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

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Abstract

We newly diagnose, illustrate, and clarify the distribution ranges of six of the most common and broadly distributed species of *Tetragnatha* Latreille, 1804 found in the Neotropical region. Twenty new junior synonyms from around the world are included, nine for *T. bogotensis* Keyserling, 1865, four for *T. mandibulata* Walckenaer, 1841, three for *T. keyserlingi* Simon, 1890, three for *T. nitens* (Audouin, 1826), and one for *T. elongata* Walckenaer, 1841. *Tetragnatha vermiformis* Emerton, 1884 is newly recorded from South America. The Argentine *T. major* Holmberg, 1876 and *T. riparia* Holmberg, 1876 are considered nomina dubia. Finally, we discuss the terminology of the structures of the chelicerae to establish a coherent nomenclature for teeth and fang cusps.

Key Words

Biodiversity, Araneoidea, Systematics, Tetragnathinae

Introduction

The long-jawed spider genus *Tetragnatha* Latreille, 1804 (family Tetragnathidae) comprises 349 species, 67 of which restricted to the Neotropics (World Spider Catalog 2019). All species share spiny and elongate chelicerae, elongate and dorsally flattened carapace, parallel eye rows, and female genital openings located at the posterior end of the procurred epigastric furrow (Levi 1981; Gillespie 1992a, b; Barrion et al. 2011). Nonetheless, many species are poorly diagnosed at the taxonomic level and their geographic ranges are imperfectly known.

Although no complete revision is available for *Tetragnatha*, species redescriptions and local revisions are frequent. The first revisionary papers on the genus addressed species from North America (Seeley 1928) and Europe (Lendl 1886; Wiehle 1939, 1963). Chickering (1957a) reviewed the Central American and Mexican species, followed by those from Jamaica (Chickering 1957b); Panama (Chickering 1957c); United States and Canada (Levi 1981); Australasia (Okuma 1987), Asia (Okuma 1988a, b), Mexico, and part of the Neotropical region (Okuma 1992), Hawaii (Gillespie (1992a, b, 2003a); Marquesas Islands (Gillespie 2003b); and Society Islands (Gillespie 2003c)).

In this paper, we analyse most of the widespread species of *Tetragnatha* in the Neotropical region. We propose 20 new synonymies for five of them and include new records from South America for one species previously known from Asia and introduced in North and Central America. We also provide new diagnoses, illustrations, and many new distribution records. Furthermore, we consider two species from Argentina as nomina dubia.
Methods

The taxonomic summary for all species is abbreviated to save space, including only the information we consider most relevant. See the World Spider Catalog (2019) for a complete list of synonymies. Terminology for chelicerae follows Okuma (1987, 1992) and Gillespie (1992a, 1992b). For the male palp, see Levi (1981), and for the female genitalia, see Álvarez-Padilla and Hormiga (2011). Colour patterns were described based on specimens preserved in 75% ethanol.

Structures were cleaned using a Cristofoli Ultrasonic Cleaner and positioned in 70% ethanol gel or glass spheres for automontage photographs and measurements. Images were taken with a Leica DFC450 camera mounted on a Leica M205C stereo microscope (Leica Camera AG, Wetzlar, Germany) at the Laboratório de Entomologia, Universidade do Brasil/Universidade Federal do Rio de Janeiro. All images were edited with Adobe Photoshop CS5.1 and figures were prepared using Adobe Illustrator CS5.1 (Adobe Inc., San Jose, California, USA). Measurements are given in millimeters. The position of teeth and fang cusps (upward, downward, distalward, and basalward) was noted when the chelicerae were attached to the body. The genital fold length was measured from the inner angle of book-lung plates to the posterior rim of the fold. The genital fold proportion is the comparison of its length versus the span between the outer angle of posterior rim of one book-lung plate to the outer angle of the other. Males were matched with conspecific females by cheliceral morphology and collection sites.

For scanning electron microscopy (SEM), samples were critically point dried, mounted on adhesive copper tape (Electron Microscopy Sciences, EMS 77802), affixed to a stub and sputter-coated with Au-Pd for examination under high vacuum with a JEOL JSM-6510 microscope at Laboratório de Imagens, Instituto de Biologia, Universidade Federal do Rio de Janeiro; a Philips XL 30 Field Emission ESEM at the Centro de Microscopia e Microanalises, Pontifícia Universidade Católica do Rio Grande do Sul, and a JEOL JSM-6390LV at Centro de Microscopia, Fundação Oswaldo Cruz.

To clear female genitalia, we used a borax solution (Álvarez-Padilla and Hormiga 2008) and digestive enzyme tablets of “Orthoplex D.E.F” (Bioconcepts Pty Ltd, Banyo, Queensland, Australia). We noted that sometimes the internal genitalia may appear darker or lighter, after clearing, usually related to the time spent in the solution. For example, the spermathecae and central membranous sac may appear dark, roundish, and well defined (Fig. 2H) or pale and partially collapsed (Fig. 2I).

Maps were produced using QGIS v. 2.14 software and geographic coordinates were extracted from original labels. When no coordinates was available, the closest nearby area coordinates were obtained from Global Gazetteer v. 2.3 (http://www.fallingrain.com/world/index.html) or Google Earth v. 9.1.39.1 (https://earth.google.com/web/).

Cited institutions and their acronyms are:

- **AMNH**: American Museum of Natural History, USA (curator: L. Prendini);
- **CAS**: California Academy of Sciences, USA (L. Esposito);
- **IBSP**: Instituto Butantan, Brazil (A. Brescovit);
- **MACN**: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina (M. Ramirez);
- **MCTP**: Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Brazil (R. Teixeira);
- **MCZ**: Museum of Comparative Zoology, Harvard University, USA (G. Giribet);
- **MIZ**: Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Poland (W. Wawer);
- **MLP**: Museo de La Plata, Argentina (L. Pereira);
- **MLPC**: Mello-Leitão’s private collection, now at Museu Nacional, Universidade do Brasil/Universidade Federal do Rio de Janeiro, Brazil (A. Kury);
- **MNHN**: Musée National d’Histoire Naturelle, France (C. Rollard);
- **MNRJ**: Museu Nacional, Universidade do Brasil/Universidade Federal do Rio de Janeiro, Brazil (A. Kury);
- **MPEG**: Museu Paraense Emilio Goeldi, Brazil (A. Bonaldo);
- **MRAC**: Royal Museum for Central Africa, Belgium (D. Van den Spiegel);
- **MZUF**: Università di Firenze, Museo Zoologico “La Specola”, Italy (L. Bartolozzi);
- **MZUSP**: Museu de Zoologia da Universidade de São Paulo, Brazil (R. Pinto-da-Rocha);
- **NHM**: Natural History Museum, United Kingdom (J. Beccaloni);
- **NHMW**: Naturhistorisches Museum Wien, Austria (C. Hörweg);
- **NHRNS**: Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Sweden (J. Stigenberg);
- **NMB**: Naturhistorisches Museum Basel, Switzerland (A. Haenggi);
- **NMV**: Museums Victoria, Australia (K. Walker);
- **OUMNH**: Oxford University Museum of Natural History, United Kingdom (Z. Simmons);
- **SMF**: Senckenberg Museum Frankfurt, Germany (P. Jäger);
- **UFRJ**: Laboratório de Diversidade de Aracnideos, Universidade Federal do Rio de Janeiro, Brazil (R. Baptista);
- **USNM**: Smithsonian National Museum of Natural History, USA (J. Coddington);
- **ZMB**: Museum für Naturkunde, Humboldt-Universität, Germany (J. Dunlop);
- **ZMH**: Zoologisches Museum Hamburg, Germany (D. Harms).
Abbreviations used below for the chelicera:

a  male dorsal apophysis, used to lock the fangs of females during copulation.
Axi  auxiliary guide tooth of the lower row, present in some species.
Axd  auxiliary guide tooth of the upper row, above Gu, present in some species.
Bc  basal cusp on the cheliceral fang of females (new terminology). Okuma applied different names to this structure: exccrescence (1987) and posterior cusp (1992).
Cb  cheliceral bulge, a protruding area between the two rows of teeth, near the base of the fang (new terminology).
Crcl  cheliceral crest, a protruding marked area on the upper row of teeth (new terminology).
Crct  cheliceral crest, a protruding marked area on the lower row of teeth (new terminology).
GC  inner cusp of fang (follows Okuma 1987, 1992) (new abbreviation).
L2-n  teeth on the lower row numbered from the distal end after Gl.
OC  outer cusp of fang (present in some species) (new terminology).
Rs1  remaining proximal teeth on the upper row of males after T (Okuma 1987; Gillespie 1992a, 1992b).
Rs2  remaining proximal teeth on the lower row of males and females after the last specialized tooth (Okuma 1987).
Sl  first major tooth after Gu in the upper row of males (absent in some species).
T  a tooth or prominence found in males of some species.
U2-n  teeth on the upper row numbered from the distal end after Gu.

Abbreviations for male and female genitalia, male palps:

E  embolus;
C  conductor;
Y  cymbium;
P  paracymbium
K  knob at the ectal side of paracymbium (new terminology).
L  translucent lobe at the mesal side of paracymbium,
N  notch at the apex of paracymbium.

Female genitalia:

GF  genitral fold;
Sp  spermatheca;
CS  central membranous sac.

Results

Order Araneae Clerck, 1757
Family Tetragnathidae Menge, 1866
Genus Tetragnatha Latreille, 1804

Tetragnatha bogotensis Keyserling, 1865
Figs 1–4, 20A, 21A–G, 22A

Tetragnatha bogotensis Keyserling 1865: 854, pl. 21, fig. 5 (♀). Tetragnatha andina Taczanowski 1878: 144, pl. 1, fig. 2 (♀); Levi 1981: 291 (removed from syn. with T. nitens) syn nov.
Tetragnatha boydi O. Pickard-Cambridge 1898: 389, pl. 31, fig. 4 (♀) syn nov.

