae, distal region, size compared to endites: (0) ending together (Fig. 2B); (1) chelicerae exceeding (CI = 0.333; RI = 0.667).
Size differences between the chelicerae and the endites in Tetragnathinae are discrepant, with the chelicerae being more than two times longer. The chelicerae are also longer in *Chrysometa zelotypa*, and *Orsinome* plus *Tylorida*, but with a less pronounced difference than in thetragnathines.

Female eyes and carapace (Ch. 60 to 71)

Unlike in other web-building spiders like Araneidae or Theridiidae, the carapace of tetragnathids is much less variable, being somewhat flat and glabrous in most species. However, variation in eye arrangement is more noticeable within this family and may be informative in studies aiming to test the monophyly of other genera from the outgroup sample, such as *Azilia* or *Diphya*. Despite this, in our study all characters related to eye morphology (Ch. 60 to 64) showed retention indices equal to zero for the reference tree. Their optimization did not provide information on relationships within the genus *Leucauge*.

Character 60. Female carapace, eyes, PLE-PME proximity: (0) separated; (1) adjacent (Fig. 7C) (CI = 0.200; RI = 0.000).

Character 61. Female carapace, PME, canoe-shaped tapetum, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.250; RI = 0.000).

These tapeta are reflective guanine patches that help regulating light entry in optical system of spiders (Land, 1985).

Character 62. Female carapace, eyes, lateral eyes and median eyes: (0) at least one AME apart (Fig. 7C); (1) almost adjacent (CI = 0.080; RI = 0.000).

Character 63. Female carapace, eyes, posterior eye row, alignment: (0) curved (Fig. 7C); (1) straight (CI = 0.040; RI = 0.000).

To infer the direction of the curvature in the eye row, it is necessary to observe the relative position of the lateral eyes in relation to the median eyes. If the PLE are facing the anterior end of the carapace, then the row is procurved. If they are facing the posterior region, then the row is recurved.

Character 64. Female carapace, eyes, posterior eye row, curvature: (0) procurve; (1) recurve (Fig. 7C) (CI = 0.250; RI = 0.000).

Character 65. Female carapace, height: (0) flat; (1) elevated (CI = 0.160; RI = 0.667)

Carapace was coded as elevated when they displayed convexity either medially or in the cephalic region. This state (1) is more common in Metainae and the *Dyphia*/*Chrysometa* clade, while the other state (0) is present mostly in Tetragnathids and in *Azilia* plus Leucauginae.

Character 66. Female carapace, postcephalic pits, occurrence: (0) absent (Fig. 7C); (1) present (CI = 0.100; RI = 0.678).

The postcephalic pits are depressions located in the transition between the cephalic and thoracic regions of the carapace, mirroring the fovea. These pits are prevalent in *Tylorida* and *Leucauge* species, shared by all internal branches except clade A. However, they are not reliable as diagnostic features because of the higher number of internal transformations.

Character 67. Female carapace, fovea, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.500; RI = 0.000)
The fovea is absent only in the two smaller species within our sample, *Dolichognatha pinheiral* and *Nanometa dimitrovi*, which are not closely related. Thus, the absence of this character seems more related to size and availability of space than to shared ancestry.

Character 68. Female carapace, fovea, shape: (0) depression; (1) deep grooves (Fig. 7C) (CI = 0.500; RI = 0.917). Inapplicable for taxa without fovea (Ch. 69; state 0)
In Leucauginae and Tetragnathinae, the fovea is very conspicuos, formed by two deep diagonal grooves. In other tetragnathids, it is a depression that gradually connects to the surrounding cuticle. This character has a low degree of homoplasies and is useful in diagnosing higher taxon.

Character 69. Female carapace, setae, coverage: (0) glabrous (Fig. 7C); (1) hirsute (CI = 0.167; RI = 0.000).
Glabrous is the predominant state of setae coverage in Tetragnathidae. Even in the few species coded as hirsute, the carapace is not nearly as covered in setae as in araneids like *Eriophora* Simon, 1864.

Character 70 (original). Female carapace, thoracic region, marginal setae, aspect: (0) inconspicuos; (1) conspicuous (CI = 0.167; RI = 0.375).

In most species, the marginal setae are barely noticeable, even when analyzed under higher magnifications. In some species, the marginal setae are more conspicuous and do not require such efforts to be observed. This condition is shared by *L. regnyi* plus *L. idonea* and *L. mariana*; and by *L. blanda* plus *L. levanderi*, but also found in other species.

Character 71 (original). Female carapace, thoracic region, posterior macroseta, occurrence: (0) absent (Fig. 7C); (1) present (CI = 0.200; RI = 0.555).

This macrosetae is present in part of the *argyrobapta* group (the branch sister to *L. atrostricta*), and also in *L. idonea* plus *L. mariana*. This macrosetae easily dettaches from the body and must be carefully analyzed. There are three thoracic marcosetae in *L. roseosignata*, which appears to be autapomorphic for this species.

Male and female legs (Ch. 72 to 80)

Legs in tetragnathids bear very valuable characters in diagnosing generic taxa, such as the very long first pair in *Metabus* (Álvarez-Padilla, 2007), and the femoral trichobotria in several genera of Leucauginae and Tetragnathinae.

Character 72 (original). Male leg I, femur, proximal macrosetae, occurrence: (0) absent; (1) present (CI = 1.000; RI = 1.000).

A group of macrosetae is observed at the ventral base of femur I in *Mesida yangbi* and *M. yini*. We did not find information on the presence of this feature in *M. argentiopunctata* in the literature. This state may be synapomorphic for *Mesida*, and its presence in other congeners not included in our sample should be investigated in future studies.

Character 73. Male legs I and II, ventral denticles, occurrence: (0) absent; (1) present (CI = 0.200; RI = 0.500).

The presence of ventral denticles was optimized as synapomorphic *Leucauge* clade A and the *argyra* group. In analyses with higher values of K (≥ 17.55), this is one of the characters supporting a different branch composed of species from clades A and D. These short macrosetae are also present in *L. tessellata*, *L. regnyi* and *Cyrtognatha atopica*.

Character 74. Female legs, femoral trichobotria, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.250; RI = 0.800).

Femoral trichobotria are present in all Leucauginae within our sample, except for *Metabus debilis*, and are among the most distinguishing charactes of the subfamily. It has been recognized as diagnostic for *Leucauge* for more than a century, as well as being used to identify other araneoid genera like *Mangora* O. Pickard-Cambridge, 1889.

Character 75. Female legs, femur IV, trichobotria, organization: (0) one row; (1) two rows (Fig. 7C) (CI = 1.000; RI = 1.000). Inapplicable for species without femoral trichobotria (Ch. 74, state 0)

The organization in two rows is a shared character in a clade of Leucauginae that excludes *Harlanethis* and the fossil *Baltleucauge*. The rows are straight in *Mesida* and in *Leucauge*, but about tortuous in the remaining genera. In contrast, *Cyrtognatha* and *Tetragnatha* species only bear one row of thricobothria in each femur.

Character 76. Female legs, femur IV, trichobotrium shaft, aspect: (0) smooth (Fig. 7C); (1) branched (CI = 0.500; RI = 0.833). Inapplicable for species without femoral trichobotria (Ch. 74, state 0).

A plumose aspect (state 1) is found on femoral thricobotria in *Cyrtognatha atopica*, *Mesida* and *Leucauge*. If the thricobothria are used to recieve sensory stimuli (Foelix, 2011), then the presence of branches led to higher contact area and probably to more acuity in capturing sensory signs.

Character 77. Female legs, femur IV, trichobotria, number: (0) up to eight (Fig. 7C); (1) more than eleven (CI = 0.500; RI = 0.900). Inapplicable for species without femoral trichobotria (Ch. 74, state 0)

Among Leucauginae, *Leucauge* exhibits the highest number of pairs of trichobotria, which was optimized as synapomorphic for the genus. Each species possesses at least 11 pairs of thrichobothria, although this number has high intra and interespecific variation. Thrichobothria are most numerous in the *grata* group.

Character 78. Female legs, tibial bristles, occurrence: (0) absent (Fig. 7C); (1) present (CI = 1.000; RI = 1.000).

The presence of bristles in some species of *Leucauge* is one of the reasons this genus was believed to be closely related to Nephilinae (Araneidae *sensu* Hormiga et al. 2023) in the last decades (Levi, 1981). This character was recovered as synapomorphic for the *grata* species group plus *Leucauge tessellata*, and is present only in Asian species, including some not available in our sample (Zhu *et al*., 2003).

Character 79 (original). Female legs, dark rings, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.167; RI = 0.300).

A disruptive pattern composed of alternating dark and thin pigmented stripes, surrounding the legs cuticle and resembling rings. Species where the extremities of the articles gradually darken towards the center were not coded as having dark rings. In this study, the optimization of rings was highly homoplastic, and within *Leucauge* it supported the grouping of *L. dromedaria* plus *L. granulata* and the *grata* group plus *L. tessellata*. This character may be even more useful when studying the morphology of outgroups like *Azilia* or *Chrsyometa*, in which it occurs more frequently and could bear a stronger phylogenetic signal.

Character 80 (original). Female legs, dots at the base of the macrosetae, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.167; RI = 0.375).

The dots are small pigmented spots circling the insertion point of the macrosetae. In general, the dots are present in the same species that have pigmented rings (Ch. 79; state 1), but they are absent in all *Leucauge* species. Futhermore, the optimization of this character in the 'smooth thricobothria clade' is identical to the previous one (Ch. 79), being synapomorphic for this group but lost in *Tylorida flava* and *Tylorida striata*.

Female genitalia (Ch. 81 to 116)

With the exception of Tetragnathinae, the remaining species in this family exhibit entelegyne genital morphology. That is, the female genitalia consist of a plate (the epigynum), with two openings leading to a pair of canals that receive the male gametes (the copulatory ducts), which are stored in twin chambers (the spermathecae) and then transported by another pair of canals leading to the unfertilized eggs (the fertilization ducts). We observed a wide variation in shapes, paths, and degrees of sclerotization of the fertilization ducts within Leucauginae. These structures are highly informative and have great potential for diagnosing clades.

Character 81. Female genitalia, morphology: (0) entelegyne (Fig. 2G); (1) secondarily haplogyne (CI = 1.000; RI = 1.000).

The reversion to a haplogyne state is a synapomorphy of Tetragnathinae. Haplogyne genitalia are characterized by the presence of a single genital duct responsible for both receiving gametes and fertilizing eggs.

Character 82 (original). Female genitalia, genital fold, occurrence: (0) absent (Fig. 2F); (1) present (CI = 1.000; RI = 1.000).

The fold is a lobe of the genital area that extends beyond the epigastric furrow towards the spinnerets. It was optimized as synapomorphic for Tetragnathinae in this study, and although only present in this subfamily, its occurrence and size are variable among species (Castanheira *et al*., 2022).

Character 83. Female genitalia, spermathecae, occurrence: (0) absent; (1) present (Fig. 2G) (CI = 1.000; RI = 1.000).

In this study, state 0 supported the grouping of *Cyrtognatha* plus *Glenognatha*. Loss of the spermathecae is synapomorphic for *Cyrtognatha* (Dimitrov & Hormiga, 2009), but not for *Glenognatha*, being present in various species (Cabra-García & Brescovit, 2016).

Character 84. Female genitalia, spermathecae, interdistance: (0) almost touching (Fig. 7E); (1) separated (CI = 0.100; RI = 0.470). Inapplicable for taxa without spermathecae (Ch. 83, state 0).

A large gap between both spermathecae is synapomorphic in Metainae and in *Mesida*. Other than that, the separated state is probably symplesiomorphic of Tetragnathidae, and it has different posterior transformations across the tree, including in some *Leucauge* species.

Character 85. Female genitalia, spermathecae, separation degree: (0) one diameter apart; (1) two diameters apart (CI = 0.333; RI = 0.600). Inapplicable for taxa without spermathecae (Ch. 83, state 0) or with almost touching spermathecae (Ch. 84; state 0).

Both Metainae and *Mesida* not only possess separated spermathecae, but also exhibit the longest interdistances of spermathecae within our sample. This condition (state 1) is also observed in other species across the tree, although it does not support the grouping of other clades. In *L. roseosignata*, the spermathecae are separated due to the very wide copulatory ducts occupying most of the internal space of the epigynum.

Character 86. Female genitalia, spermathecae, sclerotization: (0) membranous (Fig. 7E); (1) sclerotized (CI = 0.500; RI = 0.917). Inapplicable for taxa without spermathecae (Ch. 83, state 0).

Thin and soft walls are present in the spermathecae of *Nanometa dimitovi* and *Azilia histrio* plus Leucauginae, being one of the most characteristic features for the latter. The spermathecae cuticle exhibits variable degrees of independence from the cuticle of the epigynum ducts. In species like ***Gen.nov. sp.nov.***, there is noticeable contrast in their adjacency. On the other hand, in species like *L. idonea*, the cuticle appearance barely changes.

Character 87 (original). Female genitalia, spermathecae, medial constriction, occurrence: (0) absent (Fig. 2G); (1) present (CI = 0.200; RI = 0.333).

The spermathecae is classified as constricted when there is a narrowing between the region connected with the ducts and its wider apex, with this narrowing measuring approximately half the width of the apex of the spermathecae. The medial constriction is present mostly in Asian species of *Leucauge* and *Mesida*, including some not studied here (Zhu *et al*., 2003).

Character 88. Female epigynum, spermathecae, size in comparison to the plate width: (0) same or bigger (Fig. 2G); (1) about one third (CI = 0.142; RI = 0.667). All epigynum characters are inaplicabble for Tetragnathinae.

The axis of the spermathecae, usually the longitudinal one, is bigger in Leucauginae, being as long as or longer than the epigynum width. In a few *Leucauge* species like *Leucauge idonea*, the spermathecae reverts to the smaller size. Small spermathecae is one of the characters supporting a close relationship between Metainae plus the *Diphya*/*Chrysometa* clade, and also present in *Nanometa dimitrovi* and *Leucognatha acoreensis*.

Character 89. Female genitalia, spermathecae, shape: (0) subspherical; (1) oval (Fig. 2G) (CI = 0.125; RI = 0.611).

The spermathecae with oval shape are usually the big ones (Ch. 88; state 0) while the subspherical tend to be smaller (Ch. 88; state 1). Nonetheless, these two states are not redundant, since there are oval spermathecal with smaller sizes like in *Chrysometa cambara*, and big subspherical spermathecae like in *L. xiuying*.

Character 90. Female epigynum, anterior area, cuticle, sclerotization: (0) soft (Fig. 2H); (1) sclerotized (Fig. 2F) (CI = 0.333; RI = 0.913).

In *Leucauge* and the 'smooth trichobotria clade,' a sclerotized stripe covers the region between the epigynal plate and the pedicel. In these species, the big spermathecae often extend anteriorly beyond the epigynum plate, which is typically soft in other tetragnathids. We hypothesize that this anterior sclerotization has the function of protecting the delicate and thin spermathecae. This condition is absent in *Mesida* and in the *globosa* group plus *L. henryi*, which exhibit weakly sclerotized epigynum as well.

Character 91. Female epigynum, anterior cuticle, paired depressions, occurrence: (0) absent (Fig. 2H); (1) present (Fig. 2F) (CI = 0.142; RI = 0.647).

Pit-like depressions located on each side of the anterior edge of the epigynum, which may be separated in some species or connected by a shallow groove in others. This characteristic is present in *Leucauge* and the 'smooth trichobotria' clade. Its absence in ***Gen.nov. sp.nov.*** leads to ambiguity, being recovered as synapomorphic for *Leucauge* plus ‘smooth trichobotria’ under fast optimization, or as a state that originates independently in Leucauge and in *Orsinome* plus *Tylorida* in slow optimization. In either case, this trait is lost in both *L. grata* and *L. regnyi*.

Character 92. Female epigynum, plate and spermathecae, interface: (0) apart; (1) plate enclosing the spermathecae (CI = 0.500; RI = 0.667).

A species is coded with the state 1 when the spermathecae are entirely located within the epigynum. This character is optimized as synapomorphic for *Homalometa* aff *nossa* plus *Chrysometa cambara* and *Allende nigrohumeralis*. It also originates independently in *L. festiva*, one of the *Leucauge* species with the most easily recognizable autapomorphic characters.

Character 93. Female epigynum, plate and abdominal cuticle, interface: (0) contiguous (Fig. 2F); (1) prominent (CI = 1.000; RI = 1.000).

The prominent condition refers to the epyginum in which the distinction between the plate and the abdomen is very clear and abrupt. In *Chrysometa zelotypa*, for example, the whole plate has a higher relief than its surroundings and is much more sclerotized and darker. This condition is synapomorphic for a clade containing the last mentioned species and its sister branch (*Homalometa* aff *nossa* (*Chrysometa cambara*, *Allende nigrohumeralis*)). In the remaining tetragnathids, the cuticle is not abruptly different from the rest of the abdomen.

Character 94. Female epigynum, anterior keel, occurrence: (0) absent; (1) present (Figs. 2F; 7D) (CI = 0.125; RI = 0.611).

The keel is a short cuticular fold that contours the anterior margin of the epigynum, it differentiates the plate from the surrounding cuticle, but in contrast to the previous character (93), the keel involves only the upper margin of the epigyne and is usually followed by a depression rather than an elevation. This character is synapomorphic for Leucauginae, but has been lost different times within the subfamily, most notably in the *argyra* and *globosa* species groups.

Character 95. Female epigynum, keel, shape: (0) hood-like (Fig. 2F); (1) frame-like (Fig. 7D) (CI = 0.125; RI = 0.611). Inapplicable for terminals without keel in the epigynum (Ch. 94; state 0).

The keel may either be short and thin, encircling the margin of the epigynum like a frame, or extending towards the plate and covering part of it like a hood. The hood-like condition is synapomorphic for *Leucauge* clades A (lost in *Leucauge festiva*) and frequently present in clade D. In contrast, the frame-like state is synapomorphic for *Tylorida* and present in species from *Leucauge* clade C.

Character 96 (original). Female epigynum, hood, number of pockets: (0) one; (1) two (Fig. 2F) (CI = 0.200; RI = 0.428). Inapplicable for characters without epigynal hood (Ch. 95; state 0)

In species where the keel is shaped like a hood, the empty space between the hood and the covered cuticle plate can be either simple or can have two cavities, resembling pockets. The presence of only one pocket is synapomorphic for *Leucauge* clade A, but is modified in *L. blanda*. In contrast, two pockets are present in various species from *Leucauge* clade D, in *Mesida yangbi* plus *M. yini* and is synapomorphic for *Leucauge* clade B but reversed in the *grata* species group.

Character 97 (original). Female epigynum, ventral process, occurrence: (0) absent (Figs. 2F, 2H); (1) present (CI = 0.200; RI = 0.428).
The term ventral process was proposed by Barrantes et al. (2013), and although this condition is similar to the proeminence in the epigynum of taxa like *Chrysometa cambara* at first, the difference lies in the gradual nature of the ventral process, not abruptly differencing in relief and sclerotization from the whole epyginum, but rather being a swelling at the corner between the plate and the anterior cuticle. This character is synapomorphic for the *argyra* group and is again originated independently in *L. festiva* and in *Meta menardi*.

Character 98. Female epigynum, atrium, occurrence: (0) absent; (1) present (Fig. 7D) (CI = 0.111; RI = 0.200)
The atrium is a depression in the epigynum, which can be either a single or two opposite concavities near the copulatory openings. These depressions are absent in Metainae but present in nearly all other species of our sample.

