

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

Phylogenetic placement of the spider genus *Taczanowskia* (Araneae: Araneidae) and description of a new species from Ecuador

Juan Pablo Jordán Dávalos

Biología

Trabajo de fin de carrera presentado como requisito
para la obtención del título de
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Quito, 12 de marzo de 2021

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

**HOJA DE CALIFICACIÓN
DE TRABAJO DE FIN DE CARRERA**

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description of a new species from Ecuador**

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Quito, 12 de Marzo de 2021

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RESUMEN

El género *Taczanowskia* Keyserling, 1879 es uno de los grupos más raros de arañas perteneciente a la familia Araneidae con solo cinco especies descritas y 17 especímenes citados en publicaciones. Nuestro estudio proporciona nuevos conocimientos sobre las relaciones evolutivas y la diversidad de *Taczanowskia*. Utilizando datos morfológicos, inferimos las relaciones evolutivas del género dentro de la familia Araneidae y proponemos la primera hipótesis filogenética que describe las relaciones entre especies de *Taczanowskia*. Nuestros resultados sitúan a *Taczanowskia* como hermana de *Mastophora* Holmberg, 1876, y confirman la monofilia de *Taczanowskia*. Describimos la primera especie de *Taczanowskia* de Ecuador, recolectada en las tierras bajas amazónicas en una comunidad Waorani en la cuenca del río Curaray. La nueva especie puede ser fácilmente diferenciada de todas las demás especies de *Taczanowskia* si presenta dos tubérculos en el opistosoma; un patrón de coloración claro-oscuro irregular distintivo, con manchas oscuras concentradas hacia el margen anterior y en las puntas laterales; pequeños haces de setas blancas que forman un retículo a lo largo de la parte dorsal del opistosoma, y los dos primeros fémures son gruesos pero sin dientes en el margen.

Palabras clave: Taczanowskia, Filogenética, Araneidae, Araña, nueva especie.

ABSTRACT

The genus *Taczanowskia* Keyserling, 1879 is one of the rarest groups of spiders in the orb-weaving family Araneidae, with only five species described and 17 specimens cited in publications. Our study provides new insights into the evolutionary relationships and diversity of *Taczanowskia*. Using morphological data, we tested the evolutionary relationships of the genus within the family Araneidae and propose the first phylogenetic hypothesis depicting the relationships among species of *Taczanowskia*. Our results place *Taczanowskia* as sister to *Mastophora* Holmberg, 1876, and confirm the monophyly of *Taczanowskia*. We describe the first species of *Taczanowskia* from Ecuador, collected at a Waorani community on the River Curaray basin, Amazonian lowlands of Ecuador. The new species can be easily diagnosed from all other species of *Taczanowskia* by having two tubercles in the opisthosoma; a distinct patchy dark-light colouration pattern, with dark spots concentrated towards anterior margin and on lateral tips; small bundles of white setae forming a reticulum across the dorsal part of the opisthosoma, and first two femora thick but lacking teeth on the margin.

Key words: Taczanowskia, Phylogenetics, Araneidae, Spider, New Species.

TABLA DE CONTENIDO

Introduction.....	9
Materials and Methods.....	10
Results.....	16
Taxonomy.....	22
Discussion.....	30
Conflicts of Interest.....	30
Declaration of funding.....	33
Acknowledgements.....	33
References.....	34
Anex A: Character State matrix for Species phylogeny.....	41
Anex B: Table Summary of phylogenetic hypothesis.....	42
Anex C: Family Bayesian Optimal tree.....	44

ÍNDICE DE FIGURAS

Figure 1.....	19
Figure 2.....	20
Figure 3.....	20
Figure 4.....	21
Figure 5.....	21
Figure 6.....	27
Figure 7.....	27
Figure 8.....	28
Figure 9.....	29

INTRODUCTION

The Araneidae family is one of the most species-rich families of spiders, currently with 3,059 described species in 177 genera and with a worldwide distribution (World Spider Catalog 2021). Spiders of this family are commonly called “orb weavers”, building conspicuous geometric orbicular webs to catch a wide variety of airborne prey (Scharff et al. 2020). However, members of some araneid genera do not build webs and are furtive hunters, deceiving their prey by producing sex pheromones that attract male moths (Eberhard 1980; Yeargan 1994). Spiders commonly known as “bolas spiders”, including the genera *Cladomelea* Simon, 1895, *Mastophora* Holmberg, 1876 and *Ordgarius* Keyserling, 1886, hunt extending their anterior legs and swinging one or more viscid droplets at the end of a single silk line to catch their prey (Eberhard 1980; Yeargan 1994; Leroy et al. 1998; Scharff & Hormiga 2012; Tanikawa et al. 2014). *Celaenia* Thorell, 1868 and *Taczanowskia* Keyserling, 1879 also entirely lack orb webs, catching their prey by using a pair of enlarged claws at the tip of their two anterior legs, (Eberhard 1981; Scharff et al. 2020).

Taczanowskia and *Celaenia* have been considered closely related genera (included in the tribe Celaeniini = Celaeneae Simon, 1895) which are in turn related to species of the tribes Mastophorini = Mastophoreae Mello-Leitão, 1931 and Cyrtarachnini = Cyrtarachneae Simon, 1895 (Simon 1895; Eberhard 1980, 1981, 1982; Levi 2003). Recent molecular phylogenies have included *Celaenia*: Tanikawa et al. (2014) recovered a moderately supported union of *Celaenia*, *Mastophora* and *Ordgarius*; and Scharff et al. (2020) found a close relationship between *Celaenia*, *Exechocentrus* Simon, 1889, and *Mastophora*, in a clade informally termed “Mastophorines”. Scharff et al. (2020) also determined the informal clade “Cyrtarachnines” as the sister clade to “Mastophorines”, which had already been vaguely supported by the molecular phylogeny presented years earlier by Tanikawa et al.

(2014) but had not been fully tested due to the lack of relevant outgroups. Lastly Scharff et al. (2020), identifies an additional informal clade the “Nuctenines” as the basal clade to the “Cyrtrachnines” + “Mastophorines” clade. However, the phylogenetic position of *Taczanowskia* remains uncertain, since it has not been included in any phylogenetic studies (Scharff & Coddington 1997; Scharff et al. 2020).

Taczanowskia is one of the rarest genera of Neotropical araneid spiders. Just five species have been described with very patchy distributions: *T. gustavoi* Ibarra-Núñez, 2013 occurs in southern Mexico, and four species have a cis-Andean distribution: *T. sextuberculata* Keyserling, 1892 from southern Brazil and Colombia; *T. striata* Keyserling, 1879 from Brazil and Peru; and *T. trilobata* Simon, 1897 and *T. mirabilis* Simon, 1897 from northern Argentina, Brazil, Bolivia, Peru and Colombia (Levi 1996; Ibarra-Núñez 2013). Few records have been reported for the genus *Taczanowskia* and just 17 specimens from scientific collections have been cited in the literature (Levi 1996; Ibarra-Núñez 2013; Castanheira et al. 2016; Nogueira et al. 2014).

In this publication, we present the first phylogenetic hypotheses on the generic position and interspecific relationships of *Taczanowskia*, based on morphological characters, and the description of a new species in the genus from the Amazonian lowlands of Ecuador.

