

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

**From Taxonomic Puzzlement to Phylogenetic Clarity: After 142
Years, A Comprehensive Revision of the Tarantula Genus
Cyclosternum Ausserer, 1871 (Araneae, Theraphosidae)**

Pedro Joaquin Peñaherrera Romero

Biología

Trabajo de fin de carrera presentado como requisito
para la obtención del título de
Biólogo

Quito, 06 de Diciembre de 2023

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

HOJA DE CALIFICACIÓN DE TRABAJO DE FIN DE CARRERA

**From Taxonomic Puzzlement to Phylogenetic Clarity: After 142 Years, A
Comprehensive Revision of the Tarantula Genus *Cyclosternum* Ausserer,
1871 (Araneae, Theraphosidae)**

Pedro Joaquin Peñaherrera Romero

Diego Francisco Cisneros Heredia, PhD

Quito, 06 de Diciembre de 2023

© DERECHOS DE AUTOR

Por medio del presente documento certifico que he leído todas las Políticas y Manuales de la Universidad San Francisco de Quito USFQ, incluyendo la Política de Propiedad Intelectual USFQ, y estoy de acuerdo con su contenido, por lo que los derechos de propiedad intelectual del presente trabajo quedan sujetos a lo dispuesto en esas Políticas.

Asimismo, autorizo a la USFQ para que realice la digitalización y publicación de este trabajo en el repositorio virtual, de conformidad a lo dispuesto en la Ley Orgánica de Educación Superior del Ecuador.

Nombres y apellidos: Pedro Joaquin Peñaherrera Romero

Código: 00213042

Cédula de identidad: 1727122689

Lugar y fecha: Quito, 06 de Diciembre de 2023

ACLARACIÓN PARA PUBLICACIÓN

Nota: El presente trabajo, en su totalidad o cualquiera de sus partes, no debe ser considerado como una publicación, incluso a pesar de estar disponible sin restricciones a través de un repositorio institucional. Esta declaración se alinea con las prácticas y recomendaciones presentadas por el Committee on Publication Ethics COPE descritas por Barbour et al. (2017) Discussion document on best practice for issues around theses publishing, disponible en <http://bit.ly/COPETheses>.

UNPUBLISHED DOCUMENT

Note: The following capstone project is available through Universidad San Francisco de Quito USFQ institutional repository. Nonetheless, this project – in whole or in part – should not be considered a publication. This statement follows the recommendations presented by the Committee on Publication Ethics COPE described by Barbour et al. (2017) Discussion document on best practice for issues around theses publishing available on <http://bit.ly/COPETheses>.

RESUMEN

Se evaluaron los caracteres taxonómicos útiles para la diagnosis del género *Cyclosternum* Ausserer, 1871 a partir de una hembra adulta sintipo de *C. schmardae* junto con otras hembras y congéneros machos de especies, por el momento, no descritas para complementar con la determinación del género y confirmar el posicionamiento del resto de especies ecuatorianas de *Cyclosternum* en el género; siendo *C. ianthinum* la única que sí pertenece a *Cyclosternum*. Por otro lado, se sugiere que *Cyclosternum gaujoni* sea considerado como *species inquirenda* debido a que la genitalia del sintipo hembra no congeniaba con los caracteres morfológicos diagnósticos de la espermatoca de *Cyclosternum*. Se sugiere el traslado de *Cyclosternum pulcherrimaklaasi* al género *Thrixopelma* debido a las similitudes en la ilustración del bulbo palpar del holotipo macho y presencia de setas urticantes Tipo III y IV; generando la siguiente combinación *Thrixopelma pulckerrimaklaasi* comb. nov.. Adicionalmente tras una revisión preliminar de las especies de *Cymbiapophysa*, *Cymbiapophysa seldeni* es trasladada a *Cyclosternum* debido a la ausencia de la depresión media ventral del bulbo palpar en el holotipo macho de la especie; generando la siguiente combinación *Cyclosternum seldeni* comb. nov.. Además de la revisión general se propone una nueva hipótesis filogenética de Theraphosinae en base a morfología, actualizando los datos de los caracteres morfológicos utilizados por estudios previos. El árbol filogenético consenso preferido demostró la formación de un nuevo clado hermano de Lasiodoriformis. Este nuevo clado fue nombrado como Cycloformis y conformado por *Cyclosternum* y *Cymbiapophysa*, el cual fue nuevamente puesto a prueba y con firmando la formación de Cycloformis con otra matriz morfológica donde se incluyen más representantes del clado Lasiodoriformis. Por último, se discutió la relación entre las topologías generadas del árbol

filogenético de Theraphosinae obtenido en este estudio y los árboles filogenéticos basados en marcadores moleculares de otros estudios.

Palabras clave: Theraphosinae, Filogenia, Taxonomía, Morfología, Andes Norte, Lasiodoriformis

ABSTRACT

Taxonomic characters useful for the diagnosis of the genus *Cyclosternum* Ausserer, 1871 were evaluated from an syntype adult female of *C. schmardae* together with other females and male congeners of species, for the moment, not described in order to complement the determination of the genus and to confirm the placement of the rest of the Ecuadorian species of *Cyclosternum* in the genus; being *C. ianthinum* the only one that really belongs to *Cyclosternum*. On the other hand, it is suggested that *Cyclosternum gaujoni* should be considered as species inquirenda because the genitalia of the syntype female did not match the diagnostic morphological characters of the spermatheca of *Cyclosternum*. The transfer of *Cyclosternum pulcherrimaklaasi* to the genus *Thrixopelma* is also suggested due to similarities in the illustration of the palpal bulb of the male holotype and the presence of urticating setae Type III and IV; generating the following combination *Thrixopelma pulcherrimaklaasi* comb. nov. Additionally, after a preliminary revision of *Cymbiapophysa* species, *Cymbiapophysa seldeni* is moved to *Cyclosternum* due to the absence of the ventral median depression of the palpal bulb in the male holotype of the species; generating the following combination *Cyclosternum seldeni* comb. nov.. In addition to the general revision, a new phylogenetic hypothesis of Theraphosinae is proposed based on morphology, updating the morphological character data used by previous studies. The preferred consensus phylogenetic tree demonstrated the formation of a new sister clade to Lasiodoriformis. This new clade was named as Cycloformis and consisted of *Cyclosternum* and *Cymbiapophysa*, which was again tested and confirmed the formation of Cycloformis with another morphological matrix including more representatives of the clade Lasiodoriformis. Finally, the relationship between the topologies generated from the phylogenetic tree of Theraphosinae obtained in this study and phylogenetic trees based on molecular markers from other studies was discussed.

Key words: Theraphosinae, Phylogeny, Taxonomy, Morphology, Northern Andes, Lasiodoriformis

TABLE OF CONTENT

INTRODUCTION	12
MATERIALS AND METHODOLOGY	14
EXAMINATION OF SPECIMENS AND MUSEUMS	14
CANDIDATE SPECIES, SPECIES DELIMITATION, AND DESCRIPTION FORMAT	15
ABBREVIATIONS	16
PHYLOGENETIC ANALYSIS	16
RESULTS	18
PHYLOGENETIC ANALYSIS	20
TAXONOMY	26
<i>Genus Cyclosternum</i> Ausserer, 1871	26
<i>Cyclosternum gaujoni</i> Simon, 1889 <i>species inquirenda</i>	31
<i>Cyclosternum ianthinum</i> Simon, 1889	31
<i>Cyclosternum schmardae</i> Ausserer, 1871	34
<i>Cyclosternum seldeni</i> (Sherwood & Gabriel, 2023) <i>comb. nov.</i>	35
<i>Thrixopelma pulcherrimaklaasi</i> (Schmidt, 1991) <i>comb. nov.</i>	36
DISCUSSION	37
CONCLUSIONS	40
APPENDIX	45
APPENDIX A: CHARACTER LIST USED FOR GENERAL THERAPHOSINAE PHYLOGENY	45
APPENDIX B: CHARACTERS FOR CLADISTICS WITHIN CYCLOFORMIS AND LASIODORIFORMIS	47

INDEX OF TABLES

Table 1. Results from the phylogenetic analyses using implied weighting for generic placement of Cyclosternum and Cymbiapophysa within Theraphosinae.	21
Table 2. Results from the phylogenetic analyses using implied weighting for Lasiodoriformis and Cycloformis.....	23