Character 99 (original). Female epigynum, membranous halo, occurrence: (0) absent (Fig. 2F); (1) present (CI = 0.167; RI = 0.545).
The membranous halo is an area that may exist around the copulatory openings, with much lower sclerotization than its surrounding cuticle. The presence of such halos was optimized as synapomorphic for the *caudacuta* group plus *L. rubripleura*, but also for the *grata* group and *L. idonea* plus *L. mariana*.

Character 100. Female epigynum, median plate, transverse bar, occurrence: (0) absent (Fig. 2F); (1) present (CI = 0.333; RI = 0.333).
Some median plates are notably wider towards the posterior end compared to the medial region, with its shape resembling an inverted “T”. This broader section, the transverse bar, is frequently observed in *Chrysometa*, being syapomorphic for

Chrysometa opulenta plus *Chrysometa* aff. *boraceia*, but also present in *L. caudacuta* and *L. longimana*.

Character 101. Female genitalia, genital opening, shape: (0) slit-like; (1) pit-like (Fig. 2F) (CI = 0.071; RI = 0.518).

The morphology of the genital openings is very changeable within Tetragnathidae. In *Mesida*, *Leucauge* clade B, *argyra* group, most species of the *Leucauge* clade A and in *argyrobapta* group, the genital openings are slightly circular, having a pit-like shape. In contrast, the slit-like openings were synapomorphic for *Tylorida*, *caudacuta* group and *globosa* group.

Character 102. Female genitalia, genital opening, orientation: (0) in the longitudinal axis (Fig. 7D); (1) transversal (CI = 1.000; RI = 1.000).

The genital openings in Tetragnathinae are placed in transversal orientation. In the remaining species of our sample, the openings are either totally longitudinal or slightly diagonal, but still mostly longitudinally oriented.

Character 103 (original). Female epigynum, openings, morphology: (0) individual; (1) connected grooves (Fig. 2F) (CI = 0.142; RI = 0.333).

The copulatory openings may be linked to longitudinal slits that extend through the ventral region of the epigynum to its posterior portion, terminating where the fertilization ducts converge into the external secondary uterus (Zhan et al., 2019). These grooves do not seem to play a direct role in the insemination process, they may serve as anchor points for the copulatory and fertilization ducts internally. This state is present in most species from our sample and was identified as synapomorphic for Leucauginae, being absent only in *Orsinome vethi*.

Character 104. Female epigynum, copulatory opening, position: (0) ventral (Fig. 2H); (1) posterior (CI = 0.250; RI = 0.333).

Copulatory openings positioned ventrally are prevalent in most Tetragnathidae species. In contrast, posterior copulatory openings are present only in five species of our sample, being synapomorphic only for *Chrysometa cambara* plus *Allende nigrohumeralis*.

Character 105 (original). Female epigynum, copulatory opening, excavated halo, occurrence: (0) absent (Fig. 7D); (1) present (Fig. 2H) (CI = 1.000; RI = 1.000).
Reasonably similar to the membranous halo, the excavated halo is a wide circle around the copulatory openings that is present only in *Mesida*. This halo consists of a flat distinct area which is soft and lower than the surrounding cuticle.

Character 106. Female epigynum, copulatory opening, palpal plugs, occurrence: (0) absent; (1) present (CI = 0.500; RI = 0.000).
In the present study, only two species had epigynum plugged by palpal sclerites: *Homalometa* aff *nossa* and *L. melanoleuca*. Even if this character did not recover any clades herein, it can be informative while studying *Homalometa* (Levi, 1986).

Character 107. Female epigynum, copulatory duct, path: (0) curved (Fig. 2F); (1) coiled (CI = 0.200; RI = 0.500)
Taxa were classified with a coiled state when the copulatory ducts make at least one complete turn. Coiled copulatory ducts are synapomorphic for the *Diphya*/*Chrysometa* clade (although lost in *Allende nigrohumeralis*). The highest number of coils is observed in several *Chrysometa* species (Levi, 1986).

Character 108 (original). Female epigynum, copulatory duct and spermathecae, interface: (0) contiguous; (1) distinct (Fig. 7E) (CI = 0.200; RI = 0.428)
The contiguous state was assigned for species in which the spermathecae appear to be part of the copulatory duct, uniform in width and sclerotization degree. In other species (state 1, distinct) the limits between both structures are much clearer. State 0 is present in *Diphya bicolor* and *Chrysometa* species (except *Chrysometa cambara*), and in *Tylorida flava* plus *T. striata*.

Character 109. Female epigynum, copulatory duct, sclerotization: (0) soft; (1) sclerotized (Fig. 7E) (CI = 0.090; RI = 0.333).
Soft copulatory ducts originated eight times within *Leucauge* and were synapomorphic for *Metabus debilis* plus *Mesida* (but reversed in *Mesida pumilla*). Despite very homoplastic, this state is supporting the following clades: *grata* group; *L. idonea* plus *L. mariana*; and *L. rubripleura* plus *cautacuta* group.

Character 110. Female epigynum, fertilization duct, spermathecal origin: (0) anterior edge; (1) posterior edge (Fig. 2F) (CI = 0.333; RI = 0.000)

This character did not contribute to any grouping in the present study, mainly due its occurrence in genera which were not the focus of this study, only having one species sample each like *Metellina* or *Diphya*.

Character 111. Female epigynum, fertilization duct, auxiliary spermathecae, occurrence: (0) absent; (1) present (CI = 0.140; RI = 0.450).

Synapomorphic for *Leucauge* clades A and B (but lost in *L. festiva* and *L. fastigiata* respectively), fast optimization recovers the auxiliary spermathecae as symplesiomorphic for *Leucauge* as well, being lost in the clades C and D under this hypotesis. In the last clades, two unambiguous and independent origins occur, one in *L. dromedaria* plus *L. granulata* and the other at the base of the clade composed of *L. regnyi* and its sister node. The auxiliary spermathecae is usually a membranous expansion in the middle of the sclerotized fertilization ducts in species that it occurs. In *Leucauge dromedaria* this structure is sclerotized instead.

Character 112. Female epigynum, fertilization duct, path: (0) curved; (1) coiled (CI = 0.083; RI = 0.352).

Optimized as synapomorphic for the *argyrobapta* group, but highly homoplastic outside of it, fertilization ducts were coded as coiled when they make more than one complete turn. This character and the auxiliary spermathecae (Ch. 111) are mutually exclusive, that is, both being independent modifications in the fertilization ducts and not present in a same species within our sample.

Character 113 (original). Female epigynum, fertilization duct, coils, distribution: (0) sparse; (1) concentrated near the apex (CI = 0.500; RI = 0.500). Inapplicable for taxa without coiled fertilization ducts (Ch 112; state 0).

The coils in fertilization ducts are either concentrated near the posterior end or sparsely distributed, exhibiting sinuosities throughout the duct's path from its origin to the apex. The sparse organization (state 0) is synapomorphic for the *argyrobapta* group.

Character 114. Female epigynum, fertilization duct, sclerotization: (0) soft; (1) sclerotized (CI = 0.100; RI = 0.590).

Soft fertilization ducts are shared by *Metabus* plus *Mesida*, but also by species of the *caudacuta* group and most species from the *Leucauge* clade D, especially the *argyrobapta* group. In contrast, sclerotized ducts are unambiguously optimized as symplesiomorphic for Tetragnathidae, being present in *Leucauge* clades A and B (but reversed in *L. festiva*). Although highly homoplastic, this character seems useful for diagnosing species groups or even some genera.

Character 115 (original). Female epigynum, fertilization duct, width: (0) variable; (1) uniform (CI = 0.111; RI = 0.692).

Variable ducts are wider at their origin (next to the spermathecae), but with a narrowing across their paths, next to the posterior end. Ducts with about uniform widths are found in *Leucauge* clades A and B and in *argyra* species group.

Character 116 (original). Female epigynum, fertilization duct, width variation, aspect: (0) gradual; (1) abrupt. Inapplicable for taxa with uniform fertilization ducts (Ch. 115; state 1)

The terminal apices of fertilization ducts are consistently thinner and more sclerotized than the rest of the ducts in all analyzed species, while the base and path exhibit high variability. In species where the ducts are wider than the apex, two distinct conditions are observed: a gradual narrowing path, as seen in *argyrobapta* group and part of the *caudacuta* group, or a single abrupt knob preceding the narrow apical branch. The last condition is shared between *Mesida* and *Tylorida*.

Sternum and abdomen (Ch. 117 to 138)

Only one sternum character was used in the present study, in part due to the low variation of this structure in our samples, but also because of the challenges in discerning discrete variation among species. However, we focused on abdominal characters, driven by the notable species specificity observed in *Leucauge*.

Character 117. Female sternum, setae, coverage: (0) glabrous; (1) hirsute (CI = 0.090; RI = 0.230).

Glabrous sternum was synapomorphic for Tetragnathinae and *Meta menardi* plus *Metellina segmentata*. The sternal setae are important for the reproduction of Leucauge species, interacting with the modified setae in the male chelicerae (Aisenberg *et al*., 2015). The only species that does not possess both characteristics simultaneously is *Leucauge blanda*, having glabrous sternum.

Character 118 (original). Female abdomen, anterior convergence, occurrence: (0) absent; (1) present (CI = 0.333; RI = 0.333).
In most taxa we sampled, the anterior region of the abdomen is broad, and similar in width to the middle region. However, in certain species, the anterior sides of the abdomen converge towards the center, being pear-shaped. This convergence is characteristic of the *grata* group.

Character 119. Female abdomen, dorsal tubercles, occurrence: (0) absent; (1) present (CI = 0.100; RI = 0.357)
Abdominal tubercles are diagnostic for *Dolichognatha* (Dimitrov & Álvarez-Padilla, 2010) and variable in occurrence within *Leucauge*. Except for *L. rubripleura*, tubercles are present in every species from the clade C, being one of its grouping characteristics.

Character 120. Female abdomen, dorsal tubercles, number: (0) two; (1) four (CI = 0.250; RI = 0.250). Inapplicable for taxa without tubercles (Ch. 119, state 0)
The presence of four tubercles on the abdomen is synapomorphic for *L. granulata* plus *L. dromedaria*. For the remaining species of clade C, only the two anterior tubercles are present.

Character 121 (original). Female abdomen, posterior edge, morphology: (0) ending with the spinnerets (Fig. 7C); (1) projected (CI = 0.071; RI = 0.315).
The spinnerets are commonly located at the most distal portion of the venter of the abdomen. In some species, the end of the dorsal region of the abdomen is not parallel to the spinnerets, being extended. This condition is synapomorphic for *L. rubipleura* plus *caudacuta* group, and for *L. festiva* plus *L. medjensis*, besides being present in some species from the *argyrobapta* group.

Character 122. Female abdomen, posterior projection, shape: (0) triangular; (1) tail-like (CI = 0.250; RI = 0.571). Inapplicable for taxa without abdominal projections (Ch. 121; state 0).

Abdominal extensions come in two distinct shapes: as broad as the rest of the abdomen with a triangular extremity, or as a much thinner cylindrical projection resembling a tail. This tail-like shape was previously used as a diagnosing state to classify the *caudacuta* group into separate genera, namely *Alcimosphenus* and *Opas*. Triangular projections, on the other hand, are found in *Tylorida*, *Mesida*, and species from the clade D.

Character 123 (original). Female abdomen, tail-like projection, cuticle, texture: (0) smooth; (1) grooved (CI = 1.000; RI = 1.000). Inapplicable for taxa without tail-like projections (Ch. 121; state 0 and Ch. 122; state 0).

In *L. decorata* and the caudacuta group, the 'tail' is adorned with longitudinal striae or shallow grooves. In contrast, 'tails' of species like *Cyrtognatha atopica* and *Azilia histrio* remain as smooth as the rest of the abdominal cuticle.

Character 124 (original). Female abdomen, guanine crystals, organization: (0) forming bands (Fig. 7C); (1) scattered dots (CI = 0.200; RI = 0.428).

Abdominal guanine crystals are present in all Tetragnathidae of our sample. In most species, they are compacted together and organized in bands or stripes. In other species, they are sparse, unnorganized and commonly cover the whole abdomen without distinct spots. The later condition is found in *Mesida*, *Tylorida flava* plus *T. striata* and C*hrysometa* aff. *boraceia* plus *C. opulenta*.

Character 125. Female abdomen, guanine patches, aspect: (0) opaque; (1) reflective (Fig. 7C) (CI = 0.250; RI = 0.500).

Guanine crystals function as a 'canvas', allowing for the deposition of lighter and more saturated colors such as green and red (Oxford, 1997). Opaque white and metallic-like silvery guanine patches are structurally distinct, with the latter being formed by thin foils. Opaque guanine patches are identified as synapomorphic for Metainae, but they are also found in *Diphya*, *Azilia*, and *Homalometa*.

Character 126. Female abdomen, venter, longitudinal bands, occurrence: (0) absent; (1) present (CI = 0.142; RI = 0.400)

A pair of parallel longitudinal bands that extend from the epigastric furrow to the spinnerets. These bands are present in most species of the present study, and their absence was syapomorphic for *Leucauge henryi* plus *globosa* group.

Character 127 (original). Female abdomen, venter, longitudinal bands, constitution: (0) entire; (1) dashed (CI = 0.100; RI = 0.470). Inapplicable when longitudinal bands are absent (Ch. 126, state 0).

The longitudinal bands are either formed by continuous lines of guanine crystals or by sparse dots that are present along the parallel axes. Entire bands were optimized as synapomorphic for *Leucauge*, being present mostly in clades A, B and D, while dashed bands were shared among species from clade C (reversed in *L. granulata*).

Character 128 (original). Female abdomen, venter, longitudinal bands, density: (0) sparse; (1) dense (CI = 0.167; RI = 0.167). Inapplicable when longitudinal bands are absent (Ch. 126, state 0).

The longitudinal bands can either be wide and densely constituted by guanine crystals or thinner and containing spaces. This condition is present in *L. festiva* and *L. blanda*, also synapomorphic for clade B, but lost in the *grata* group.

Character 129 (original). Female abdomen, venter, medial bands, occurrence: (0) absent; (1) present (CI = 0.500; RI = 0.933).

In addition to the longitudinal parallel bands, a transversal band may be present between the epigastric furrow and the spinnerets, positioned at the midpoint. This band is present in *Metabus*, along with some *Mesida* species, and in the internal branch of clade D that is sister to *L. volupis*. The bands present in species of the clade D are bow-shaped, and exhibit a bright orange color in living specimens, noticeable when the spiders are resting with their ventral sides facing upwards on the orb webs.

Character 130 (original). Female abdomen, venter, medial bands, aspect: (0) conected; (1) separated (CI = 0.500; RI = 0.500). Inapplicable for taxa lacking these bands (Ch. 129, state 0).

In *L. globosa* plus *L. trilineata*, also in *L. taczanowskii*, the medial band is separated in two halves not connected at their middle, with the shape resembling an inverted “V”. The saturated orange color is still present in living species.

Character 131 (original). Female abdomen, dorsum, paired dark circles: (0) absent; (1) present (CI = 0.100; RI = 0.500).
When present, these dark circles occupy the anterolateral regions of the abdomen, one on each side of the cardiac area. This is a homoplastic character present in species of clades A and B, synapomorphic for C, and absent in most species from D.

Character 132 (original). Female abdomen, dorsum, posterior black patches, occurrence: (0) absent; (1) present (Fig. 7C) (CI = 0.111; RI = 0.111).
These patches are highly variable and present within most species of our sample. Despite their absence does not recover any clades, this state is partially congruent with guanine crystal without organization (Ch. 124, state 1), with the abdomen being homogeneously covered and completely reflective. State 1 can be observed in some species of *Mesida* and *Chrysometa*.

Character 133 (original). Female abdomen, dorsum, posterior black patches, organization: (0) single; (1) subdivided (Fig. 7C) (CI = 0.142; RI = 0.333). Inapplicable when black patches are absent (Ch. 132, state 0).
In the *caudacuta* group, the posterior patches form a single band the covers the tail projection, which was synapomorphic for this clade. In most remaining species, the posterior black patches are divided in at least two parallel lines or rows of spots.

Character 134 (original). Female abdomen, dorsum, posterior black patches, number of rows: (0) two (Fig. 7C); (1) three (CI = 0.500; RI = 0.917). Inapplicable when black patches are absent (Ch. 132, state 0) or present in a single row (Ch. 133, state 0).
Patches organized in three rows are synapomorphic for *L. volupis* plus its sister group inside clade D.

Character 135 (original). Female abdomen, dorsum, posterior black patches, aspect: (0) intermittent (Fig. 7C); (1) continuous (CI = 0.250; RI = 0.863). Inapplicable when black patches are absent (Ch. 132, state 0).

As the longitudinal bands, the continuity of the black bands is variable within species of the target group, being mostly intermittent in outgruoups and in clade B. While the bands in clades A, C and D are usually continuous.

Character 136 (original). Female abdomen, dorsum, posterior intermittent black patches, type: (0) dots (Fig. 7C); (1) grid (CI = 0.333; RI = 0.750) Inapplicable when black patches are absent (Ch. 132, state 0) or continuous (Ch. 135, state 1).

For species with sparse posterior patches, the grid is a form of organization in which the patches are subdivided in sequences of longitudinal and transversal lines forming some kind of grid made of rectangular cells. This condition is very common for Metainae plus the *Diphya*/*Chrsyometa* clade and present in *Tylorida tianlin* plus *Tylorida ventralis*. In contrast, patches in rows of dots or circular marks are present in species of *Mesida*, remaining species from the ‘smooth trichobothria’ clade and in *Leucauge* clade B.

Character 137. Female abdomen, dorsum, posterior continuous black patches, type: (0) spots; (1) lines (CI = 0.250; RI = 0.700). Inapplicable when black patches are absent (Ch. 132, state 0) or intermittent (Ch. 135, state 0).

Black patches in the shape of broad spots are present in all *Leucauge* species (except for those of clade B), and is synapomorphic for *Leucauge medjensis* plus *Leucauge festiva*, and for the whole clade C except its basalmost species, *Leucauge xiuying*. In *Leucauge levanderi* plus *Leucauge blanda* and most species of the clade D, the thinner lines (state 1) are prevalent.

Character 138 (original). Female abdomen, dorsum, posterior lines, type: (0) interconnected; (1) isolated (CI = 1.000; RI = 1.000). Inapplicable when black patches are absent (Ch. 132, state 0) or not organized in continuous lines (Ch. 137, state 1).

Long isolated lines are present in species of clades A and B, while *Leucauge xiuying* and most species of clade D have smaller lines connects transversally, forming ‘isles’ of guanine patches inside them. The shape and size of these patterns are useful in recognizing some species like *Leucauge volupis*.

Character 139. Males and females, degree of sexual dimorphism: (0) extreme; (1) moderate (CI = 0.500; RI = 0.500).

