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Article



Phylogenetic placement and redescription of the spider genus *Atelidea* Simon, 1895 (Araneae, Tetragnathidae)

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Abstract

The spider genus *Atelidea* Simon, 1895 previously included two described species, *A. spinosa* Simon, 1895 and *A. globosa* Yamaguchi, 1957. In this study we describe for the first time the female of *A. spinosa*, and provide illustrations and scanning electron microscope images of external and internal features. The phylogenetic placement of this genus was investigated by including *A. spinosa* in a recent phylogenetic analysis with 23 tetragnathids. Parsimony analyses under equal and implied weights were performed. Our results suggest that *Atelidea* belongs to Tetragnathidae and in particular nests within Leucauginae, this last node is well supported and expected to endure future analysis; however, the relationships of *Atelidea* to other leucaugine species and its validity as a genus need to be assessed in future studies with a larger sample of leucaugine taxa. The second species described in the genus, *A. globosa*, is only known from its now lost type specimen from Japan and it is proposed as a *nomen dubium* leaving *Atelidea* monotypic.

Key words: Cladistics, Taxonomy, Sri Lanka, Oriental region

Introduction

The members of the orb weaving spider family Tetragnathidae have a worldwide distribution and are particularly diverse in tropical and subtropical ecosystems. Near one thousand species of tetragnathids have been described, classified in 46 genera (Platnick 2010) and is estimated that at most only half of the species have been described, as for many other spider families (Platnick 1999). The other half of undescribed species are mainly concentrated in the tropical areas. Describing the unknown biota, among other organisms, is first step for understanding and preserving our biodiversity. Tetragnathids usually build typical orb webs either along bodies of water, within the forest vegetation or inside caves. Tetragnathidae belong to the superfamily Araneoidea, sharing with these taxa several morphological and behavioral synapomorphies such as the presence of aggregate silk glands (which produce the viscid sticky silk) (Fig 6D), the loss of the cribellum and the presence of the paracymbium (Fig 5A) (Griswold et al. 1998 and references therein for more synapomorphies). Based on morphological and behavioral data tetragnathids have been proposed as sister to Nephilidae (Coddington 1990; Hormiga et al. 1995; Alvarez-Padilla 2007; Dimitrov & Hormiga 2009), or as sister to a clade that includes representatives of Linyphildae, Pimoidae, Theridiosomatidae, Nesticidae and Theridiidae, with nephilids proposed as sister to all other araneoids (Kuntner et al. 2008). Recent analyses that combined morphological, molecular and behavioral data found that Tetragnathidae is sister to Mimetidae or at least some of its representatives (Rix et al. 2008; Blackledge et al. 2009; Dimitrov & Hormiga in press).

The monophyly of Tetragnathidae has been recovered in several studies that include molecular, behavioral and morphological data and explore different analytical criteria (Álvarez-Padilla *et al.* 2009; Dimitrov & Hormiga in press). Tetragnathids differ from other araneoids by their somewhat simpler male pedipalps with only one tegular sclerite, the conductor, which often is coiled with the embolus (Figs. 2E and 5D); by their spinneret spigot morphology which usually lacks aciniform spigots over the PMS anterior surface (Fig 6C), by having the ALS piriform spigot bases distal edge separated from the column base leaving a torus (Fig. 6B) and by their web building behav-

iors (Eberhard 1982, 1987, 1988, 2001). The anatomy, diversity and taxonomy of tetragnathids have been studied since the 19th century and it is still being actively studied (e.g., Simon 1894; Levi 1980, 1981, 1986, 2008; Levi and Eicksted 1989; Hormiga *et al.* 1995; Kuntner 2005, 2006; Kuntner *et al.* 2008; Álvarez-Padilla *et al.* 2009, Dimitrov *et al.* 2007, Dimitrov & Hormiga 2009).

Currently some stability has been achieved within tetragnathid internal relationships by combining molecular and morphological data. Recent studies have recognized three subfamilies: Tetragnathinae, Leucauginae, Metainae and the "Nanometa clade" (Álvarez-Padilla *et al.* 2009) or recognizing these three subfamilies plus an additional clade that includes *Azilia* Keyserling, 1881, *Diphya* Nicolet, 1849 and *Mollemeta* Álvarez-Padilla, 2007 (Dimitrov and Hormiga in press). These two studies differ in the taxonomic composition of Metainae which according to Dimitrov and Hormiga (in press) includes *Metleucauge* Levi, 1981; contrary to Álvarez-Padilla *et al.* (2009) analyses that place it as a basal Leucauginae.