Tetragnatha bozogen Banks 1898: 246, pl. 15, fig. 12 (♂); Levi (1981): 291 (removed from syn. with T. nitens) syn nov.
Tetragnatha praedator Tullgren 1910: 147, pl. 3, fig. 69 (♂)
Tetragnatha mandibulata bidentata Gravely 1921: 442, fig. 3c, f (♀). Tetragnatha eremita Chamberlin 1924: 645, figs 89, 90 (♂); Levi 1981: 292 (removed from syn. with T. nitens) syn nov.
Tetragnatha nitens Lawrence 1927: 27, pl. 3, fig. 61, pl. 4, fig. 77 (♀) misidentified.
Tetragnatha bencalco Mello-Leitão 1939: 67, figs 42–44 (♀) syn nov.
Tetragnatha ramboi Mello-Leitão 1943: 193, fig. 24, 24a, b (♀) syn nov.
Tetragnatha haitiensis Bryant 1945: 408, fig. 37 (♀); Levi 1981: 292 (removed from syn. with T. nitens) syn nov.
Tetragnatha nitens Kilimandjaro and Meru, examined (photos).
Tetragnatha praedator Schmidt and Krause 1993: 6, fig. 5 (♀) syn nov.

Figure 1. *Tetragnatha bogotensis* Keyserling, 1865, male (UFRJ 0035). A. Dorsal habitus; B. Ventral habitus; C. Chelicerae upper row and eyes; D. Chelicerae lower row and maxilla; E–H. Left chelicera: E. Upper view; F. Inner view; G. Lower view; H. Outer view; I–K. Left male palp: I. Mesal view; J. Dorsal view; K. Ventral view (paracymbium). Scale bars: 2 mm (A, B); 1 mm (C, D, E, F, G, H); 0.5 mm (I, J, K).
Keyserling (1865) described this species in *Tetragnatha nitens* (Audouin, 1826) and share chelicerae with an elongated ‘a’, and AXu and ‘t’ extremely elongated and distally bent. AXu and ‘t’ differ as follows: thick and triangular in *T. bogotensis* (Figs 1C, E, F, 3B), but thinner and ‘t’ sickle-like in *T. nitens* (Figs 14C, D, F, 16A). Gu longer, sharper, straight and larger than U2 in *T. bogotensis* (Figs 1C, E, F, 3B) while it is shorter than U2 and slightly curved downward in *T. nitens* (Figs 14C, D, 16A). Palps share medium-sized conductors without pleats (Figs 11, 3A, 14G, 15D, E). *Tetragnatha bogotensis* palps differ by shorter tibiae (ca 3× longer than wide) (Figs 11–K, 3A), conductors not twisted at their distal halves, with completely folded apexes enclosing the emboli tips (Figs 11, J; 3A, E; 20A) and longer paracymata, overreaching the upper border of tegulae, each bearing deeper notch, resulting in an elongated tip of the paracymbium proper, and thinner and relatively narrow translucent lobe (Figs 11, K; 3D). In *T. nitens*, palps have longer and thinner tibiae (almost 4× longer than wide) (Figs 14G–I, 16E), conductors twisted in distal half with their apexes rounded and excavated, exposing the emboli tips (Figs 14G, H, 16D–F, 20E) and shorter paracymata that do not reach the upper border of tegulae, with expanded and very wide translucent lobes (Figs 14I, J, 16F). The epipandial field is straight, with 19 fusules, in *T. bogotensis* (Fig. 3F) but arched and smaller, with only 15 fusules, in *T. nitens* (Fig. 16C).

Females are similar to *T. nitens* and also *T. mandibulata* Walckenaer, 1841, sharing: bulky body, wide and pointed at the terminal end (Figs 2A, B, 12A–C, 15A, B), and elongate genital fold (Figs 2G, 12H, 15I). Their chelicerae also bear an evident basal cusp (BC) in the fang (Figs 2D, E, 12D–G, 13C, D, 15D, F–I, 16B), Gu elongated and not contiguous to U2 (Figs 2C, D, 12D, E, 13C, 15C, E, F, 16B); Gl large and pointed distally, followed by smaller L2 and L3 (Figs 2D, E, 3C, 12E, F, 13D, 15D, F, H, 16B). *T. bogotensis* and *T. mandibulata* differ from *T. nitens* by distinct bulky AXi, which are elongated, pointed and with large bases, clearly visible and overreaching the claws even in upper view (Figs 2C–F, 3C, 12D–G, 13C, D), while in *T. nitens* it is short and not pointed (Figs 15F–H, 16B). *T. bogotensis* and *T. mandibulata* also differ by the conspicuous bulge (CB) in the area between both rows (Figs 2C, E, 3C, 12D, F, 13C, D), which is absent in *T. nitens*. *Tetragnatha bogotensis* chelicerae can be distinguished from *T. mandibulata* by the following characters: more robust basal cusp (BC), placed at the middle line of the lower side of the claw, compared to a smaller BC, displaced towards the outer face of the claw (Figs 2D, E, 3C–F, 12D–G, 13C, D). Gu straight with a large basis, being separated from U2 by a wide and deep furrow, versus both teeth not quite spaced (Figs 2C, D, 3C, 12D, E, 13C); AXI bulkier, with much larger basis, compared to a thinner and shorter tooth (Figs 2C–F, 3C, 12D–G, 13C, D); Gl shorter, straight and pointed, with wider basis, and much smaller than AXI, versus a longer and slanted GI, regularly tapered and just a bit smaller than AXI (Figs 2D, E, 12E, F, 13D); and CB rounded and wide, extending from a bit above L2 to L3, and placed in the middle line between both rows of teeth, contrasting to a smaller and lower CB, extending from the basis of GI to the middle of the gap between L2 and L3, and adjoined to the basis of L2 (Figs 2C, E, 3C, 12D, F, 13C, D). In *T. nitens*, BC is placed at a similar position to *T. bogotensis*, but is larger (Figs 15D, F–I, 16B) and Gu is connected to U2 by a thin and dark ridge, with a gap of similar size to *T. bogotensis* (Figs 15C, E, F, 16B). The genital fold (Figs 2G, 12H, 15J) is similar in all three species but shorter in *T. nitens* (genital fold length around 0.6× the width), intermediate in *T. bogotensis* (0.8×) and longer in *T. mandibulata* (1.1×). The internal genitalia of *T. bogotensis* is more similar to *T. mandibulata*, with medium-sized spermathecae and a sclerotized and rounded fundus (Figs 2H, I, 12I), in contrast to wider spermathecae without a well-defined fundus in *T. nitens* (Fig. 15K, L). The central membranous sac (CS) of *T. bogotensis* is medium-sized, with almost the same size of the spermathecae, and placed at the same level of their bases (Fig. 2H, I), while in *T. mandibulata* it is massive, longer, and placed at the same level as the spermathecae (Fig. 12I). In *T. nitens*, the CS is about the same size as in *T. bogotensis*, but with a stalk of variable size, sometimes longer than the spermathecae, placing the apical portion of the CS at the same level or anteriorly to the spermathecae (Fig. 15K, L).

**Synonymy and notes.** Keyserling (1865) described this species based on female specimens from “Nova Granada”, which encompasses a large area ranging from Panama to Ecuador, and which were collected by Alexander Lindig, who gathered many animals and plants in Bogotá (Colombia) from 1859 to 1863 (Meagher 2012). Therefore, the type specimens were most likely collected, at least partially, in this city, as indicated by the name *T. bogotensis*. The drawing of one female by Keyserling (1865: pl. 21, fig. 5) allows the recognition of the species by showing the long and robust AXI placed near to a smaller and traverse GI of the right chelicera. In the original description, Keyserling wrote that he had “many copies in my collection”, without citation of any males (Keyserling 1865: 855).

The first author of this paper visited three collections with type material by Keyserling: MIZ; NHM (Beccaloni 2012), and ZMB (Kretschmann 2006), and we also contacted curators of NHMW and USNM. Possible well-preserved type specimens were found in two vials at only the NHM. In the first vial (Fig. 4A), there were three females labeled “type” and originated from “Taquara” (originally “Taquara do Mundo Novo”, state of Rio Grande do Sul, Brazil). In the second vial (Fig. 4B), there were two females and one male labeled “Bogotá”, but with no clear indication as type. All five females from both vials are *T. bogotensis* but the male from Bogotá belongs to *T. nitens*. 


Figure 2. Tetragnatha bogotensis Keyserling, 1865, female. A. Dorsal habitus (UFRJ 1314); B. Lateral habitus (UFRJ 1314); C–F. Left chelicera (UFRJ 1314): C. Upper view; D. Inner view; E. Lower view; F. Outer view; G–I. Genital area: G. Genital fold, ventral view (MCTP 3381); H. Internal genitalia, cleared, ventral view (UFRJ 1314); I. Internal genitalia, cleared, ventral view (MCTP 13581). Scale bars: 2 mm (A, B); 1 mm (C, D, E, F, G); 0.2 mm (H); 0.1 mm (I).
Figure 3. *Tetragnatha bogotensis* Keyserling, 1865, SEM photos. **A.** Left male palp, mesal view (MCTP 4299); **B.** Left male chelicera, upper view (MCTP 4299); **C.** Left female chelicera, upper view (MCTP 4299); **D.** Left male palp paracymbium, ventral view (UFRJ 0044); **E.** Left palp conductor detail, mesal view (MCTP 4299); **F.** Epiandrous field, ventral view (UFRJ 0044). Scale bars: 0.2 mm (**A**); 0.5 mm (**B, C**); 0.1 mm (**D**); 0.05 mm (**E**); 0.02 mm (**F**).
We consider Keyserling’s syntypes to be lost, as there is no clear indication that the specimens above were used to describe the species: females from Taquara are not syntypes because Keyserling had not cited any specimens from that Brazilian locality, and females from Bogotá are also not syntypes as they were not labeled as type or “N. Grana-da” and are kept in the same vial as the additional male. Therefore, the confirmation of the identity of Keyserling’s species relies on the illustration in the original description and the fact that specimens collected in Bogotá and other cities from Colombia clearly display the key cheliceral teeth characters that allow the diagnosis of *T. bogotensis*. 