INDEX OF FIGURES

<p>Figure 1. Preferred phylogeny of Theraphosinae (L= 162, CI = 0.40; RI = 0.64) obtained by implicit weights with symmetric resampling and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles.20</p>	20
<p>Figure 2. Preferred phylogeny of Lasiodoriformis and Cycloformis (L = 132, CI = 49, RI = 0.79) obtained by implicit weights with symmetric resampling and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles.....24</p>	24
<p>Figure 3. Close up view of Lasiodoriformis + Cycloformis (Cyclosternum + Cymbiapophysa) from the preferred phylogeny within theraphosinae (L= 169, CI = 0.43, RI = 0.67) obtained by implicit weights with symmetric resampling method and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles. Male palpal bulbs from top to bottom: <i>Cyclosternum</i> sp. Ilalo, <i>Cymbiapophysa carmencita</i>, <i>Lasiodora klugi</i> (Gabriel, 2016), <i>Nhandu sylviae</i> (Sherwood et al., 2023), <i>Vitalius australis</i> (Galleti-Lima et al., 2023).27</p>	27

INTRODUCTION

The genus *Cyclosternum* Ausserer, 1871 was established to house a single species *C. schmardae* Ausserer, 1871. Ausserer (1871) defines the genus by having an ovate cephalothorax with prominent caput; a deep procurved fovea with radial furrows which are distinct at the sides of the caput; a labium as long as broad, and a sternum almost a little broader than long which is also described as swollen. He then describes the species as (translated): “covered with dense hair coffee brown... almost olive-green in colour with longer hairs on the legs and abdomen especially long on the underside of the shanks”; with a large spot of black hairs on the upper abdomen ...while the sternal sigillae are only apparent opposite coxa III. Ausserer (1871) further describes the legs as weakly spined, with only patella III having a single spine. Moreover, giving length measurements as “cephalothorax with mandibles 20mm; without mandibles 15mm; breadth of the same 13.5mm. Whole animal 45mm.

Currently the genus *Cyclosternum* Ausserer, 1871 (Mygalomorphae: Theraphosidae) includes 12 described species: *Cyclosternum schmardae* Ausserer, 1871, type species; *C. familiare* (Simon, 1889); *C. gaujoni* Simon, 1889; *C. janthinum* (Simon, 1889); *C. rufohirtum* (Simon, 1889); *C. kochi* (Ausserer, 1871), *C. garbei* (Mello-Leitão, 1923), *C. viridimonte* Valerio, 1982, *C. pulcherrimaklaasi* (Schmidt, 1991); *C. spinopalpus* (Schaefer, 1996); *C. palomeranum* West, 2000; and *C. ledezmae* (Vol, 2001) (World Spider Catalog 2023). As currently defined, *Cyclosternum* is distributed in Mexico, Costa Rica, Colombia, Venezuela, Brasil, Ecuador, and Paraguay, among the main neotropical biogeographical zones of the northern Andes, tropical savannas of Venezuela and deciduous and tropical forests of Central America (Perafán, 2017). Fortunately, almost all non-Ecuadorian species were previously revised and redistributed to other

genera, due to clear morphological differences (Peñaherrera-R. et al., *in press*); leaving only the Ecuadorian species.

C. schmardae, *C. gaujoni*, *C. janthinum*, and *C. pulcherrimaklaasi* have been described using type specimens from Ecuador (Perafán, 2017; World Spider Catalog, 2022). While *C. pulcherrimaklaasi* was considered *nomen dubium* by Gabriel & Sherwood (2020), the other three species have been recognized for populations with overlapping distributions across the Andes of Ecuador (See map 1, Dupérré & Tapia, 2021). However, most recent records are based on locality points from specimens deposited in museums whose identity has not been confirmed (Perafán, 2017; Dupérré & Tapia, 2021). Actually, the taxonomy of the genus *Cyclosternum* is problematic due to the limited descriptive data and vague (or inexistent) illustrations provided in original descriptions; poor understanding of their distribution and biogeography, with many records from widely different and distant ecosystems; limited information about the type material, especially for the type species of the genus (*C. schmardae*); and few recent studies including relevant taxonomic characters from an evolutionary perspective. Original descriptions of *Cyclosternum* species date from 1871 to 2001 (*C. ledezmae* being the most current) and in most cases the type material from different species was not compared with other specimens determined by different authors (e.g., Bücherl et al., 1971; Gerschman & Schiapelli, 1973; Schmidt, 1986; Schmidt, 1993; Esche, 2014; Dupérré & Tapia, 2021; Gabriel & Sherwood pers. comm.). Additionally, several potentially undescribed species from the genus *Cyclosternum* have been reported across a wide altitudinal range (250-4500 m) from different ecosystems and climates in Colombia and Ecuador (Perafán, 2017).

The taxonomy of *Cyclosternum* faces complications stemming from limited descriptive as well as a poor understanding of distribution and biogeography, with records spanning diverse and distant ecosystems. After three years of intensive examination and search of historical material deposited in the Natural History Museum of Vienna, The Natural History Museum, and Muséum National d'Histoire Naturelle by colleagues and in a joint effort by the Mygalomorphae Group of the Laboratory of Terrestrial Zoology of Universidad San Francisco de Quito USFQ to collect fresh material from several localities in Ecuador. The first taxonomic revision of the genus *Cyclosternum* is hereby presented, accompanied with a phylogenetic analysis based on morphology to determine its position and relationship among the tarantulas' tree of life. Hypothesising that the inclusion of new and updated morphological data of several genera within the latest matrix could demonstrate similar topologies to the ones recovered by molecular data presented by Turner et al. (2017). The monophyly of the genus based on exclusive synapomorphies as well as the recovery possible phylogenetic relationship of morphologic closest genera like *Cymbiapophysa*, *Lasiadora*, and *Nhandu*.

MATERIALS AND METHODOLOGY

Examination of specimens and museums

Direct examined specimens are deposited in the invertebrate collection of Museo de Zoología of Universidad San Francisco de Quito, Museo de Zoología of Pontificia Universidad Católica del Ecuador, Museo de Historia Natural Gustavo Orces V. of Escuela Politécnica Nacional, and Instituto Nacional de Biodiversidad del Ecuador. Specimens examined from The Natural History Museum, Muséum National d'Histoire Naturelle, and Natural History Museum of Vienna were

via photographs of the principal structures of historical material shared by Danniella Sherwood and Ray Gabriel.

Note: The specimens deposited in the invertebrate collection of INABIO are not yet properly managed or digitised. Therefore, these specimens do not have the current coding numeration (MECN-AR) like the rest of invertebrates of this collection, but each specimen presents a unique catalogue specimen code (AE).

Specimens deposited at Museo de Zoología of Universidad San Francisco de Quito (ZSFQ-i) and Instituto Nacional de Biodiversidad del Ecuador (INABIO) were examined and measured under an Olympus SZX16 stereomicroscope with an Olympus DP73 digital camera and an Olympus CX22 microscope with an OMAX A35180U3 digital camera. Specimens deposited at Museo de Zoología of Pontificia Universidad Católica del Ecuador were examined under Olympus SZX16 stereomicroscope with an Olympus DP73 digital camera. Measurements were recorded with Micro Imaging Software Olympus and OMAX. All measurements are presented in millimetres.

Candidate species, species delimitation, and description format

The delimitation of candidate species is based on the separation and support of branches in the preferred phylogenetic tree. However, the proposal of their description is avoided as these species are associated with a collaborative work with several authors. On the other hand, the previously described species are subject of taxonomic actions. Due to the large number of proposed taxonomic assessments, the diagnosis of each species was based on the next closest relative format. In the case a species required further redescription, the description format proposed by Sherwood et al. (2021a) was considered within spination pattern description proposed by Pérez-Miles et al. (2008).

Palpal bulb terminology follows Bertani (2000), Gabriel (2016), Gabriel & Sherwood (2020), Sherwood *et al.* (2021a), Ferretti *et al.* (2023), and Peñaherrera-R. *et al.* (2023).

Abbreviations

Morphology: Somatic characters: AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes. Male genitalia: A, apical keel; D, dorsal median depression; PI, prolateral inferior keel; PS, prolateral superior keel; PACK, prolateral accessory central keel; PASK, prolateral accessory superior keel; PAIK, prolateral accessory inferior keel, RI, retrolateral inferior keel; RS, retrolateral superior keel; ER, embolic ridge; MDGA, median dorsal granular area; PC, prolateral crease; PR, prolateral ridge; PAR, prolateral apical ridge; TH, tegular heel.