The spider genus *Atelidea* Simon, 1895 previously included two described species, *A. spinosa* Simon, 1895 and *A. globosa* Yamaguchi, 1957 (Platnick 2010). Simon (1895) proposed this genus to include *A. spinosa* from Sri Lanka and mentioned that it was similar to *Argyroepeira* Thorell, 1881 (currently a junior synonym of *Leucauge* White, 1841) in having a shiny abdomen of silver guanine patches (Fig. 1A–C) and a brush of trichobothria on the fourth femur (Figs. 3E, G). Most *Argyroepeira* species have been transferred to *Leucauge*, and to other genera such as *Chrysometa* Simon, 1894 and *Cyrtognatha* Keyserling, 1881. Simon's description of *A. spinosa*, although very old, was accurate enough to allow species identification. However, *A. spinosa* was only known from male specimens, and the original descripton did not have any illustrations of the diagnostic features and did not provide any details of the anatomy of the species. This state of affairs has complicated the study of *Atelidea* and it has made impossible to establish its phylogenetic placement in relation to other species of *Atelidea, namely A. globosa*, was recorded exclusively from Japan and is known only after the type material. We redescribe here *A. spinosa* and provide illustrations and SEM images to document its anatomy, describe for the first time the female and test the phylogenetic placement of this genus.

Methods

Taxonomic methods. General taxonomic methods and the format of the descriptions follow Álvarez-Padilla (2007). Morphological observations and illustrations of external structures were made using Leica MZ APO dissecting and Leica DMRM compound microscopes with camera lucidae. Internal genitalic structures were cleared in methyl salicylate (Holm 1979) and mounted on temporary slides (Grandjean 1949; Coddington 1983). All measurements were taken with a reticule calibrated in millimeters using dissecting and compound microscopes. In addition, a LEO 1430 VP scanning electron microscope (SEM) was used to study the ultrastructure of many morphological internal and external features. Soft tissues surrounding internal structures were effectively digested following the protocol described by Álvarez-Padilla & Hormiga (2008).

Phylogenetic analysis. We added *A. spinosa* to the morphological and behavioral partition of the data matrix of Álvarez-Padilla *et al.* (2009) to test if *A. spinosa* is a tetragnathid and to investigate its phylogenetic placement within this family. This data partition included 213 characters, several of them also included in a previous phylogenetic analysis (Hormiga *et al.* 1995; Álvarez-Padilla 2007; Kuntner *et al.* 2008). Its taxonomic sample includes 22 tetragnathid terminals representing 20 genera, an undescribed Australian tetragnathid species, six araneoid families represented by 22 species, the deinopoid genus *Uloborus* Latreille, 1806 (Uloboridae) are used as outgroups and *Oncodamus bidens* (Karsch 1878) (Nicodamidae) as the root (Fig. 7A). *Deinopis* sp. (Deinopidae) was removed from the present analysis because it was coded only for the molecular partition of the study. Refer to Álvarez-Padilla et al (2009) for character states and character names and definitions.

Parsimony analyses under equal and implied weights were performed with TNT 1.1 (Goloboff *et al.* 2004) and characters optimizations were carried out using WinClada 1.00.08 (Nixon 2002). For the equal weights analyses five replicates of 1,500 random additions of taxa were performed, with sectorial searches and tree fusing algorithms. The parameters for all algorithms were the program defaults. Jackknife support values (Farris *et al.* 1996) were calculated with 1,000 replicates, with a probability of 36% of character removal and search parameters per replica of 200 random additions of taxa followed by TBR. For the implied weights analyses (Goloboff 1993) 500

random additions of taxa followed by TBR algorithms. Implied weight concavities from one to 100 were performed with a script and the set of these cladograms that was among the most parsimonious trees (MPTs) were chosen as working hypothesis. Symmetric Resampling (Goloboff *et al.* 2003) support values were calculated with 1,000 with a change probability of 33% and search parameters per replica of 200 random additions of taxa followed by TBR. The random seed for both analyses was one.

One new character was added to this data set: Character 214. Male metatarsus I ventral surface: (0) without modified macrosetae; (1) armed with a line of short and thick macrosetae (Fig. 1F; 3D, F). The presence of short and thick macrosetae was observed only in the species representing the genera *Atelidea, Mesida* and *Opadometa*. Tarsi and metatarsi of all other species were also revised. All multistate characters were treated as non-additive (Fitch 1971).