*Tetragnatha boydi* has been redescribed and illustrated many times (see World Spider Catalog 2019). Pickard-Cambridge (1898) described this species based on a female from Socotra (Yemen), giving detailed illustrations of the lower and inner views of the chelicerae (Pickard-Cambridge 1898: fig. 4a, b). Males were first described as *T. praedator* Tullgren, 1910 from Kenya, a species considered junior synonym afterwards (see below). Unfortunately, the female type material was not located at NHM or in OUMNH, institutions where O. Pickard-Cambridge normally deposited his specimens, and remains lost. Lawrence (1927) (sub *T. nitens*) and Okuma (1983) were the first authors to correctly match both sexes in their papers. Lawrence (1927) gave very detailed illustrations of the male left palp and chelicera, clearly showing the diagnostic characters of this species. On the other hand, the females were not illustrated, but his description points to the “inferior margin with a large apical tooth” (Lawrence 1927: 28), thereby rejecting the identification as *T. nitens*. Okuma (1983) also correctly matched the couples, gave very detailed drawings of chelicerae and genitalia, synonymised *T. mandibulata bidentata* and *T. nitens kullmanni* with *T. boydi*, and gave the first records for Brazil. Later, Okuma (1992) also provided new drawings of the species. After examining illustrations by Keyserling (1865: pl. 21, fig. 5), the NHM specimens of *T. bogotensis* from the type locality (Bogotá), and making comparisons with O. Pickard-Cambridge’s (1898) illustrations and the later illustrations by Tullgren (1910), Lawrence (1927), and Okuma (1983, 1992), we conclude that all specimens belong to the same common species and establish that *T. boydi* is a junior synonym of *T. bogotensis*.

*Tetragnatha praedator* Tullgren (1910: fig. 69a, b) was described from four male specimens from Kilimandjaro and Meru (Kenya). Lessert (1915) also cited males of *T. praedator*, and the species was later synonymised with *T. boydi* by Roewer (1942). Finally, it was treated as a subspecies of *T. boydi* by Schmidt and Krause (1993), who also described females from Comoros Island, forming the combination *T. boydi praedator* Tullgren, 1910. After comparing Tullgren’s (1910) illustrations and photos of the syntypes we received (Fig. 21C) with the specimens we identified as *T. bogotensis*, we observed that they clearly match. Thus, *T. boydi praedator* is synonymised here with *T. bogotensis*. On the other hand, the females assigned to *T. boydi praedator* by Schmidt and Krause (1993: fig. 5) probably belong to a different species judging by their illustrations, which are, however, too poor to allow a proper evaluation.

*Tetragnatha bemalcuei* was described by Mello-Leitão (1939: 68, figs 42–44), who mentioned on the original description “a robust conical forward apophysis” (AXI) on the lower row of the chelicerae. We examined detailed images of the holotype (NMB) that show the characters of *T. bogotensis* (Figs 4D, 21E) and establish *T. bemalcuei* as a junior synonym of *T. bogotensis* Keyserling, 1865.

Mello-Leitão (1943) described *T. ramboi* based on males and females from Rio Grande do Sul, south Brazil. He indicated the vial MNJR 42467 as “tipo” (type in Portuguese) in the description, but did not label it as “typus”, in contrast to his common practice (Fig. 4C). We examined the type series (one male, two females, and one immature specimen) and agree with Silva-Moreira et al. (2010) that the whole series of specimens should be treated as syntypes. In the original description, the male was cited first and its diagnostic chelicerae and palps were illustrated (Mello-Leitão 1943: fig. 24a, b), whereas only the habitus of the female was illustrated (Mello-Leitão 1943: fig. 24). Under the rule of the “First Reviser” (ICZN 1999, article 24), we consider the sequence of descriptions and the presence of diagnostic illustrations in establishing the male as the lectotype of the species. This male clearly belongs to *T. bogotensis* according to the chelicerae and palp diagnostic characters (Figs 1C, E, J, 3A, B, E, 20A, 21F; Mello-Leitão 1943: fig. 24b) and must be newly synonymised with this species. Finally, we consider the male and juveniles of the type series of *T. ramboi* as misidentified specimens of *T. argentinensis* Mello-Leitão, 1931 which were erroneously attributed to *T. ramboi*.

We also note that several species previously considered junior synonyms of *T. nitens* should be newly synonymised with *T. bogotensis*. For example, Levi (1981: 291, 292) established 13 junior synonyms of *T. nitens*. Indeed, most of those species are correctly junior synonyms of it, but at least four should now be regarded as junior synonyms of *T. bogotensis* (see *T. nitens* below). It also seems that Levi (1981: figs 23–29) matched males of *T. nitens* with at least some females of *T. bogotensis*, as it is evident by the female illustrations he gave. These clearly depict the large AXI of *T. bogotensis* (Levi 1981: figs 23–25) and similar genitalia (Levi 1981: figs 26–29), with a pattern very different from *T. nitens* (Fig. 15K, L, Zhu and Zhang 2011: fig. 125G). In the “Variation” and “Diagnosis” sections of his paper, Levi (1981: 292) pointed out “On Panamanian specimens the diagnostic tooth at the posterior base of the Fang is as long as the chelicerae are wide, and is sometimes smaller than illustrated on the most northern specimens” and “The female chelicerae have a large posterior lateral tooth at the insertion of the Fang”. Unfortunately, he did not provide the collection site for the female specimen he illustrated, and although there is no formal record for *T. bogotensis* or any of its synonyms from the United States, at least some of the females from the southern USA cited as *T. nitens* may belong to that species instead.

and female syntypes from Amable Maria, Peru, however, Taczanowski’s (1878: fig. 2) poor illustration of the female chelicerae allows its recognition as T. bogotensis, as verified in the photos we received from MIZ (Fig. 21A). Thus, T. andina is here removed from the synonymy of T. nitens and newly synonymised with T. bogotensis.

Banks (1898) described T. peninsulana from two males and “several females” from San José del Cabo, Baja California Sur, Mexico. Photos of females provided by the MCZ (Fig. 21B) include three specimens of T. bogotensis and one of T. nitens, which we consider a misidentification. Additionally, according to Levi (1981), the male syntypes were destroyed. Based on the elongated AXl (Fig. 21B), this species must also be removed from the synonymy of T. nitens and be newly synonymised with T. bogotensis.

Tetragnatha eremita Chamberlin, 1924 was based on a male holotype from Baja California, Mexico. Chamberlin (1924: figs 89, 90) provided a short description and two good illustrations that clearly show the characteristic shape and teeth formula of T. bogotensis, besides citing a female paratype collected at the same time. The male holotype is represented by the right pedipalp in the MCZ (MCZ 15283, RVC 1111), and by the whole specimen in CAS 1430. We were able to examine the holotype’s chelicerae through photos (Fig. 21D), and thus confirmed its identity, removing T. eremita from the synonymy with T. nitens and newly synonymising it with T. bogotensis.

Furthermore, Levi (1981: 292) followed Chickering (1957b: 2) in the synonymization of T. haitiensis Bryant, 1945, which was based on a female from Haiti, with T. nitens. Bryant (1945: fig. 37) illustrated the huge AXI tooth typical of T. bogotensis, which we also observed in the photos we received from MCZ (Fig. 21G). Therefore, T. haitiensis Bryant, 1945 is also removed from the synonymy of T. nitens and newly synonymised with T. bogotensis.

Wunderlich (1992: 365) also mistook T. bogotensis as T. nitens, removing T. nitens kullmanni from its proper synonymy with T. boydi (Okuma 1983: 70). We agree with Okuma (1983) that this species is “undoubtedly identical with T. boydi”, as both males and females of T. nitens kullmanni bear the same diagnostic characters of T. bogotensis in comparison with T. nitens: male chelicerae with Gu longer than U2 (Figs 1E, 3B; Wiehle 1962: fig. 9) and female chelicerae with a long AXl (Figs 2D–F, 3C; Wiehle 1962: fig. 15). Therefore, the synonymy with T. nitens is rejected and T. nitens kullmanni is a junior synonym of T. bogotensis.

Variation. Males (n = 18): total length, 7.36–11.60; females (n = 17): total length, 7.52–11.76. The gap between Gu and U2 is variable in males of this species and can have almost the double of the length of the specimen illustrated.

Distribution. This species is widespread in the Neotropics and Mexico, but potentially north into the southern United States; it also occurs in the Old World, with records from Africa, Yemen, India, Nepal, and China (Fig. 22A).

Tetragnatha elongata Walckenaer, 1841
Figs 5–7, 20B, 22B

Tetragnatha elongata Walckenaer 1841: 211 (♂ ♀).
Tetragnatha tropica O. Pickard-Cambridge 1889: 11, pl. 2, fig. 3 (♀); F. O. Pickard-Cambridge 1903: 431, pl. 40, figs 10, 11 (♂ ♀) syn. nov.

Type material. Tetragnatha elongata: GUADELOUPE: ♀ ♂ syntypes, lost; UNITED STATES OF AMERICA: ♀ neotype, Raleigh, North Carolina (Coll. C. S. Brimley, 21–31.vii.1944, MCZ 21192), not examined. Tetragna-
Figure 5. Tetragnatha elongata Walckenaer, 1841, male (MCTP 28045). A. Dorsal habitus; B. Lateral habitus; C. Ventral habitus; D–G. Left chelicera: D. Upper view; E. Inner view; F. Lower view; G. Outer view; H–K. Left male palp: H. Mesal view with tibia; I. Mesal view detail; J. Dorsal view; K. Ventral view (paracymbium). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G, H); 0.5 mm (I, J, K).
Figure 6. *Tetragnatha elongata* Walckenaer, 1841, female. A. Dorsal habitus (MCTP 28045); B. Lateral habitus (MCTP 28045); C–F. Left chelicera (MCTP 28045): C. Upper view; D. Inner view; E. Lower view; F. Outer view; G, H. Genital area: G. Genital fold, ventral view (MCTP 28045); H. Internal genitalia, cleared, ventral view (MCTP 28306). Scale bars: 5 mm (A, B); 1 mm (C, D, E, F); 0.5 mm (G); 0.2 mm (H).
**Extended diagnosis.** Females of *T. elongata* can be distinguished from all other Neotropical species by their elongated body, abdomen anteriorly enlarged and much narrower posteriorly, large chelicerae with an outer cusp (OC), and a short genital fold (Figs 6A–G, 7B). The unique internal genitalia has large spermathecae with two thick tubular lobes connected mid-way, forming a kidney-shaped structure, with the median lobe more than twice as long as its width and parallel to each other and to the longitudinal axis of the abdomen (Fig. 6H). The lateral lobe is smaller and thinner than the median lobe and may vary in position, with the fundus directed dorsally (Fig. 6H) or laterally (Levi 1981: fig. 76). Central membranous sac (CS) is small and poorly sclerotized (Fig. 6H; Levi 1981: fig. 76).