Museum collections: BMNH = The Natural History Museum, London, United Kingdom; MNHN = Muséum National d'Histoire Naturelle, Paris; NHMV = Natural History Museum, Vienna; QCAZ = Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; ZSFQ = Museo de Zoología, Universidad San Francisco de Quito, Quito, Ecuador.

Phylogenetic analysis

The morphological characters (see Annex 1) used for Theraphosinae phylogeny were based on somatic and female and male sexual structures found during direct examination of specimens, considering also that each character to be used can be extracted from the descriptions of the previously known species and genera and be updated within the matrix of Ferretti *et al.* (2023). Theraphosinae phylogeny was informed by 45 characters with 41 terminal taxa. Due to the lack of ecological information, any potential behavioral character was avoided. To infer genus level relationships within species of the target genera, a second data character matrix (see Annex 2) was

made with few modifications of the matrix used in Galleti-Lima & Guadanucci (2018), including additional character stages; comprising 61 characters.

The character matrix was edited in Mesquite 2.74 (Maddison & Maddison 2019). Unknown states are presented as “?”. Since the evolution of all the multi-state characters are unknown, these characters are not treated as non-additive (Fitch minimum mutation model; Fitch, 1971). Cladistic analyses were conducted using TNT 1.1. For out-group selection, the entry of *Catumiri* (Ischnothelinae), as used in Ferretti et al. (2023), since the latest molecular-based phylogeny showed that Ischnothelinae is one of the closest subfamilies to Theraphosinae. The dataset was analysed under equal weights (EW) and implied weights (IW). Heuristic EW search strategies were performed using new technology options of TNT using the command ‘hold 1000; mult 30 = tbr drift’, proposed by Hazzi et al. (2018). Heuristic IW search strategies were performed using the script “aaa” proposed by Mirande (2009) with the following command ‘aaa 3 10 70 95 7’. As a support measures, IW trees were analysed under symmetric resampling and EW trees under jackknife values. Trees during searches were collapsed under ‘rule 1’ (Coddington & Scharff 1994). The sensitivity of IW results (*sensu* Wheeler 1995) was assessed using varying and not pre-selected K-values given by the script “aaa”. WinClada 10.00.08 (Nixon 2002) was used for character optimisations on the preferred cladogram using slow transformation (DELTRAN), as also tree edition.

RESULTS

The morphology of *Cyclosternum* was considerably sketchy. The updated data and diagnosis provided by Pérez-Miles et al. (1996) based on the revision of a supposed type material of *C. schmardae*, females and males (Pérez-Miles et al., 1996: fig. 12, 13), were in fact non-type specimens revised and identified by Eugène Simon as *C. schmardae*. Being possible that there may have been a bias on determining the identity of *Cyclosternum*, in fact through the development of this study and revision of Simon's material we had determined that the revised material of *C. schmardae* by Pérez-Miles et al. (1996) correspond to an undescribed species [see Remarks on *C. schmardae*]. Furthermore in 2016, the first graphic evidence of a spermatheca from a female syntype of *C. schmardae* was provided by Gabriel (2016; fig. 69) but no taxonomic account was proposed for the species or genus. However, this addition allowed us to know the exact spermatheca morphology of *C. schmardae*, demonstrating that it possesses short and globose twin receptacles and guard plates below the receptacles [see Description of *C. schmardae*].

Upon the examination of approximately 238 Ecuadorian specimens from different 18 localities across the inter-Andean and Western Ecuador regions, two groups were found with similar spermatheca morphology of *C. schmardae*, one being the genus *Cymbiapophysa*, but clearly separated by the presence [in *Cymbiapophysa*] or absence [unknown group] of a dorsal median depression in the male palpal bulb of each group. Resulting in a clear need to obtain additional useful data to differentiate the females of these groups and to determine their relationship to *C. schmardae*. Simultaneously, through collaboration with Ray Gabriel and Danniella Sherwood, between 2022 and 2023 the type material of *C. schmardae* was reexamined in order to further

analyse the spermatheca of the female syntype as well as the type of urticating setae and presence of stridulatory setae. As a result of the reexamination by Gabriel and Sherwood, it was determined that the syntype female of *C. schmardae* presents urticating setae Type I and short spiniform stridulatory setae in coxa I–IV and trochanter I–IV. Based on these results, although both groups showed short spiniform stridulatory setae in both segments, the females of *Cymbiapohysa* were differentiated from the syntype of *C. schmardae* by having urticating setae Type Id. In contrast, the females of the unknown group present urticating setae Type I, showing congruence with the syntype female of *C. schmardae* but not so much similarity as to identify at least a portion of the revised material as belonging to this species. Under these evidences this group was associated and identified as *Cyclosternum*, allowing preliminarily to complement the missing morphological data of the males of the genus on the basis of male specimens of undescribed species of the genus; thus, making a new diagnosis for the genus as well as assigning an identity to the clade obtained on the basis of the following phylogenetic study.

Phylogenetic analysis

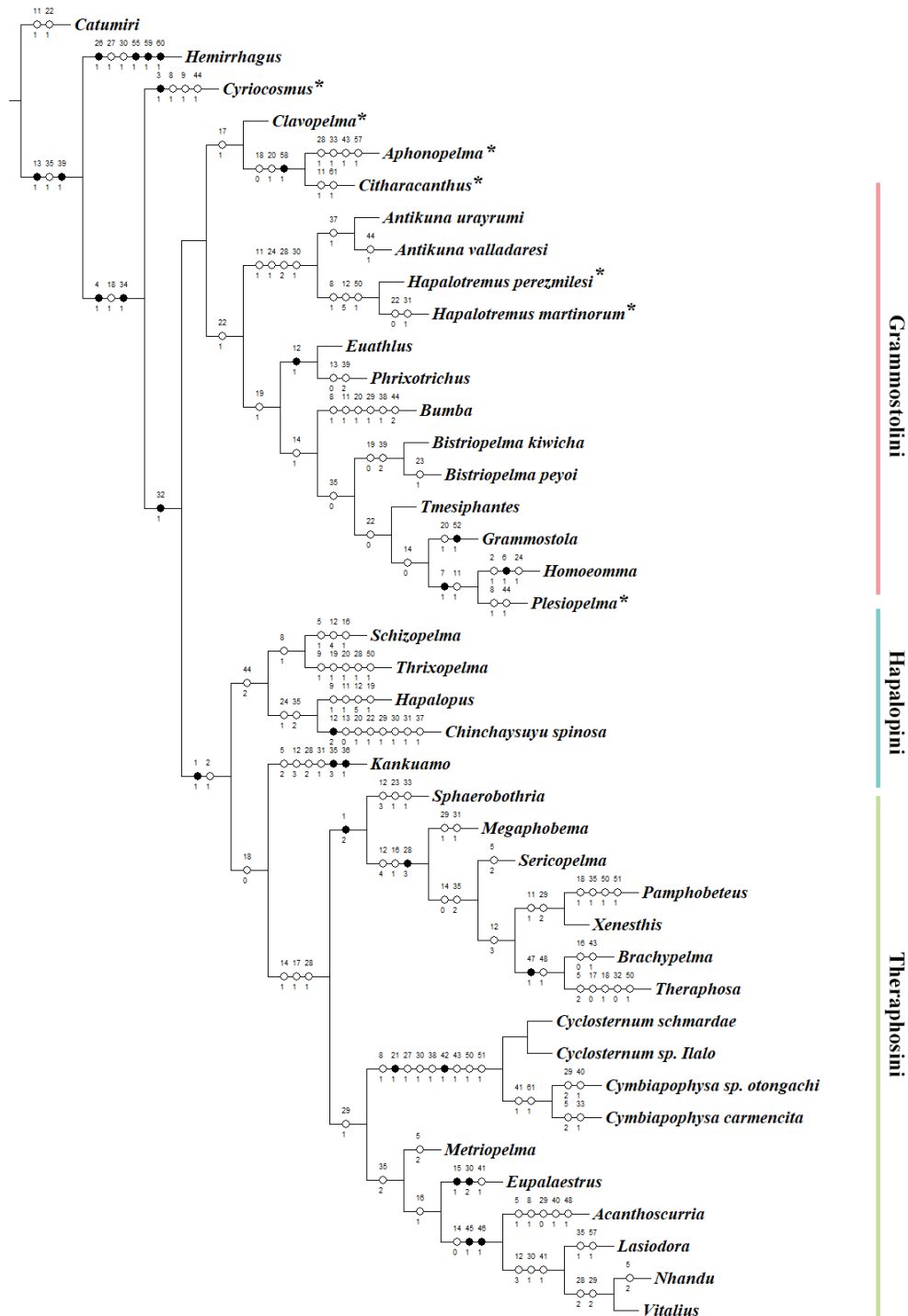


Figure 1. Preferred phylogeny of Theraphosinae (L= 162, CI = 0.40; RI = 0.64) obtained by implicit weights with symmetric resampling and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles.