MATERIALS AND METHODS

Field Work

We organised an expedition to the tropical rainforest of the Middle Curaray River basin, province of Pastaza, Ecuador. Arachnological surveys were conducted at two Waorani communities: Gomataon (1.1659722°S, 77.1676944°W, 275 m) on 15–20 October 2018, and Geyepade (1.294683°S, 77.069783°W, 240 m) on 21–25 October 2018. Surveying techniques

included manual trapping along 200 m transects, sampled three times per day: morning, evening, and night. Coordinates were obtained by means of a Garmin eTrex10 Handheld Navigator GPS (WGS84). Spiders were photographed alive in the field, using a Canon 7D camera body with a 60 mm macro lens. Specimens were preserved in 75% ethanol and are deposited at the Museo de Zoología, Universidad San Francisco de Quito, Ecuador (ZSFQ).

Morphological description of the new species

Description format, definitions, terminology, abbreviations, and measurements follow standards proposed by Levi (1993, 1996, 2002). The following abbreviations are used: ALE= anterior lateral eyes, AME= anterior median eyes, PLE= posterior lateral eyes, PME= posterior median eyes. Leg measurements were made from the dorsal side. Morphological analyses, measurements, and photographs were produced with an Olympus SZX16 stereomicroscope outfitted with an Olympus DP73 digital colour camera. Measurements were recorded using Micro Imaging Software CellSens for Olympus. Colour descriptions were based in live colour photographs taken in the field, following standards presented by Köhler (2012; colour codes in parentheses). Line drawings were based on proportions measured using Olympus SZX16 stereo-microscope photographs; morphological structures were first sketched using transformed proportions, illustrated with ink and digitised with a graphic tablet and Adobe® Photoshop CS6 software.

Phylogenetic Analyses

We used two different morphological data matrices for our phylogenies. To determine the placement of *Taczanowskia* within the family Araneidae, we used the morphological dataset presented by Scharff and Coddington (1997), which included 57 genera and 13 outgroup taxa (70 terminal taxa). The analysis was informed by 82 characters including: male and female sexual characters, somatic characters, and behavioural characters. The character descriptions and polarizations were presented by Scharff and Coddington (1997). We

downloaded the original dataset from TreeBASE (www.treebase.org), adding the new species of *Taczanowskia* herein described as a representative of the genus, resulting in a final matrix with 71 terminal taxa. Only female characters of *Taczanowskia* were used due to the lack of male individuals and final data were coded as follows (“-” = inapplicable, “?” = unknown): “?” 1-24, 0, 0, 0, 1, 0, 0, 0, ?, ?, ?, 0, 0, 0, 0, 1, 1, 0, 0, ?, 0, ?, 0, 0, 0, 0, 1, 1, 1, 0, 0, 0, 0, -, 0, ?, 1, ?, 0, 0, 1, 0, 0, 0, 1, 0, 0, 2, ?, 0, 2, -, -, -, -, -, 1, 1, -. Scharff and Coddington (1997) remains the most comprehensive morphological study of the family Araneidae available to date. Several studies have used the dataset by Scharff and Coddington (1997) to place other araneid genera within the overall family phylogeny (Tanikawa 2000; Kuntner 2002; Kuntner & Hormiga 2002; Smith 2006; Harmer & Framenau 2008; Schmidt & Scharff 2008; Framenau *et al.* 2010a; Framenau *et al.* 2010b; Framenau 2011; Magalhães & Santos 2012). We refrained from using more recent versions of the dataset by Scharff and Coddington (1997) or adding all *Taczanowskia* species to the large family data matrix because including a large number of new taxa without adding new informative characters may result in trees with little to no resolution (Harmer & Framenau 2008; Schmidt & Scharff 2008).

To infer relationships among species of *Taczanowskia* and test the taxonomic position of various genus of the sub-family clade, we developed a new character data matrix (different from the family matrix mentioned before), comprising 14 terminal taxa scored for 29 morphological and behavioural characters. Outgroups used for the species phylogeny (*Gasteracantha*, *Cyrtarachne*, *Mastophora*, *Argiope*, *Kaira*, *Nuctenea*, *Celaenia* and *Exechocentrus*) were informed by the hypothesised placement of the genus within the family phylogeny of previous publications (Simon, 1895; Scharff & Coddington 1997; Tanikawa 2000; Scharff *et al.* 2020). The outgroups *Kaira* and *Celaenia* were chosen to test the speculation made by Levi (1996) in which he argued that these genus are closely related. *Cyrtarachne* and *Mastophora* were included to test the “cyrtarachninae” clade presented by

Scharff and Coddington (1997) and by Tanikawa et al. (2014). The outgroup genus *Nuctenea* and *Exechocentrus* were specifically added to test the phylogenetic hypothesis of the larger clade in which *Taczanowskia* is contained presented by Scharff et al. (2020). Finally, the outgroup genus *Argiope* and *Gasteracantha* were included to anchor tree along as basal araneid genus. Character state information for comparative diagnoses was obtained from original species descriptions, taxonomic reviews (Levi 1978, 1996, 2003; Ibarra-Núñez 2013; Scharff and Hormiga, 2012), historical data sets (Scharff & Coddington 1997), and examined specimens.

Both character data matrices were edited using Mesquite, version 3.61 (Maddison & Maddison 2019). Cladistic analyses were performed using TNT 1.5 (Goloboff & Catalano 2016). We performed a heuristic search strategy using the new technology option in TNT to determine generic placement of *Taczanowskia* within Araneidae. We performed searches using the command “hold 1000; mult 30 = thr drift” as described by Hazzi *et al.* (2018). Trees found during searches were collapsed under “rule 1” (Coddington & Scharff 1994). We analysed the dataset under equal weights (EW) and implied weights (IW) (Goloboff 1993). We used various values of concavity for the IW analysis ranging from 1-11. To specify the concavity constant, we used the command “Piwe = k value” as described by Hazzi *et al.* (2018). For IW analysis, we used symmetric resampling as support measures and for EW analysis we used Jackknife values; both were run for 1000 replicates (Goloboff *et al.* 2003). For the species phylogeny, the smaller dataset was resolved using implicit enumeration and analysed using EW and IW, as described above. We ran a total of 24 parsimony analyses. To study character optimization, we used WinClada 10.00.08 (Nixon, 2002) on the consensus topology using accelerated transformation (ACCTRAN) (Swafford & Maddison 1987). Bayesian inference analyses were done in Mr. Bayes version 3.2.7a, using a variant of the Markov Chain Monte Carlo algorithms based upon the posterior probability distribution of

possible trees (Ronquist., et al 2019). We applied the morphological discrete Markov K model (Mkv Γ) for morphological data (Lewis 2001; Nylander 2004), which allows a gamma distribution in the rate variation between characters. Bayesian inference analyses sampled trees every 1000 generations using four chains (one cold and three heated) (Hazzi *et al.* 2018). For tree manipulation and final modelling, we used the software Figtree (Rambaut 2012).

Character descriptions and polarization

In the following section we describe the morphological characters used for the species phylogeny, following the format proposed by Scharff and Coddington (1997). Character states are presented in Table S1. Many of the characters used in the phylogenetic analyses were previously described and used in phylogenetic studies. To reference these studies and any relevant figures exemplifying the morphological character, we use the following codes: L96 = Levi (1996); L78 = Levi (1978); L03 = Levi (2003); SC97 = Scharff and Coddington (1997); IB13 = Ibarra-Núñez (2013).