Male chelicerae of *T. elongata* are similar to those of *T. laboriosa* Hentz, 1850, insofar as sharing elongated apophyses with excavated tips, elongated and robust ‘T’, and long Gl, the last as the longest teeth of both lower rows (Figs 5D–G; Okuma 1992: fig. 11A–C). *Tetragnatha*...
Tetragnatha mandibulata: L. Koch 1872: 194, pl. 17, figs 2a, b, 3a, b (♀ Misidentified).
Tetragnatha keyserlingi Simon 1890: 134 (♀ ♂).
Tetragnatha mandibulata: Thorell 1890: 221 (♀ misidentified)
Tetragnatha maxillosa Thorell 1895: 139 (♀ ♂) syn. nov.
Tetragnatha kochi Thorell 1895: 140 (♀ ♂) syn. nov.
Tetragnatha japonica Bösenberg and Strand 1906: 177, pl. 15, fig. 409a-d (♀ ♂).
Tetragnatha conformans Chamberlin 1924: 9, pl. 2, figs 13–15 (♀ ♂).
Tetragnatha propioides Schenkel 1936: 89, fig. 31 (♀ ♂).
Tetragnatha ethodon Chamberlin and Ivie 1936: 64, pl. 17, figs 144–146 (♀ ♂) syn. nov.


Extended diagnosis. Males of T. keyserlingi are similar to T. elongata. Both species have a long body, a very long paturon, AXI and GI placed on a common base and displaced to a lower position than the remaining lower teeth, and conductor tips not extended in tail-like projections (Figs 5A–J, 7A, C–E, 20B). Palps of both species are similar by having pairs of black dots on the posterior-dorsal region of the abdomen, a′ placed closer to the external border of the paturon and directed upwards and outwards, t′ present, s′ absent, a crest filling the gap from Gu to ‘T’, a large gap between ‘T’ and ‘rsu’, lower teeth onwards from L3 placed in a shallow concave row (Figs 5A–E, 7A, 8A–E, 10A). Palps of both species are also similar, but those of T. keyserlingi have shorter and wider tibias (2.3× vs 4.7×), conductors with one pleat that only partially enfold the ribbon-like and twisted emboli, and paracymbia that are elongated, boomerang-shaped with slanted, basally projecting knobs and clearly visible translucent lobes (Figs 8H–J, 10C–E, 20C). The epandrial field has a spinning area which is not as high and with undivided notches, narrow, thin translucent lobes, and thumb-like projecting knobs (Figs 5K, 7C, F).

Female chelicerae have elongated Gu, U2, and U3, where Gu is set apart from U2 by a very large gap and is lo-

Tetragnatha tropica was described from a single female from Guatemala (Menché, currently Atxchilan, near the Mexican border), not located in NHM or OUMNH collections. Thus, we rely on the original illustrations and subsequent descriptions of both sexes to diagnose this species (O. Pickard-Cambridge 1889: pl. 2, fig. 3; F. O. Pickard-Cambridge 1903: pl. 40, figs 10, 11; Chickering 1957c: figs 97–102). We compared these illustrations with our specimens and the drawings of both sexes and SEM images of the conductor tip of T. elongata by Levi (1981), who proposed a neotype for this species (MCZ 21192) and identified many specimens from northern Mexico, and with Okuma (1992), who identified specimens from Mexico, Costa Rica, and Panama. Based on our investigations, T. tropica can be diagnosed as a junior synonym of T. elongata because the morphology of male palps and the chelicerae of both sexes perfectly match.

We also highlight that Mello-Leitão (1943, 1945, 1947, 1949) repeatedly recorded T. elongata from Brazil and Argentina, but all his specimens we analysed belong to other common species, especially T. bogotensis and T. nitens. However, after analyzing many other specimens, we were able to confidently record this species for these two countries.

Variation. Males (n = 8): total length, 7.20–13.45; females (n = 15): total length, 8.88–13.90.

Distribution. Tetragnatha elongata is a very common species in the Nearctic and Neotropical regions, recorded from Canada (Dondale et al. 2003) to Misiones, northeastern Argentina (Fig. 22B).

Tetragnatha keyserlingi Simon, 1890
Figs 8–10, 20C, 21H, I, L, M, O, 22C

Tetragnatha mandibulata: Keyserling 1865: 848, pl. 21, figs 6–9 (♀ ♂ misidentified).
ated on an upper crest (CRu) (Figs 9D, E, 10B). U2 and remaining upper side teeth form a row displaced to lower side of paturon, following the slanted fangs closing (Figs 9D, E, 10B). AXl very small and located near Gl base and lower row with first three teeth on a lower crest (CRI); Gl straight, elongated, bulky, pointed, its base large, and projected slightly upwards (Fig. 9E, F). Cheliceral fang enlarged in middle portion and apical third slanted and tapering to the acute tip, also harboring a narrow ridge (Figs 9D, E, 10B). Internal genitalia unique, with two rounded spermathecae linked by two thick tubes to a median, slender and very elongated stalk, which places CS at a far anterior position (Fig. 9I; Zhu and Zhang 2011, sub T. maxillosa: fig. 123G).

**Synonymy and notes.** This species is widespread in the Old World tropics and has been cited and illustrated many times under *T. maxillosa* (World Spider Catalog 2019), especially by Okuma (1983, 1987) and Zhu and Zhang (2011).

*Tetragnatha keyserlingi* was named by Simon (1890: 134) for the specimens described and illustrated as *T. mandibulata* by Keyserling (1865: 848, pl. 21, figs 6–9) from “Neu Granada” (currently Colombia) and *T. mandibulata*? by L. Koch (1872: 194, pl. 2, figs 2, 3) from Fiji (Ovalau), Samoa (Upolu), and Tonga in the Pacific. The illustrations by Keyserling (1865) and L. Koch (1872) already clearly show, for example, the large ‘T’ and small ‘t’ in male chelicerae and the characteristic Gu and Gl of the female chelicerae of *T. keyserlingi* (Figs 8D, E, G, 9D–F, 10A, B).

*Tetragnatha keyserlingi* was also recorded from Java (Indonesia) (Thorell 1890: 221) and in his paper on Burmese spiders, Thorell (1895: 139) newly named this species as *T. maxillosa*, based on the female from Java he described in 1890 and on males and females from Singapore collected by C. Workman: he pointed out that he considered *T. maxillosa* to be distinct from *T. keyserlingi*. One page later, he (Thorell 1895: 140) named the specimens reported by L. Koch (1872) from the Pacific islands as another new species: *T. kochi*, heavily relying on geographical distributions to separate the specimens from South America, Southeast Asia, and the Pacific Islands. The only morphological differences mentioned in his paper (Thorell 1895: 139–140) are minor details in eye position and cheliceral teeth arrangement in females; no male characters were mentioned. In particular for *T. maxillosa* and *T. keyserlingi*, he compared the position of the second tooth on upper row of female chelicerae (U2 in our terminology) in relation to teeth of the lower row. According to Thorell, U2 of *T. maxillosa* would face the 6th or 7th tooth of the lower row, while in *T. keyserlingi* it would face the 4th or 5th tooth. However, the apparent position of teeth of one row in relation to the teeth of the opposite row is not easy to evaluate, as small changes on chelicerae inclination may change the apparent alignment. In addition, small changes in the relative position of teeth of the upper and lower rows are very common in this and other species.

We agree with Simon (1890) that the detailed illustrations given by Keyserling (1865) from “Neu Granada”, and L. Koch (1872), from Pacific Islands (Fig. 21H), allow the clear recognition of just one species, despite the great distances between localities. Moreover, the specimens from Southeast Asia that Thorell (1895) named *T. maxillosa* also belong to the same widespread species. As Simon (1890) and Thorell (1895) had never seen the specimens they named as new species, no type specimens have ever been designated. No type or non-type material from the type localities of *T. keyserlingi* or *T. maxillosa* could be located in NHM, NMV, and ZMH. However, we received photos of two females from Upolu, collected in 1869 and deposited at NHRS, both identified as *T. mandibulata* (labeled Museum Godeffroy, NIHRS-GU-L1000069809). These specimens are surely part of the material which L. Koch (1872) designated and illustrated as “*T. mandibulata*?” (Fig. 21H) and Thorell (1895) afterwards named *T. kochi*. Thus, these specimens represent part of the type series of *T. kochi*. As *T. keyserlingi* Simon, 1890 was proposed five years before both Thorell’s names (1895), it is senior synonym of *T. maxillosa* and *T. kochi*.

Bösenberg and Strand (1906: 177, pl. 15, fig. 409a–d) provided comprehensive illustrations of male and female chelicerae and genitalia of *T. japonica*. Based on photos of the chelicerae of syntypes of both sexes from Osaka (Japan) deposited at ZMH (Fig. 211–K), we confirm that the female is *T. keyserlingi* (Fig. 21I) and that the male actually belongs to *T. nigrita* Lendl, 1866 (Fig. 21J, K). Nonetheless, the illustrations of the male by Bösenberg and Strand (1906: fig. 409c, d) are like *T. keyserlingi*, with a laterally directed apophysis, large Gu, absent or not noticeable ‘t’, and apical portion of embolus and conductor curved in a gentle slope. Thus, we consider that at least the originally illustrated male syntype belongs to *T. keyserlingi* and that it may be deposited in SMF instead. The female specimen of *T. japonica* should be considered as name bearing, as it was described, measured, and illustrated first by Bösenberg and Strand (1906: fig. 409a, b). We agree here with Okuma’s synonymy (1983) of *T. japonica* with *T. maxillosa* (= *T. keyserlingi*) and consider the male syntype from Bamburg and any other possible similar male syntype as misidentified specimens of *T. nigrita*. Unfortunately, we were not able to examine the syntypes from Saga deposited in SMF.

Chamberlin (1924: 12, pl. 3, figs 21–23) described *T. conformans* (Fig. 21L, M) and *T. cliens* Chamberlin, 1924 (Fig. 21N–Q), each based on a couple from Suzhou [Soochow on the labels (Fig. 21P, Q), but Kuliang (Fuzhou) in the original paper], China. Later, Schenkel (1936: 89–91, fig. 31) described *T. propiioides* based on a couple from Sichuan, also in China. All were separately synonymised with *T. keyserlingi* (under *T. maxillosa* or its junior synonyms): Zhu (1983) for *T. conformans* (sub *T. japonica*) and Okuma (1983: 72, 73) for *T. japonica*, *T. cliens*, and *T. propiioides*.