Anatomical abbreviations: AC = aciniform gland spigot(s); AG = aggregate gland spigot(s); ALE = anterior lateral eyes; ALS = anterior lateral spinnerets; AME = anterior median eyes; BH = basal hematodocha; C = conductor; CB = cymbium; CDBP = cymbio dorso-basal process; CD = copulatory ducts; CO = copulatory opening; CY = cylindrical gland spigot(s); E = embolus; F = fundus; FD = fertilization duct; FL = flagelliform gland spigot(s); MAP = major ampullate gland spigot; mAP = minor ampullate gland spigot; P = paracymbium; PI = piriform gland spigot(s); PLE = posterior lateral eyes; PLS = posterior lateral spinnerets; PME = posterior median eyes; S = spermatheca; ST = subtegulum; T = tegulum; TO = tarsal organ.

Results

Phylogenetic analyses

Twelve most parsimonious cladograms were found (1043 steps, CI 26, RI 59) regardless of how zero-length branches were treated (Coddington & Scharff 1995; Platnick *et al.* 1991). The strict consensus collapsed seven nodes, six within Leucauginae affecting the relationships of *Atelidea* with the other members of this subfamily (Fig 7 A). Nevertheless *Atelidea* in nested within the subfamily Leucauginae, and more precisely in a group that excludes *Metleucauge* Levi, 1980, with 66% and 88% of support in both analyses. Implied weights analyses under all concavities recovered *Atelidea* as sister to a clade that includes *Mesida* and *Opadometa* (support values less that 51%) and the two species of *Leucauge* as sister taxa (72%). The clade that includes *Atelidea, Mesida* and *Opadometa* (Figs. 3D, F and I), and the procurved PME row which is straight in most leucaugines except in *Metleucauge* and *Tylorida* (character 97 state 1 in Álvarez-Padilla *et al.* 2009). A total of eight different cladograms were obtained by the different concavities and their strict consensus collapsed 15 nodes mainly within Tetragnathidae (Fig. 7B). These analyses converged in only one of the most parsimonious tree was used to calculate the Symmetric Resampling support values.

Discussion

The inclusion of *Atelidea* within Leucauginae is well supported and expected to endure future analyses (Figs. 7A-B). *Atelidea* shares with other leucaugine taxa, except *Metleucauge*, the following diagnostic characters: sperm duct with multiple coils, a ventrally enlarged tegulum, (Figs. 2D and 5A-F), the elongated shape of the base of the embolus, a filiform embolus completely coiled inside the conductor (Fig. 2D-E) and the mesally displaced subtegulum (Fig. 5E). Female *Atelidea* share with leucaugines characters such as: fertilization ducts coiled (Fig. 2B-C), copulatory ducts cuticle flexible, the particular acorn-shaped sperm glands openings of the spermatheca (Figs. 4A-D), the flexible cuticle of the spermathecae (homoplastic in *Metleucauge, Azilia* and other tetragnathids) and the presence of paired rows of trichobothria on femur IV (absent in *Metabus*, presumably lost).

A recent phylogenetic analysis (Dimitrov & Hormiga, in press), including for the first time molecular data for *Metleucauge*, have found that this latter genus does not belong into Leucauginae. This latter subfamily, as delimited by these authors, was recovered monophyletic with different analytical criteria and has been recovered well supported. These authors included representatives of seven out of the twelve genera that can be unambiguously assigned to Leucauginae (Platnick 2010 and references therein; Dimitrov & Hormiga in press). These results suggest that Leucauginae represents a natural group, however more work is needed to resolve its internal phylogenetic relationships, in particular to test the monophyly of the currently valid genera, reassess the status of other monotypic genera, and to understand the evolution of the features that characterize these spiders, among other questions. The proposed monotypic status of *Atelidea* also needs to be taken with caution until more intensive survey of the Sri Lankan spiders is done. There are ca. 240 described species of leucaugines, but the diversity of this subfamily is far greater taking into account specimens revised at museum collections, in particular for tropical areas, in addition to the estimates of the new species that are alive in forest (e.g., see comments by Dimitrov & Hormiga 2010). We expect that the data presented in this study will aid in a more comprehensive exploration of Leucauginae biodiversity and phylogenetics.

Taxonomy

Tetragnathidae Menge1886

Atelidea Simon, 1895

(Figs. 1-6)

Type species. Atelidea spinosa Simon, 1895.