Heuristic search under EW & IW: During the first for a general phylogenetic hypothesis of theraphosinae under EW, 237 trees were obtained for the subfamily theraphosinae; nevertheless, topologies of each tree was considerably similar between clades members. In the case of IW, between 3–6 different topologies or pattern trees were obtained according to each K-value (Table 1) and a strict consensus tree was obtained from all the trees of all K values (L= 171, CI = 0.40, RI = 0.60).

Table 1. Results from the phylogenetic analyses using implied weighting for generic placement of *Cyclosternum* and *Cymbiapophysa* within Theraphosinae.

K-value	Tree length	Trees	Total fit
3.38	178	6	14.52
3.87	178	6	13.54
4.48	171	3	12.49
5.24	171	3	11.37
6.22	171	3	10.20
7.54	171	3	8.97
9.42	170	3	7.67
12.28	169	3	6.28
17.18	169	3	4.79
27.53	169	6	3.19

The topologies of IW trees obtained under symmetric resampling showed better resolution than EW trees resulted from this support measure. In fact, EW results showed almost 93% of unresolved branches. For this reason, a consensus tree obtained under IW + Symmetric resampling was selected for evaluating the placement for both genera and as the preferred phylogenetic hypothesis for Theraphosinae. Although a consensus tree was obtained based on all the trees under different IW values, consensus tree under k-value of 12.28 (L= 169, CI = 0.43, RI = 0.67) was selected as a replicative measure to the previous phylogeny proposed by Ferretti et al. (2023).

In the case of the second phylogenetic hypothesis within the closest relatives to *Cyclosternum* and *Cymbiapophysa*, EW searches were unavailable since none of the principal branches was resolved but some group of species in *Cyclosternum* were resolved but without logic within the tree. Furthermore, IW searches recovered between 378–882 different topologies or pattern trees were obtained according to each K-value (Table 1) and a strict consensus tree was obtained from all the trees of all K values (L= 133, CI = 0.50, RI = 0.80). In this case, the preferred hypothesis for Lasiodoriformis + Cycloformis was based on the consensus tree under k-value of 13.45 (Figure 2) (L = 132, CI = 49, RI = 0.79) since presented a most parsimonious organisation.

Table 2. Results from the phylogenetic analyses using implied weighting for Lasiodoriformis and Cycloformis.

K-value	Tree length	Trees	Total fit
3.70	134	882	0
4.24	134	882	10.25
4.90	133	378	9.41
5.74	133	378	8.54
6.82	133	378	7.64
8.27	133	378	6.69
10.32	133	378	5.70
13.45	132	378	4.66
18.83	132	378	3.54
30.17	378	378	2.36

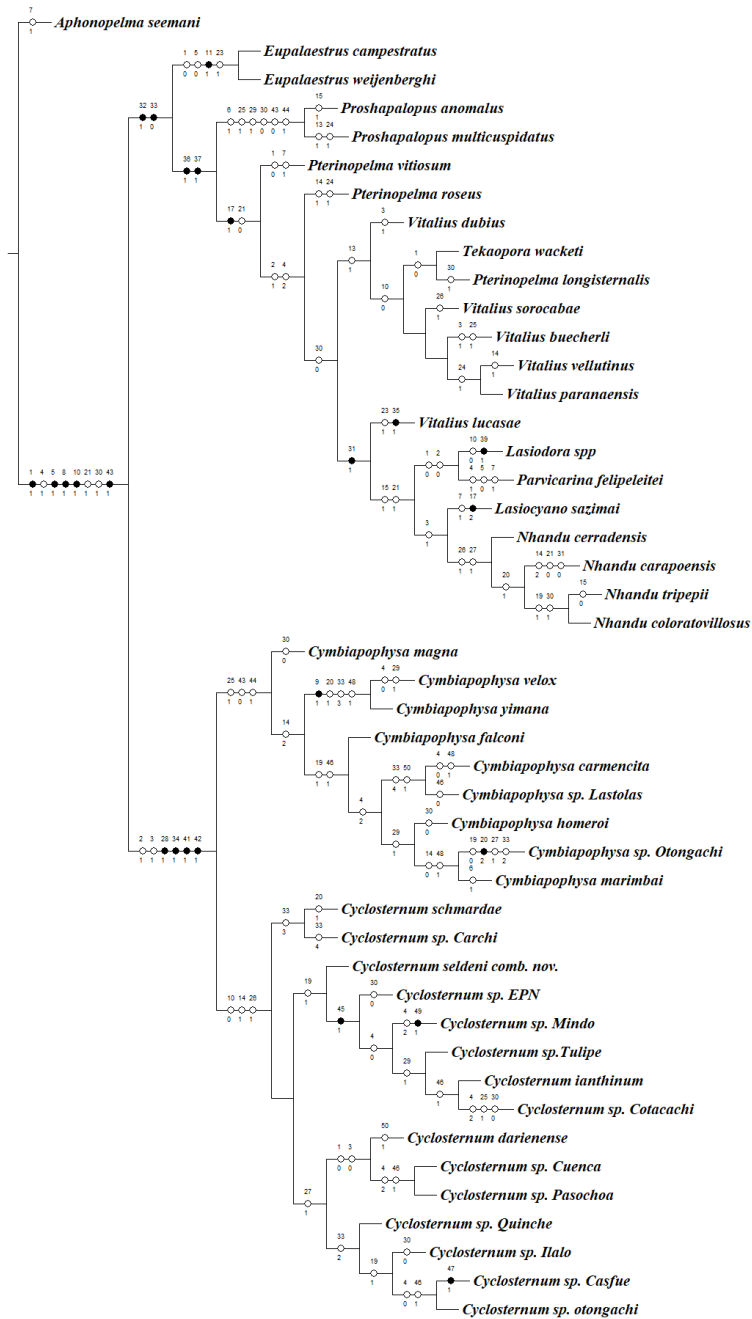


Figure 2. Preferred phylogeny of Lasiodoriformis and Cycloformis (L = 132, CI = 49, RI = 0.79) obtained by implicit weights with symmetric resampling and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles.

Clades: In general, the general phylogenetic hypothesis for theraphosinae tree (Figure 1) (L= 169, CI = 0.43, RI = 0.67) showed groupings already proposed in the last morphological phylogeny (Ferretti et al., 2023) and tribes proposed by a 16S/NDI-based phylogeny (Turner et al., 2017), with the exception of the formation of a new clade (*Brachypelma* + *Megaphobema* (*Sericopelma* + *Theraphosa*) (*Pamphobeteus* + *Xenesthis*)) and the relocation of *Chinchaysuyo* within the Hapalopini tribe. This new clade is supported by one synapomorphy (apical keel being strongly elongated) and tree homoplasies: the presence of a retrolateral scopula in Femur IV, apical region of palpal bulb being convex, and spermathecae with two seminal receptacles widely fused.

Within the placement of *Cyclosternum* and *Cymbiapophysa* in the general phylogenetic hypothesis for theraphosinae, both genera were recovered as a sister group (Figure 1, Figure 2, Figure 3) supported by two exclusive synapomorphies in the general theraphosinae hypothesis: (21) the presence of weakly developed coxal spinules and (42) the presence of a retrolateral cymbial apophysis; seven homoplasies also supported the grouping of both genera. The separation of *Cyclosternum* and *Cymbiapophysa* was supported by the following characters: (41) ventral median depression [absent in *Cyclosternum*, present in *Cymbiapophysa*] and (61) presence of urticating subtype Id [absent in *Cyclosternum*, present in *Cymbiapophysa*]. Additionally, these genera were recovered as closest relatives to the clade of the Lasiodoriformis group (*Metriopelma* (*Eupalaestrus* (*Acanthoscurria* (*Lasiodora* (*Nhandu* + *Vitalius*))) which is supported by one synapomorphy (presence of an embolic ridge) and two homoplasies: subapical keel generally not serrated and retrolateral keel/s present but not pronounced. Although the inclusion of *Metriopelma* and *Acanthoscurria* within the Lasiodoriformis group is shown in the presented phylogeny, this should be compared with molecular data and possibly with more updated data.