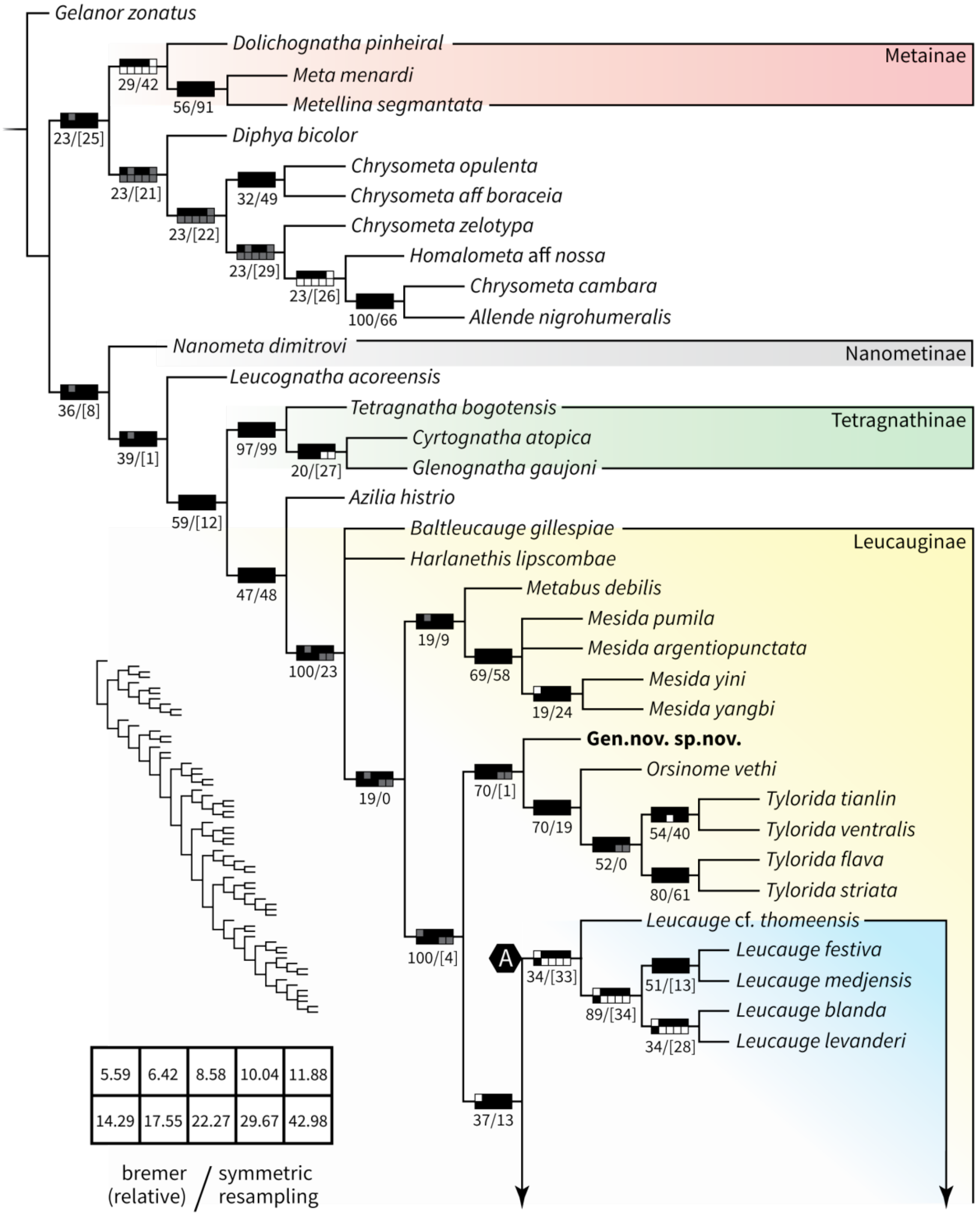
Extreme sexual dimorphism (SSD) is not common in tetragnathids, and both well-documented cases are found within distinct clades of *Leucauge*. SSD originated two times within this genus, in the *caudacuta* group (Levi, 2005; 2008) and in the *grata* group.

Phylogenetics

Our analyses recovered the monophily of *Leucauge* in 10 of the 11 tested concavity values, including the reference tree: wfit value of 99.23452, CI = 0.204 and RI = 0.568. The genus is unambiguously supported by the combination of these following six characters: basal tubercle on the cymbium; presence of a setae cluster close to the paracymbium base; eleven or more pairs of trichobothria on femur IV; pit-shaped genital opening; female abdomen with contiguous longitudinal bands ventrally, and contiguous black patches dorsally. Under fast optimization, this list also includes the presence perpendicular paracymbia, epyginal hood and auxiliary spermathecae. The genus *Leucauge*, as delineated by these characters, was stable in most of our analyses, although having low support (37). In contrast, its internal branches were more sensible to variations in homoplasy downweight values, but some of them with higher value. The four clades present in the reference tree were also found under *K* values spanning from 6.42 to 14.29 and are listed below.

Clade A include Afrotropical species along with the Asian *L. blanda*, characterized by short denticle-like macrosetae on the first two male legs, a paracymbium with uniform sclerotization with the cymbium, and an epigynum hood (when present) with only one pocket. This grouping has a low Bremer support (34) and was the most affected by different concavities. At *K* values of 17.55 and 22.27, the four species in clade A do not form a distinct monophyletic branch, but instead appear as basal terminals for clade D. At higher *K* values (29.67 and 42.98), *L. levanderi* and *L. blanda* remain at the base of the Neotropical clade D, while *L. medjensis* plus *L. festiva* are positioned as sisters to clade C.

Clade B consists of well-known species from tropical Asia, including the ones previously described under *Opadometa* (*grata* group here) and the very widely distributed *L. decorata*. In this group, the base of the embolus is concealed by the cymbium, and the bands on the venter of the abdomen are wide and conspicuous, a character later modified in the *grata* group.Species from both Clades A and B exhibit dorsobasal processes on the pedipalp, epigynum with sclerotized fertilization ducts, auxiliary spermathecae, and longitudinal bands with a bright bluish-green coloration in living specimens.



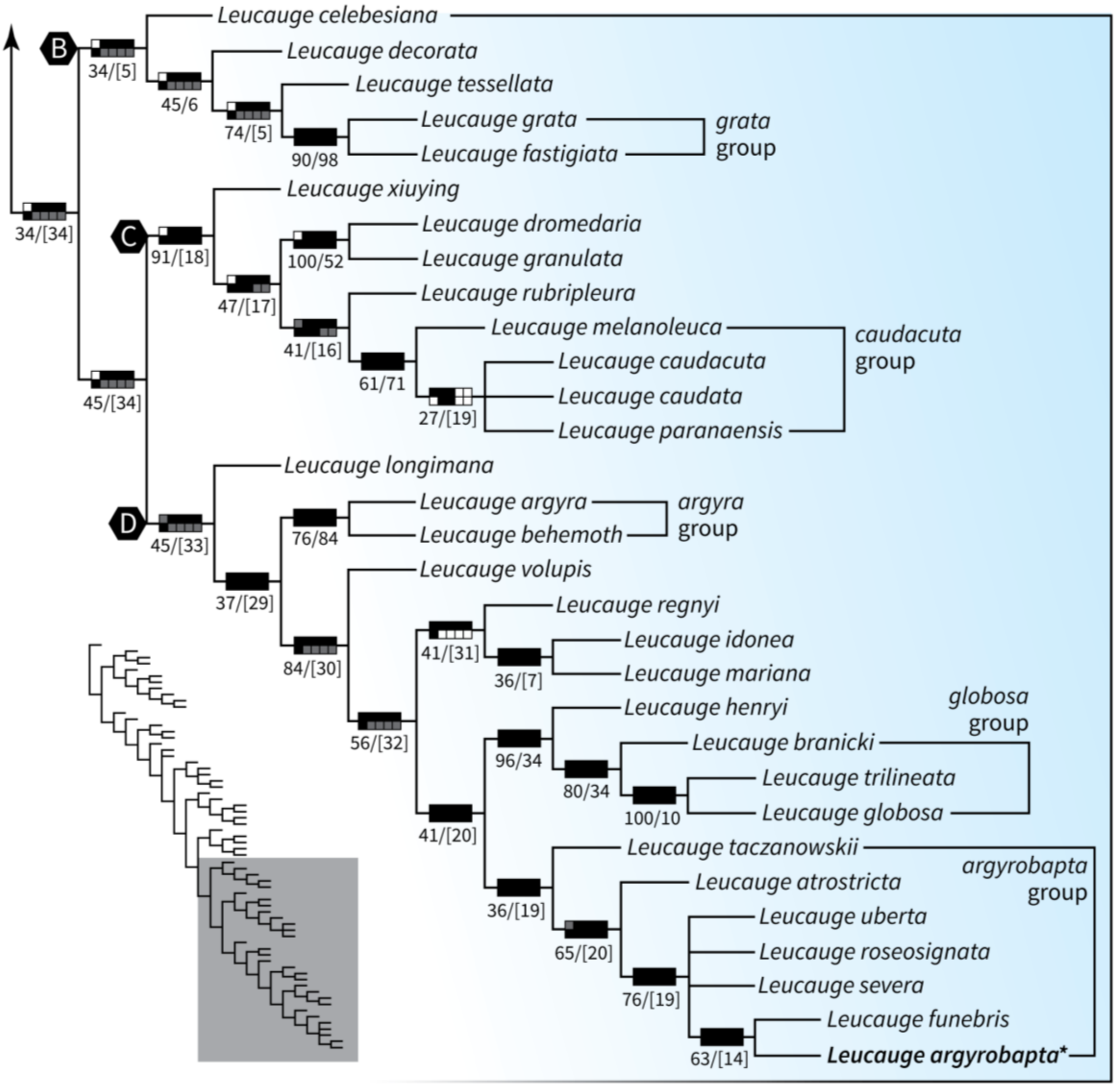


Figure 3. Strict consensus of the three most parsimonious trees obtained through implied-weight analysis with K = 7.40, which recovered the most frequent topology. Relative Bremer support and symmetric resampling values are given below navajo rugs, on left and right of the bar respectively.

These conditions appear to be plesiomorphic for *Leucauge* in general. Exceptions include *L. festiva*, with its highly modified epigynum and chelicerae, as well as the *grata* group with reduced or lost auxiliary spermatheca and unique coloration patterns. At higher K values (≥ 17.55), clade B does not include *L. celebesiana*, which is instead positioned as the sister taxon to Clades C plus D.

Clade C is composed of taxa from Asia, Australasia, and the Neotropics, including species previously classified under the genus ‘*Opas’*. These species share abdominal tubercles covered by black circles, longitudinal bands formed by spaced spots, and the males lack cymbial dorsobasal processes or modficiations used in cheliceral clasping. Living specimens have predominantly silver, red, and black coloration. Despite grouping species that are geographically incongruent (see discussion), clade C has high Bremer support (91) and is consistently recovered with all values of *K*.

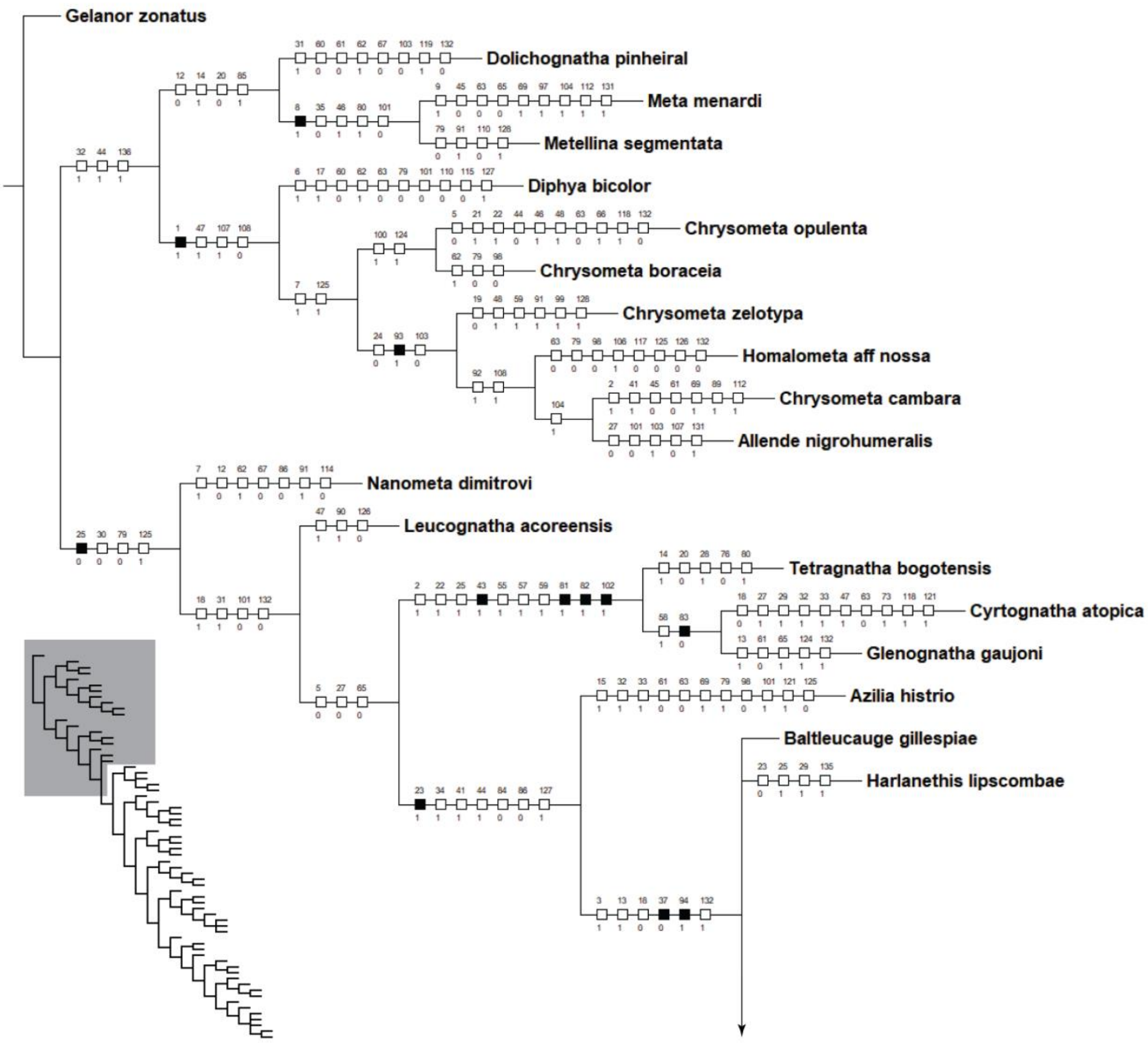


Figure 4. Unambiguous optimization of characters for the reference tree (*K* = 7.40). Black squares indicate non-homoplastic characters (1 of 3).

Finally, Clade D has 18 terminals, half of the analyzed *Leucauge* species and is exclusively Neotropical. The type species, *L. argyrobapta*, is recovered within this group, as well as the most studied species of the genus, *L. argyra* and *L. mariana*. The clade has a low Bremer support value (45), but its subsequent branches are well supported (76 for *argyra* group and 84 for *L. volupis* plus remaining species). Clade D is grouped by the modified male chelicerae with numerous setae and a distal constriction. Except for *L. longimana*, all taxa in this clade are consistently grouped under every value of *K*.

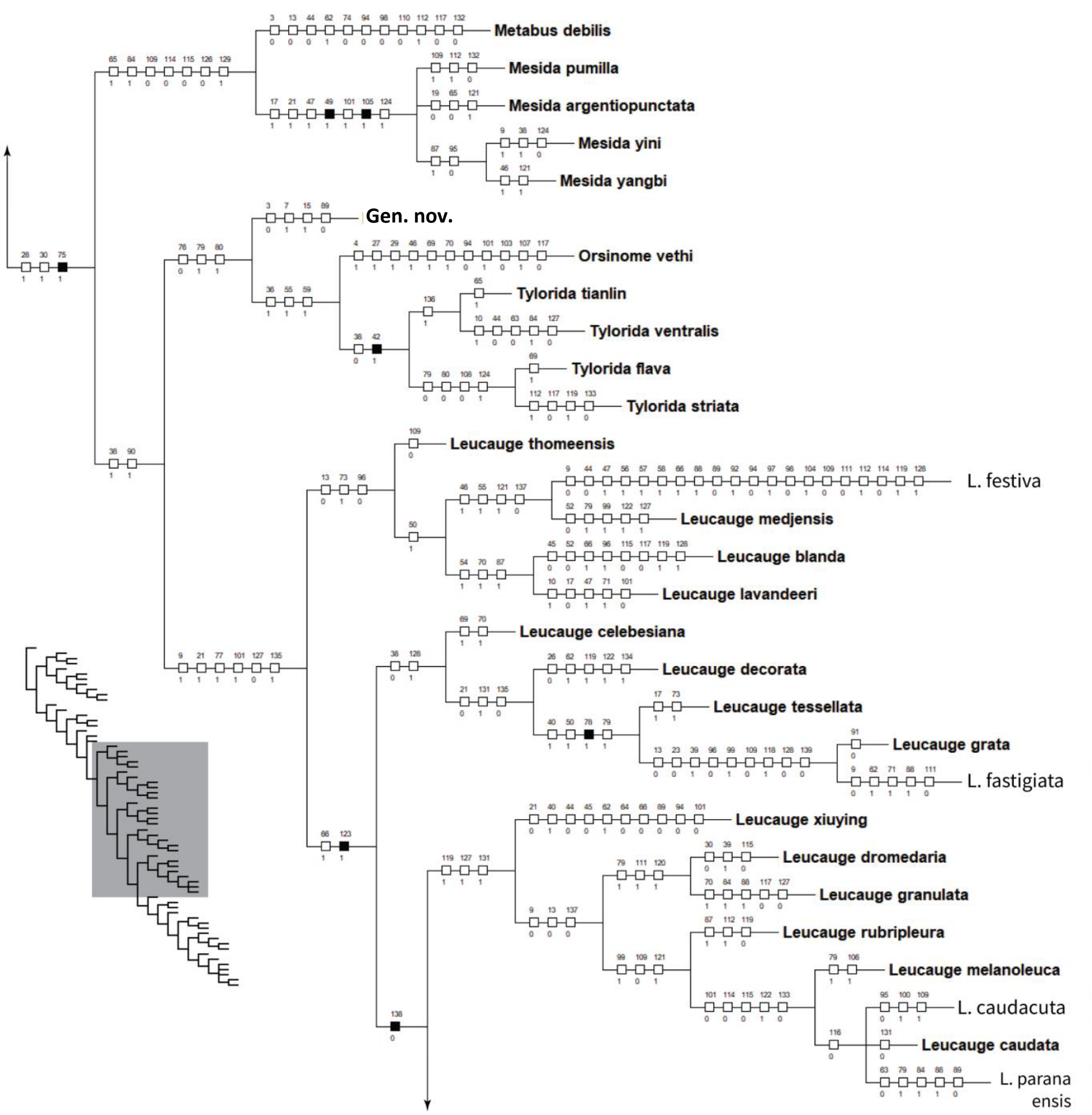


Figure 5. Unambiguous optimization of characters (2 of 3) for the reference tree (*K* = 7.40). Black squares indicate non-homoplastic characters.

The subfamily Leucauginae was represented in our study by *Leucauge*, *Metabus*, *Mesida*, *Tylorida*, *Orsinome, Baltleucauge* (extinct), the recently described *Harlanethis* and the ***Gen.nov***. This clade has been consistently recovered as monophyletic in present analyses, with the most noteworthy difference occurring under the lower value of K (= 5.59), where *Leucauge* is recovered as paraphyletic, comprising almost every other Leucauginae genera as internal branches, with the exception of *Harlanethis* and *Baltleucauge*. In the present study, at least six characters support the monophyly of Leucauginae: presence of a dorsobasal process; paracymbium without projections, more sclerotized than its surroundings; embolus with proximal plate; keeled epigynum and presence of abdominal posterior black patches. With concavity curve values equal to 6.42 and above, the monophyletic *Leucauge* appears as sister to the 'smooth trichobothria' branch, which includes ***Gen.nov. sp.nov.***, *Orsinome vethi* and four species of *Tylorida*. All these taxa were grouped by the presence of a sclerotized stripe between the epigynum and the pedicel, a character later lost in the *globosa* group plus *Leucauge henryi*.