Diagnosis. *Atelidea* can be distinguished from similar tetragnathid genera by the following combination of characters: dark-brown cephalothorax and chelicera; abdomen decorated with black patches in preserved specimens (Figs. 1A–C); male pedipalps white colored in dead specimens; male metatarsus I armed with a ventral line of short and thick macrosetae (Simon 1895: 737; Figs. 3D, F). *Mesida* and *Opadometa* males also possess these ventral macroseta. In *Opadometa* the macrosetae are similar in size to those of *Atelidea*, but extend to the venter of the tarsus (Figs. 3F, I). Females of *Opadometa* also can be differentiated by the presence of a brush of macrosetae on the distal third of tibiae IV and males have the paturon dorsal surface covered with large spine-like macrosetae. *Mesida* also has a ventral line of short and thick macrosetae on metatarsus I; however they are smaller than those of *Atelidea. Mesida* and *Leucauge* females can be differentiated by their green to yellow coloration and the considerably more dense rows of trichobothria on femora IV.

Composition. Monotypic. *Atelidea globosa* Yamaguchi, 1957, the second species previously included in this genus is proposed as a *nomen dubium* because its description and illustrations do not clearly specify if the type specimen is a female or an immature and the type specimen is lost. The original work only mentions the locality and coloration of the specimens (Yamaguchi 1957; Yaginuma 1960; Tanikawa, *in litt.*)

Atelidea spinosa Simon, 1895

A. spinosa Simon, 1895 (male holotype examined, deposited at the Museum National d'Histoire Naturelle, Paris)
Atelidea spinosa The genus Atelidea was described in 1894 but the type species A. spinosa was described later in 1895 in a different publication, making the nomenclatural act of 1894 a nomen nudum.

Material examined. SRI LANKA: Kandy, district, Udawattekelle Sanctuary, 19 October 1973, collector/s unknown (1 female); Ampara district, Ekgal-Aru Sanctuary Jungle, 9–11 March 1979, K. V. Krombein, T. Wijesinhe, S. Siriwardana, L. Jayawickrama (1 male 2 female); Ratnapura district, Gilimale, Induruwa Jungle, 13–15 March 1979. K. V. Krombein, T. Wijesinghe, S. Siriwardana, L Jayawickrama (1 male; 2 females); Sabaragamuwa prov. Ratnapura district, Rubber plantation at Gallella Village, 29 January 1995, M. Kuntner & M. Skoberne (2 males). All specimens are deposited at the National Museum of Natural History, Smithsonian Institution. This species is known after nine specimens: five males (identical to the holotype of *A. spinosa* in their morphological characteristics) and three females.



FIGURE 1. *Ateleidea spinosa*, somatic morphology. A, female habitus. B, male habitus. C, female lateral view. D, male cephalothorax frontal view. F male femur and metatarsus I. Scale bars 0.5 mm, A–C same scale, D–E same scale.



FIGURE 2. *Ateleidea spinosa*, genital morphology. A, epigynum ventral view. B, epigynum ventral view cleared. C, epigynum dorsal view cleared. D, male pedipalp ventral view cleared. E male pedipalp expanded. Scale bars 0.2 mm, A–C same scale, D–E same scale.



FIGURE 3. *Ateleidea spinosa* and *Opadometa* sp. (B, I). cephalothorax and legs morphology. A, female cephalothorax dorsal view. B, *Opadometa* sp female cephalothorax tangential view. C, female metatarsus I. D, male metatarsus I. E, female femur IV trichobothria at the base. F, male metatarsus I spine. G, femur IV trichobothria detail. H, male tarsus I. I, *Opadometa* sp., male tarsus I.

Description. *Female*: specimen from Udawattakele, Kandy District, Sri Lanka. Total length 4.6. Cephalothorax 1.9 long, 1.3 wide, 0.4 high. Sternum 0.8 long, 0.7 wide. Finding the female of *Atelidea spinosa* was difficult for us taking into account that only diagnostic characters of male specimens were known. Nonetheless, the unique abdominal pattern, dark coloration of the cephalothorax (Figs. 1A, C) and the geographic distribution of the female specimens described in this study were our clues to match both sexes to the same species. Chelicerae with a boss



FIGURE 4. *A. spinosa* and *Leucauge venusta* (Walckenaer, 1841) (C, D) genitalic morphology. A, *A. spinosa* epigynum anterior view. B, *A. spinosa* accessory glands over the copulatory ducts. C, *L. venusta* epigynum dorsal view. D, *L. venusta* accessory glands over the copulatory ducts. E, *A. spinosa* male pedipalp apical view. F, *A. spinosa* embolus and conductor.