In the other hand, the preferred phylogenetic hypothesis for Lasiodoriformis + (*Cyclosternum* + *Cymbiapophysa*) (Figure 2) showed a better organisation between these major clades, implicit, and all the known representants of *Cyclosternum* and *Cymbiapophysa* species as also undescribed species confirms the monophyly of both genera. In this case *Cyclosternum* was supported by three homoplasies: (10) absence of ventral median depression, (14) reduced tibial apophysis, (26) female chela with long marginal soft hairs.

Since both phylogenetic trees showed similar organisation in relation to *Cyclosternum* and *Cymbiapophysa*, herein this clade is proposed as Cycloformis as a way to identify its members in the rest of this manuscript and future studies. In the case of the specific phylogenetic hypothesis (Figure 3), Cycloformis is supported by four exclusive synapomorphies: (28) Presence of male palpal tibial retrolateral process, (34) coxal spinules present, (41) (42) presence of spiniform stridulatory setae in trochanters and coxae.

Taxonomy

Family **Theraphosidae** Thorell

Genus *Cyclosternum* Ausserer, 1871

Adranochelia Simon, 1889; Raven, 1985: 148. (jun. synonym).

Chaetorhombus Ausserer, 1871; Raven, 1985: 151. (jun. synonym).

Drytopelma Simon, 1889; Pérez-Miles et al., 1996: 46. (jun. synonym).

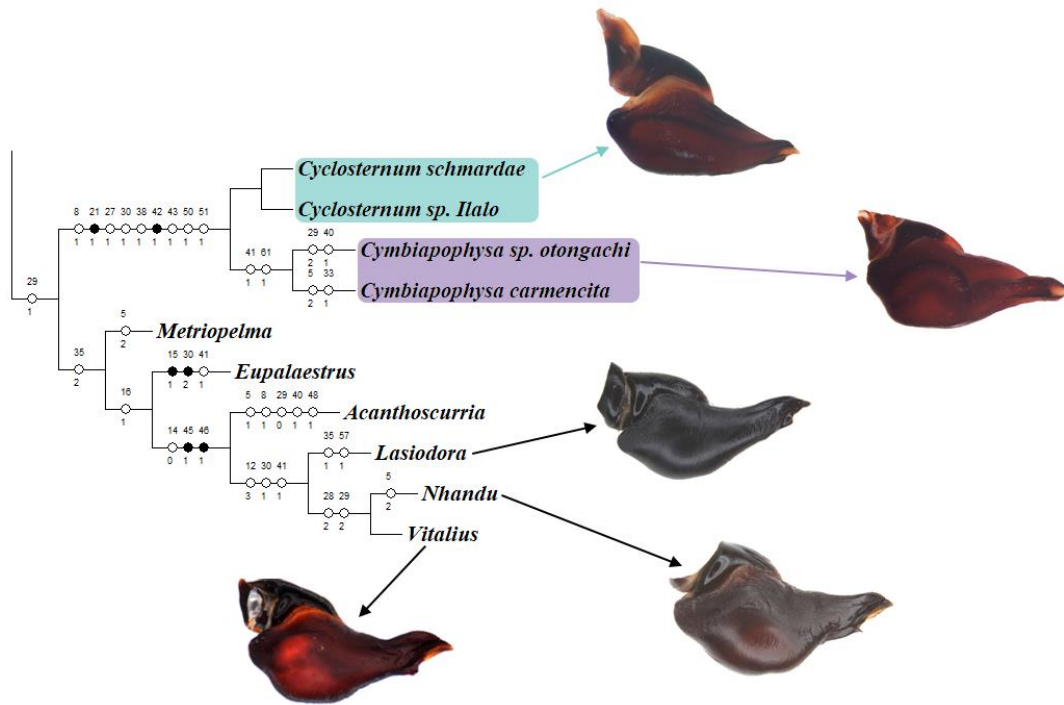


Figure 3. Close up view of Lasiodoriformis + Cycloformis (*Cyclosternum* + *Cymbiapophysa*) from the preferred phylogeny within theraphosinae ($L= 169$, $CI = 0.43$, $RI = 0.67$) obtained by implicit weights with symmetric resampling method and slow character optimisation. Synapomorphies are indicated by black circles and homoplasies with white circles. Male palpal bulbs from top to bottom: *Cyclosternum* sp. *Ilalo*, *Cymbiapophysa carmencita*, *Lasiodora klugi* (Gabriel, 2016), *Nhandu sylviae* (Sherwood et al., 2023), *Vitalius australis* (Galleti-Lima et al., 2023).

Type species: *Cyclosternum schmardae* Ausserer, 1871.

Diagnosis: Males of *Cyclosternum* differ from other theraphosinae genera by the presence of a distal-retrolateral apophysis on the male cymbium; along with the combination of morphological characters of palpal bulb: D absent, PR and ER present, RS and RI keel weakly developed, convergent PI and PS keels following the axis and the acuminate curvature of distal embolus, and a rounded SA keel. Males of *Cyclosternum* resemble males of *Spinostatibiapalpus* by

comparatively having similar prolateral keels morphology as also general palpal bulb shape, as well as A and SA keel morphology and absence of D. Therefore, males of *Dryptopelma* can be differentiated from the previously mentioned genus by the presence of paired tibial apophysis, distal-retrolateral apophysis on the male cymbium, weakly developed retrolateral process in male palpal tibia, comparatively shorter SA keel, and the absence of PAR (paired tibial apophysis absent or a single-branched apophysis, comparatively elongated SA keel, presence of PAR, and the absence a distal-retrolateral apophysis on the male cymbium in *Spinostatibiapalpus*). Additionally, males of *Cyclosternum* relatively resembles males of *Acentropelma* and *Pseudoschizopelma* by comparatively having a similar and general palpal bulb morphology. Therefore, males of *Cyclosternum* differs from *Acentropelma* and *Pseudoschizopelma* by having a PS keel prolaterally positioned, SA keel comparatively short but rounded [protruding], and the absence of plumose setae in trochanter I, femur I, and palpal trochanter (dorsally positioned PS keel, SA keel comparatively large and slightly projected, and presence of plumose setae in trochanter I, femur I, and palpal trochanter in *Acentropelma* and *Pseudoschizopelma*).

Females of *Cyclosternum* differs from other theraphosinae genera by the combination of a twin spermathecae and the presence of guard plates. Females of *Cyclosternum* resemble to females of *Aphonopelma*, *Cyrtopholis*, *Cymbiapophysa*, *Lasiadora*, *Phormictopus*, and *Spinostatibiapalpus* by the general shape of twin spermathecae and the presence of guard plates in the last four genera. Therefore, females of *Dryptopelma* can be differentiated from *Aphonopelma*, *Cyrtopholis*, and *Phormictopus* by comparatively having shorter receptacles, >1.5x wide of each receptacle (elongated receptacles, >2x wide of each receptacle in *Cyrtopholis*, *Aphonopelma*, and *Phormictopus*); from *Lasiadora* and *Spinostatibiapalpus* by having non-globose receptacles (globose receptacles in *Lasiadora* and *Spinostatibiapalpus*); finally form *Cymbiapophysa* by the

absence of urticating setae subtype Id (urticating setae subtype Id in *Cyclosternum*). Additionally, females of *Cyclosternum* differs from some species of *Cyrtopholis* by the absence of lateral lobes on each receptacle (e.g. fig. 9 in Fabiano-da-Silva *et al.*, 2020) and from *Lasiadora* by the presence of guard plates. Also, females can further differ from *Cyrtopholis*, *Lasiadora*, *Spinosatibiapalpsu*, and *Phormictopus* by the presence of weakly developed coxal spinules on coxa I and II (absent in *Cyrtopholis*, *Lasiadora*, *Spinosatibiapalpsu*, and *Phormictopus*) and from all the compared genera [excepting *Cymbiapophysa*] by the presence of ventro-basal dilatation of coxae (Gerschman & Schiapelli, 1973; Gabriel, 2016; Rudloff, 2008; Fabiano-da-Silva *et al.*, 2020; Peñaherrera-R., 2023)

Tentatively, males and females of *Cyclosternum* can also be differentiated from all the previously mentioned groups, excepting *Cymbiapophysa*, by the presence of maxillary spiniform setae and putative presence of spiniform stridulatory setae on the retrolateral and dorsal faces coxae I–III or I–IV, respectively, and on prolateral face of trochanters I–IV.