Another mismatching of *T. keyserlingi* and *T. nigrita* occurred with the type series of *T. cliens*, as observed by Song (1988: 127), who removed *T. cliens* from the synonymy with *T. maxillosa*. The male holotype of *T. cliens*
Figure 8. *Tetragnatha keyserlingi* Simon, 1890, male (UFRJ 1553). A. Dorsal habitus; B. Lateral habitus; C. Ventral habitus; D–G. Left chelicera: D. Upper view; E. Inner view; F. Lower view; G. Outer view; H–J. Left male palp: H. Mesal view; I. Dorsal view; J. Ventral view (paracymbium). Scale bars: 2 mm (A, B, C); 0.5 mm (D, E, F, G); 0.2 mm (H, I, J).
Figure 9. Tetragnatha keyserlingi Simon, 1890, female. A. Dorsal habitus (UFRJ 1351); B. Lateral habitus (UFRJ 1351); C. Ventral habitus (UFRJ 1351); D–G. Left chelicera (MCTP 14749): D. Upper view; E. Inner view; F. Lower view; G. Outer view; H, I. Genital area: H. Genital fold, ventral view (MCTP 14749); I. Internal genitalia, cleared, ventral view (UFRJ 1504). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G); 0.5 mm (H); 0.1 mm (I).
is clearly *T. nigrita* and was wrongly coupled with the female, which belongs to *T. keyserlingi* (Fig. 21N, O). Song (1988) noted that the male was labeled as “type” and the female as “paratype” in the original vials in USNM (Fig. 21P, Q). Like Song (1988), we were also able to analyse the type material and agree with the synonymy. Nonetheless, this mismatching was not noticed by Oku-

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**Figure 10.** *Tetragnatha keyserlingi* Simon, 1890, SEM photos. A. Left male chelicera, upper and lower views (MCTP 43319 ex 6944); B. Left female chelicera, upper and lower view (MCTP 14749); C. Left male palp, mesal view (MCTP 43319 ex 6944); D. Left palp conductor tip, mesal view (UFRJ 1552); E. Left male palp paracymbium, ventral view (UFRJ 1552); F. Epiandrous field, ventral view (MCTP 43319 ex 6944). Scale bars: 0.5 mm (A, B); 0.1 mm (C, E); 0.02 mm (D); 0.05 mm (F).
type photos we received. Additionally, we also confirm the synonymy of *T. propioides* (see Schenkel 1936: fig. 31), but its syntypes were not located.

Finally, *T. ethodon* was described by Chamberlin and Ivie (1936: pl. 17, figs 144–146) based on specimens from both sexes collected in Panama. This species was redescribed by Chickering (1957c: 316, figs 27–31) who transferred Chamberlin and Ivie’s females to *T. tenensisima* O. Pickard-Cambridge, 1889 and pointed out that the rather damaged male holotype was the only known specimen of the species from Panama. Okuma (1992: 228, fig. 7) also redescribed and illustrated *T. ethodon*, expanding its distribution to Puerto Rico and Barbados and adding a new description for females. She pointed out that this species was very similar to *T. maxillosa* (= *T. keyserlingi*) and separated both species by its wider genital fold. Comparing our specimens with previous illustrations under *T. maxillosa*, we consider the differences pointed out by Okuma (1992) to fall within the observed intraspecific variations, and hereby synonymise *T. ethodon* with *T. keyserlingi*.

**Variation.** Males (*n* = 11): total length, 5.29–7.28; females (*n* = 14): total length, 6.59–9.03. In Okuma (1968 sub *T. japonica*, 1983, 1992 under *T. ethodon*) and Bösenberg and Strand (1906 under *T. japonica*: fig. 409a), there is no visible upper crest (CRu) or lower crest (CRI). In fact, female syntypes of *T. kochi* (Fig. 21K), the paratype of *T. ciens* and holotype of *T. conformans* (Fig. 21M, O) do not have crests on the patumon. In contrast, other publications (e.g. Okuma 1987, 1988b, Zhu and Zhang 2011), the female syntype of *T. japonica* from Osaka (Fig. 21I), and all female specimens we examined from South America clearly possess CRu and CRI. So far, we cannot disregard the possibility that the absence of crests in some of the illustrated specimens is real or simply an artefact of poor illustration.

**Distribution.** Pantropical, including Africa, Asia, Polynesia, Central America, and Brazil (Fig. 22C).

*Tetragnatha mandibulata* Walckenaer, 1841

Figs 11–13, 20D; 21R–X, 22D

*Tetragnatha mandibulata* Walckenaer 1841: 211 (♀ ♂).  
*Tetragnatha confrentera* Banks 1909: 207, pl. 6, fig. 34 (♀ ♂) syn. nov.  
*Tetragnatha necatoria* Tullgren 1910: 149, pl. 3, fig. 72 (♂) syn. nov.  
*Tetragnatha petrunkevichii* Caporiacco 1947: 24 (♀ ♂) syn. nov.  
*Tetragnatha petrunkevichii* Caporiacco 1948: 646 (♀).  
*Tetragnatha infascata* Benoit 1978: 667, fig. 2D, E (♂); Saaristo 2003: 23, figs 21A, B, 25 (removed from syn. with *T. boydi*) syn. nov.


**Diagnosis.** For females, see the extended diagnosis of *T. bogotensis*. Males can be distinguished by the elongated body (Fig. 11A–C), chelicerae with pointed undivided apophyses (Figs 11D–G, 13A), Gu extremely distinctive, thick, bulky and distally projected, followed by a tiny U2, contiguous to Gu (Figs 11D, E, 13A), two very small and almost connected AX1 and GI (Figs 11E, F, 13B) and palps with shorter tibias (ca 3× longer than large); conductor tips projected, large, flattened and winglet-shaped (Figs 11H–J, 13F, 20D) and paracymbia with divided notches and large membranous translucent lobes that constitute the mesal halves of the notches, as in *T. bogotensis* and *T. nitens* (Figs 1K, 3D, 11K, 13E, G, 14I, J, 16D–F). Differing from *T. bogotensis*, the translucent lobes of the other two species fill more than half of the total width of the paracymbia (Figs 1K, 3D, 11K, 13G, 14I, J, 16F). Finally, *T. mandibulata* can be distinguished from *T. nitens* by the narrower lobes (Figs 11K, 13G, 14I, J, 16F).

**Synonymy and notes.** We identified many specimens of *T. mandibulata* from northern to southeastern Brazil. Unfortunately we were not able to study the type material of this species from Guam. It was not available at the MNHN and NHM and is likely lost. However, this well-known and widely distributed species has been repeatedly redescribed and illustrated in many papers (e.g. Simon 1900; Gravely 1921; Okuma 1983, 1987).

After comparing our specimens with illustrations from redescriptions, we noticed close similarities between *T. mandibulata* and *T. confrentera* (Fig. 21R–V; Chickering 1957c: 312, figs 19–26; Okuma 1992: 223, fig. 4), similar to Okuma (1983), who pointed out that both species might be synonyms. Banks (1909) described *T. confrentera* from Costa Rica and published a simple illustration of the male chelicerae. Later on, Chickering (1957c) and Okuma (1992) provided better illustrations of chelicerae and genitalia of specimens from Panama and Costa Rica, respectively. Okuma (1992) also redescribed *T. confrentera* based on many specimens from various localities in Costa Rica and reaffirmed its relationship with *T. mandibulata*, acknowledging that *T. confrentera* “may be barely distinguished from the latter by the female cheliceral fang” (Okuma 1992: 225). We received photos of five males and one
Figure 11. Tetragnatha mandibulata Walckenaer, 1841, male (UFRJ 1356). A. Dorsal habitus; B. Lateral habitus; C. Ventral habitus; D–G. Left chelicera: D. Upper view; E. Inner view; F. Lower view; G. Outer view; H–K. Left male palp: H. Mesal view with tibia; I. Mesal view detail; J. Dorsal view; K. Ventral view (paracymbium). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G); 0.5 mm (H); 0.2 mm (I, J, K).
Figure 12. *Tetragnatha mandibulata* Walckenaer, 1841, female. A. Dorsal habitus (UFRJ 1552); B. Lateral habitus (UFRJ 1552); C. Ventral habitus (UFRJ 1552); D–G. Left chelicera (UFRJ 1552): D. Upper view; E. Inner view. F. Lower view; G. Outer view; H, I. Genital area: H. Genital fold, ventral view (UFRJ 1552); I. Internal genitalia, cleared, ventral view (UFRJ 1124). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G, H); 0.1 mm (I).
female syntypes from two different vials, all bearing the diagnostic characters of *T. mandibulata* (Fig. 21R–V). Based on the characteristic morphology of males and females of *T. mandibulata*, we consider the small differences pointed out in Okuma (1992) as representing intraspecific variation, and we propose that *T. confratrena* is a junior synonym of *T. mandibulata*.

*Tetragnatha necatoria* Tullgren, 1910 was based on a male specimen from the Pare Mountains in Tanzania. After studying one photo of the upper row of teeth of this male holotype and the original illustration of the distal part of the left chelicera of this species (Fig. 21W; Tullgren 1910: fig. 72), we noticed the large Ga had the U2 adjoined, which is typical of *T.
mandibulata. So, T. necatoria is a junior synonym of T. mandibulata.

We received photos of one of the many specimens of T. petrunkevitchi Caporiacco, 1947 from Potaro and Georgetown, Guyana. This female (MZUF 529) clearly belongs to T. nitens, but there are also four specimens of T. mandibulata in the same vial. Additionally, all specimens in vials MZUF 527 and MZUF 528 are T. mandibulata, but the male and only adult specimen (amongst 25 immatures) in the vial MZUF 530 also belong to T. nitens. As the illustrations of chelicerae by Caporiacco (1948: figs 51, 52) of male and female specimens that he had preliminarily described in 1947 also match well with T. mandibulata, we conclude this species is another junior synonym of T. mandibulata.

Finally, based on photos of the male holotype of T. infuscata from the Seychelles (MRAC 143319), we observed that it also has the diagnostic characters of T. mandibulata (Fig. 21X). Saaristo (2003: figs 21A, B, 25; 2010: figs 27, 31) illustrated the genitalia of one male and one female from the same locality and placed this species in the synonymy of T. boydi (= T. bogotensis), but without any evidence for his claim. Ironically, Saaristo (1978: 121, figs 224–231) was the first to correctly identify T. mandibulata from the Seychelles and gave reliable illustrations of the typical female chelicerae and much elongated genital fold. However, Saaristo (2003, 2010) unexplicably considered his former identification as erroneous and attributed it to T. boydi instead. Hence, we correct this misidentification, removing T. infuscata from the synonymy with T. boydi, and consider it to be a junior synonym of T. mandibulata.