Prosoma

Character 1. Carapace shape (SC97). (0) longer than wide; (1) wider than long. Females present a broad carapace structure (SC97 fig. 31).

Character 2. Carapace (SC97). (0) hirsute; (1) Glabrous (SC97 figs. 31, 35).

Character 3. Cephalic area dimension (L96). (0) Cephalic area narrower than half the carapace's widest diameter; (1) Cephalic area not narrower than half the carapace's widest diameter. Females present a narrow cephalic area, proportionally half compared to the carapace's width (L96 figs. 2, 8, 12, 16).

Character 4. Total length of female (L96). (0) Less than 7.0 mm.; (1) Between 7-8 mm (L96 fig. 39).

Opisthosoma

Character 5. Dorsal tubercles in the opisthosoma (L96). (0) present; (1) absent. Opisthosoma with any number of dorsal tubercles (L96 figs. 8, 12, 16).

Character 6. Number of dorsal tubercles in the opisthosoma (L96). (0) One pair; (1) More than one pair (L96 figs. 8, 12, 16).

Character 7. Dorsal tubercle morphology (IB13). (0) Nipple like tubercles; (1) Non nipple like tubercles. Dorsal tubercles with nipple-like morphology (L96 fig. 12; IB13 fig. 2, 3).

Character 8. Opisthosoma widest area (L96). (0) in the middle; (1) rear of opisthosoma; (2) adjacent to the prosoma. Widest measurement of the opisthosoma found in the middle (L96 fig. 8, 12, 16, 18, 20).

Character 9. Bundles of white setae in the opisthosoma (L96). (0) present; (1) absent. opisthosoma covered with sparse bundles of white setae (L96 fig. 16).

Character 10. Abdominal sigillae (SC97). (0) present; (1) absent. Sclerotized discs in the opisthosoma (L78 fig. 72; SC97 fig. 39, 40).

Character 11. Abdominal spines (SC97). (0) present; absent (1). Female opisthosoma with three pairs of spines (L78 fig. 72; SC97 fig. 39).

Female genitalia

Character 12. Epigynum (L96). (0) sclerotized; (1) not sclerotized (L96 figs. 6, 7, 10, 11).

Character 13. Scape with distal pocket (L96). (0) present; (1) absent (L96 figs. 6, 10, 14).

Character 14. Ventral area to the median plate in posterior view (L96). (0) sclerotized; (1) non-sclerotized (L96 figs. 7, 11, 15).

Character 15. Scape (SC97). (0) present; (1) absent (SC97 fig. 24).

Character 16. Genital tubercle (SC97). (0) present (*Gasteracantha cancriformis* (Linnaeus, 1758), SC97 fig. 23); (1) absent.

Legs

Character 17. First pair of legs with a pair of claws (L96). (0) present; (1) absent. Females present a pair of claws in the two anterior legs. Unique for new world orb-weavers (L96 plate 1; fig. 22).

Character 18. First two pairs of femora armed with rows of teeth (L96). (0) present; (1) absent. Row of teeth present along the edge of the first and 0 femora. Unique for new world orb-weavers (L96 plate 1; fig. 16, 21).

Character 19. Thickness of the first pair of femora (L96). (0) thick (enlarged); (1) straight (not enlarged). (L96 fig. 16, 21).

Behaviour

Character 20. Orb-web (L03). (0) present; (1) absent.

Character 21. Hunting technique (L03). (0). Sticky silk in web; (1) use legs.

Character 22. Reported use of pheromones (L96). (0) present; (1) absent.

Character 23. Resting place (L03). (0) exposed; (1) same as hunting position.

Male genitalia & Size ratio

Character 24. Male abdominal shape (SC97). (0) Normal; (1) Star Shped; (2) U-shaped; (3) Heart-shaped.

Character 25. Sustentaculum (SC97). (0) absent; (1) present.

Character 26. Female / male size ratio (SC97). (0) < 2 times; (1) > 2 times.

Accesories

Character 27. Serrate accesory claw setae (SC97). (0) absent; (1) present.

Character 28. Ventral Condyles (SC97). (0) present; (1) absent.

Character 29. Number of trichobothria on metatarsus (SC97). (0) 0–1; (1) many.

RESULTS

Phylogenetic analyses

Heuristic search under EW in TNT yielded 12 most parsimonious trees for the family Araneidae. Topologies found under IW analysis were unstable and showed little resolution; varying in the number of most parsimonious trees recovered, their length, and the comparison indexes (Table S2). For this reason, we chose the EW strict consensus tree (L = 312, CI = 0.31, RI = 0.70) as the preferred phylogenetic hypothesis (Fig. 1). The topology found with Bayesian inference resembles topologies found under IW analysis, and was generally congruent with EW parsimony topology (Fig. S1). All analyses placed *Taczanowskia* as sister taxa to *Mastophora*, forming a clade sister to *Cyrtarachne* and *Pasilobus* Simon, 1895; relationships with high posterior probability support in the Bayesian inference topology (Fig. S1) but relatively low symmetric resampling support in the parsimony topology (Fig. 1). Grouping of *Taczanowskia* and *Mastophora* is morphologically supported by four homoplastic conditions: absence of patellae with macrosetae (char. 4), presence of sustentaculum (char. 40), absence of abdominal sigillae (char. 56), and loss of orb-web (char. 74). The clade formed by (*Taczanowskia* + *Mastophora*) + (*Cyrtarachne* + *Pasilobus*) is supported by the following synapomorphies: absence of low-shear sticky silk lines (char. 79), absence of very sticky silk lines (char. 80), and the absence of extreme 4th leg combing (char. 81) (Fig. 2).

Parsimony analysis of the species data matrix yielded six most parsimonious trees under EW and IW analysis. Trees found under both weighting regimes (EW and IW) were stable, showing the same retention/consistency index and similar resampling average support (Table S3). All trees found in the heuristic search in TNT presented the same topology. All trees found under IW had a length of 46 steps, unlike the topology found under EW with 47 steps. We choose, the strict consensus tree under implied weight K= 3 (L = 46, CI = 0.74, RI

= 0.72) as the preferred phylogenetic hypothesis, because it had the highest branch support values and was less parameter-dependent (Fig. 3). Bayesian and parsimony topologies were largely congruent, carrying into their relationships between species (Fig. 4).

All analysis recovered a monophyletic *Taczanowskia*, supported by high symmetric resampling and posterior probability values (Fig. 4). Monophyly of *Taczanowskia* is supported by seven morphological synapomorphies: cephalic area narrower than half the carapace widest diameter (char. 3), non-sclerotized epigynum (char. 12), presence of a scape with distal pocket (13), ventral area to the median plate in posterior view (char. 14), first pair of legs with a pair of claws (char. 17), first two pairs of femora armed with rows of teeth (char. 18), thick (enlarged) first pair of femora (char. 19). All parsimony trees have *T. trilobata* as the most basal species and group in one clade: *T. sextuberculata*, *T. striata*, *T. gustavoi*, *T. mirabilis* and the new species herein described. Bayesian trees recovered two clades within the genus polytomy, grouping *T. sextuberculata* and *T. gustavoi* as sister taxa and *T. striata*, *T. mirabilis* and the new species in another clade, both supported by relatively high posterior probability values (Fig. 3, 4).