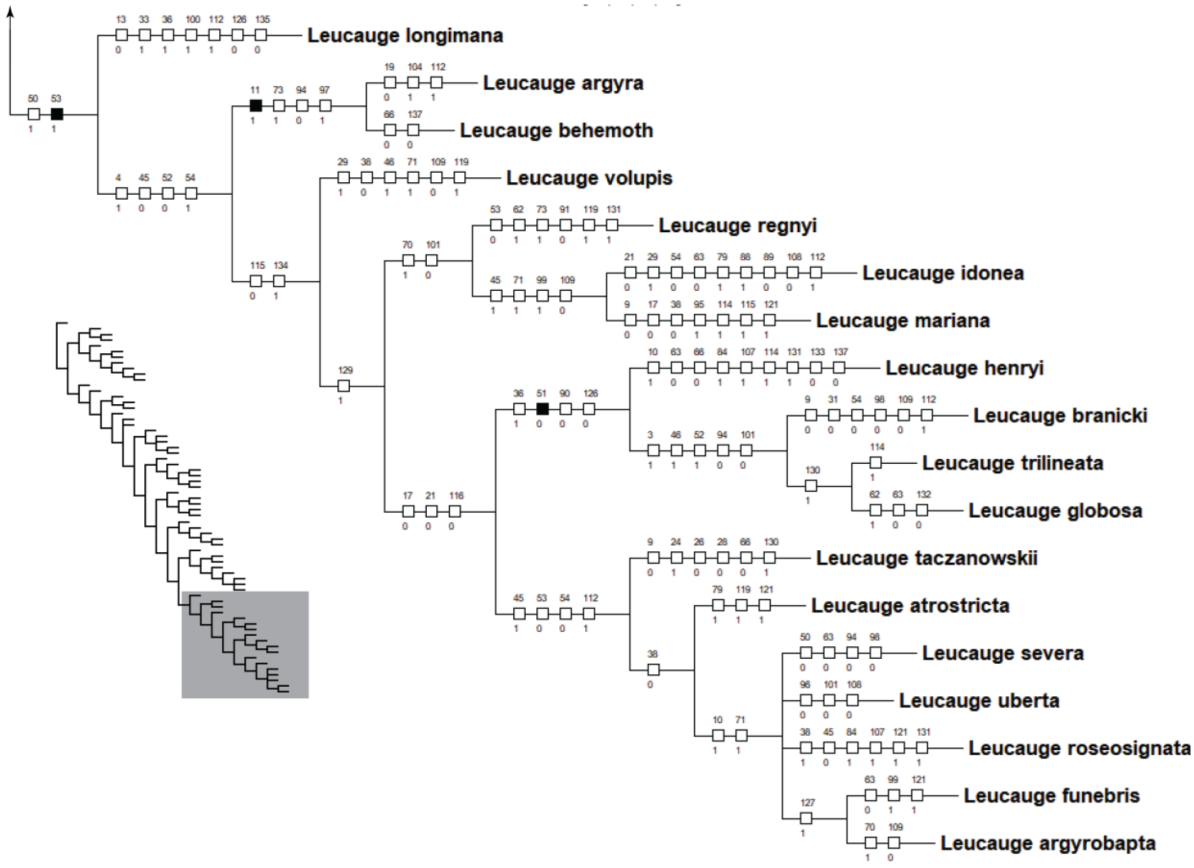


Figure 6. Unambiguous optimization of characters (3 of 3) for the reference tree (*K* = 7.40). Black squares indicate non-homoplastic characters.

Taxonomy implications

Leucauge operational species group

Most shared conditions supporting the genus *Leucauge* in this study are very homoplastic, undergoing numerous subsequent transformations on internal branches. Therefore, they can be unreliable in providing a universal diagnosis for a genus with so many species. In contrast, many internal branches of *Leucauge* exhibt stable shared characteristics, viable to diagnose them. We propose five distinct species groups consisting of species from our sample, as well as tentatively assigning other species not analyzed in the present study.

argyrobapta group

Species within this group exhibit the following combination of characteristics: fertilization ducts soft, coiled, variable in diameter, and lacking auxiliary spermathecae. The coils are distributed throughout the entire duct path rather than being concentrated in one area. Male chelicerae typically have a boss (with the exception of *L. roseosignata*) and modified setae (except for *L. severa*), but lack distal constriction. Females often possess a posterior triangular abdominal projection and dorsal black patches organized in three connected lines. Species from our sample belonging to this group are: *L. argyrobapta*, *L. atrostricta*, *L. funebris*, *L. roseosignata*, *L. severa*, *L. taczanowskii*, and *L. uberta*. Additionally, the characters supporting this group are found in the following species, potentially close to the aforementioned: *L. acuminata* (O. Pickard-Cambridge, 1889), *L. argentea* (Keyserling, 1865), *L. bituberculata* Baert, 1987, *L. polita* (Keyserling, 1893), and *L. venusta* (Walckenaer, 1841). This group contains the highest number of undescribed species.

globosa group

A group that includes the former '*Mecynometa*' (sensu Levi, 2008), as well as other small and delicate spiders. These species are recognizable by their distinct body morphology, with short bodies and slender legs. Unlike other groups, the abdomen is almost as wide as long, rather than long and cylindrical. The unambiguous optimization grouped these species by the following shared characteristics: presence of a dorsobasal process; embolus base located at the side of the tegulum; male chelicerae with a proximal swelling; modified setae sparse and very heterogenous in thickness; female epigynum with slit-like copulatory openings, lacking a hood or keel; absence of the sclerotized stripe between the pedicel and the epigynum; and an abdomen without longitudinal bands but with very conspicuous and wide medial bands. This group consists of *L. branicki*, *L. globosa*, and *L. trilineata*. It may also include *L. simplex* F. O. Pickard-Cambridge, 1903 and many undescribed species. We did not include *L. henryi*, despite the similarities with this group, because it bears many distinct characteristics, and the group would need to have a more comprehensive and less precise diagnosis.

***argyra* group**

This group consists of species formerly attributed to *Plesiometa*: *L. argyra* and *L. behemoth*. These species are large and widely distributed, distinguished by the following characteristics: presence of a unique cymbial apophysis bearing a large and thick apical macroseta; male legs I and II with ventral denticles; male chelicerae with modified setae, distal constriction, and a sclerotized notch; a projected epigynum without chilia and bearing a ventral process; abdomen with longitudinal bands but without medial bands. The *argyra* group is not as diverse as many other internal clades of *Leucauge*, but species in this group are highly valued for studying ecology and biological aspects. For instance, *L. behemoth* possesses one of the most complex social organizations ever described among spiders.

***caudacuta* group**

The "tailed" Neotropical species of *Leucauge* belong to the *caudacuta* group, which includes species formerly classified in the genus '*Opas*'. In addition to the prominent tail-like abdominal projection, diagnostic characters include the following: dorsum of the abdomen with tubercles; venter with longitudinal bands organized in dots; epigynum with slit-like copulatory openings circled by a membranous halo; fertilization ducts soft, wider than the apex, and without coils or auxiliary spermathecae; extreme sexual dimorphism, with very small males lacking modifications on the chelicerae. This group includes *L. caudata*, *L. caudacuta*, *L. melanoleuca*, and *L. paranaensis* from our sample, and may also include *L. licina*, *L. lugens*, and various unnamed species. Besides the challenge of describing new taxa, an equally challenging task is matching males to females of species in this group, as they are not congruent in color patterns and are not frequently collected together, as is the case in other lineages. *Leucauge rubripleura* was not included because it would require a much broader diagnosis, and it could potentially belong to its own species group (see below).

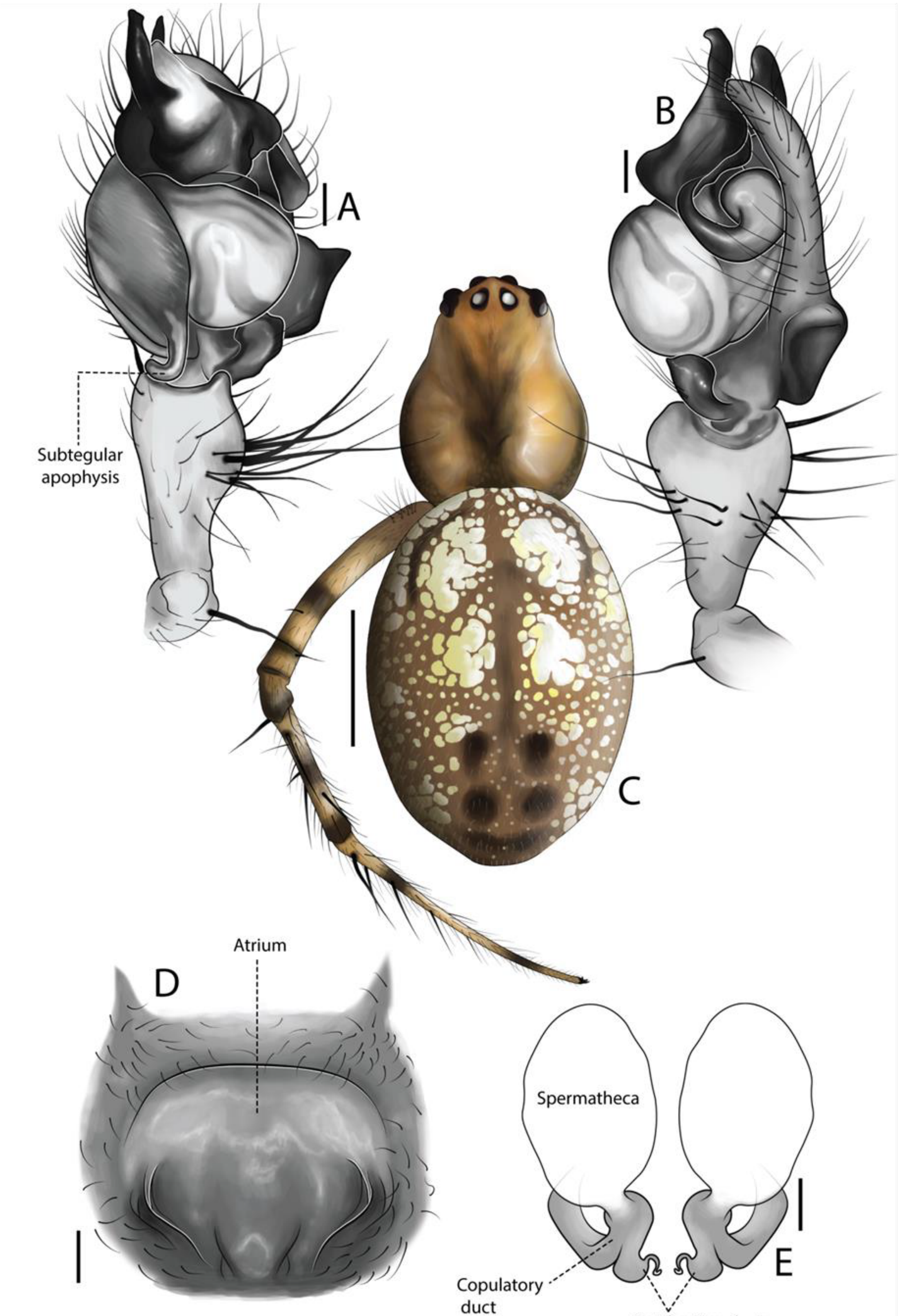


Figure 7. ***Gen.nov. sp.nov.*** A-B, male pedipalp. A, ventral view, showing the autapomorphic subtegular apophysis. B, lateral view. C, female habitus, dorsal. D-E female epigynum. D, ventral view. E, dorsal view, cleared. Scale bars A-B, D-E = 0.1 mm. C = 1 mm.

grata **group**

Composed by Asian species from the old '*Opadometa*' genus, *grata* group is characterized by the following combination of characteristics: subtegulum under the tegulum; embolus base mesally positioned and its path not forming a switchback: male chelicerae with uniformly distributed thick macrosetae; female epigynum with only one hood, containing membranous halos around the copulatory openings; copulatory ducts long and soft; sclerotized and thin fertilization ducts with reduced or absent auxiliary spermathecae; legs with dark rings and tibial bristles; pear shaped abdomen with a convergent anterior region; presence of extreme sexual dimorphism. This group includes *L. fastigiata* and *L. grata* from our sample and should also comprise at least *L. kuchingensis* (Dzulhelmi & Suriyanti, 2015) and *L. sarawakensis* (Dzulhelmi & Suriyanti, 2015).

New genus of Leucauginae

In addition to the species group, we propose a new monotypic genus. The species described below is assigned to a new genus due to having unique characteristics that do not fit in any of the currently circumscribed Leucauginae genera, including those not analyzed here. This new genus is sister to *Orsinome* plus *Tylorida*, also resembling *Harlanethis,* although this similarity is not reflected in the topology. We believe that it is partly due to the large number of missing data in *Harlanethis lipscombae*, scored exclusively from the literature.

Gen.nov **new genus**

Type species. *Gen.nov. sp.nov* is the type by monotypy.

Diagnosis. ***Gen.nov*** is most similar to *Orsinome*, *Tylorida* and *Harlanethis*. ***Gen.nov*** is distinct from *Orsinome* because it has a much shorter embolus, not reaching the paracymbium. Males of ***Gen.nov*** lack modifications on promarginal teeth like in *Orsinome* and *Tylorida*. Females of ***Gen.nov*** are similar to *Tylorida* by the shape of the epigynum, with a short anterior keel and broad atrium, but ***Gen.nov*** is different by having a much lower atrium (Fig. 7D) and shorter internal ducts (Fig.

7E). Males of ***Gen.nov*** and *Harlanethis* have very large conductor and embolus, wider than in remaining Leucauginae, but they differ because the subtegulum in ***Gen.nov*** is positioned side by side of the tegulum (Fig. 7A), instead of underneath it. The embolus in ***Gen.nov*** is much more exposed than in *Harlanethis*. Females of both genera have very wide epygina, almost as big as the sternum; however, the epigynum in ***Gen.nov*** is well sclerotized and lacks the longidutinal grooves (Fig. 7D). Additionally, ***Gen.nov*** can be distinguished from other Leucauginae by having an ectomedial process in the cymbium, and from all remaining tetragnathids by the presence of a unique hook-shaped apophysis in the subtegulum.

Gen.nov sp.nov new species

Holotype: Male from Sabah, Borneo, Malaysia 15/VIII/2022, C. X. Wong coll., DZUB 10953. **Paratypes:** female (collected with the holotype) DZUB 12500.

Diagnosis. The genus is monotypic. Diagnosis of *Gen.nov sp.nov* is as described above.

Description. Male holotype. Total length 3.60. Carapace glabrous, light beige with three longitudinal orange stripes, 1.84 long, 0.71 high. Cephalic region 0.89 wide, thoracic region 1.37 wide. Clypeus 0.17. Eyes with black rings.0 Eyes measurements: AME 0.14, ALE 0.11, PME 0.13, PLE 0.11; Eyes interdistances: AME-AME 0.08, AME-ALE 0.08, AME-PME 0.07, ALE-PLE touching, PME-PME 0.08, PME-PLE 0,11. Chelicerae 0.72 long, 0.33 wide, light orange, without modified setae or apophyses. Fangs 0.30 long, dark orange. Endites 0.54 long, 0.30 wide, labium 0.24 long, 0.35 wide, colors as in chelicerae. Sternum 0.71 long, 0.66 wide, beige and covered with setae. Legs beige with brown rings and sparse macrosetae. Fermurs bear unbranched trichobothria organized in two rows, more conspicuous on the fourth leg. Leg formula: 1243. Leg measurements: Leg I femur 3.67 / patella 0.75 / tibia 3.39 / metatarsus 4.37 / tarsus 1.02 / total 13.22; II 2.22 / 0.72 / 1.82 / 2.16 / 0.76 / total 7.68; III 1.18 / 0.34 / 0.90 / 1.10 / 0.46 / total 3.98; IV 2.37 / 0.52 / 1.55 / 1.70 / 0.66 / total 6.80. Pedipalp measurements: femur 1.29 / patella 0.19 / tibia 0.49 / cymbium 0.90. Pedipalp with wide tibia covered with macrosetae; very sclerotized cymbium with ectobasal process and dark tegular sclerites; conductor with wide with a soft apical area; wide and exposed embolus sheathead distally by the conductor. Abdomen 2.25 long, 1.34 wide, 1.24 high, beige with numerous guanine patches and with posterior dark bands both in the venter and the dorsum.

Female paratype. Total length 4.94, most color pattens as in the male above. Carapace 1.95 long, 0.54, cephalic region 0.85 wide. Thoracic region 1.37 wide. Clypeus 0.13. Eyes measurements: AME 0.12, ALE 0.10, PME 0.11, PLE 0.10; Eyes interdistances: AME-AME 0.09, AME-ALE 0.13, AME-PME 0.08, ALE-PLE touching, PME-PME 0.09, PME-PLE 0.14. Chelicerae 0.83 long, 0.42 wide, middle region beige with orange edges. Fangs 0.93 long. Endites 0.54 long, 0.33 wide, dark orange. Labium 0.32 long, 0.40 wide, dark orange. Sternum 1.01 long, 0.74 wide. Leg formula: 1243. Leg measurements: Leg I. femur 3.28 / patella 0.74 / tibia 2.55 / metatarsus 3.76 / tarsus 0.97 / total 11.30; II. 2.06 / 0.59 / 1.49 / 2.08 / 0.80 / total 7.02; III 1.07 / 0.37 / 0.58 / 0.82 / 0.46 / total 3.30; IV 1.93 / 0.48 / 1.35 / 1.56 / 0.52 / total 5.82. Pedipalp measurements: femur 0.71 / patella 0.18 / tibia 0.54 / tarsus 0.65. Abdomen 3.16 long, 1.99 wide, 2.22 high. Dorsum beige, covered with guanine patches, dark bands organized in two rows of three spots each. Venter with a dark continuous area between the epigastric furrow and the spinnerets, longitudinal guanine patches thin, surrounded by sparse dark lines. Epigynum 0.47 long, 0.71 wide, very sclerotized with a deep atrium. Ducts wide, short and very sclerotized. Spermathecae oval and soft.

Matching sexes. Both specimens were collected together and are similar in size and coloration patterns. The male has longer legs, with larger macrosetae, while the female has a larger body and slightly darker coloration.

Distribution. North of Sabah, Malaysia.

Natural history. Unknown.

DISCUSSION

Leucauginae have been recovered as monophyletic in all phylogenetic studies conducted so far, inferred through different types of data sources including morphology, molecular data, and behavioral traits. In addition to the genera present in this study, Leucauginae should include at least *Okileucauge* Tanikawa, 2001 (Ballesteros & Hormiga, 2021; Zhu *et al*., 2003) and *Atelidea* Simon, 1895 (Álvarez-Padilla & Benjamin, 2011). The sister group of Leucauginae, however, is a conundrum that is still far from clarification. Several genera have been recovered in this position, namely *Azilia* (present study, Álvarez-Padilla, 2007; Álvarez-Padilla & Hormiga, 2011; Álvarez-Padilla *et al*., 2020), *Diphya* (Álvarez-Padilla *et al*., 2020; Kallal & Hormiga, 2018), *Metleucauge* Levi, 1980 (Álvarez-Padilla *et al*., 2009;

Álvarez-Padilla & Hormiga, 2011; Ballesteros & Hormiga, 2021; Dimitrov *et al*., 2010; Tanikawa, 2001; Zhu *et al*., 2003) and *Wolongia* Zhu, Kim & Song, 1997 (Zhu *et al*., 2003). The phylogenetic relationships of these genera remain uncertain, mainly because it is common for them to behave like rogue taxa in cladistic analyses, while *Wolongia* is likely part of the Nanometainae subfamily (Wan & Peng, 2013). In the present study, *Diphya* emerges as close to *Chrysometa*, while *Metleucauge* and *Wolongia* were not included.