Variation. Males (n = 6): total length, 7.12–11.89; females (n = 20): total length, 7.54–11.63.

Distribution. Known from Africa, Asia, Australia, Central America, the Caribbean, and South America (Brazil and Guyana) (Fig. 22D).

Tetragnatha nitens (Audouin, 1826)

Figs 14–16, 20E, 22E.

Euglena nitens Audouin 1826: 118, pl. 2, fig. 2 (♀). Euglena pelusia Audouin 1826: 119, pl. 2, fig. 3 (♂ ♀).

Tetragnatha nitens Walckenaer 1841: 209.

Tetragnatha peruviana Taczanowski 1878: 142, pl. 1, fig. 1a–e (♂ ♀) syn. nov.

Tetragnatha andina Taczanowski 1878: 144, pl. 1, fig. 2 (♀); Levi 1981: 291 (syn. rejected, see T. bogotensis).

Tetragnatha peninsula Banks 1898: 246, pl. 15, fig. 12 (♂ ♀); Levi 1981: 291 (syn. rejected, see T. bogotensis).

Tetragnatha eremita Chamberlin 1924: 645, fig. 89, 90 (♂); Levi 1981: 292 (syn. rejected, see T. bogotensis).

Tetragnatha decipiens Badoeck 1932: 13, fig. 9 (♀) syn. nov.

Tetragnatha haitiensis Bryant 1945: 408, fig. 37 (♀); Levi 1981: 292 (syn. rejected, see T. bogotensis).

Tetragnatha tullgreni Caporiacco 1947: 24 (♀ preoccupied by T. tullgreni Lessert, 1915)

Tetragnatha caporiaccou Platnick 1993: 381 (replacement name of T. tullgreni) syn. nov.

Tetragnatha nitens kullmanni Wiehle 1962: 379, figs 1–5, 6b, 9–11, 14, 15 (♂ ♀); Wunderlich 1992: 365 (syn. rejected, see T. bogotensis).


Diagnosis. See the extended diagnosis under T. bogotensis for the diagnostic characters of T. nitens.

Synonymy and notes. Tetragnatha nitens was first described from Egypt, but its syntypes are lost according to Levi (1981). This common species has been diagnosed and redescribed many times, with plentiful illustrations of its body, chelicerae and genital morphology (e.g. L. Koch 1872; O. Pickard-Cambridge 1872; Simon 1898; F. O. Pickard-Cambridge 1903; Chickering 1957c; Okuma 1983, 1987, 1988b, 1992). Furthermore, it is a senior synonym for 17 species or subspecies according to the World Spider Catalog (2019). As it is easily mistaken for other large-bodied species, misidentified specimens are commonly found in museum collections.

Levi (1981: 291, 292), for example, listed 13 synonyms of T. nitens, of which 11 were new. We highlight that T. festina Bryant, 1945 was listed as a new synonym by Levi (1981) but was previously synonymised by Chickering (1957b: 2), T. aptans Chamberlin, 1920 was a new synonym but not listed as such, and T. eremita Chamberlin, 1924 was not included in the synonymic list of the World Spider Catalog (2019). Indeed, Levi (1981: figs 23–29) clearly misidentified at least some of the females he ascribed to T. nitens, whose illustrations belong to T. bogotensis instead (see above Synonymy and notes for T. bogotensis). Based on the original illustrations, we are able to confirm the synonymy of the following taxa: T. pelusia Audouin, 1826, T. antillana Simon, 1897, T. vicina Simon, 1897, T. galapagoensis Banks, 1902, T. aptans Chamberlin, 1920, T. seminola Gertsch, 1936, T. steckleri Gertsch & Ivie, 1936, T. elmorla Chamberlin & Ivie, 1942, and T. festina Bryant, 1945. On the other hand, four species are in turn synonyms of T. bogotensis (see Synonymy and notes for that species).

Another lapsus occurred with T. nitens kullmanni from Sardinia, Italy (Wiehle 1962: 379, figs 1–5, 6b, 9–11, 14, 15). It was first synonymised with T. nitens by Wunder-
Figure 14. Tetragnatha nitens (Audouin, 1826), male (MCTP 1426). A. Dorsal habitus; B. Ventral habitus; C–F. Left chelicera: C. Upper view; D. Inner view; E. Lower view; F. Outer view; G–J. Left male palp: G. Mesal view. H. Dorsal view; I. Ventral view (paracymbium); J. Paracymbium detail, ventral view. Scale bars, 2 mm (A, B); 1 mm (C, D, E, F); 0.5 mm (G, H, I); 0.2 mm (J).
Figure 15. *Tetragnatha nitens* (Audouin, 1826), female. A. Dorsal habitus (UFRJ 1528); B. lateral habitus (UFRJ 1528); C. Chelicerae upper row and eyes (UFRJ 1528); D. Chelicerae lower row and maxilla (UFRJ 1528); E–I. Left chelicera (UFRJ 1528): E. Upper view. F. Inner view. G. Lower view. H. Outer view. I. Basal cusp detail, distal view; J–L. Genital area: J. SEM of genital fold, ventral view (MCTP 11555); K. Internal genitalia, cleared, ventral view (MCTP 43323 ex 7313); L. Internal genitalia variation, cleared, ventral view (UFRJ 1528). Scale bars: 2 mm (A, B); 1 mm (C, D, E, F, G, H, J); 0.2 mm (I, K, L).
Figure 16. Tetragnatha nitens (Audouin, 1826), SEM photos. A. Left male chelicera, upper and lower views (MCTP 1618). B. Left female chelicera, upper and lower views (MCTP 11555). C. Epiandrous field, ventral view (MCTP 1618). D. Left male palp, bulb detail, mesal view (MCTP 5985). E. Left male palp, mesal view (MCTP 5985); F. Left male palp paracymbium, ventral view (MCTP 5985). Scale bars: 1 mm (A, B); 0.1 mm (C); 0.5 mm (D, E, F).
lich (1992: 365), but we disagree with this synonymy and consider *T. nitens kullmanni* as a synonym of *T. bogotensis* (see Synonymy and notes for that species).

Mainly based on our observations of the morphology of the chelicerae, we propose three new synonymies for *T. nitens: T. peruviana* from Peru, *T. decipiens* from Paraguay, and *T. caporiaccoi* from Guyana. The type materials of all species were studied; for *T. peruviana* images from MIZ were examined, and for *T. decipiens* and *T. caporiaccoi* specimens were studied on visits to NHM and MZUF, respectively.

*Tetragnatha decipiens* and *T. caporiaccoi* were described only from females, while descriptions of *T. peruviana* were based on males and females, with males described first, even though only females were illustrated. Females of the three species and males of *T. peruviana* clearly show the diagnostic characters of *T. nitens* (see Diagnosis above).

**Variation.** Males (*n* = 23): total length, 7.22–9.04; females (*n* = 30): total length, 7.42–11.44. The internal genitalia of females is also variable, with CS stalk shorter or longer than CS head, which places this structure at the same level or anterior to the spermathecae, which also vary in size (Fig. 15K, L; Zhu and Zhang 2011: fig. 125G).

**Distribution.** This species was first described from Africa (Egypt), but it has a cosmopolitan distribution, with many new records from the Neotropics (Fig. 22E).

*Tetragnatha vermiformis* Emerton, 1884

Figs 17–19, 20F, 22F

**Type material.** UNITED STATES OF AMERICA: ♂ lectotype, ♀ paralectotype (Levi 1981). ♀ lectotype, 3 ♀ paralectotypes in MCZ database, Beverly, Essex, Massachusetts (Coll. J. H. Emerton, 15.xiii.18xx), not examined.

**Extended diagnosis.** Males and females of *T. vermiformis* are most similar to *T. pallescens* F. O. Pickard-Cambridge, 1903. Males have similar length and width of chelicerae (Figs 17D–G, 19A, Banks 1892: 51, pl. 5, fig. 88 as *T. pallida*; Okuma 1992: 236, fig. 16A–E); ‘T’ and ‘rsu’ very alike, sclerotized and pointed; GI very sclerotized, thick and pointed, with a very large base, remaining teeth set apart by similar gaps. They also share similar elongated paracymbia, with finger-like notches and straight lateral knobs (Figs 17J, 19E; Okuma 1992: 236, fig. 16D). The epandrial field sets this species apart as it is flat and wide, with 20 furrows in two bands (Fig. 19F).

Females of both species have similar small, rounded and laterally bulging chelicerae (Figs 18D–G, 19B; Okuma 1992: 236, fig. 16F, G); Gu isolated from U2; Gl from L2 by large gaps, with all teeth very pointed; and similar short genital folds (Fig. 18H; Okuma 1992: 236, fig. 16J). Nonetheless, males and females of *T. vermiformis* differ from *T. pallescens* in having eyes much smaller and delicate and abdomen not as long and projecting (Figs 17A–C, 18A–C; Okuma 1992: 236, fig. 16H, I).

**Variation.** Males (*n* = 4): total length, 6.29–7.29; females (*n* = 7): total length, 6.99–10.98. The spermathecal lobes are variable in size and form. Both lobes may be more regularly cylindrical and the external lobe may be much smaller than the inner one (Levi 1981: figs 178–180) or regularly cylindrical and the external lobe may be much smaller than the inner one (Levi 1981: figs 178–180) or more elongated conductors, with thicker projected tips completely enfolding the emboli, not ending in long tails (Figs 17H–J, 19C, D, 20F). Females differ in lacking both AXu and AXI and having smaller and triangular Gu, longer and wider U2, and lack of a small denticle and groove near the base of L2 (Figs 18D–F, 19B; Okuma 1992: 236, fig. 16G). Females of *T. vermiformis* and *T. pallescens* have similar internal genitalia, with two curved kidney-shaped spermathecae on edge of plate, lacking central membranous sacs (Fig. 18I; Levi 1981: 311, fig. 131). However, *T. vermiformis* has longer spermathecae, without a median membranous area (Fig. 18I).