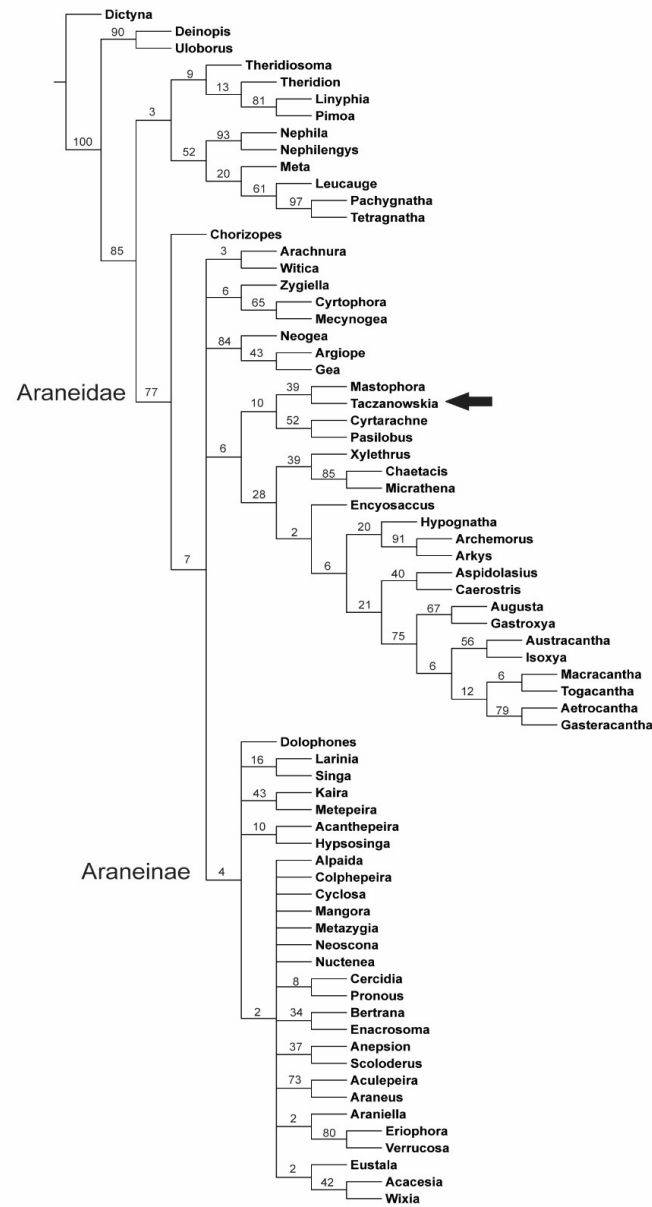


Figure 1. Strict consensus of the most parsimonious tree obtained by cladistic analysis of Araneidae under equal weights. Arrow shows the position of Taczanowskia. Support values by Jackknife for 1000 replicates. Support values for groups are symmetric resampling expresses as GC (Group present/Contradicted) frequency differences of 1000 replicates.

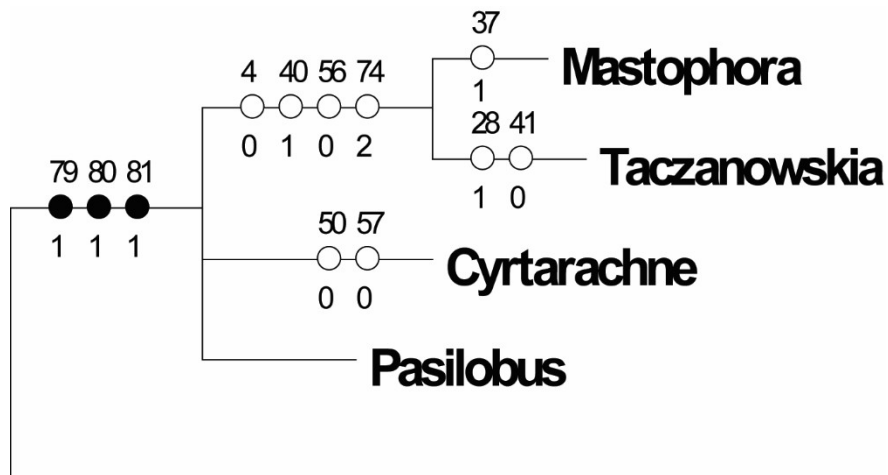


Figure 2. Strict consensus of the most parsimonious tree under EW for Araneidae. Non-homoplasious and homoplasious transformations (ACCTRAN) indicated by black and white circles. Character numbers are above the branches and character states are below the branches.

Figure 3. Strict consensus of the most parsimonious species tree obtained by cladistic analysis using implied weights ($K=3$). Support values for groups are symmetric resampling expresses as GC (Group present/Contradicted) frequency differences of 1000 replicates.

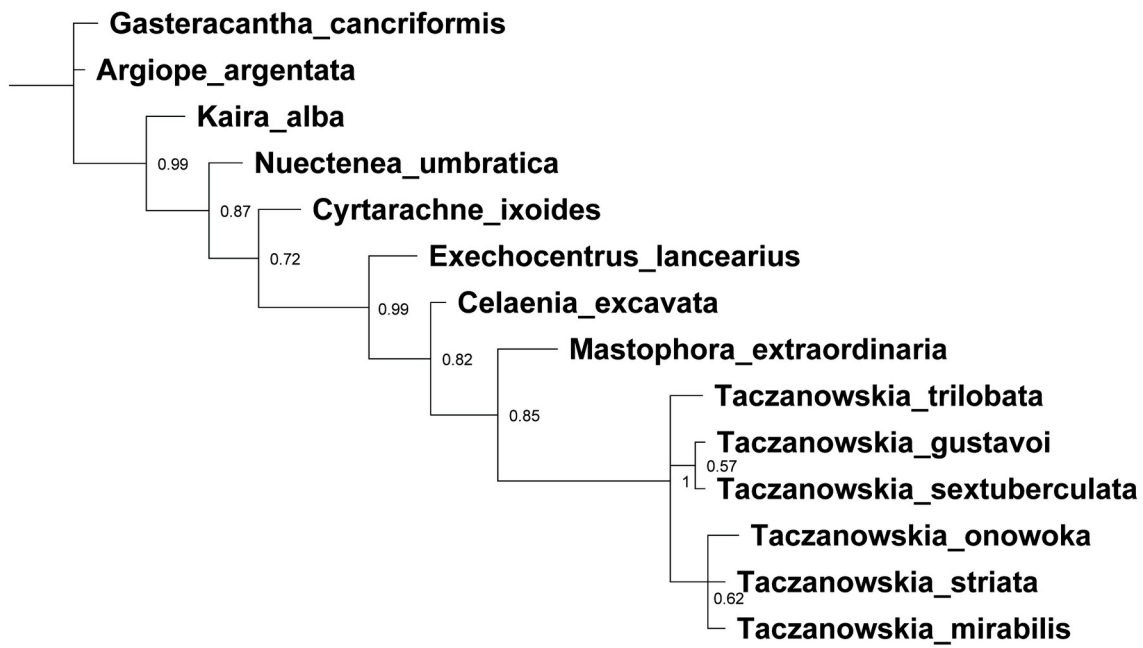


Figure 4. Bayesian optimal tree obtained under the (Mkv Γ) model of the species. Values in nodes represent posterior probabilities.