Generic description: Small to medium theraphosine spiders (18.83 mm body length). Carapace ovate, hirsute, caput not raised, slightly raised or raised, ocular tubercle slightly raised or raised, with an anterior eye row straight, slightly procurved or procurved, posterior eye row slightly recurved and ocular arrangement AME > PLE > ALE > PME. Clypeus narrow with fringe of short setae or clypeus wide with fringe of medium to long setae. Fovea deep, transverse or slightly recurved. Labium wider than long, with between 25–73 cuspules. Labio-sternal mounds separate. Maxilla longer than wide, disperse and thin maxillary spiniform setae present in posterior margin and medial to apical section. Sternum ovate or almost circular, with three pairs of ovate sigilla, at varying distances from the edge of the sternum. Legs and palps all of approximate equal thickness (except femora III of males of most species), hirsute, generally spinose and with golden shades.

One pair of tarsal claws on tarsi I–IV, both claws with medial serration, and a single claw on palpal tarsus. Ventral faces of tarsi I–IV fully scopulate. Metatarsi I–IV all with ventral scopulae, of varying extents. Weakly developed coxal spinules present. Various modified setae on the retrolateral and dorsal faces of coxae I–III and I–IV, respectively. Trochanters I–IV with modified spiniform setae on prolateral face. Tibiae I–IV and palpal tibia with small group of short and coarse setae with thickened trichobothria, extending in the basal part of prolateral and retrolateral faces. Metatarsi I–IV with small group of short and coarse setae with thickened trichobothria, extending from basal to medial of retrolateral face to dorsal face. Opisthosoma with Type I urticating setae present dorsally (males with subtype Ia; females with regular Type I). Opisthosoma covered with long and short setae. Male tibia I with paired tibial apophysis, PB and RB short, almost of equal length, and emerging from basal nodules. Male metatarsus I unmodified. Male cymbium with distal-retrolateral apophysis.

Remarks: Currently the genera *Adrenochelia* and *Chaetorrombus* are considered as junior synonyms, nevertheless both genera as also the non-Ecuadorian species that were originally described as *Cyclosternum* were reviewed on an additional work (*in press.*) whereby each species was distributed to other genera, or at the same time restoring any genus. For this reason, these species are not considered for these phylogenetic and taxonomic analyses; with the exception of *Cyclosternum darienensis* and *Cyclosternum seldeni* **comb. nov.**, which was included in the phylogenetic analyses due to the similar male palpal bulb morphology of some undescribed species [revised material].

Distribution: Ecuador and Panama; between the Chocó-Darien or Ecuador and Panama, Western Ecuador, and Northern Andes biogeographic provinces of the Western Cordillera of the Andes of

Ecuador, 10–2785 m. (Ausserer, 1871; Simon, 1892; Gabriel & Sherwood, 2022; Sherwood & Gabriel, 2023).

Cyclosternum gaujoni Simon, 1889 species inquirenda

Remarks: Spermatheca morphology of the syntype of *C. gaujoni* showed a different morphology than known for *Cyclosternum*, specifically the absence of GP as also having thin and enlarged receptacles emerging from a width and membranous base. Due to these differences and inconsistencies, it is most likely that this species may belong to an undescribed genus, however herein the species is proposed as *specie inquirenda* since it is advisable to establish the new genus with fresh material and the inclusion of male specimens.

Cyclosternum ianthinum Simon, 1889

Drytopelma ianthinum Simon, 1889: 402 (*lapsus*).

Drytopelma janthinum Simon, 1892: 137.

Drytopelma janthinum Simon, 1903: 920.

Drytopelma janthinum Schmidt, 1986: 41.

Drytopelma janthinum Schmidt, 1993d: 65.

Cyclosternum janthina Pérez-Miles et al., 1996: 47.

Drytopelma janthinum Schaefer, 1996: 24, f. 13.

Cyclosternum janthinum Schmidt, 2003: 156.

Diagnosis: Males of *Cyclosternum ianthinum* differs from males of *C. seldeni* **comb. nov.** by comparatively having an elongated distal part of embolus, PI keel developed, PS and SA keels weakly developed, and RS and RI keels absent (comparatively having a shorter distal part of

embolus, SA keel well developed, PS and PI keels developed, RS keel weakly developed, and the absence of RS keel in *C. ianthinum*). Females of *Cyclosternum ianthinum* differ from females of *C. schmardae* by having symmetrical receptacles, inner and external lateral constrictions at one third, and ovate GP (asymmetrical receptacles, inner and external lateral constrictions at two thirds, and quadrate GP in *C. schmardae*).

Material: 1 ♂ syntype (MNHN), Ecuador, environs de Quito, M. A. Cousin leg., examined via photographs. 2 ♂ and 2 ♀ syntypes (MNHN-AR 4637), Ecuador, Quito, M. A. Cousin leg., examined via photographs. 2 ♂ syntypes (MNHN-AR 4636), Equateur, Casitagna [sic = Casitagua], 3600 m.a.s.l., 1903, Dr. Rivet leg., examined via photographs. 1 ♂ (MNHN-AR 4636), Equateur, El Vinculo, 1902, Dr. Rivet leg., examined via photographs. 3 ♂ 4 ♀ (MEPN) Ecuador, Quito, Escuela Politécnica Nacional, examined. 1 ♂ 1 ♀ (QCAZ I) Ecuador, Quito, Pontificia Universidad Católica del Ecuador, examined.

Redescription of male (MEPN): Total length including chelicerae: 18.83. Carapace: length 9.85, width 8.87. Caput: slightly raised. Ocular tubercle: raised, length 1.18, width 1.54. Eyes: AME > PLE > ALE > PME, anterior eye row procurved, posterior row slightly recurved. Clypeus: narrow; clypeal fringe long. Fovea: deep, transverse. Chelicera: length 3.60, width 2.62. Abdomen: length 8.98, width 4.70. Maxilla with 112-127 cuspules covering approximately 30% of the proximal edge. Labium: length 1.19, width 1.75, with 33 cuspules most separated by 1-1.5 × the width of a cuspule. Labio-sternal mounds: separate. Sternum: length 3.94, width 2.43, with three pairs of sigilla. Tarsi I–IV fully scopulate. Metatarsal scopulae: I 100%; II 50%; III 40%; IV 0%. Lengths of legs and palpal segments: see table 2, legs 4,2,1,3. Spination: Femora II 1D; III 2D; IV 1D. Patellae I 1D, 1P; II 3V; palp 1P. Tibiae I 2D,3V, 1P, 2R; II 6V, 3P; III 11V, 7P, 3R; IV 4V; and palp 3D. Metatarsi I 1D,4V; II 6V, 45P; III 3D,7V, 3R; IV 3D, 8V, 2P, 2R. Tibia I with paired

tibial apophysis, RB longer than PB, PB with two median size megaspines with a pointed apex (one on retrolateral and other in ventral surface of PB), RB with one short megaspines with a pointed apex. Femur III: incassate. Posterior lateral spinnerets with three segments, basal 0.98, median 1.05, digitiform apical 1.16. Lateral median spinnerets with one segment 0.98. Palpal bulb with developed TH; PI developed; A, SA, and PS weakly developed, ER, PR and PC present, PC constricted along apical half; D and PAR absent; RS, RI, PACK, PAIK, and PASK keels absent. MDGA absent. Distal part of embolus considerably elongated. Urticating setae: Type Ia present dorsally.

Description of female (QCAZ I): Total length including chelicerae: 33.18. Carapace: length 13.33, width 11.08. Caput: raised. Ocular tubercle: slightly raised, length 1.41, width 1.85. Eyes: ALE > PLE, PLE < AME, AME > PME, anterior row procurved, posterior row recurved. Clypeus: very narrow; clypeal fringe: very narrow. Fovea: deep, straight. Chelicera: length 5.81, width 3.23. Abdomen: length 15.24, width 10.21. Maxilla with 131-134 cuspules, covering approximately 20% of proximal edge. Labium: length 1.85, width 2.66, with 35 labial cuspules most separated by 0.5–1.0 × the width of a single cuspule. Labio-sternal mounds: joined. Sternum: length 6.63, width 5.73, with three pairs of sigilla. Tarsi I–IV fully scopulate. Metatarsal scopulae: I 70%; II 50%; III 35%; IV 20%. Lengths of leg and palpal segments: see table 2, legs 4,1,2,3. Spination: Femora I 1P; II 1P; III 2P, 2R; IV 1P, 1R; palp 1P. Patellae I 0; II 1P; III 2P; IV 1P, 2R; palp 0. Tibiae I 3V, 1P; II 5V, 3P; III 8V, 3P, 6R; IV 3V, 3P, 4R; palp 4V, 1P. Metatarsi I 1V, 1P; II 4V, 3P, 1R; III 6V, 5P, 4R 3D; IV 14V, 4P, 3R, 6D. Tarsi I-IV and palp 0. Posterior lateral spinnerets with three segments: basal 2.60, medial 1.56, digitiform apical 2.34. Lateral median spinnerets with one segment 2.17. Spermathecae with twin short, symmetrical, and squat receptacles, placed

above ovate GP; inner and external lateral constrictions present at one third of receptacle length; spermathecae with conspicuous atriobursal orifice. Urticating setae: Type I present dorsally.