and three teeth on both margins (Figs. 1D–E). Abdomen oval 2.9 long, 2.1 wide, 2.2 high, venter with two parallel lines lighter than the surrounding cuticle and with few silver guanine patches. Ocular area lower than the carapace margin (Fig. 3A). AME diameter 0.12. ALE 0.13. PME 0.14. PLE 0.11. Clypeus height 0.7 x AME diameters. AME separation 1.0 x AME diameter. AME-ALE separation 0.8 x AME diameter. PME separation 1.0 x PME diameter. Spinnerets (Figs. 6A–D). ALS with more than 50 piriform spigots and with their bases separated from the column leaving a torus (Fig. 6B). PMS with three aciniform spigots between the cylindrical spigot and the minor ampullate, nubbin present (Fig. 6C). PLS with a field of ca. 12 aciniform spigots, aggregate spigots apex separated from the flagelliform spigot tip and cylindrical spigots peripheral (Fig. 6D). Leg I length 10.4, leg II 7.2, leg III 3.9, leg IV 6.1, pedipalp 1.8. Leg IV with two parallel rows of rami-

fied trichobothria extended more than half the femur length (Figs. 3E, G). Epigynum flat with a rectangular atrium longer than wide, anterior edge with a sclerotized arch (Figs. 2A–B). Genital openings inside small curved grooves located at the center of the atrium (Figs. 2B–C). Copulatory ducts weakly sclerotized and entering the spermatheca near the fertilization ducts origin. Fertilization ducts well sclerotized, coiled and separated from the copulatory ducts path, spermathecae weakly sclerotized (Figs. 2B–C). One accessory gland duct per opening, with its base thicker than twice the duct length, and resembling an inverted acorn (Fig. 4A–B).



FIGURE 5. *Ateleidea spinosa* and *Leucauge venusta* (D), male genitalic morphology. A, *A. spinosa* pedipalp ectal view. B, *A. spinosa* paracymbium and CDBP. C, *A. spinosa* conductor. D, *L. venusta* pedipalp ectal view. E, *A. spinosa* pedipalp mesal view. F, *A. spinosa* pedipalp ventral view.



FIGURE 6. *Ateleidea spinosa* spinnerets. A, female right spinning field. B, female ALS. C, female PMS. D, female PLS. E, epiandrous fusules. F, male PLS.

Male: from Sabaragamuwa province, Ratnapura district, Rubber plantation at Gallella Village. Habitus as in female (Fig. 1B). Total length 3.4. Cephalothorax 1.7 long, 1.2 wide, 0.2 high. Sternum 0.8 long, 0.7 wide. Abdomen oval longer than wide, venter as in female. 1.7 long, 0.9 wide, 1.5 high. Chelicerae anterior margin with three teeth, posterior cheliceral margin with five. Male chelicerae larger than the female and slightly divergent (Fig. 1D–E). Epiandrous plate anterior margin swollen, fusules concentrated in one irregular line and immersed in the plate (Fig. 6E). PLS and PMS cylindrical and aggregate spigots reduced to nubbins (Fig. 6F). AME diameter 0.14. ALE 0.11. PME 0.13. PLE 0.10. Clypeus height 0.7 x AME diameters. AME separation 0.8 x AME diameters. AME-ALE separation 0.7 x AME diameter. PME separation 0.9 x PME diameter. PME-PLE separation 0.8 x PME diameters. Leg I length 11.6, leg II 7.9, leg III 3.7, leg IV 6.2, pedipalp 1.8. Pedipalp tibia 2.2 times longer than wide (Figs. 5A, E–F). Cymbium tarsal organ diameter larger than the diameter of the contiguous macrosetae bases (Fig. 4E). CDBP at the base of the cymbium, parallel to the longitudinal axes of the cymbium and dorsally projected



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FIGURE 7. Cladograms from the equal and implied weights analyses. A, strict consensus (1074 steps, CI 25, RI 57) of 12 MPTs (1043 steps, CI 26, RI 59) obtained by equal weights. B, strict consensus of all the topologies obtained by the implied weights analyzes concavities 1 to 100. Numbers under nodes Jackknife and Symmetric Resampling values respectively, arrows indicate the position of Atelidea.

(Figs. 5A–B). Tegulum ventrally swollen, subtegulum mesally displaced (Figs. 5E–F). Paracymbium fused to the tegulum and hook-shaped (Fig. 5B). Conductor cup-shaped with a terminal apophysis that supports the embolus tip, conductor attachment to the tegulum membranous (Figs. 2E; 5C). Embolus base more that twice longer than wide, embolus filiform, embolus attachment to the tegulum membranous (Figs. 2E; 4F). Sperm duct coiled, diameter considerably enlarged towards the fundus and fundus same diameter as the sperm duct. Sperm duct entering the embolus base at the opposite end where the flagellum originates (Fig. 2D).

Variation. Female total length 4.2–4.3, cephalothorax length 1.8–1.9. Male total length 3.4–3.9, cephalothorax length 1.9–2.2.

Distribution. A. spinosa is only known from Sri Lanka.

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