Figure 5. Strict consensus of the most parsimonious species tree under implied weights (K=3). Non-homoplasious and homoplasious transformations (ACCTRAN) indicated by black and white circles. Character numbers are above the branches and character states are below the branches.

TAXONOMY

Family **ARANEIDAE** Clerck

Genus *Taczanowskia* Keyserling

Identification key for females of the genus Taczanowskia (modified from Levi 1996 and Ibarra-Nuñez 2013)

1. Sides of opisthosoma with two lobes; opisthosoma widest near its posterior end ...
Taczanowskia trilobata Simon, 1897
- Opisthosoma without such lobes; widest in the middle ... 2
2. Opisthosoma almost circular in dorsal view; femora III with a ventral row of teeth ... *T. gustavo* Ibarra-Nuñez, 2013
- Opisthosoma clearly wider than long in dorsal view; femora III without ventral row of teeth ... 3
3. Dorsum of opisthosoma with three pairs of tubercles ... *T. sextuberculata* Keyserling, 1892
- Opisthosoma with one pair of dorsal tubercles (Fig. 7B) ... 4
4. Opisthosoma with coloured patches, black feather-like setae and bundles of white setae on each side; carapace with radiating dark lines; total length less than 5.5 mm, narrower opisthosoma (1.4 times its length) ... *T. striata* Keyserling, 1879
- Opisthosoma without feather-like setae, carapace without radiating dark lines; total length usually more than 6.0 mm, wider opisthosoma (1.8 times its length) ... 5
5. Opisthosoma with patchy dark-light colouration, dark spots concentrated towards anterior margin and on lateral tips; bundles of white setae across the entire surface, forming a distinct reticulum (Fig. 6); first two femora thick but lacking teeth on margin ... *T. onowoka* sp. nov.
- Opisthosoma not as above, with different colouration patterns; bundles of setae absent; first two femora with teeth on margin ... *T. mirabilis* Simon, 1897

Taczanowskia onowoka, sp. nov.

(Fig. 6–8)

ZooBank registration: urn:lsid:zoobank.org:act:60E8265B-BC21-48F3-A193-96CA63314096

Holotype

Adult female; **República del Ecuador**, provincia de Pastaza, cantón Arajuno, parroquia Curaray, comunidad Waorani de Gomataon [southern side of River Nushino]; - 1.1659722, -77.1676944; 275 m; 16.x.2018; Mariela Domínguez Trujillo leg.; ZSFQ-I4972.

Diagnosis

Taczanowskia onowoka sp. nov. differs from all other species of the genus by having two tubercles in the opisthosoma; a distinct patchy dark-light colouration pattern, with dark spots concentrated towards anterior margin and on lateral tips; small bundles of white setae forming a reticulum across the dorsal part of the opisthosoma, and first two femora thick but lacking teeth on the margin, a character otherwise present in all other congeneric species (Fig. 6–7).

Description of holotype

Prosoma (Fig. 6): Cephalic region Jet Black (300) with Army Brown (46) accents towards the middle. Thoracic region adjacent to opisthosoma Pale Cinnamon (55), bordered by patches of Jet Black extending from PLE to opisthosoma. Thoracic region much wider than cephalic region. Chelicerae mostly Jet Black, with two pro-marginal teeth and without teeth on retromargins. Labium and endites Jet Black, endites present marginal golden-brown setae. Anterior sternum Jet Black, posterior sternum Mikado Brown (42). Sternum shaped like a nicked-top heater shield, longer than wide, widest at coxae II. Coxae I Jet Black with scattered Mikado Brown patches; coxae II mostly Mikado Brown with longitudinal Jet Black

lines on the middle; coxae III and IV mostly Mikado Brown with reduced middle Jet Black patches adjacent to trochanters in ventral view. Trochanters I and II Jet Black; trochanters III and IV half Jet Black/Mikado Brown (half contiguous to sternum, half contiguous to femur). Legs I and II have distinct alternate banded pattern, with Walnut Brown (27) proximal to body alternating with Pale Pinkish Buff (3). Femora of legs III and IV with Walnut Brown patch adjacent to trochanter; patella, tibia, and tarsus Light Buff (2). Femora of legs I-II wider and longer than femora of legs III-IV. All legs are coated by reduced setae-like structures, colour coinciding with leg colouration pattern. Spines and additional distinct morphological structures absent. Retro-lateral claws of legs I-II significantly larger than pro-lateral claws (Fig. 7A).

Opisthosoma (Fig. 6-7B): Marginal to carapace, widest in the middle, about 2× wider than long. Anterior margin with two small projections, giving the margin a slight M-shape. Opisthosoma covered by non-symmetrical, size varying, white bundles of setae forming a distinct reticulum. Chestnut (30) spots present along anterior margin of opisthosoma, bordered by white setae reticulum. Two large Chestnut spots present on lateral edges of opisthosoma, located towards widest section of opisthosoma. Dorsum with two small lobed tubercles, symmetrically located on widest section of opisthosoma. Four small Jet Black spots on centre of opisthosoma, distributed like the four vertices of a trapezoid. Two Sepia (279) marks shaped like inverted V towards mid-posterior opisthosoma. Venter and posterior margin of opisthosoma with Mikado Brown venation-like marks. Epigynum anterior to epigastric furrow located on transversely margin. Epigynum with short and translucent scape projecting anteriorly from its base, slightly sclerotized. Scape barely visible with the naked eye due to its reduced size, smooth texture (Fig. 8).

Preserved specimen maintains colouration patterns. Vibrant colour tones were lost in preservative and remaining colour pigments became opaque. Legs banded pattern remains

visible, but lighter tones became translucent. Same discolouration is observed in opisthosoma with a brownish colour predominant over the whole opisthosoma. Venation pattern became translucent. All setae-like and setae structures remain intact.

Measurements of holotype (in mm): Total length 7.71; carapace 3.03 long; 3.45 maximum wide in thoracic region, 1.1 wide behind PLE. Diameter of AME 0.18, PME 0.98 of an AME, laterals 0.68 diameter, AME 0.96 diameters apart, ALE 1.46 diameters from AME, PME 0.65 diameters apart, PLE 1.77 diameters from PME, ocular quadrangle as wide behind as in front; clypeus height 1.4 diameters of AME. Right side leg measurements (femur, patella, tibia, metatarsus, tarsus): Leg I. 4.92, 1.13, 2.89, 1.76, 6.55; Leg II. 5.08, 1.02, 3.13, 1.66, 0.64; 3. 2.11, 1.13, 1.25, 0.74, 0.50 4. 2.99, 1.19, 1.83, 1.00, 0.51. Opisthosoma length (in the middle) 4.54, maximum width 7.97; ratio with to length 0.97.

Distribution and Natural History

Currently known only from the type locality, in the vicinity of Gomataon, a Waorani community on the Nushino River, an affluent of the Curaray River, Ecuador (Fig. 9). The holotype was collected in non-flooded Lowland Evergreen forest, during a night hike while conducting manual active surveys in a trail crossing secondary forest with fairly open canopy, between forest clearings and near small Waorani settlements. It was perched in the middle of the upper side of a leaf, ca. 1.75 meters above ground, at 22h00. The night was misty and with an overcast moon. The spider lacked the second leg of the left side, amputated from the base of the trochanter (Fig. 6). No additional specimens were found despite intensive surveys.