Remarks: Is most likely that the material collected from Casitagua could belong to an undescribed species of *Cyclosternum*, resembling the morphology of the Simon's *C. schmardae* males and Berland's *C. gaujoni* males [see Remarks of *C. gaujoni* and *C. schmardae*].

***Cyclosternum schmardae* Ausserer, 1871**

Diagnosis: Females of *Cyclosternum schmardae* differs from females of *C. ianthinum* by having asymmetrical receptacles, inner and external lateral constrictions at two thirds, and quadrate GP (symmetrical receptacles, inner and external lateral constrictions at one third, and ovate GP in *C. ianthinum*).

Material: Lectotype ♀ (NHMV) (designated herein), Cordillera 4000–5000', Prof. Schmarda leg., examined via photographs. 29 paralectotypes juv. (NHMV), same data as lectotype.

Redescription of female: Developed ventro-basal dilatation of coxae III and IV. Weakly developed coxal spinules only extended over basal area of prolateral face in coxae I and II. Spermathecae with twin short, asymmetrical, and squat receptacles, placed above quadrate GP; inner and external lateral constrictions present at two thirds of receptacle length; spermathecae with conspicuous atriobursal orifice. Urticating setae: Type I present dorsally.

Remarks: The specimen is in a fragile state; thus, general measures like scopulation, leg lengths, leg spination, and posterior lateral spinnerets segments were avoided to prevent fragmentation and loss of leg and pedipalp segments of this historical material. Nevertheless, the most important characteristics to diagnose this species are presented.

In 1889, Eugène Simon stated that the species was described from specimens collected from Quito, stating also that he had several specimens collected from the same locality by Boucier as also from the surroundings of Quito, Rumipamba, and Los Puentes [near Tandayapa] collected by M. A. Cousin, and from Cuenca collected by Father Gaujon. For this reason, between the confusion, Gerschman & Schiapelli (1973) and Pérez-Miles et al. (1996) led to consider that these were specimens that belong to this species and even included Simon's male specimens for the diagnosis of the genus. By reviewing Simon's material deposited in MNHN as also fresh material collected by the author and colleagues, we determined that the material from Quito and Cuenca certainly belonged to *Cyclosternum*. However, these were undescribed species since the females do not match with the spermatheca morphology of the lectotype of *C. schmardae*. Although the justification of Pérez-Miles et al. (1996) on the synonymy of *Dryptopelma* Simon, 1889 to *Cyclosternum* was based on these specimens [especially the males], herein the morphologic comparison between the lectotype of *C. schmardae*, syntypes and non-type material of *C. ianthinum*, and other undescribed material provided robust information that confirms this synonymy.

***Cyclosternum seldeni* (Sherwood & Gabriel, 2023) comb. nov.**

Cymbiapophysa seldeni Sherwood & Gabriel, 2023.

Diagnosis: Males of *Cyclosternum seldeni* are easily differentiated from *C. ianthinum* by comparatively having a shorter distal part of embolus, SA keel well developed, PS and PI keels developed, RS keel weakly developed, and the absence of RS keel (comparatively elongated distal part of embolus, PI keel developed, PS and SA keels weakly developed, and RS and RI keels absent in *C. ianthinum*).

Material: Holotype ♂ (BMNH 1903.7.1.137), Carondelet, N.W. Ecuador, 60f, examined via photographs.

Description: See Sherwood & Gabriel (2023).

Remarks: Sherwood & Gabriel (2023) described the male of *Cyclosternum seldeni* **comb. nov.** by having a palpal bulb with a weakly developed ventral medial depression, nevertheless this character is absent in this species. Due to the absence of this character and the addition of the species within the phylogenetic analysis (Figure X), the species is considered as a member of *Cyclosternum*.

***Thrixopelma pulcherrimaklaasi* (Schmidt, 1991) comb. nov.**

[for complete reference of the taxonomic account for the species see WSC, 2023]

Material: ♂ Holotype *Paraphysa pulcherrimaklaasi* (SMF 37585), Mittel-Südamerika, Ecuador, A. Tinter leg., G. Schmidt det., not examined.

Remarks: Although male cymbia and palpal bulb of the male holotype are considered lost (Perafán & Pérez-Miles, 2014; Gabriel & Sherwood, 2020), being one of the major character for species and genera delimitation, herein the conflictive species *Paraphysa pulcherrimaklasasi* is relocated to the genus *Thrixopelme* due to the following reasons: (1) The presence of urticating setae type III and IV were reported by Perafán & Pérez-Miles (2014) [absent in *Cyclosternum*, but confused within the work of Pérez-Miles et al. (1996) in which reported the presence of type III], indicating a possible relationship within Hapalopini. (2) illustrations provided by Schmidt (1991), of which indicated two enlarged prolateral keels resembling to the general morphology of *Thrixopelma* [in fact possible keels with crests] (Sherwood et al., 2021b; pers. obs.). (3) Finally, Schmidt (1991) described the species from a male specimen supposedly collected from Ecuador,

of which it makes coherence between the distribution of *Thrixopelma*. It should be noted that due to the loss of the palpal bulb, the species will continue to be considered as *nomen dubium*.

DISCUSSION

Within the morphologic phylogenetic hypotheses and revision of type material of the Ecuadorian species of *Cyclosternum* and undescribed species, we confirm the monophyly of *Cyclosternum* and recovered as sister genus of *Cymbiapophysa*, both genera conform the new major clade herein named as Cycloformis based on morphological data and simultaneously recovered as sister clade of Lasidoriformis. Although these hypotheses showed as sister clade, it is important to state that organisation of each branch in relation to the phylogeny could not recover a true organisation in time relation to the evolution of each group. Meaning that morphological states of the used character for both matrixes were considered as unordered [forcing the root of groups based in a timeline scale of evolution] and were not compared against morphological characters found in fossil records as recovered in different studies related to other organisms (*e.g.* Hippa & Vilkamaa, 2006; Tarasov et al., 2016; Bardua et al., 2019).

Nevertheless, the separation of genera within both phylogenetic hypothesis [excepting the paraphyly of *Vitalius* and *Pterinopelma* in the second hypothesis] and tribe segregation in the case of the first hypothesis seems to present natural groupings instead of artificial groupings at a medium level as for major clades. It is imperative that the grouping of Cycloformis should be tested with other genera that shows similar male palpal bulb and spermathecae morphology such as *Acentropelma*, *Pseudoschizopelma*, and *Spinostatibiapalpus* (Gabriel & Sherwood, 2020; Gabriel et al., 2020). However, as mentioned above, it is possible that this grouping is an artificial

formation, so it is recommended that future studies also evaluate morphological data within molecular sequences in order to infer ancestral states and determine the basal groups of theraphosini and their evolutionary connections between taxonomic groups with similar morphology and even cryptic groups. Through this, the use of morphological phylogenies would have more informative characters that demonstrate a more accurate and natural grouping between clades and connected with a more precise evolutionary approach.

Despite this drawback, when compared to molecular-based studies we can find a character that can demonstrate an ancestral origin for the theraphosini tribe. This character is the ventral median depression, during the analysis of theraphosinae tribes by Turner et al. (2017) the Lasiodoriformis group was recovered as the second basal clade of the tribe, indicating that in future studies this character could be used as a forcing character for the root of the result dendrograms. However, this character seemingly demonstrates multiple pathways of losses (*e.g.* *Cyclosternum*, *Metriopelma*, *Megaphobema*) as well as reintegration of the character as for example in *Xenesthis*, but in a degenerated or slightly developed state character, which is very distant from Lasiodoriformis and possibly from Cycloformis (Turner et al., 2017; Sherwood et al., 2023). Based on this, it is possible that natural groups containing representatives with a developed or well-developed ventral median depression may indicate that they belong to a more basal branch because they do not demonstrate degenerated state characters.