Orsinome and *Tylorida* are placed next to each other in our study and in other papers (Álvarez-Padilla et al., 2009; Dimitrov & Hormiga, 2011; Kallal & Hormiga, 2018) but their position in relation to *Leucauge* vary depending on data sources and analytical approaches. *Leucauge* was more commonly recovered as close to *Mesida* (Álvarez-Padilla *et al*., 2009; Álvarez-Padilla & Hormiga, 2011; Ballesteros & Hormiga, 2021) or as sister to all "core" Leucauginae (Álvarez-Padilla *et al*., 2020; Dimitrov & Hormiga, 2011; Taniwaka, 2001). Instead, herein *Mesida* is positioned as sister to the Neotropical *Metabus*, sharing characteristics such as a very soft epyginum, spaced spermathecae, and similar abdominal guanine patches organization.

Regardless of topological hypothesis for Leucauginae among the available phylogenies, tracing the biogeographic history of this subfamily is puzzling due lineages with very different distributions being recovered as sister clades. In calibrated phylogenies, the origin of Leucauginae is estimated to have occurred between approximately 46 million years ago (Ballesteros & Hormiga, 2021; Magalhães *et al*., 2020) to around 75 million years ago (Álvarez-Padilla et al., 2020; Kallal & Hormiga, 2018), with the older limit of these estimates reaching up to around 105 million years. Whatever the case, Leucauginae likely originated after the breakup of the the Mesozoic supercontinents (see Gondwana breakup dates in Jokat *et al*., 2003). This suggests that intercontinental dispersion events occurred multiple times. Long-distance dispersion mechanisms like ballooning potentially play a more significant role in the distribution of these species than viacariance. This is observed for many web-building spiders (Decae, 1987; Scharff *et al*., 2020; Su *et al*., 2011). Clade C presents a potential subject of study to better understand long-distance dispersal in spiders.

A similar group to the present study clade C was recovered in the molecular phylogeny of *Leucauge* (Ballesteros & Hormiga, 2021). It contains, among others, *L.*

granulata, the former '*Opas*' species, *L. argentina* (van Hasselt, 1882), and *L. moerens* (O. Pickard-Cambridge, 1896) The last two were not scored by us but are very similar to other species within our sample, respectively *L. xiuying* and *L. rubripleura*.

Except for the topological unstable Clade A of the present study, the congruences between our analyzes and the molecular phylogeny go even further. Clade B of the present study aligns with tropical Asian branch recovered in Ballesteros & Hormiga (2021). Clade D also can be mirrored to their branch of Neotropical "core" *Leucauge*, albeit with a distinct internal topology. *Leucauge argyrobapta* was not placed as next to *L. argyra* under any concavity value.

Beyond *Leucauge* and the Leucaugines, the monophyly of *Chrysometa* was not corroborated in this study. Nonetheless, neither the characters explored are focused on representing the morphological diversity within the genus, nor the sample is representative enough to jump to conclusions. *Chrysometa* is a genus with 147 species (World Spider Catalog, 2024), and dozens of others not yet described (Levi, 1986). It is possible that some of these species may belong to other genera, but this needs to be investigated with a more comprehensive taxon sampling.

other possible species group

The following relationships are speculative and require testing. We refrained from proposing species groups without phylogenetic background, but there are striking similarities overall. *Leucauge xiuying* might be related to *L. argentina*, *L. crucinota*, *L. nanshan* Zhu, Song & Zhang, 2003, and *L. argyrescens* Benoit, 1978. Some of them have been grouped together in a phylogenetic framework elsewhere (Ballesteros & Hormiga, 2021). All these species have small bodies with at least four tubercles, predominantly black coloration with spaced silvery bands on both the dorsum and the venter. Males lack the dorsobasal process. As mentioned above, *L. rubripleura* might be related to *L. moerens* but also to *L. mesomelas (*O. Pickard-Cambridge, 1894), *L. pulcherrima* (Keyserling, 1865), and many similar undescribed species. They exhibit similar color patterns on the abdomen and a wide epigynum slightly projected with very distant copulatory openings, with males lacking both the dorsobasal process and cheliceral clasping mechanisms. Future studies aiming to further understand the internal lineages of Leucauge should also investigate these supposed relationships.

CONCLUSIONS

This work corroborates the monophyly of *Leucauge* as a genus containing three to four major internal lineages, depending on the analytical approach used. As lineages are not necessarily linked to continental distribution, the occurrence of multiple dispersal events over long distances is deduced. Part of the clades recovered by this study were proposed as operational groups of species, opening perspectives for targeted studies as well as taxonomic revisions. As the value of *Leucauge* as model organisms increase, the contributions of the present study can bring new interpretations of biological aspects in the light of the evolutionary relationships.

REFERENCES

Aisenberg, A. (2009). Male performance and body size affect female re-mating occurrence in the orb-web spider *Leucauge mariana* (Araneae, Tetragnathidae). *Ethology*, 115(12), 1127-1136.

Aisenberg, A., & Barrantes, G. (2011). Sexual behavior, cannibalism, and mating plugs as sticky traps in the orb weaver spider *Leucauge argyra* (Tetragnathidae). *Naturwissenschaften*, 98, 605-613.

Aisenberg, A., Barrantes, G., & Eberhard, W. G. (2014). Hairy kisses: tactile cheliceral courtship affects female mating decisions in *Leucauge mariana* (Araneae, Tetragnathidae). *Behavioral Ecology and Sociobiology*, 69, 313-323.

Aisenberg, A., Barrantes, G., & Eberhard, W. G. (2015). Post-copulatory sexual selection in two tropical orb-weaving *Leucauge* spiders. *Cryptic female choice in arthropods: Patterns, mechanisms and prospects*, 79-108.

Alvarez-Padilla, F. (2007). Systematics of the spider genus *Metabus* O. P.-Cambridge, 1899 (Araneoidea: Tetragnathidae) with additions to the tetragnathid fauna of Chile and comments on the phylogeny of Tetragnathidae. *Zoological Journal of the Linnean Society*, 151(2), 285-335.

Alvarez-Padilla, F., & Benjamin, S. P. (2011). Phylogenetic placement and redescription of the spider genus *Atelidea* Simon, 1895 (Araneae, Tetragnathidae). *Zootaxa*, 2761(1), 51-63.

Álvarez-Padilla, F., Dimitrov, D., Giribet, G., & Hormiga, G. (2009). Phylogenetic relationships of the spider family Tetragnathidae (Araneae, Araneoidea) based on morphological and DNA sequence data. *Cladistics*, 25(2), 109-146.

Alvarez-Padilla, F., & Hormiga, G. (2011). Morphological and phylogenetic atlas of the orb-weaving spider family Tetragnathidae (Araneae: Araneoidea). *Zoological Journal of the Linnean Society*, 162(4), 713-879.

Álvarez-Padilla, A., Kallal, R. J. & Hormiga, G. (2020). Taxonomy and phylogenetics of Nanometinae and other Australasian orb-weaving spiders (Araneae: Tetragnathidae). *Bulletin of the American Museum of Natural History* 438: 1-107.

Ballesteros, J. A., & Hormiga, G. (2018). Species delimitation of the North American orchard-spider *Leucauge venusta* (Walckenaer, 1841) (Araneae, Tetragnathidae). *Molecular Phylogenetics and Evolution*, 121, 183-197.

Ballesteros, J. A., & Hormiga, G. (2021). Molecular phylogeny of the orb-weaving spider genus *Leucauge* and the intergeneric relationships of Leucauginae (Araneae, Tetragnathidae). *Invertebrate Systematics*, 35(8), 922-939.

Briceño, R. D., & Eberhard, W. G. (2011). The hub as a launching platform: rapid movements of the spider *Leucauge mariana* (Araneae: Tetragnathidae) as it turns to attack prey. *The Journal of Arachnology*, 39(1), 102-112.

Barrantes, G., Aisenberg, A., & Eberhard, W. G. (2013). Functional aspects of genital differences in *Leucauge argyra* and *L. mariana* (Araneae: Tetragnathidae). *The Journal of Arachnology*, 41(1), 59-69.

Brazeau, M. D. (2011). Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*, 104(3), 489-498.

Cabra-Garcia, J., & Brescovit, A. D. (2016). Revision and phylogenetic analysis of the orb-weaving spider genus *Glenognatha* Simon, 1887 (Araneae, Tetragnathidae). *Zootaxa*, 4069(1), 1-183.

Castanheira, P. de S., Baptista, R. L. C., Pizzetti, D. D. P. & Teixeira, R. A. (2019b). Contributions to the taxonomy of the long-jawed orb-weaving spider genus *Tetragnatha* (Araneae, Tetragnathidae) in the Neotropical region, with comments on the morphology of the chelicerae. *Zoosystematics and Evolutio*n 95(2), 465-505.

Coddington, J. A. (1990). Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology, 496, 1-52.

Danielson-François, A., & Sullivan, H. N. (2021). Do exaggerated chelicerae function as weapons or genitalia in a long-jawed spider? Functional allometric analysis yields an answer. *Journal of Morphology*, 282(1), 66-79.

Decae, A. E. (1987). Dispersal: ballooning and other mechanisms. *Ecophysiology of spiders*, 348-356.

Dimitrov, D., & Hormiga, G. (2009). Revision and cladistic analysis of the orbweaving spider genus *Cyrtognatha* Keyserling, 1881 (Araneae, Tetragnathidae). *Bulletin of the American Museum of Natural History*, 2009(317), 1-140.

Dimitrov, D., & Hormiga, G. (2010). Mr. Darwin's mysterious spider: on the type species of the genus *Leucauge* White, 1841 (Tetragnathidae, Araneae). Zootaxa, 2396(1), 19-36.

Dimitrov, D., Álvarez-Padilla, F. & Hormiga, G. (2010). On the phylogenetic placement of the spider genus *Atimiosa* Simon, 1895, and the circumscription of *Dolichognatha* O.P.-Cambridge, 1869 (Tetragnathidae, Araneae). *American Museum Novitates* 3683, 1-19.

Eberhard, W. G. (1987). Effects of gravity on temporary spiral construction by *Leucauge mariana* (Araneae: Araneidae). *Journal of Ethology*, 5(1), 29-36.

Eberhard, W. G. (1990). Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. *Journal of Arachnology*, 205-234.

Eberhard, W. G., & Huber, B. A. (1998). Courtship, copulation, and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. *Journal of Arachnology*, 342-368.

Giribet, G. (2003). Stability in phylogenetic formulations and its relationship to nodal support. *Systematic Biology*, 52(4), 554-564.

Goloboff, P. A. (1999). Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, 15(4), 415-428.

Goloboff, P. A., & Farris, J. S. (2001). Methods for quick consensus estimation. *Cladistics*, 17(1), S26-S34.

Goloboff, P. A., Farris, J. S., Källersjö, M., Oxelman, B., Ramıacute; rez, M. N. J., & Szumik, C. A. (2003). Improvements to resampling measures of group support. *Cladistics*, 19(4), 324-332.

Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, 39(2), 144-153.

Gonzaga, M. O., Moura, R. R., Pêgo, P. T., Bang, D. L., & Meira, F. A. (2015). Changes to web architecture of *Leucauge volupis* (Araneae: Tetragnathidae) induced by the parasitoid *Hymenoepimecis jordanensis* (Hymenoptera: Ichneumonidae). *Behaviour*, 152(2), 181-193.

Griswold, C. E., Coddington, J. A., Hormiga, G., & Scharff, N. (1998). Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society*, 123(1), 1-99.

Hénaut, Y., García-Ballinas, J. A., & Alauzet, C. (2006). Variations in web construction in *Leucauge venusta* (Araneae, Tetragnathidae). *The Journal of Arachnology*, *34*(1), 234-240.

Hormiga, G., Eberhard, W. G., & Coddington, J. A. (1995). Web-construction behavior in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). *Australian Journal of Zoology*, 43(4), 313-364.

Hormiga, G., Kulkarni, S., Arnedo, M. A., Dimitrov, D., Giribet, G., Kallal, R. J. & Scharff, N. (2023). Genitalic morphology and phylogenomic placement of the Australian spider *Paraplectanoides crassipes* Keyserling, 1886 (Araneae, Araneidae) with a discussion on the classification of the family Araneidae. Invertebrate Systematics 37(12), 797-818.

Huber, B. A. (2003). Rapid evolution and species-specificity of arthropod genitalia: fact or artifact?. *Organisms Diversity & Evolution*, 3(1), 63-71.

Jokat, W., Boebel, T., König, M., & Meyer, U. (2003). Timing and geometry of early Gondwana breakup. *Journal of Geophysical Research: Solid Earth*, 108(B9).

Kallal, R. J. & Hormiga, G. (2018). An expanded molecular phylogeny of metaine spiders (Araneae, Tetragnathidae) with description of new taxa from Taiwan and the Philippines. *Invertebrate Systematics* 32(2), 400-422. doi:10.1071/IS17058

Kuntner, M. (2005). A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian 'coin spiders'. *Invertebrate Systematics* 19(5), 391-436.

Kuntner, M. (2006). Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). *Zoologica Scripta* 35(1), 19-62.

Kuntner, M., Coddington, J. A. & Hormiga, G. (2008). Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24(2), 147-217.

Land, M. F. (1985). The morphology and optics of spider eyes. In *Neurobiology of arachnids* (pp. 53-78). Berlin, Heidelberg: Springer Berlin Heidelberg.

Levi, H. W. (1980). The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 149, 271-318.

Magalhaes, I. L., Azevedo, G. H., Michalik, P., & Ramírez, M. J. (2020). The fossil record of spiders revisited: implications for calibrating trees and evidence for a major faunal turnover since the Mesozoic. *Biological Reviews*, 95(1), 184-217.

Maddison, W. P. and D.R. Maddison. (2023). Mesquite: a modular system for evolutionary analysis. Version 3.81 http://www.mesquiteproject.org

Mirande, M. J. (2009). Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 25(6), 574-613.

Nixon, K. C. (1999). The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15(4), 407-414.

Nixon, K. C. (2002). WinClada, version 1.00. 08. published by the author, Ithaca, New York.

Oxford, G. S. (1997). Guanine as a colorant in spiders: development, genetics, phylogenetics and ecology. In *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh (pp. 121-131).

Pádua, D. G., Salvatierra, L., Sobczak, J. F., & Oliveira, M. L. (2016). Parasitism of *Hymenoepimecis manauara* Pádua & Oliveira (Hymenoptera: Ichneumonidae: Pimplinae) on *Leucauge henryi* Mello-Leitão (Araneae: Tetragnathidae) in Brazilian Amazonian. *Biodiversity Data Journal*, (4), e11219.

Preston-Mafham, K. G., & Cahill, A. (2000). Female-initiated copulations in two tetragnathid spiders from Indonesia: *Leucauge nigrovittata* and *Tylorida ventralis*. Journal of Zoology, 252(4), 415-420.

Saaristo, M. I. (2003). Tetragnathid spiders of Seychelles (Araneae, Tetragnathidae). *Phelsuma* 11, 13-28.

Salomon, M., Sponarski, C., Larocque, A., & Avilés, L. (2010). Social organization of the colonial spider *Leucauge* sp. in the Neotropics: vertical stratification within colonies. *The Journal of Arachnology*, 38(3), 446-451.

Scharff, N., Coddington, J. A., Blackledge, T. A., Agnarsson, I., Framenau, V. W., Szűts, T., Hayashi C. Y. & Dimitrov, D. (2020). Phylogeny of the orb-weaving spider family Araneidae (Araneae: Araneoidea). *Cladistics*, 36(1), 1-21.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9(7), 671-675.

Sereno, P. C. (2007). Logical basis for morphological characters in phylogenetics. *Cladistics*, 23(6), 565-587.

Simon, E. (1903). Arachnides de la Guinée espagnole. *Memorias de la Real Sociedad Española de Historia Natural* 1(3), 65-124.

Strong, E. E., & Lipscomb, D. (1999). Character coding and inapplicable data. *Cladistics*, 15(4), 363-371.

Tanikawa, A. (2001). *Okileucauge sasakii*, a new genus and species of spider from Okinawajima Island, southwest Japan (Araneae, Tetragnathidae). *Journal of Arachnology* 29, 16-20.

Tahir, H. M., Butt, A., & Alam, I. (2010). Relationship of web characteristics and body measures of *Leucauge decorata* (Araneae: Tetragnathidae). *Pakistan Journal of Zoology*, 42(3).

Wan, J. L., & Peng, X. J. (2013). The spiders of the genus *Wolongia* Zhu, Kim & Song, 1997 from China (Araneae: Tetragnathidae). Zootaxa, 3691(1), 87-134.

Wheeler, W. C. (1995). Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology*, 44(3), 321-331.

World Spider Catalog (2024). World Spider Catalog. Version 25.0. Natural History Museum Bern, online at http://wsc.nmbe.ch, accessed on 08 March 2024. doi: 10.24436/2

Wunderlich, J. (2008). Descriptions of fossil spider (Araneae) taxa mainly in Baltic amber, as well as certain related extant taxa. *In* Wunderlich, J. (ed.). *Beiträge zur Araneologie*, 5, 44–139.

related extant taxa. In Wunderlich, J. (ed.). Beiträge zur Araneologie, 5: 44–139.

Yoshida, M. (2000). Predatory Behavior of *Leucauge magnifica* (Araneae: Tetragnathidae). *Acta Arachnologica*, 49(2), 117-123.

Zhu, M. S., Song, D. X. & Zhang, J. X. (2003). Fauna Sinica: Invertebrata Vol. 35: Arachnida: Araneae: Tetragnathidae. Science Press, Beijing, 418 pp.

Apêndice I

CHARACTER MATRIX

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Apêndice II

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The more, the merrier: a new colonial species of the orb weaving spider genus *Leucauge* White, 1841 (Araneae: Tetragnathidae) from the Amazon rainforest

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Abstract

A new *Leucauge* species, widespread in the Amazon rainforest, is described and illustrated. *Leucauge behemoth* **n. sp.** lives in colonies, usually positioned above turbulent waters. Both males and females have a unique color pattern, especially on the abdomen, which makes this species easily identifiable. Males are distinguished from most congeners by the long hook of the cymbium and from their closest relatives by the lack of a cymbial dorsobasal process. Females of this species differ from their congeners by the presence of a rounded ventral process in the epigynum. *Leucauge argyroaffins* Soares & Camargo, 1948 is proposed as a junior synonym of *Leucauge argyra* (Walckenaer, 1841).

Key words: spider, Amazonia, biodiversity, Neotropical

Introduction

The genus *Leucauge* was proposed by White (1841) as a subgenus of *Linyphia* Latreille, 1804, with only one species, *Linyphia (Leucauge) argyrobapta* White. Later, several new species of *Leucauge* were described from tropical regions around the world (World Spider Catalog 2023). This genus is composed of small to medium-sized orb web builders (1.6 to 12 mm) that inhabit mostly tropical environments (Dimitrov & Hormiga, 2010). These tetragnathid spiders are mainly diagnosable by the presence of two rows of long and conspicuous feathered trichobothria on the fourth femur (Levi, 1980, Figs 50, 51, 67). Other remarkable feature is the abdominal coloration, covered by silvery guanine crystals. This is highlighted by the generic name etymology, which refers to the brightness of the guanine patches (Cameron, 2005).

Ballesteros & Hormiga (2021) tested the monophyly of *Leucauge* in a study where they recovered *Alcimosphenus* Simon, 1895, *Mecynometa* Simon, 1894, *Opadometa* Archer, 1951 and *Opas* O. Pickard-Cambridge, 1896 as junior synonyms of this genus. As a result, the already high number of valid species was further increased to 183 (World Spider Catalog, 2023), making it one of the most speciose spider genera in the world. Many of these *Leucauge* species also have particularities that make them interesting research subjects of various biological aspects, such as studies of parasitoid and prey interactions (Gonzaga *et al*., 2015) and reproductive ecology (Aisenberg *et al*., 2015).