Etymology

The specific epithet *onowoka* is a noun in apposition, meaning spirit in Wao Tededo, language spoken by the Waorani people. This name honours the Waorani, their strong spirit, their unique culture, and their fights to save the Amazon rainforest. Waorani are intimately familiar with Amazonian biodiversity, and we are deeply thankful for their permission and

support to explore their lands and describe this spider as a new species for science. The epithet also refers to the project where the new species was collected: “*Proyecto Descubre Napo—NUNA*”, since *nuna* also means spirit but in the Kichwa language.

Remarks

Taczanowskia onowoka sp. nov. is most similar to *T. mirabilis* and *T. striata*. *Taczanowskia mirabilis* differs by lacking bundles of setae and by the colouration of its opisthosoma; while *T. striata* has bundles of setae restricted to the sides of the opisthosoma, shows black feather-like setae and carapace with radiating dark lines. The female of *T. onowoka* sp. nov. is larger than all other species with a total length of 7.71 mm, except *T. mirabilis* which has a variable total length of up to 8 mm.

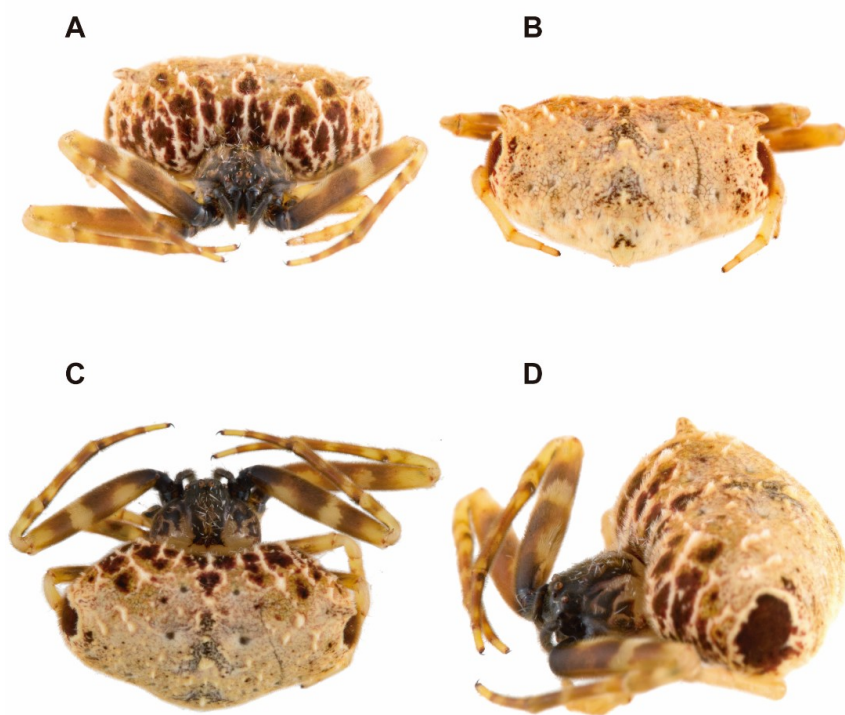


Figure 6. *Taczanowskia onowoka* sp. nov., female holotype. Photographs of living holotype showing habitus in: A: anterior view; B: posterior view; C: dorsal view; and D: latero-dorsal left view.

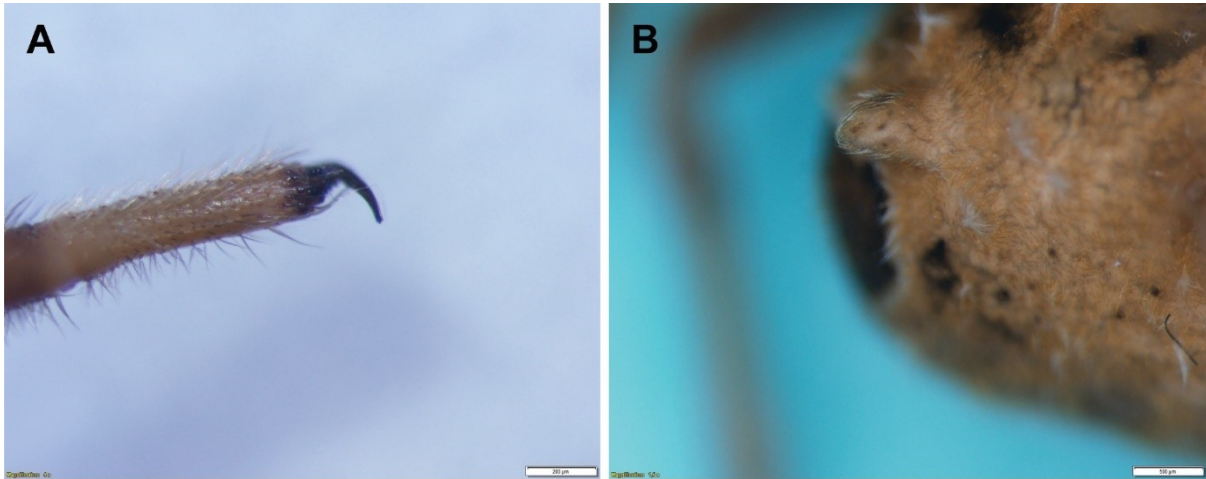


Figure 7. *Taczanowskia onowoka* sp. nov, female holotype. **A** Leg I claw; **B** Left tubercule lateral view.

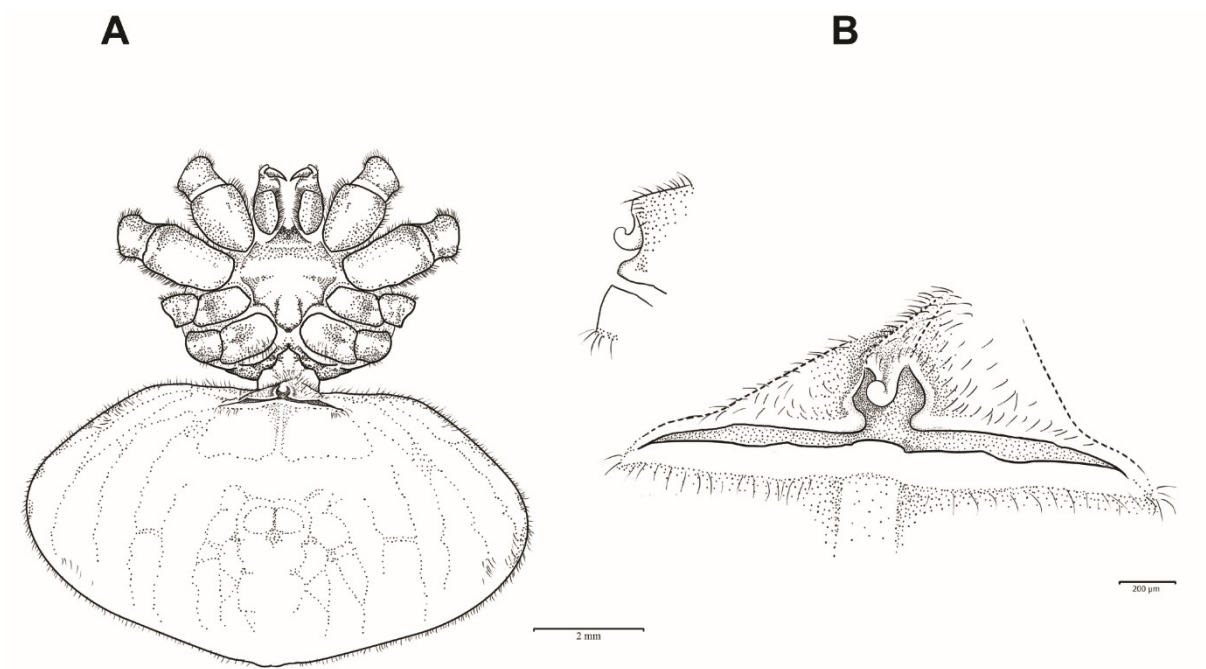


Figure 8. *Taczanowskia onowoka* sp. nov, female holotype illustration. **A** Habitus ventral view; **B** Epigyne anterior and lateral view.