**Distribution.** Temperate and tropical Asia, North and Central America, newly recorded from South America (Brazil) (Fig. 22F).

*Tetragnatha major* Holmberg, 1876 and *Tetragnatha riparia* Holmberg, 1876

**Remarks.** *Tetragnatha major* and *T. riparia* were described by Holmberg (1876), but the original descriptions are very short, without any suitable characters to correctly diagnose the species. There is a lack of illustrations and no type materials are specified because Holmberg did not collect the specimens he described. No specimens labeled as types of either species were found in MACN during our visit to that collection; Galiano and Maury (1979) had previously determined this. Despite the lack of information on these two species, both were subsequently reported from many localities from Argentina (e.g. Melo-Leitão 1941, 1942). However, we re-examined many of these specimens at the MACN and MNJR and they belong to either *T. argentinensis* or *T. nitens*. Therefore, we treat both species as nomina dubia.
Figure 17. Tetragnatha vermiformis Emerton, 1884, male (UFRJ 1556). A. Dorsal habitus. B. Lateral habitus. C. Ventral habitus; D–G. Left chelicera: D. Upper view; E. Inner view; F. Lower view; G. Outer view; H–J. Left male palp: H. Mesal view; I. Dorsal view; J. Ventral view (paracymbium). Scale bars, 2 mm (A, B, C); 0.5 mm (D, E, F, G); 0.2 mm (H, I, J).
Figure 18. *Tetragnatha vermiformis* Emerton, 1884, female. A. Dorsal habitus (UFRJ 1556); B. Lateral habitus (UFRJ 1556); C. Ventral habitus (UFRJ 1556); D–G. Left chelicera (UFRJ 1556): D. Upper view; E. Inner view; F. Lower view; G. Outer view; H, I. Genital area: H. Genital fold, ventral view (UFRJ 1556); I. Internal genitalia, cleared, ventral view (MCTP 43339 ex 11333). Scale bars: 2 mm (A, B, C); 0.2 mm (D, E, F, G, H, I).
**Figure 19.** *Tetragnatha vermiformis* Emerton, 1884, SEM photos (MCTP 43339 ex 11333). **A.** Left male chelicera, upper and lower views; **B.** Left female chelicera, upper and lower views; **C.** Left male palp, mesal view; **D.** Left palp conductor detail, mesal view; **E.** Male palp paracymbium, ventral view; **F.** Epiandrous field, ventral view. Scale bars: 0.5 mm (**A, B, C**); 0.05 mm (**D**); 0.1 mm (**E**); 0.02 mm (**F**).

**Discussion**

In the literature the importance of the chelicerae for correctly diagnosing species has often been ignored. Old publications (e.g. Audouin 1826; Walckenaer 1841; Emerton 1884) usually had short descriptions, basically describing the body size, shape of abdomen, and eye length. On the other hand, some later authors like F. O. Pickard-Cambridge (1903), Chickering (1957c), Levi (1981), Okuma (1983, 1987, 1988a, 1988b, 1992) and Gillespie (1992a, 1992b), paid attention to chelicerae morphology and also genitalic features. Levi (1981), for example, based most of his determinations only on genital morphology, because he believed intraspecific variation on chelicerae was too high to allow clearcut species separation. In contrast, Okuma (1983, 1987, 1988a, 1988b, 1992) based her determinations mostly on chelicerae morphology, with additional drawings of male palps and genital folds. Gillespie (1992a, 1992b) followed Okuma, but also paid attention to leg spines on some *Tetragnatha*. In the same way, we also heavily rely on cheliceral features for species diagnoses, but add genitalic and other somatic characters whenever possible. In our opinion, taxonomy in *Tetragnatha* cannot...
Figure 20. Embolus and conductor tip detail, dorsal view, SEM photos. **A.** *T. bogotensis* (MCTP 4299); **B.** *T. elongata* (MCTP 43306 ex 0370); **C.** *T. keyserlingi* (MCTP 43319 ex 6944); **D.** *T. mandibulata* (UFRJ 1356); **E.** *T. nitens* (MACN 2252); **F.** *T. vermiformis* (MCTP 43339 ex 1133). Scale bars: 0.05 mm (A, B, C, E, F); 0.02 mm (D).
Figure 22. Records of the material we analysed (circles), including the type localities of Neotropical junior synonyms cited in the text (stars and triangles). A. Tetragnatha bogotensis; B. Tetragnatha elongata; C. Tetragnatha keyserlingi (excluding Haiti); D. Tetragnatha mandibulata; E. Tetragnatha nitens; F. Tetragnatha vermiformis.

only be based on genital morphology because there are many cryptic species with identical genitalia. Unfortunately, Okuma and Gillespie lacked consistency on their nomenclature. For example, Okuma called “U2” the more elongated tooth on the upper row (Okuma 1987: figs 1A, 2A), instead of “T” (Okuma 1992: figs 6A, 21A) and variously named fang cusps as excrescence (Okuma 1987) or posterior cusps (Okuma 1992). Besides, Gillespie (1992a) ignored Gu and Gl on females, renaming these structures U1 and L1, respectively.

The inconsistent terminology for chelicerae in Tetragnatha has hampered the recognition of homologies be-
tween species, shown by the lack of such characters in family phylogenies including morphological data (Álvarez-Padilla et al. 2009; Álvarez-Padilla and Hormiga 2011). Besides the lack of a straightforward set of homologies based on comprehensive phylogenies at the subfamily and genus levels, we believe that a practical system for naming chelicerae teeth and fang details in adult Tetragnatha is valuable for taxonomic purposes. Although some teeth may slightly vary in shape and size, teeth position in the groove row is less prone to variation. In that way, Okuma’s terms are a good basis for a classification system, despite the observed inconsistencies.

In Tetragnatha, adults normally bear guide teeth on upper (Gu) and lower rows (Gl). It is the usually robust first tooth on each margin (e.g. Figs 1E–G, 2E, 3B, C, 5D–F, 6C–E) which receives and guides the folding of the fang. Adjoined to the guide teeth, but not placed on the furrow, we can find additional teeth of variable size near the fang basis, from a small AXu (Figs 15E, F, 16B) or AXl (Figs 8E, F, 9E, F, 10A, B) to an extremely elongated AXu (Figs 14C, D, 16A) or a bulky and elongated AXl (Figs 2C, D, 12E, F, 13D). Okuma (1987) named ‘rsu’ “the upper row of small teeth”. As this is not very consistent, we kept the name, with some minor changes. In the same paper, she named ‘rs’ “the lower row of small teeth” after Gl or L2 (Okuma 1987: 38). In both sexes ‘rsu’ and ‘rsl’ refer to the teeth after the last specialized teeth position in the groove row is less prone to variation.

Males usually have specialized teeth, longer, more conspicuous, and more numerous than in females. There is an apophysis (spur) on the upper surface, which varies in shape and position, from the middle portion on distal part of paturon (Figs 5A, 7A) to its outer margin (Figs 8D, 10A). In some species, there is an additional ‘t’, a unique tooth near the apophysis basis, sometimes reduced to a nub (Figs 8D, E, 10A) or in other species elongated (Figs 1C, E, F, 3B, 14C, D, 16A). Considering the row itself, some males also bear a conspicuous and more elongated tooth on the upper row, named ‘T’, which replaces U2 or U3 (Figs 5D, E, 7A, 8D, E, 10A, 17D, E, 19A), and it can sometimes be slightly displaced from the furrow (Figs 17D, E, 19A). Okuma (1987, e.g. fig. 5F) also named ‘T’ in some females. We think the use of ‘T’ for females is inconsistent, as sometimes it is not the most elongated tooth, but just larger than ‘rsu’.

Moreover, we can find ‘sl’, a tooth on the upper row of males of some species with an elongated ‘T’. It is always the last tooth before ‘T’, normally basally projected (Figs 5A, B, 7A). Again, Okuma (1987, e.g. fig. 5F) considered it to be present in females, named as ‘e’. As we do not use ‘T’ in females, ‘e’ is deemed to be just a regular tooth. Therefore, in males with a ‘T’, we consider all remaining teeth after this elongated tooth to be ‘rsu’ (Figs 5D, 8D).

In relation to fangs, we call the massive pointed projection placed at lower side and near fang basis the basal cusp (BC) (Figs 2D, E, 12D–G, 13C, D, 15D, F–I, 16B) and the spiky projection placed at outer side, varying in distance from fang basis, the outer cusp (OC) (Figs 6C–F, 7B; Okuma 1988b: fig. 1A–C; 1992: fig. 21E, F). The projection placed near or on the inner face of fang is named the inner cusp (IC) (Figs 17D, F, 19A; Okuma 1992: fig. 3A, C). Finally, we name very robust forking projection at the upper side and near the middle of fang the median cusp (MC) (e.g. Zhu et al. 2003: fig. 59C–E; Mello-Leitão 1931: fig. 1).

We also introduce new terminology for modifications of the paturon. Some have a rounded elevated cheliceral bulge (CB) in the area between both rows of teeth (Figs 2C, E, 3C, 12D, E, 13C) or bear well-marked crests or thick keels on gaps alongside the teeth. There may be an upper crest (CRu) departing from Gu (Figs 9D, 10B; Okuma 1992: fig. 21E) or a lower crest (CRI) occupying the total length of furrow (Figs 9F, 10B). Nonetheless, those crests and bulges may not always be illustrated or simply do not occur in some specimens (see Variation in T. keyserlingi).

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References


Appendix

Material examined

**Tetragnatha bogotensis**

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Tetragnatha elongata


Tetragnatha keyserlingi

Brazil: 1♂, 1♀, Amapá: Uaçá [Uassa, ex French Guyana], 3.534001, 51.524370, K. Jelski leg. (MIZ 225530-225531, mixed with samples of Tetragnatha filiformata Roewer, 1942); Amazonas: 1♂, 1♀, Humaitá, -7.532108, -53.525047, J. C. de M. Carvalho et al. leg. (MACN 24582); 1♀, Potaro-Siparuni, Tuutamari, 5.2615047, -59.1659206, 19.ix.1936 (MZUF); 1♂, 1♀, Ouest, Port-au-Prince, 18.579024,-72.3545005, 1961, Duret leg. (MACN 39718 ex 26276).