Despite highly diverse and abundant, the genus *Leucauge* has been taxonomically neglected and was never revised outside of eastern countries like China, Korea and Taiwan. In the Tropical Americas, *Leucauge* specimens are difficult to identify at species level, since most of the taxonomic literature is poorly illustrated (World Spider Catalog, 2023), and dozens of species remain undescribed (Álvarez-Padilla and Hormiga, 2011). This is no surprise,

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since the Neotropical region is usually recognized as the most species-rich region in the world (Raven *et al.*, 2020), but also has been drastically threatened by anthropogenic action (Antonelli, 2022).

Therefore, given that taxonomy is the base of conservation biology (Valdecasas & Camacho, 2003), increasing the knowledge of the species that occur in the neotropics is a necessary step to implement policies of biodiversity protection to mitigate adverse actions upon our biomes. In this article we describe a new colonial species of *Leucauge* from moist environments on the Amazon rainforest. This species, recognizable by its colonial structure which is rare among Leucauginae, has been previously studied and suggested as a new species (Áviles *et al*., 2001; Salomon *et al*., 2010). Here, we provide a formal description of this species along with a discussion about the identity of *Leucauge argyroaffins* Soares & Camargo, 1948, which is proposed as a junior synonym of *Leucauge argyra*, a common and widespread spider.

Material and methods

The studied specimens are deposited in the following collections (acronym and curator in parentheses): Instituto Butantan, São Paulo (IBSP, A. D. Brescovit); Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ, A. B. Kury); Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe (SMNK, H. Höfer); Universidade Federal do Mato Grosso, Cuiabá (UFMT, A. Chagas Junior); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG, A. J. Santos); Museu Paraense Emílio Goeldi (MPEG, A. B. Bonaldo); Coleção de História Natural, Universidade Federal do Piauí (CHNUFI, L. S. Carvalho); Museu de Zoologia, Univerisdade de São Paulo (MZSP, R. Pinto da Rocha); Universidade de Brasília, Brasília (DZUB, P.C. Motta).

We examined the specimens using a Leica S8 APO stereoscope, equipped with an external camera AmScope MU500, connected to the software AmScope version 3.7. The spiders were identified based on the available literature (World Spider Catalog, 2023), as well as the illustrations of the congeneric holotypes by H. W. Levi (available on http://surl.li/ndavo). This reference material was compared with a large sample of *Leucauge* specimens, including almost 40 Neotropical species.

We took photographs that were used as basis for both the illustrations and measurements. The measurements were taken through the software ImageJ (Schneider *et al*., 2012) in reference to a scale given by graph paper. We made the illustrations on the software packages Photoshop and Illustrator CC 2019 from Adobe, and used both specimens of the type series and photographs of living individuals as reference. The species description follows the format used by Lise *et al.* (2015). We followed the morphological terminology used by Álvarez-Padilla & Hormiga (2011).

For scanning electron microscopy (SEM) images, the structures were removed and dehydrated through a series of graded ethanol (80–100%), dried by critical-point drying, mounted on metal stubs using adhesive copper tape for fixation, and sputter coated with gold. SEM images were taken with a FEI Quanta 250 scanning electron microscope at the Laboratório de Biologia Estrutural of the Instituto Butantan, São Paulo.

We used QGis version 2.16.3 with the plugin QuickMapServices to make the distribution maps. We included data from citizen science uploaded on iNaturalist in addition to the register sites of the museum specimens on the map. It is not always possible to identify spider species with accuracy only by images; however, the distinct and unique coloration of the species herein described allows confident identification from photographic records.

Abbreviations follow Álvarez-Padilla & Hormiga (2011). Eyes: AME, anterior median eyes; ALE, anterior lateral eyes, PME; posterior median eyes; PLE, posterior lateral eyes. Male palp: C, conductor; CB, cymbium; CH, cymbial hook; DP, dorsobasal process; E, embolus; P, paracymbium; ST, subtegulum; T, tegulum. Epigynum: A, atrium; CD, copulatory ducts; CO, copulatory opening; FD, fertilization ducts; LR, lateral ridge; S, spermatheca; VP, ventral process.

Taxonomy

Family Tetragnathidae Menge, 1866

Genus *Leucauge* White, 1841

Leucauge argyra (Walckenaer 1841)

Figs 1A–D, 7

Tetragnatha argyra Walckenaer, 1841: 219, pl. 19, figs. 1a–d. Type specimens from Guadeloupe, lost according to Levi, 1980: 28.

Linyphia aurulenta C. L. Koch, 1845: 127, pl. 425, fig. 1049. Type specimen from St. Thomas. Levi, 1980: 28 (Syn.)

Linyphia ornata Taczanowski, 1874: 66. Type material from Cayenne and Saint-Laurent-du-Maron, French Guiana. Banks, 1909: 163 (Syn.).

Meta argyra: Keyserling, 1881: 563, pl. 16, figs. 12–12a.

Argyroepeira argyra: Keyserling, 1893: 343, pl. 18, figs. 253a–d; McCook, 1894: 243, pl. 24, figs. 2–3b; Simon, 1894: 730, fig. 806.

Argyroepeira aurulenta: Simon, 1898: 871.

Plesiometa argyra: F. O. Pickard-Cambridge, 1903: 438, pl. 41, figs. 15–16a.

Leucauge argyra: Banks, 1909: 163.

Leucauge aurulenta: Archer, 1951: 6, figs 5–6 (Removed from synonymy of *Leucauge venusta* Walckenaer, 1841).

Leucauge argyroaffins Soares & Camargo, 1948: 381, figs. 40–42. Male holotype from Nova Xavantina, Mato Grosso, Brazil, X/1946, deposited in MZSP 1330. We have examined photographs of the holotype. **New synonymy**.

Other material examined. MEXICO, female from unknown location, 05/IX/1952, unknown coll. (IBSP 11884). **CUBA**, two males and female from Rio La Mula, Guamá, Santiago de Cuba, 16/VI/1999, A. Sánchez coll. (IBSP 169936). **DOMINICAN REPUBLIC**, female from Punta Cana, La Altagracia, VII/2009, G. R. S. Ruiz coll. (IBSP 214480). **PUERTO RICO**, male and female from Jayuya, 20/III/1986, H. L. Levi, coll. (IBSP 6233). **MARTINIQUE**, three males and six females from Carrere, 08-21/VI/2013, A. Sanchéz coll. (IBSP 169861). **BRAZIL**, male from Usina Hidrelétrica de Balbina (01°54′56,7″S 59°28′25″W), Presidente Figueiredo, Amazonas, 01/IV/1994, Naldrand coll. (IBSP 14503); fourteen males, thirty-four and five juveniles from Mina do Sossego (06°26’33.4”S 50°54’57.2”W), Marabá, Pará 05/III/2004, E. Wanzeler coll. (MPEG 4122); male and female from Riacho Cheio D’água, povoado Cheio D’água, Aldeias Altas (4°38’16.7”S 43°29’46.4”W), Maranhão, 30/XII/2021, G. S. Lustosa et al. Coll. (CHNUFPI 4350); twelve females from Rio Igaraçu, Parnaíba (2°53’40.11”S 41°45’10.25”W), Piauí 01/VI/2010, L. S. Carvalho *et al.* coll. (CHNUFPI 4137); male and four females from João Pessoa (07°06’54”S 34°51’03”W), Paraíba 23/XII/1982, M. C. Santos coll. (IBSP 14286); male and nine females from Campus UFSe, São Cristóvão (11°0′54″S 37°12′21″W), Sergipe, 12/VI/1996, A. D. Brescovit coll. (IBSP 7635); three females from Usina Hidrelétrica Luís Eduardo Magalhães (9°45’21”S 48°22’23”W), Palmas, Tocantins, 10/I/2002, D. M. Cândido & M. Costa coll. (IBSP 40561); male from Estação Experimental Biológica (15°44’10.8”S 47°53’00.4”W), Asa Norte, Brasília, Distrito Federal, 05/V/2006, P. C. Motta *et al.*, coll. (DZUB 4595); four females from Campus Darcy Ribeiro (15°45’55.9”S 47°51’22.8”W), Asa Norte, Brasília, Distrito Federal, 03/V/2004, J. Roger coll. (DZUB 3022); male and three females from Salvador (12°57’48”S 38°24’44”W), Bahia, X/2012, T. S. Melo *et al.* coll. (IBSP 235737); three males and four females from Parque Estadual do Rio Doce (19°39’31”S 42°34’32”W), Marliéria, Minas Gerais 13-16/VII/2018, T. G. Kloss coll. (UFMG 22436); male and three females from Ilha Solteira (20°25’58”S 51°20’33”W), São Paulo, 25/VI/1973, M. P. Bueno coll. (IBSP 2665); male, two females and three juveniles from Usina Hidrelétrica Engenho Sérgio Motta (22°28′46″S 52°57′25″W), Presidente Epitácio, São Paulo, 16/I-13/II/1999, team IBSP coll. (IBSP 23124);

Justification of the synonymy. *Leucauge argyroaffins* was described by Soares and Camargo (1948) based on a single male collected in Nova Xavantina, state of Mato Grosso (Fig 1A). This specimen is damaged, having lost both palps and most of the color pattern, but the chelicerae remain undamaged, where a distal constriction typical of *L. argyra* is seen. The authors used two main diagnostic features to differentiate *L. argyroaffins* from *L. argyra*: the shape of the cymbial hook and the presence of a dorsobasal process, against its supposed absence on *L. argyra*, which is inaccurate. The fig. 40 of their work depicts a palp with these structures, same as those presented by *L. argyra* males. It should be noted that the curvature of the cymbial hook is not a reliable diagnostic feature because

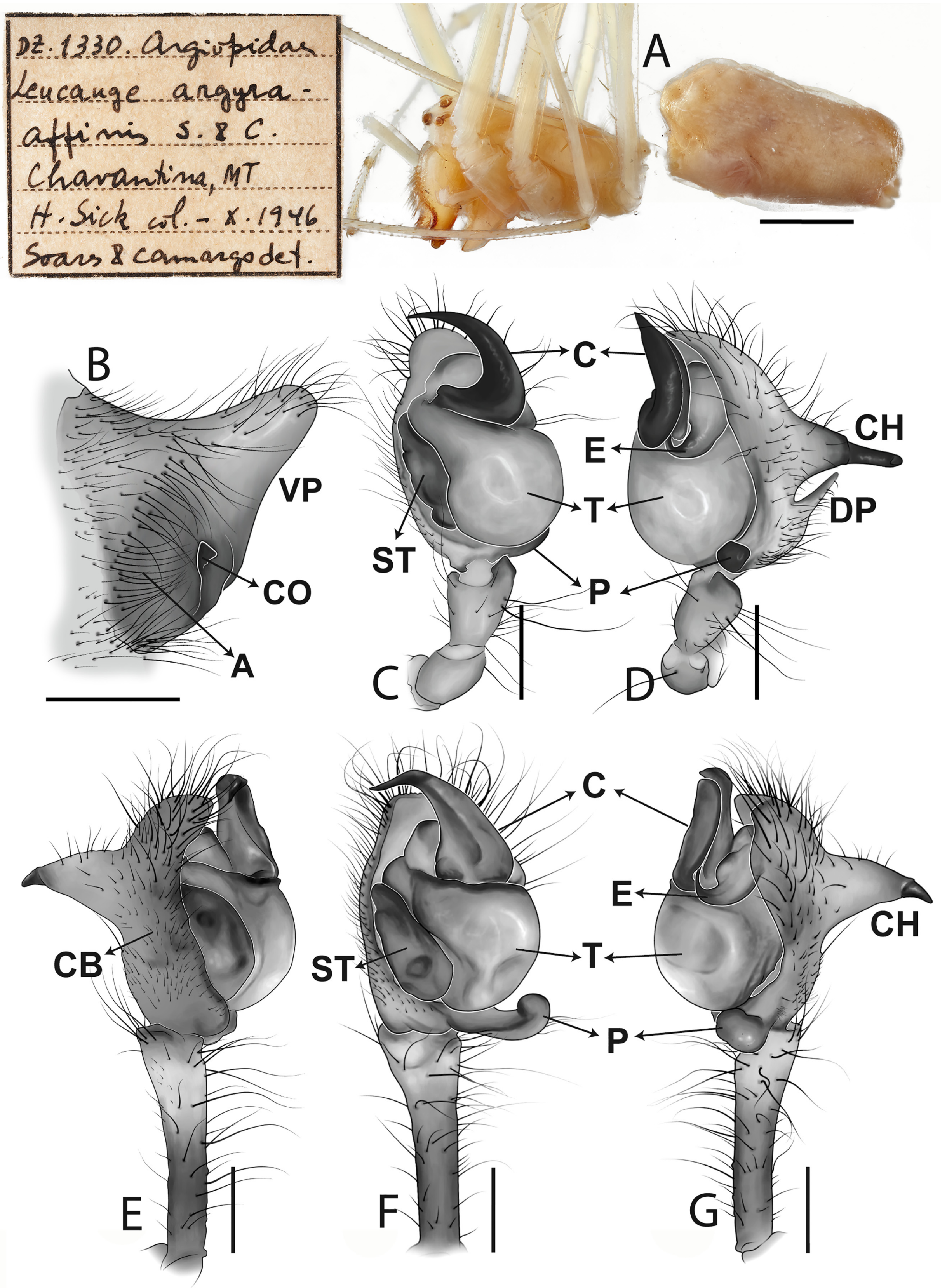

FIGURE 1. *Leucauge argyra* (Walckenaer, 1841). A, Holotype and original label of *Leucauge argyroaffins* Soares & Camargo 1948 (MZSP 1330) (images by Nadine Dupérré). B, Female from Brasília, epigynum in lateral view (DZUB 3022). C–D pedipalp of male from Brasília (DZUB 4595). C, ventral view. D, retrolateral view. *Leucauge behemoth* **n. sp.,** pedipalp of male paratype from Reserva Florestal Adolfo Ducke, Manaus **(**IBSP 97726). E, prolateral. F. ventral. G, retrolateral.Scale bars, A, 1.0 mm; B–G, 0.5 mm.

it may vary slightly within populations. Furthermore, in the original description of the *L. argyroaffins* holotype, the color described for the male is the same as that shown by *L. argyra.* The combination of these factors led us to propose the synonymy of these species.

Diagnosis. This species differs from most congenerics by its unique genitalia: females are distinguished by their projected epigynum with a ventral process (Fig 1B) only shared with the species herein described (see below), but differ by the conical shape of the projection. Males share the presence of dorsobasal process covered with setae with of *Leucauge globosa* (O. Pickard-Cambridge, 1889), but *L. argyra* differs by the presence of a very sclerotized sickle-shaped conductor, bigger body size (more than 4 mm) and thicker legs. The species described below and *L. argyra* are the only known to possess the cymbial hook, however *L. argyra* is distinct for carrying both cymbial apophyses. (Fig 1D).

Leucauge behemoth **new species**

Figs 1E−6

Plesiometa sp.: Avilés *et al*., 2001: 625, fig. 4.
Leucauge sp.: Salomon *et al*., 2010: 446, fig. 1C.

Holotype: Female from ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Amazonas, Brazil, 15/VIII/2003, A. Pacheco coll., (IBSP 342780). **Paratypes:** male and four females from Reserva Florestal Adolfo Ducke (2°55'22.0"S 59°58'29.0"W), Manaus, Amazonas, Brazil, 20/XI/2013, B. Faleiro coll. (UFMG 18051); four males and six females from Igarapé do Acampamento, ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Amazonas, Brazil, 15/VIII/2003, A. Pacheco coll. (IBSP 97726); male and two females, same data (IBSP 97728); four males and two females, same data (IBSP 97729).

Other material examined. **BRAZIL**, three females from Parque Nacional da Serra do Divisor (8°2′39″S 73°33′55″W), Cruzeiro do Sul/Mâncio Lima, Acre 14/III/1997, L. Resende & R.S. Vieira coll. (IBSP 12638); two males and four females, same data (IBSP 12634); female, same data, 18/III/1997 (IBSP 12211); female and two immature from Rodovia Transamazonica, Km 530, Amazonas 26/VI/1979, E. Froelich coll. (IBSP 5855); female and immature, same data, II/1987 (IBSP 5865); three females from Parque Nacional do Jaú (2°15'0"S 62°38'0"W), Novo Airão, Amazonas 18/VI/2012, R.A.K. Ribeiro coll. (UFMT); male and two females from Benjamin Constant (4°22′58″S 70°1′51″W), Amazonas, VII/1985, A. Pontual coll. (IBSP 97724); male and four females, same locality, VII/1984, A. Cerrutti coll. (MNRJ 13047); male, female and two immature from Fazenda Esteio, Reserva do km 41 (02°22'34"S 59°52'39"W), Manaus, Amazonas, 29/VIII/1994, E. Venticinque coll. (IBSP 6238); seven females and immature, same data, (IBSP 6237); two females and four immature, same data (IBSP 6235); male, two females and immature, same data (IBSP 6234); four females, same locality, VIII/1994, E. Venticinque coll. (IBSP 6094); male and female from ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Km 41, Igarapé do Acampamento (02°22'34"S 59°52'39"W), Manaus, Amazonas, 15/VIII/2003, A. Pacheco (IBSP 97725); two males and six females, same data (IBSP 97727); male and female from Reserva Florestal Adolfo Ducke (2°54'2.14"S 60°5'12.24"W), Manaus, Amazonas, VII/1999, M.O. Gonzaga & G.F. Dutra coll. (IBSP 26695); male and two females, same locality, 21/VI/1995, Delgado coll. (IBSP 7382); male and two females from Barra dos Bugres (15°4′22″S 57°10′51″W), Mato Grosso, XI/1984, A. Cerrutti coll. (IBSP 315621); three males, nine females and six immatures, same data (MNRJ 13048). **COLOMBIA**, Male and three females from Puerto Asis Road, (0°40'36"N 76°52'38"W), Orito, Provincia Putamayo ,24-25/VIII/1973, V. Leist coll. (SMNK). **ECUADOR**, two males and five females from Estacíon Biológica Jatun-Sancha (1°03'57.5"S 77°37'00.2"W), Napo, 5/XII/2009, A.J. Santos coll. (UFMG 9125). **PERU**, two males and one female from Centro de Investigaciones Jenaro Herrera (4°53'44.8"S 73°38'50.1"W), Provincia de Requena, Distrito Jenaro Herrera, Región Loreto, 4/IV/2013, C.A. Rheims and R.P. Indicatti coll. (IBSP 233558); female, same data (IBSP 233629); male and two females, same data (DZUB 11010); three females, same data (IBSP 237055).

Etymology. The specific name is a noun in apposition taken from the mythological beast behemoth. The epithet was chosen to reference the remarkable size of this species.