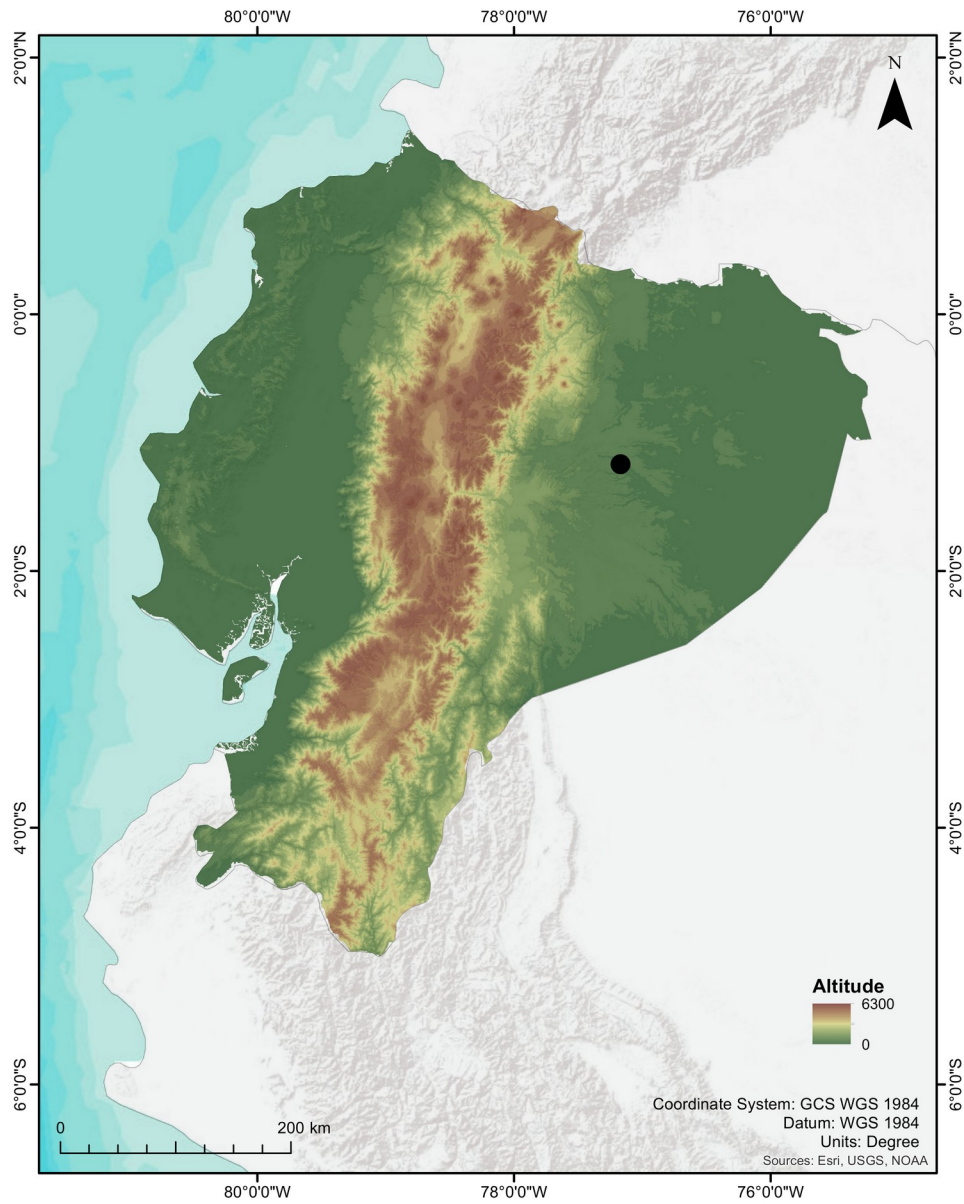


Figure 9. Map of Ecuador showing the type locality (black dot) of *Taczanowskia onowoka* sp. nov.: Gomataon (-1.1659722, -77.1676944; 275 m), a Waorani community on the southern side of River Nushino, Amazonian lowlands of Ecuador.

DISCUSSION

Our data place *Taczanowskia* as the sister genus of *Mastophora*, and both as sister to *Cyrtarachne* + *Pasilobus*, with high support in both parsimony and Bayesian analyses (Fig. 1), confirming previous hypotheses about the close relationships between Celaeniini, Mastophorini and Cyrtarachnini (Simon 1895; Levi 1996; Eberhard 1980, 1981, 1982; Levi 2003; Tanikawa et al. 2014; Scharff et al. 2020). Additionally, our results place *Taczanowskia* within the “Mastophorines” clade (sensu Scharff et al. 2020) with a minor change, recovering *Celaenia* as the sister clade to *Mastophora* + *Taczanowskia*, instead of *Exechocentrus* (Fig. 3,4). This slight change of the phylogenetic relationships in the “Mastophorines” clade could be due to the constraint of informative morphological characters. Interestingly, Levi 1996, suggested *Celaenia* as the closest relative to *Taczanowskia*, even including the species *Celaenia excavata* for reference and morphological comparison in his taxonomic revision of *Taczanowskia*. Eventough our outgroup genus selection does not fully represent the “Cyrtarachnines” clade depicted in Scharff et al. 2020, our data strongly supports a sister group relationship between the two informa clades, relationship that had already been recovered in previous studies based on behavioral characters (Eberhard, 1980; Robinson, 1982; Stowe, 1986; Scharff and Coddington, 1997).