Tetragnatha mandibulata

ARGENTINA: Buenos Aires province: 1♂, 1♀, Córdoba province: 3♂, 2♀, 24–29.i.1990, A. Peretti leg. (MACN 24567); 1♂, 1♀, Cabana, -31.236160, -64.328100, 08.v.1947, Max Birabén leg. (NHM); 1♀, Calamuchita, -31.916670, -64.633330, 1962, Viana leg. (MACN 24426); 1♀, Córdoba, Arguello, -31.416667, -64.183333, xiii.1944, De Carlo leg. (MACN 39600 ex 1957); 1♂, 1♀, Villa Giardino, -31.033333, -64.483333, i.1990, T. Devoto leg. (MACN 24582); 1♂, 2♀, Corrientes: Manantiales, -27.9249206, -58.1102847, ix.1960, Apóstol leg. (MACN 5265); 1♀, same data (MACN 39611 ex 5266); Entre Ríos: 1♀, Paraná, Canal 6, -31.733333, -60.533333, ii.1963, A. Bachmann leg. (MACN 24425); 1♂, Villa Elisa, Balnearía, -32.166670, -58.4, i.1989, A. Olive leg. (MACN 22252); 1♀, La Pampa: Combello, -36.60556, -64.3075, ii.1940, Prof. P. Gomez leg. (MACN 24451); La Rioja: 1♂, 1♀, 1j, Villa Giardino, -27.9249206, -58.1102847, ix.1960, Apóstol leg. (MACN 5265); 1♀, same data (MACN 39611 ex 5266); Entre Ríos: 1♀, Paraná, Canal 6, -31.733333, -60.533333, ii.1963, A. Bachmann leg. (MACN 24425); 1♂, Villa Elisa, Balnearía, -32.166670, -58.4, i.1989, A. Olive leg. (MACN 22252); 1♀, La Pampa: Combello, -36.60556, -64.3075, ii.1940, Prof. P. Gomez leg. (MACN 24451); La Rioja: 1♂, 1♀, x.1965, Mauny leg. (MACN 24406); 1♀, Patquia, Guayapa, -30.05, -66.883, xii.1940, Prof. P. Gomez leg. (MACN 24475); 1♀, Mendoza: -28.833333, -68.816667, iv.1970, Willian leg. (MACN 24471); Misiones: 1♂, “Misiones/ Corrientes”, 03–12.i.1989 (MCTP 0836); 2♀, 1♂, J., “Puerto Yayá”, -25.985922, -54.4420392, viii.1959, Nuñez leg. (MACN 24424); 1♀, Cataratas del Iguazú, -25.683611, -54.453889, xi.54, B. C. Schiapelli leg. (MACN 24526); 3♀, Posadas, -27.361667, -55.902788, xii.1947, De Carlo and D’Amico leg. (MACN 2435); 1♀, San José, Pondapay, -27.51785, -55.8405244, xii.1941, Max Birabén leg. (MLP 16425 wrongly mixed with a male syntype of Tetragnatha longidens Mello-Leitão, 1945); 1♀, same data (MACN 60016 ex 2308 wrongly mixed with a male syntype of Tetragnatha longidens Mello-Leitão, 1945); 2♀, Santa Maria: -27.934526, -55.407083, x.1956, Viana leg. (MACN 39615 ex 24423); 1♀, Tobuna, -26.47, -53.891389, i.1952, W. Partridge leg. (MACN 39610 ex MACN 4078); 2♀, 29♂, Rio Negro: General Roca, Balsa, -39.033333, -67.583333, i.1962, A. Bachmann leg. (MACN 5480); 4♀, 4♂, 1j, Santa Fé: xi.1969, Arce leg. (MACN 24544); 1♂, 1♀, Estancia Las Gamas, 20 Km W of Vera, -29.4265464, -60.3702699, 300 m a.s.l., 30.x.1994, M. Ramirez and J. Fainovich leg. (MACN 24543); 1♀, same locality, 20–24.iii.2014, M. Ramirez, C. Grisiamo, L. Piactenitz and M. González Marquez leg. (MACN 5480).
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31323); 1♂, same data (MACN 31341); 2♂, 2♀, same data (MACN 31612); 4♀, 4♂, same data (MACN 31613);

BRAZIL. 6♂, 2♀, 1♂, Espírito Santo: Ilha de Trindade -20.524722, -29.324722, no further data (MNRJ 02601);
1♂, same locality (MNRJ 02608); 1♀, same locality (MNRJ 04361); 17♂, 23♀, 7♂, same locality, 17.vii.1957,
Wolfgang (Exp. Inst. Butantan) leg. (IBSP 1323, 1328, 1329, 1330, 1334, 1368); 2♂, 2♀, 4♂, 4♀, Goiás: São José
Alexandre Barrigossi leg. (MCTP 19598); 2♂, 1♀, Mato Grosso: Chapada dos Guimarães, -15.460833, -55.75, 20–
29.vii.2000, C. Strüssman leg. (MCTP 11314); 1♀, same data (MCTP 11555); 2♂, 1♀, same locality, 20–
30.viii.2000, C. Strüssman leg. (MCTP 11534); 1♂, 1♀, Pontes e Lacerda, Usina Hidrelétrica de Guaporé,
-15.1353576, -58.988965, 01–14.x.2002, Operação Coatá leg. (MCTP 43320 ex 13581); Mato Grosso do Sul: 4♂,
2♀, 5♂, 2♀, 5♀, 5♂, 7♀, 1♀, 3♀, 1♀, 4♀, Parque do Homem, Ilha do Mel, -23.6666666, 53.977778, 11–
14.vi.2001, F. S. Cunha & J. P. L. Guadanucci leg. (IBSP 39358); 1♂, 2♀, same locality, Usina Hidrelétrica Engenho
Sérgio Motta, 12–19.iii.2001, F. S. Cunha & C. A. R. Souza leg. (IBSP 39500); 1♀, Corumbá, -19.008889,
-57.652778, 1994, J. Raizer leg. (IBSP 6479); 1♀, Passo do Lomtra, Base de Estudos do Pantanal (UFMS),
-19.5750615, -57.0381845, 20–29.v.1995, A. A. Lise et al leg. (MCTP 43324 ex 7578); 1♂, Xangrilá, -29.800833,
-50.043889, 05.ii.1995, A. A. Lise et al. leg. (MCTP 43324 ex 7578); 1♂, Nova Santa Rita, -29.856944,
-51.273889, 23.v.2009, A. Oliveira leg. (MCTP 37269); 3♂, Novos Cabrais, Parque Witeck, -29.735,
-52.947778, 01.xi.2008, A. M. Petersen leg. (MCTP 43321 ex 19627); 5♂, 7♀, 1♀, same locality, 26.iii.1990,
D. Linck leg. (MCTP 5973); 4♂, 1♀, same locality, 28.ii.1990, D. Linck leg. (MCTP 43323 ex 7313); 1♀, São Borja,
Rio Uruguai, -27.1751176, -53.552525, 11–
21.v.1989 (MCTP 0840); 1♂, Alvorada, -29.99,
-51.083889, 17.v.1992, M. Cunha leg. (MCTP 1540); 1♀, Barra do Ribeiro, -30.290833, -51.300833, 20.ii.2002,
G. M. Petersen leg. (MCTP 016672); 1♀, Cachoeira do Sul, Porteira Sete, -30.038889, -52.938889, 31.x.1992, R.
G. Buss leg. (MCTP 41820 ex 3386); 1♀, same locality, Cordilheira, 04.x.1992, R. G. Buss leg. (MCTP 41823 ex
3381); 1♀, Candelária, -29.668889, -52.788889, 14.x.2017, F. Biondo leg. (MCTP 41584); 1♂, Capão da
Canoa, Arroio Teixeira, -29.6458034, -49.9478308, 24.x.1984, F. C. Quadros leg. (MCTP 1939); 1♀, Caxias
do Sul, Fazenda Souza, -29.121444, -51.018557, 11–
12.x.1995, Eq. Lab Aracnologia PUCRS leg. (MCTP 43323 ex 7313); 1♂, Cidreira, -30.160833, -50.233889,
(MCTP 37269); 3♂, Novos Cabrais, Parque Witeck, -29.735,
-52.947778, 01.xi.2008, A. M. Petersen leg. (MCTP 43321 ex 19627); 5♂, 7♀, 1♀, same locality, 24.ii.2005,
R. G. Buss leg. (MCTP 40256); 6♂, 8♀, same locality, 15.ii.2011, R. Linck leg. (MCTP 40287); 1♂,
2♀, same locality, 15.x.1998, C. B. Kotzian and L. Indrusiak leg. (MCTP 43322 ex 40632); 1♂, same locality,
v.1988, Eq. Def. Fitos leg. (MCTP 4882); 4♀, same locality, v.1988, Eq. Def. Fitos leg. (MCTP 4883); 2♂,
2♀, 1♀, same locality, 18.v.1990, Eq. Def. Fitos leg. (MCTP 4884); 1♂, 5♀, same locality, 26.iii.1990, D. Linck leg.
(MCTP 5971); 1♀, same locality, 30.i.1990, D. Linck leg (MCTP 5972); 1♂, 1♀, same locality, 26.iii.1990, D. Linck leg.
(MCTP 5973); 4♂, 1♀, same locality, 28.ii.1990, D. Linck leg. (MCTP 5980); 1♂, 2♀, same locality, 28.ii.1990,
D. Linck leg. (MCTP 5985); 3♂, 2♀, same locality, 28.ii.1990. D. Linck leg. (MCTP 5987); 1♂, São Borja,
Rio Uruguai, -28.660833, -53.060389, 03–12.i.1998 (MCTP 0883); 1♀, same locality, Reserva Biológica São Donato,
10–25.v.2012, Miguel Machado leg. (MCTP 36184); 1♀, São Francisco de Paula, -29.447778, -50.583889,
09–12.i.1997, A. A. Lise et al. leg. (MCTP 10845); 1♂, Torres,
(MCTP 1426); 1♀, same locality, Colônia São Pedro, 07–
09.iv.1992, A. Brall leg. (MCTP 1618); 1♀, Viamão,
-30.072391, -51.097196, 07.xi.1995, A. A. Lise et al. leg. (MCTP 43325 ex 7807); 1♀, same locality, Est. Exp.
Fiotécnica, 25.viii.1995, A. A. Lise et al. leg. (MCTP 43324 ex 7578); 1♂, Xangrilá, -29.800833, -50.043889, 05.

Tetragnatha vermiformis