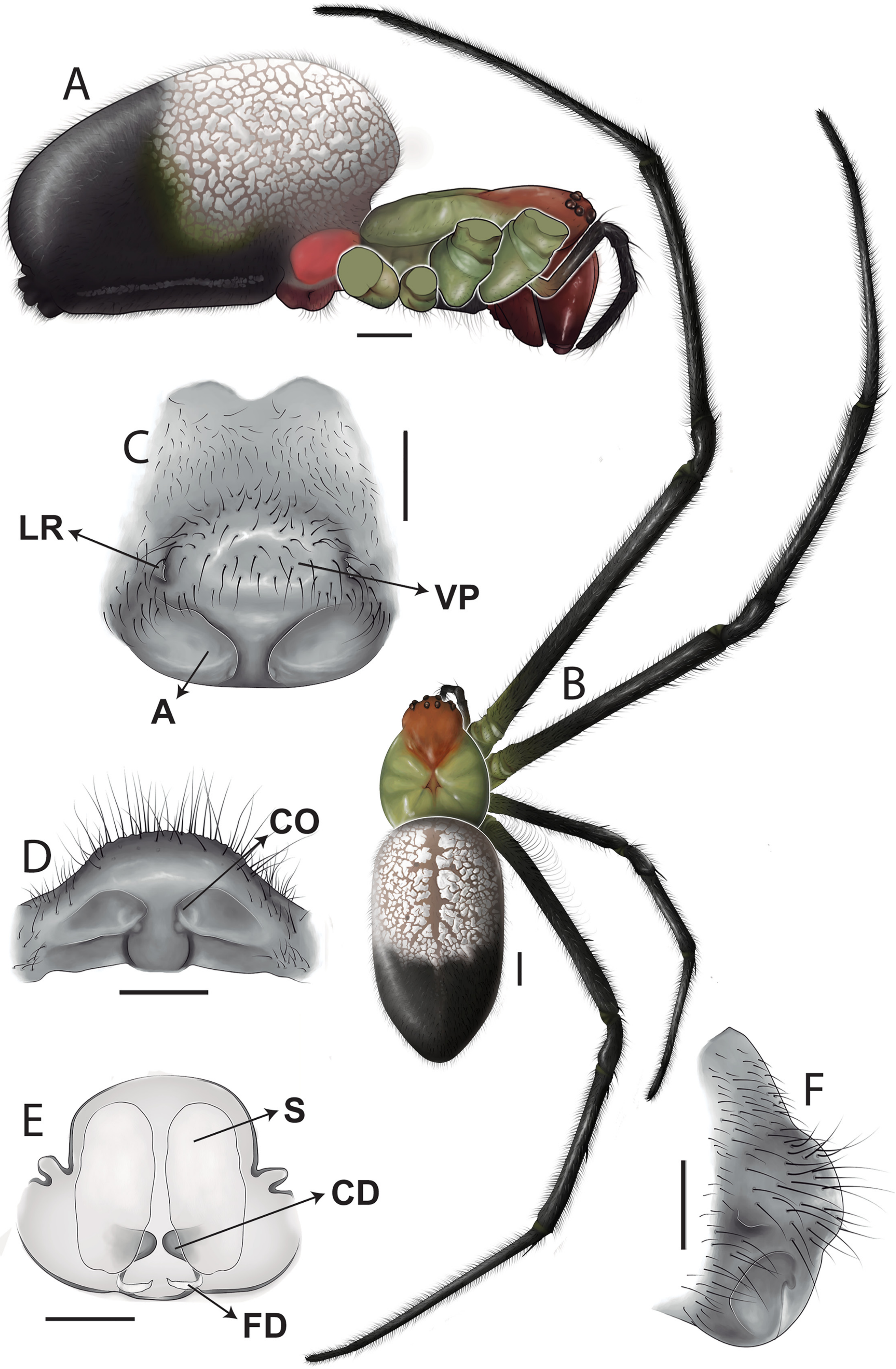

FIGURE 2. *Leucauge behemoth* **n. sp.**, female paratype from ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus (IBSP 97726). A,habitus, lateral . B, same, dorsal. C–F, Epigynum. C, ventral. D, posterior. E, dorsal, cleared. F, lateral. Scale bars, A, B, 1 mm; C–F, 0.5 mm.

Diagnosis. The males of *Leucauge behemoth* **n. sp.** resemble *Leucauge argyra* by the presence of a dorsal hook on the cymbium of the palp (Figs 1C−G, 4C−E,5A), but can be distinguished by the longer paracymbium and by lacking the dorsobasal process(Figs 1E, 1G, 4C−D; Levi, 1980: fig 69). The females of *L. behemoth* **n. sp.** also share with *L. argyra* the lateral ridge and the ventral process on the epigynum (Figs 1B, 2C−F). They differ by the shape of the ventral process, rounded instead of conical in *L. behemoth* **n. sp.** (Figs 2C−F, 4A−B). This species differs from most *Leucauge* species by the lack of an anterior hood on the epigynum of females, by its large size compared to other Neotropical congenerics (8.8 to 11.9 mm) and posterior half of abdomen black in dorsal view (Figs 2A−B, 3).

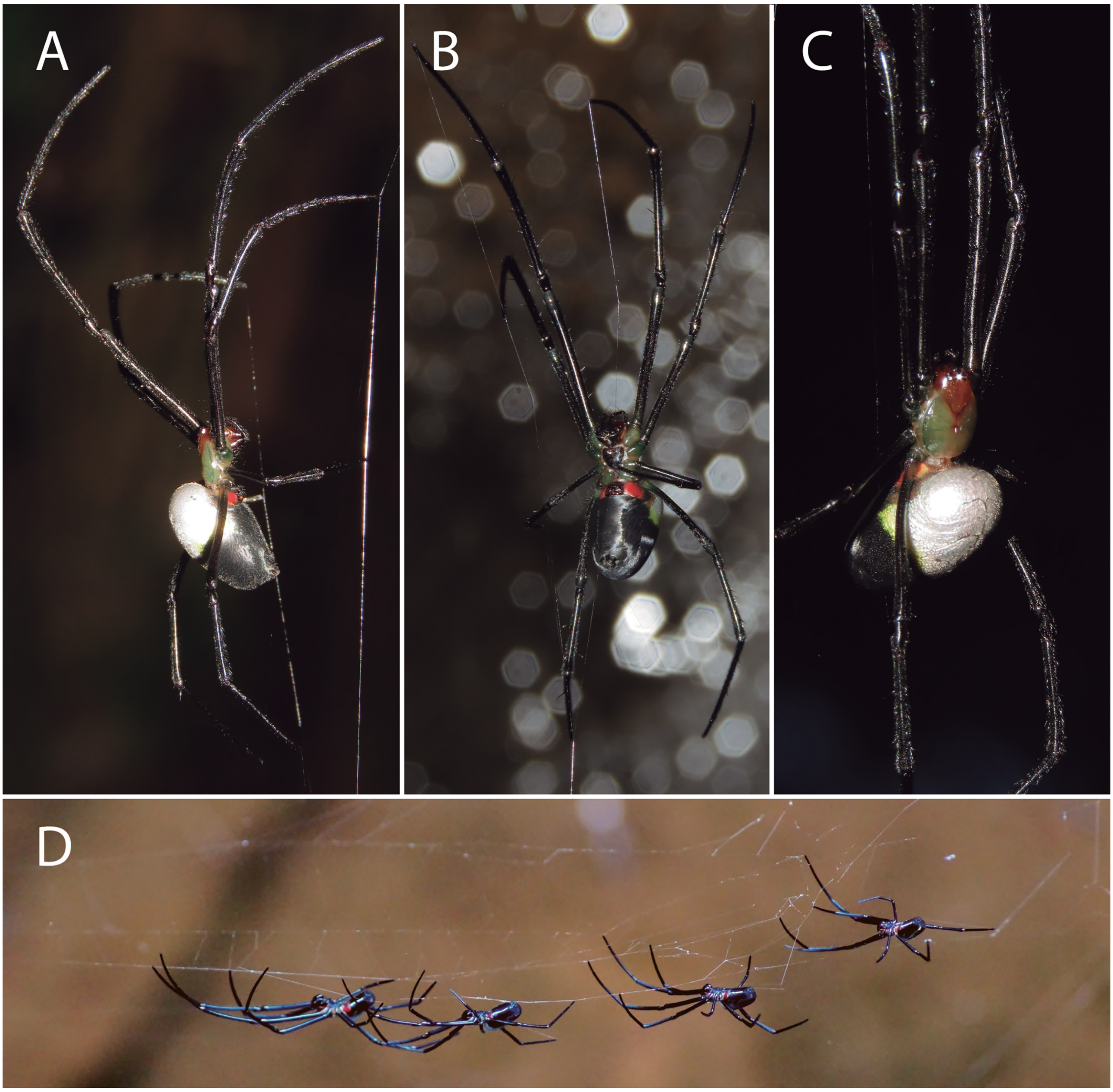

FIGURE 3. Living specimens of *Leucauge behemoth* **n. sp.** Female from Tambopata, Peru (photographed by Rich Hoyer/ Birdernaturalist in 20/IV/2019): A, female habitus, lateral. B, ventral. C, dorsolateral. D, specimens from Cantón Baños, Ecuador, coexisting without aggression outside their individual webs (photographed by Hederd Torres in 17/XII/2013).

Description. Female. Paratype from ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Amazonas, Brazil (IBSP 97726). Total length 10.76. Carapace 4.60 long, 0.60 high, glabrous, light orange. Cephalic region 1.98 wide, slightly darker. Thoracic region 3.68 wide. Clypeus 0.26. Eyes with small black rings. Eyes measurements: AME 0.21, ALE 0.19, PME 0.17, PLE 0.19; Eyes interdistances: AME-AME 0.16, AME-ALE 0.29, AME-PME 0.22, ALE-PLE touching, PME-PME 0.25, PME-PLE 0.33. Chelicerae 2.14 long, 0.98 wide, brownish orange with dark edges. Fangs 0.97 long, dark brown. Endites 1.26 long, 0.62 wide, brown with proximal edges orange. Labium 0.64 long, 0.76 wide, brown. Sternum 1.68 long, 1.72 wide, brownish orange with sparse setae. Coxae and trochanter light orange with few setae, other articles blackish brown with dense setae and very sparse macrosetae. All femurs bear feathered trichobothria, but they are more conspicuous on leg IV. Leg formula: 1243. Leg measurements: Leg I. femur 10.32 / patella 2.26 / tibia 8.58 / metatarsus 10.36 / tarsus 2.23 / total 33.75; II. 8.46 / 2.04 / 7.06 / 9.10 / 1.96 / total 28.62; III 4.76 / 1.16/ 2.98 / 4.39 / 1.40 / total 14.69; IV 8.36 / 1.60 / 5.61 / 7.49 / 1.66 / total 24.72. Palp measurements: femur 1.43 / patella 0.63 / tibia 0.92 / tarsus 1.57. Abdomen 7.00 long, 3.99 wide, 4.23 high. Dorsum covered with silver guanine patches on the anterior half, heart line and its branches without patches, posterior half black with two median parallel lines of guanine dots. Lateral colors as in dorsum, black half without guanine patches laterally. Venter black from the epigastric furrow to the spinnerets, with a pair of lateral parallel silver lines. Booklungs area yellowish beige. Spinnerets reddish brown. Epigynum 1.62 long, 1.55 wide, dark orange with broad rounded ventral process, covered with setae anteriorly. Atrium and posterior region of ventral process glabrous (Figs 2C–D, 2F, 4A–B). Copulatory ducts short and wide, oval spermathecae with thin and translucid walls, almost inconspicuous (Fig 2E).

Male. Paratype from ARIE do Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Amazonas, Brazil (IBSP 97726). All colors as in females. Total length 9.10. Carapace 4.49 long, 0.82 high, cephalic region 1.89 wide, thoracic region 3.39 wide. Clypeus 0.26. Eyes measurements: AME 0.20, ALE 0.19, PME 0.19, PLE 0.19; Eyes interdistances: AME-AME 0.20, AME-ALE 0.30, AME-PME 0.23, ALE-PLE touching, PME-PME 0.19, PME-PLE 0.34. Chelicerae long 2.06, wide 0.99, covered with small setae. Fangs 0.92 long. Endites 1.18 long, 0.61 wide, labium 0.51 long, 0.63 wide. Sternum 1.52 long, 1.67 wide. Leg formula: 1243. Leg measurements: Leg I femur 12.46 / patella 2.33 / tibia 11.71 / metatarsus 15.17 / tarsus 2.50 / total 44.17; II 10.25 / 2.16 / 8.91 / 11.55 / 2.00 / total 34.87; III 5.49 / 1.22 / 3.35 / 4.73 / 1.21 / total 16.00; IV 9.03 / 1.56 / 6.96 / 9.66 / 1.58 / total 28.79. Palp measurements: femur 3.21 / patella 0.55 / tibia 1.34 / cymbium 1.58. Palp with paracymbium curved, shorter than the tibia; conical cymbial hook with an apical spine; conductor with broad base and tapered apex, covered with small projections; tubular embolus widened in the base, sheathed by the conductor (Figs 1E–G, 4C–F, 5) Abdomen 5.82 long, 2.62 wide, 2.29 high.

Notes. The main description and measurements were taken from paratypes to prevent causing any damage to the holotype. The holotype and the paratypes chosen for the description came from the same population and were collected together.

This species was studied before its formal description was carried out (see synonymy list). Although the voucher specimens from Avilés *et al*. (2001) and Salomon *et al*. (2010) were not examined, they were recognized as conspecifics based on their size, color and colonial structure, high similarity to *L. argyra* and same locality (Estación Biológica Jatun-Sancha).

Variation. Female total length, 8.8 to 11.8 (n=10), male 8.2 to 11.1 (n=10). Females and males are very similar in size and in color. Females have slightly larger bodies, but shorter legs. The chelicerae are covered by more setae in males, and their legs have larger macrosetae than in females.

Living specimens. Males and females have a brownish orange cephalic region and a green thoracic region. Chelicerae brownish red, darker distally. Endites, labium and sternum blackish brown, lighter on their edges. Legs mostly black, trochanter and coxae green as the thoracic region. Abdomen white on the anterior dorsal half, posterior half black. Lateral edge between these halves with either a large and bright yellow stripe, a thin greenish yellow border, or even absent. Venter black. Booklung covers bright red (Fig 2A–B, 3).

Distribution. Brazil, Colombia, Ecuador and Peru (Fig 6).

Natural history. We observed 26 colonies in the ARIE (Área de Relevante Interesse Ecológico) Dinâmica Biológica de Fragmentos Florestais, north of Manaus, Brazil. The number of individuals of *L. behemoth* **n. sp.** per colony ranged from 3 to 22 adult and young spiders (2 to 27 in Solomon *et al*., 2010, median size of 19; 25 in Áviles *et al*., 2001). The colonies seemed to be more common in stretches of the “igarapé” with turbulent waters, which possibly has relation to the increase of number of flying insects or the high emergency of adult insects that have aquatic larval form. This phenomenon was observed in other tetragnathid species that coexist in similar areas with high prey abundance. These species, *Tetragnatha praedonia*, L. Koch, 1878; *T. keyserling* Simon, 1980, and *T. pinicola* L. Koch, 1870 primarily tolerate themselves through variations in the vertical placement of their webs (Yoshida, 1980).

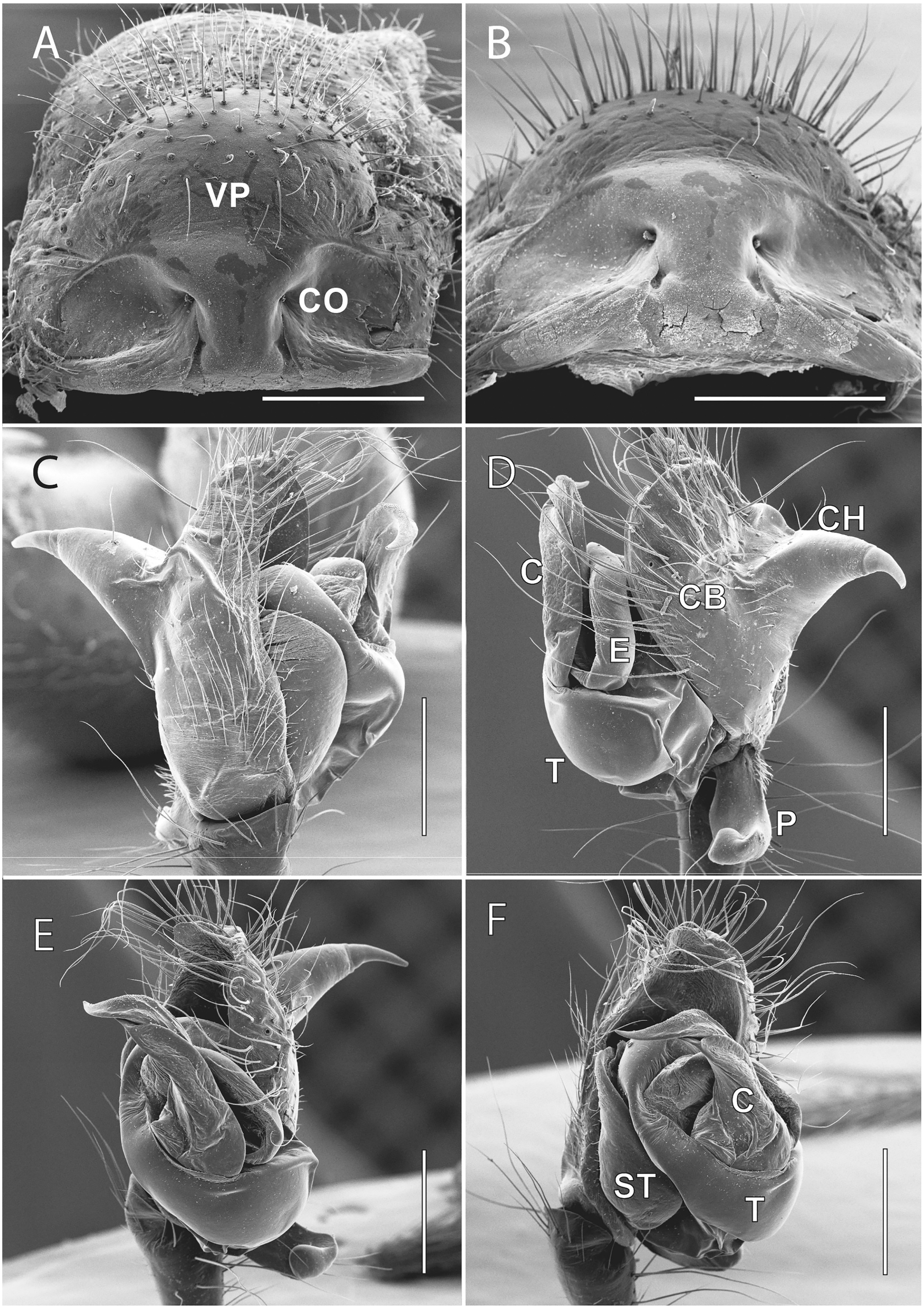

FIGURE 4. *Leucauge behemoth* **n. sp.** male and female from Manaus (IBSP 7382). A–B, epigynum. A, ventral. B, posterior. C–F, male palp. C, prolateral. D, retrolateral. E, retroventral. F, ventral. Scale bars, 0.5 mm.