Our results also support the monophyly of *Taczanowskia* (Fig. 3), but the intrageneric relationships were not fully resolved due to a hard polytomy found in the Bayesian and parsimony analyses. Tree topologies recovered are not congruent with each other, differing in the interspecific grouping. The taxonomic delimitation of the araneid sub-family Cyrtarachninae has been very problematic since it first was described by Simon (1892). Subsequent studies investigating the systematics of Cyrtarachninae have included or excluded various genus in their analysis, thus not fully resolving the relationships among the genus of

the family (Scharff and Coddington 1997; Tanikawa et al. 2014; Scharff et al. 2020). This has perpetuated the taxonomic incongruencies of the group, and until date no study – including this one – has presented a complete analysis of the relationships of the Cyrtarachninae family. For this reason we have to constrain the interpretation of our results for each particular scenario. For instance, the tribes proposed by Simon (1892) are supported by our phylogenies. The phylogeny presented by Scharff and Coddington (1996) that excluded *Celaenia* is rejected since, in both the latter work in Scharff et al. (2020) and our results, *Celaenia* is recovered in the same monophyletic clade as *Taczanowskia*. The hypothesis presented by Tanikawa et al. (2014) can not be rejected by our data since we not include *Ordgarius* but, we speculate that the closest relative of *Mastophora* would be *Taczanowskia* therefore displacing *Ordgarius*. Lastly our results strongly corroborate the informal clade “mastophorines” proposed by Scharff et al. (2020). We recognize the limitations of a phylogenetic study based solely on morphological characters, however we consider the need for a first hypothesis depicting the phylogenetic relationships of *Taczanowskia*, despite its limitations. Studies including additional evidence (e.g., molecular data, morphological characters from males) may provide a better understanding of the evolutionary relationships within *Taczanowskia* and in the larger “mastophorines” clade sensu Scharff et al. (2020).

Due to the apparent natural rarity of spiders of the genus *Taczanowskia*, available taxonomic descriptions are based on very few specimens and little is known about morphological and chromatic intraspecific variation and dimorphism. Levi’s (1996) revision of *Taczanowskia* reported almost no phenotypic variation for most species. However, important colour variations seem to exist in *T. mirabilis*, either due to natural intraspecific differences or it may suggest that more than one species is currently included under the name. Levi (1996) and Ibarra-Nuñez (2013) reported the opisthosoma of *T. mirabilis* as evenly

coloured. However, the opisthosoma in the holotype of *T. mirabilis* was described as mostly black with light marks on lateral tips (Simon 1897; Levi 1996), and the opisthosoma of the holotype of *T. pulchra* Soares, 1944 (placed in the synonymy of *T. mirabilis* by Levi (1996)) was white, irregularly stained pinkish and black, with large pink marks on the lateral tips. Levi (1996) reported a female from Rio Grande do Sul (Brazil) with a spotted opisthosoma, and another one from Irupana (Bolivia) with a median black band on the opisthosoma and lateral black tips.

The Curaray River basin, type locality of the new species, is part of one of the most important biodiversity hotspots in the world: the Napo River Basin, which holds outstanding species richness and endemism levels (Dinerstein et al. 1995; Olson DM et al. 2001; Bass et al. 2010). Although expected due to the generic distribution, the discovery of this new species remarks how little is known about the diversity of spiders in Ecuador. High diversity of spiders of the family Araneidae has been reported throughout the Neotropics, with biodiversity hotspots in central and western Amazonia, the Atlantic Forest, the Pacific lowlands and Andes of Colombia, and across Panama (Santos *et al.* 2017). Still, the number of species of Araneidae recorded in Ecuador is low, in comparison with neighbouring countries and when considering species richness in other spider families (Santos *et al.* 2017). For example, Ecuador is a diversity hotspot for Oonopidae, and a single expedition in 2009 yielded 3 new generic records and 43 new species (Santos et al. 2017). Low araneid species richness in Ecuador is most certainly caused by collecting bias and limited sampling effort, aggravating Linnaean (large number of undescribed species) and Wallacean (species with unknown geographical distribution) shortfalls (Bini et al. 2006). Information on the diversity, ecology and biogeography of araneid spiders of Ecuador is largely absent. Aside from seminal works by Herbert Levi and collaborators (see Levi 2002), little has been published on

the Ecuadorian fauna of Araneidae in recent years (Cisneros-Heredia & Carrasco-Montalvo 2016)

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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ANEX A: CHARACTER STATE MATRIX FOR SPECIES PHYLOGENY

<i>Species</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Gasteracantha cancriformis</i>	1	0	1	0	1	-	-	0	1	0	0	0	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0
<i>Argiope argentata</i>	1	0	1	0	1	-	-	0	1	0	0	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0
<i>Kaira alba</i>	1	0	1	0	1	-	-	2	1	0	1	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
<i>Cyrtarachne ixoides</i>	1	1	1	1	1	-	-	0	1	0	1	0	1	0	0	1	1	1	1	0	0	1	0	1	1	0	1	
<i>Nuctenea umbratica</i>	1	1	1	0	1	-	-	2	1	0	1	?	?	1	1	1	1	1	1	0	0	1	0	0	1	0	1	
<i>Exechocentrus lancearius</i>	1	1	1	0	1	-	-	0	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	2	1	0	1	
<i>Celaenia excavata</i>	0	1	1	0	1	-	-	0	1	1	1	0	1	0	0	1	1	1	1	1	1	0	1	3	1	0	0	
<i>Mastophora extraordinaria</i>	0	1	1	0	1	-	-	2	1	1	1	0	1	0	1	1	1	1	1	0	1	0	0	3	0	1	0	
<i>Taczanowskia mirabilis</i>	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	3	0	1	0	
<i>Taczanowskia sextuberculata</i>	0	1	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	3	0	1	0	
<i>Taczanowskia striata</i>	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	3	0	1	0	
<i>Taczanowskia trilobata</i>	0	1	1	0	1	-	-	1	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	3	0	1	0	
<i>Taczanowskia gustavoii</i>	0	1	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	1	1	0	1	3	0	1	0	
<i>Taczanowskia onowoka</i>	0	1	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	1	0	1	1	0	1	3	0	1	0	

ANEX B: TABLE SUMMARY OF PHYLOGENETIC HYPOTHESIS

Summary of phylogenetic hypotheses of the most parsimonious trees (MTPs) under EW and IW analysis (k values form 1-11) of the phylogeny of Aranidae. Av. Sym. = average support fo summetric resampling.

	Length	MPTs	Consistency index	Retention index	Av. Sym.
EW	312	12	0.31	0.70	30
1	428	10	0.23	0.54	29.2
2	391	8	0.25	0.59	29.4
3	394	3	0.25	0.59	29.9
4	388	1	0.25	0.60	30.4
5	377	79	0.26	0.61	30.8
6	381	36	0.26	0.61	30.8
7	373	11	0.26	0.62	31.2
8	359	4	0.27	0.64	31.5
9	355	3	0.29	0.67	31.5
10	337	3	0.29	0.67	31.6
11	333	3	0.29	0.67	31.7

Summary of phylogenetic hypotheses of the most parsimonious trees (MTPs) under EW and IW analysis (k values form 1-11) of the species phylogeny. Av. Sym. = average support fo summetric resampling.

	Length	MPTs	Consistency index	Retention index	Av. Sym.
EW	47	6	0.73	0.70	43
1	46	6	0.75	0.75	42.2
2	46	6	0.75	0.75	43
3	46	6	0.75	0.75	42.2
4	46	6	0.75	0.75	42.9
5	46	6	0.75	0.75	43
6	46	6	0.75	0.75	42.9
7	46	6	0.75	0.75	42.2
8	46	6	0.73	0.72	43.3
9	46	6	0.75	0.75	42.9
10	46	6	0.75	0.75	43.3
11	46	6	0.75	0.75	43

ANEX C: FAMILY BAYESIAN OPTIMAL TREE

Bayesian optimal tree obtained under the (Mkv Γ) model indicating the generic placement of the genus *Taczanowskia* (arrow) in the phylogeny of the family Araneidae. Values in nodes represent posterior probabilities.