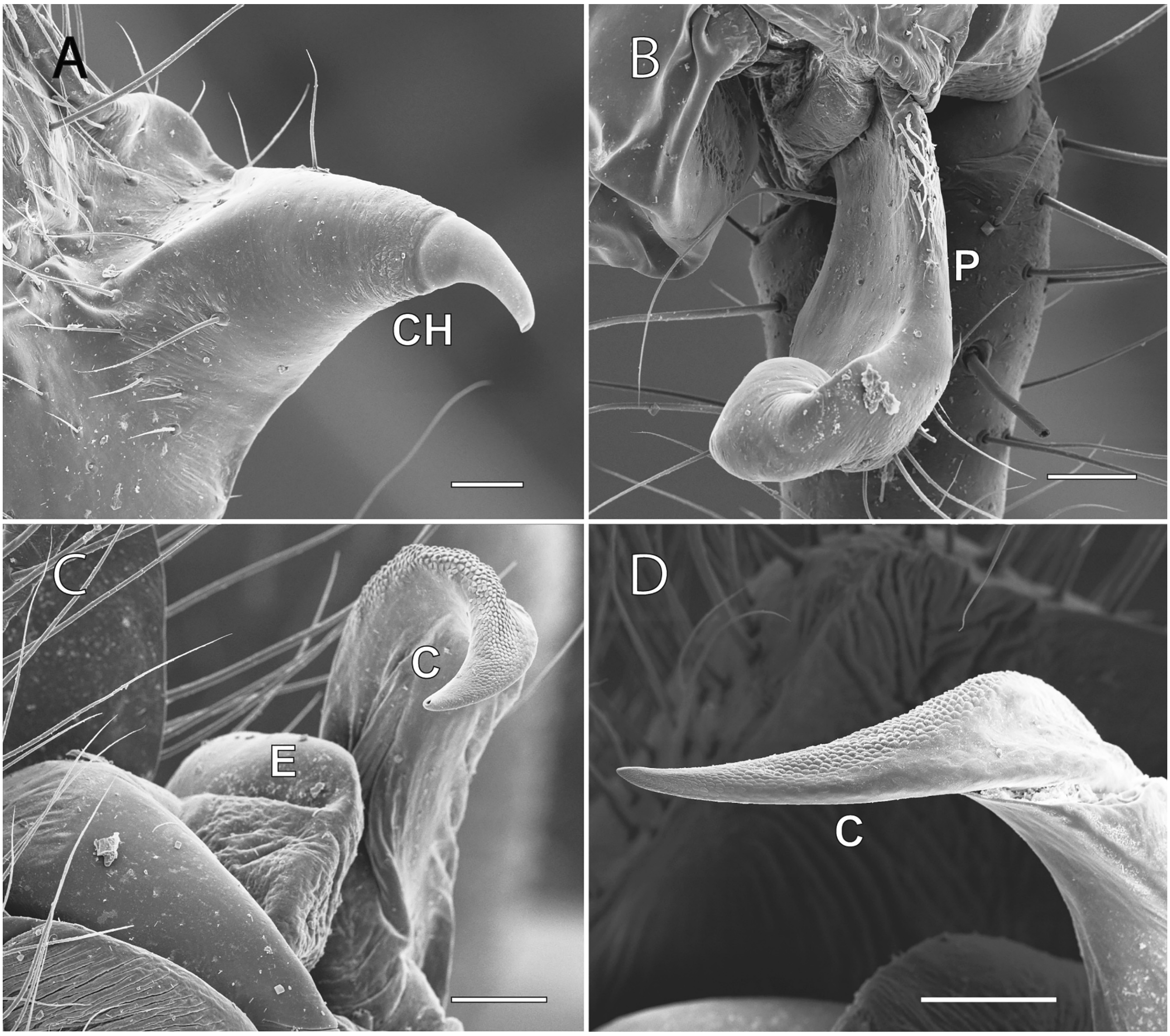

FIGURE 5. *Leucauge behemoth* **n. sp. (**IBSP 7382) male palp details. A, cymbial hook. B, paracymbium. C, embolus base and conductor. D, conductor tip. Scale bars, 0,1 mm.

Vertical stratification is also present in colonies of *L. behemoth* **n. sp.**, and it has been speculated (Salomon *et al*., 2010) that this colonial organization leads to spiders in different heights having access to different prey communities. We observed between VII/1984-VII/1985 that spiders smaller than 2 mm do not spin individual orb webs, living on the supporting threads of orbicular webs of colony in aggregations of up to five individuals close to the vegetation. Spiders around 2 mm spin small webs (6–10 cm) positioned a little further away from the vegetation towards the center of the watercourse. Individuals around 4–6 mm spin webs generally close to the surface of the water, whereas larger individuals (body size about 9–11 mm) occupy the intermediate and higher parts of the colonies. Specimens studied in Napo (Ecuador) by Salomon *et al*. (2010) behaved the same way. When disturbed, the spiders fled in groups to the leaves of the surrounding vegetation. Generally, the escape behavior varies according to the size of the colony. In small colonies all spiders fled to the same leaf, but in larger colonies, groups of two to five spiders fled to the underside of different leaves, returning after 10–20 minutes. Another observed behavior indicates tolerance between conspecific of the same colony, since spiders stayed together without aggression in encounters that take place outside the orb webs (Fig 3D).

Even though other congeneric species such as *L. argyrobapta* can have aggregate behaviors in the reproductive season (Buskirk, 1986), this is the first species where a complex coloniality with generation overlap has been documented. Its only close relative with similar behaviors is *Metabus ocellatus* (Keyserling, 1864) (Burskirk, 1975), a Leucauginae from riparian habitats in Central America.

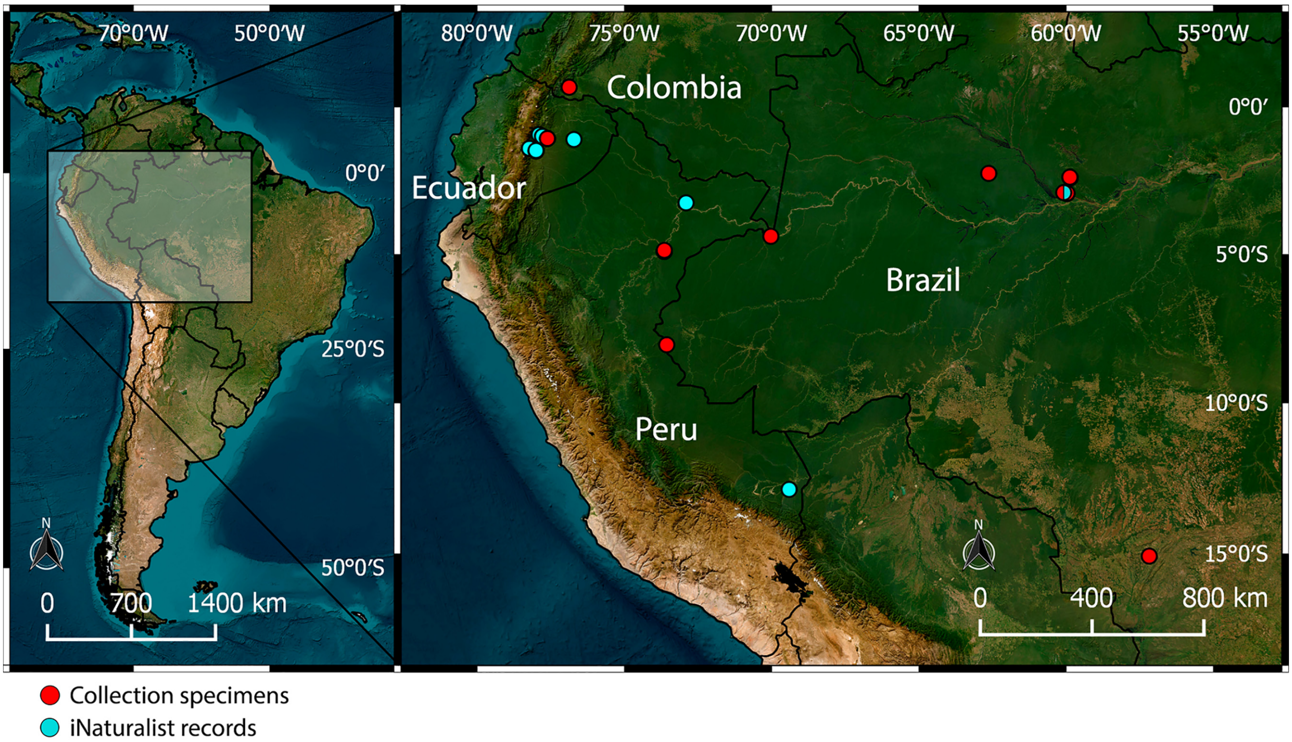

FIGURE 6. Distribution of *Leucauge behemoth* **n. sp.**

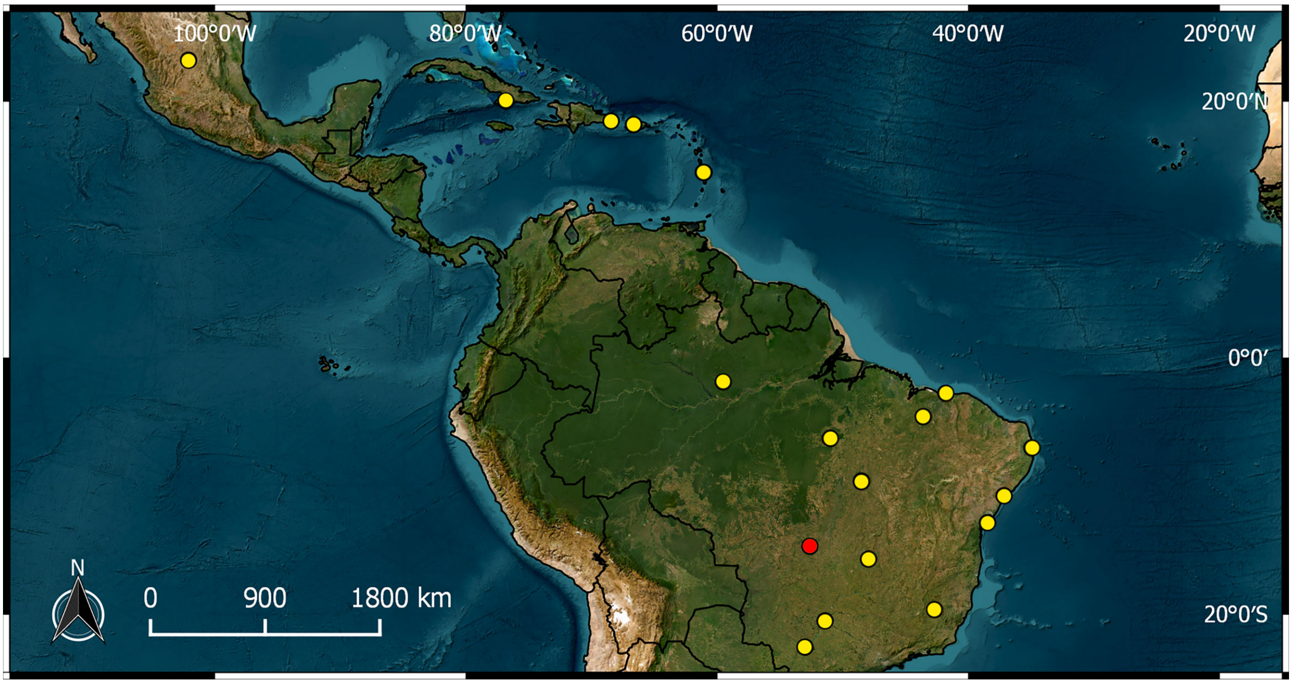

FIGURE 7. Distribution of *Leucauge argyra*. New records (yellow) and holotype of *Leucauge argyroaffins* (red).

Discussion

Cymbial apophyses are common among tetragnathids (Álvarez-Padilla & Hormiga, 2011). However, the cymbial hook present in *L. argyra* and *L. behemoth* **n. sp.** appears to be different from all other tetragnathid apophyses, which is highlighted by the topological positioning (dorsomedial) and the presence of a large modified seta apically. Thus, their cymbial hook might be a putative synapomorphy suggesting a close relationship between these two species, supported as well by the ventral epigynal process of the females. The cymbial hook is directly used in copulation: according to Barrantes *et al*. (2013; fig. 7), the conductor and the cymbial hook are locked inside the epigynal atria in *L. argyra*. The same is probably true to *L. behemoth* **n. sp.**, as in this species the atrium is large and concave enough for both palpal sclerites to fit. After mating, the epigynum can be plugged, possibly to block the copulatory openings and prevent posterior copulation attempts. The plug persists in collection specimens of both *L. argyra* and *L. behemoth* **n. sp.** and is composed mainly by a whitish matrix that covers part of the atrium.

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References

Aisenberg, A., Barrantes, G. & Eberhard, W.G. (2015) Hairy kisses: tactile cheliceral courtship affects female mating decisions in *Leucauge mariana* (Araneae, Tetragnathidae). *Behavioral Ecology and Sociobiology*, 69, 313–323. https://doi.org/10.1007/s00265-014-1844-2

Antonelli, A. (2022) The rise and fall of Neotropical biodiversity. *Botanical Journal of the Linnean Society*, 199 (1), 8−24. https://doi.org/10.1093/botlinnean/boab061

Archer, A.F. (1951) Studies in the orbweaving spiders (Argiopidae). 1. *American Museum Novitates,* 1487, 1−52.

Álvarez-Padilla, F. & Hormiga, G. (2011) Morphological and phylogenetic atlas of the orb-weaving spider family Tetragnathidae (Araneae: Araneoidea). *Zoological Journal of the Linnean Society,* 162 (4), 713−879. https://doi.org/10.1111/j.1096-3642.2011.00692.x

Avilés, L., Maddison, W.P., Salazar, P.A., Estévez, G., Tufiño, P. & Cañas, G. (2001) Arañas

sociales de la Amazonía ecuatoriana, con notas sobre seis especies sociales no descritas previamente Social spiders of the Ecuadorian Amazonia, with notes on six previously undescribed social species. *Revista Chilena de Historia Natural,* 74 (3), 619−638.

Ballesteros, J.A. & Hormiga, G. (2021) Molecular phylogeny of the orb-weaving spider genus *Leucauge* and the intergeneric relationships of Leucauginae (Araneae, Tetragnathidae). *Invertebrate Systematics,* 35 (8), 922−939. https://doi.org/10.1071/IS21029

Barrantes, G., Aisenberg, A. & Eberhard, W.G. (2013) Functional aspects of genital differences in *Leucauge argyra* and *L. mariana* (Araneae: Tetragnathidae). *Journal of Arachnology,* 41 (1), 59−69. https://doi.org/10.1636/B12-63.1

Buskirk, R.E. (1975) Coloniality, activity patterns and feeding in a tropical orb-weaving spider. *Ecology*, 56 (6), 1314−1328. https://doi.org/10.2307/1934699

Buskirk, R.E. (1986) Orb-weaving spiders in aggregations modify individual web structure. *Journal of Arachnology*, 14 (2), 259−265.

Dimitrov, D. & Hormiga, G. (2010) Mr. Darwin's mysterious spider: on the type species of the genus *Leucauge* White, 1841 (Tetragnathidae, Araneae). *Zootaxa,* 2396, 19−36. https://doi.org/10.11646/zootaxa.2396.1.2

Gonzaga, M.O., Rios Moura, R., Teixeira Pêgo, P., Lee Bang, D. & Meira, F.A. (2015) Changes to web architecture of *Leucauge volupis* (Araneae: Tetragnathidae) induced by the parasitoid *Hymenoepimecis jordanensis* (Hymenoptera: Ichneumonidae). Behaviour, 152 (2), 181−193. https://doi.org/10.1163/1568539X-00003238

iNaturalist. (2023) Available from: https://www.inaturalist.org. (Accessed 16 March 2023)

Keyserling, E. (1881) Neue Spinnen aus Amerika. II. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 30, 547−582. https://doi.org/10.5962/bhl.part.20318

Keyserling, E. (1893) *Die Spinnen Amerikas. Epeiridae*. Bauer & Raspe, Nürnberg, 192 pp. https://doi.org/10.5962/bhl.title.64832

Koch, C.L. (1845) *Die Arachniden*. C. H. Zeh'sche Buchhandlung, Nürnberg, 166 pp.
https://doi.org/10.5962/bhl.title.4374

Koch, L. (1870) Beiträge zur Kenntniss der Arachnidenfauna Galiziens. *Jahrbuch 0der Kaiserlich-Königlichen Gelehrten Gesellschaft in Krakau* 41, 1–56.

Koch, L. (1878) Japanesische Arachniden und Myriapoden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien,* 27 (1877), 735–798.

Latreille, P.A. (1804) Tableau methodique des Insectes. *Nouveau Dictionnaire d'Histoire Naturelle, Paris,* 24, 129−295.

Levi, H.W. (1980) The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology,* 149, 1−74.

Lise, A.A., Kesster, C.C. & Silva, E.L.C. da (2015) Revision of the orb-weaving spider genus *Verrucosa* McCook, 1888 (Araneae, Araneidae). *Zootaxa,* 3921 (1), 1−105. [Erratum, 3956 (4), 600.]
https://doi.org/10.11646/zootaxa.3921.1.1

McCook, H.C. (1894) *American spiders and their spinningwork. A natural history of the orbweaving spiders of the United States with special regard to their industry and habits*. *Vol. III*. Academy of Natural Sciences of Philadelphia, Philadelphia, 346 pp.
https://doi.org/10.5962/bhl.title.2681

Pickard-Cambridge, O. (1896) Arachnida. Araneida. *In:* Godman, F.D. & Salvin, O. (Ed.), *Biologia Centrali-Americana, Zoology, Botany and Archaeology. Vol. 10*. Dulau & Co, London, pp. 161−224.

Pickard-Cambridge, O. (1889) Arachnida. Araneida. *In*: Godman, F.D. & Salvin, O. (Ed.), *Biologia Centrali-Americana, Zoology*. London 1–57 pp.

Pickard-Cambridge, F.O. (1903) Arachnida - Araneida and Opiliones. *In*: Godman, F.D. & Salvin, O. (Ed.), *Biologia Centrali-Americana, Zoology*. London, 425−464 pp.

Raven, P.H., Gereau, R.E., Phillipson, P.B., Chatelain, C., Jenkins, C.N. & Ulloa Ulloa, C. (2020) The distribution of biodiversity richness in the tropics. *Science Advances*, 6, 1−5.
https://doi.org/10.1126/sciadv.abc6228

Salomon, M., Sponarski, C., Larocque, A. & Avilés, L. (2010) Social organization of the colonial spider *Leucauge* sp. in the Neotropics: vertical stratification within colonies. *The Journal of Arachnology,* 38, 446–451.
https://doi.org/10.1636/Hi09-99.1

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9 (7), 671–675.
https://doi.org/10.1038/nmeth.2089

Simon, E. (1894) *Histoire naturelle des araignées. Deuxième édition, tome premier*. Roret, Paris, pp. 489−760.
https://doi.org/10.5962/bhl.title.51973

Simon, E. (1895) *Histoire naturelle des araignées. Deuxième édition, tome premier*. Roret, Paris, pp. 761−1084.
https://doi.org/10.5962/bhl.title.51973

Simon, E. (1898) On the spiders of the island of St Vincent. III. *Proceedings of the Zoological Society of London*, 65 (4), 860–890.
https://doi.org/10.1111/j.1096-3642.1898.tb01390.x

Simon, E. (1890) Etudes arachnologiques. 22e Mémoire. XXXVI. Arachnides recueillis aux îles Mariannes par M. A. Marche. *Annales de la Société Entomologique de France,* 10 (6), 131–136.

Taczanowski, L. (1874) Les aranéides de la Guyane française. *Horae Societatis Entomologicae Rossicae*, 10, 56−115.

Valdecasas, A.G. & Camacho, A.I. (2003) Conservation to the rescue of taxonomy. *Biodiversity & Conservation*, 12, 1113−1117.
https://doi.org/10.1023/A:1023082606162

Walckenaer, C.A. (1841) *Histoire naturelle des Insects*. *Aptères*. *Tome deuxième*. Roret, Paris, 549 pp.
https://doi.org/10.5962/bhl.title.61095

White, A. (1841) Description of new or little known Arachnida. *Annals and Magazine of Natural History,* 7 (46), 471−477.
https://doi.org/10.1080/03745484109443624

World Spider Catalog (2023) World Spider Catalog. Version 24. Natural History Museum Bern. Available from: http://wsc.nmbe.ch (Accessed on 13 January 2023)
https://doi.org/10.24436/2

Yoshida, M. (1981) Preliminary study on the ecology of three horizontal orb weavers, *Tetragnatha praedonia*, *T. japonica*, and *T. pinicola* (Araneae: Tetragnathidae). *Acta Arachnologica*, 30 (1), 49–64.
https://doi.org/10.2476/asjaa.30.49