Another consideration to consider about morphological characters during these and previous phylogenies is that many characters related to keels may have the potential to be represented as independent characters and not as a conglomerate of multiple stages of a single character development. Although the framework of Bertani (2000) tried to stabilize these structures and find the way as homologous features in Theraphosinae, many new structures resembling to keel

morphology have been found across new descriptions and even redescriptions of older taxa. Characters such as the presence or absence of a prolateral accessory keel below the prolateral inferior keel used in the Theraphosinae morphologic phylogeny since the creation of the matrix by Pérez-Miles et al. (1996) should be reexamined and potentially partitioned as different type of prolateral accessory keels. In fact, there could be a strong possibility that these new keels could fall under the recent definition of accessory keels proposed by Ferretti et al. (2023). Nevertheless, this can only be done if these structures can be compared with the bulbs of more basal groups, bearing in mind that keel-shaped structures have been reported in the more basal subfamily of Theraphosidae, Eumenophorinae, as well as in closer (e.g. Barychelidae) and distant (e.g. Paratropididae) families. Although it is possible that due to the broadening of the embolus in Theraphosidae, although there are groups that still maintain thin and elongated embolus (e.g. *Aphonopelma*), may have allowed the redistribution of keels, so perhaps another route to really know the homology of the structures is to look at the internal development of the bulb in the tarsus of juvenile males as well as to compare with reproductive structures in fossil representatives of Theraphosidae.

CONCLUSIONS

Concluding, this study finally clarified the identity of the genus *Cyclosternum* as well as the Ecuadorian species. As a result, a correct diagnosis for the group was made and a clear comparison with morphologically similar groups can be approached. Due to the large number of examined specimens from the visited museums, it was possible to show a clear definition in the formation of the clade Cycloformis grouped by *Cyclosternum* and *Cymbiapophysa*; being a sister clade to Lasiodoriformis. The construction of phylogenetic trees based on morphology seems to be still useful in Theraphosinae, demonstrating a clear separation between clades. Although groupings at tribe level may still be artificial for some genera. Because of the great variation of structures found in the male palpal bulbs in Theraphosinae, it is possible that a reclassification of some characters used in both morphological matrices may be needed for future phylogenies. It is estimated that with this clarification of the characters, more accurate topologies similar to those obtained in molecular phylogenies can be obtained. Nevertheless, these morphologic based methods still represent as an important tool to know the position of groups where only one specimen is known worldwide or in collections where for various reasons it is not possible to extract tissues for molecular analysis.

BIBLIOGRAPHIC REFERENCES

- Ausserer, A. (1871). Beiträge zur kenntniss der arachniden-familie der territelariae thorell (mygalidae autor). *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen gesellschaft in wien* 21: 117-224
- Bardua, C., Evans, S. E., & Goswami, A. (2019). Phylogeny, ecology and deep time: 2D outline analysis of anuran skulls from the Early Cretaceous to the Recent. *Palaeontology*, 62(3): 417-431.
- Bertani, R. (2000). Male palpal bulbs and homologous features in Theraphosinae (Araneae, Theraphosidae). *Journal of Arachnology* 28: 29-42.
- Bertani, R., Nagahama, R. H. & Fukushima, C. S. (2011). Revalidation of *Pterinopelma* Pocock 1901 with description of a new species and the female of *Pterinopelma vitiosum* (Keyserling 1891) (Araneae: Theraphosidae: Theraphosinae). *Zootaxa* 2814: 1-18.
<http://dx.doi.org/10.11646/zootaxa.2814.1.1>
- Bücherl, B., Timotheo da costa, a. & Lucas, S. (1971). revisão de alguns tipos de aranhas caranguejeiras (orthognatha) estabelecidos por cândido de mello-leitão e depositados no museu nacional do rio. *Memórias do Instituto Butantan* 35: 117-138.
- Coddington, J. & Scharff, N. (1994). Problems with zero-length branches. *Cladistics* 10, 415–423. <https://doi.org/10.1111/j.1096-0031.1994.tb00187.x>
- Dupérré, N. & Tapia, E. (2021). The endless search for type specimens; illustrations of eleven spider (araneae, mygalomorphae) species described by Eugène Simon. *Zootaxa* 4951(2): 259-282. <http://dx.doi.org/10.11646/zootaxa.4951.2.3>
- Esche, S. (2014). Bestimmung einer theraphosinae mit unterscheidung von *Cyclosternum* und *Pseudhupalopus*. *Arthropoda Popularis* 3(1): 18–26.
- Fabiano-da-Silva, W., Guadanucci, J. P. L., Alayón García, G., Lucas, S. M. & Silva, M. B. da (2020). Taxonomy of the genus *Cyrtopholis* Simon, 1892 (Araneae, Mygalomorphae, Theraphosidae): Cuban species described by Pelegrín Franganillo Balboa. *Zootaxa* 4779(1): 79-90. <http://dx.doi.org/10.11646/zootaxa.4779.1.5>
- Ferretti, N., Chaparro, J. C., Ochoa, J. A. & West, R. (2023). A new tarantula (Mygalomorphae: Theraphosidae) genus endemic from Peru with a novel genitalic morphology among theraphosinae and its phylogenetic placement. *Zoologischer Anzeiger* 302: 102-112.
<http://dx.doi.org/10.1016/j.jcz.2022.11.011>
- Fitch, W. M. (1971). Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* 20, 406–416. <https://doi.org/10.2307/2412116>

Gabriel, R. (2016). revised taxonomic placement of the species in the central american genera *Davus* O. Pickard-Cambridge, 1892, *Metriopelma* Becker, 1878, and *Schizopelma* F. O. Pickard-Cambridge, 1897, with comments on species in related genera (Araneae: Theraphosidae). *Arachnology* 17(2): 61–92. <http://dx.doi.org/10.13156/arac.2006.17.2.61>

Gabriel, R. & Sherwood, D. (2020). Revised taxonomic placement of *Pseudhapalopus* strand, 1907, with notes on some related taxa (Araneae: Theraphosidae). *Arachnology* 18(4): 301–316. <http://dx.doi.org/10.13156/arac.2020.18.4.301>

Gabriel, R., Sherwood, D. & Longhorn, S. J. (2020). The revised taxonomic placement of the genus *Acentropelma* Pocock, 1901 and restoration of the genus *Pseudoschizopelma* Smith, 1995 (Aranei: Theraphosidae). *Arthropoda Selecta* 29(4): 453–466.

Galleti-Lima, A., Hamilton, C. A., Borges, L. M. & Guadanucci, J. P. L. (2023). Phylogenomics of Lasiodoriforms: reclassification of the South American genus *Vitalius* Lucas, Silva and Bertani and allied genera (Araneae: Theraphosidae). *Frontiers in Ecology and Evolution* 11(1177627): 1-19. <http://dx.doi.org/10.3389/fevo.2023.1177627>

Gerschman, B. S. & Schiapelli, R. S. (1973). La subfamilia Ischnocolinae (Araneae: Theraphosidae). *Revista del museo argentino de ciencias naturales bernardino rivadavia* (ent.) 4: 43-77.

Hazzi, N. A., Polotow, D., Brescovit, A. D., González-Obando, R. & Simó, M. (2018). Systematics and biogeography of *Spinoctenus*, a new genus of wandering spider from Colombia (Ctenidae). *Invertebrate Systematics* 32(1): 111-158. <http://dx.doi.org/10.1071/IS17022>

Hippa, H., & Vilkamaa, P. (2006). Phylogeny of the Sciaroidea (Diptera): the implication of additional taxa and character data. *Zootaxa*, 1132(1): 63-68.

Maddison, W.P., Maddison, D.R. (2019). Mesquite: a Modular System for Evolutionary Analysis. Version 3.61. Accessed 31 March 2023. <http://www.mesquiteproject.org>.

Mirande, J.M., 2009. Weighted parsimony phylogeny of the family characidae (Teleostei: characiformes). *Cladistics* 25: 574–613. <https://doi.org/10.1111/j.1096-0031.2009.00262.x>
Nixon, K. C. (2002). 'Winclada (BETA) Ver. 10.00.08.' (Published by the author: Ithaca, NY.)

Peñaherrera-R., P. (2023) increasing knowledge of *Cymbiapophysa* Gabriel & Sherwood, 2020 (Araneae, Theraphosidae): general distribution, key to species, and three new species from Ecuador. *Zookeys* 1178: 17–38. <http://dx.doi.org/10.3897/zookeys.1178.105703>

Peñaherrera-R., P., Guerrero-Campoverde, A., León-E., R. J., Pinos-Sanchez, A. & Facón-Reibán, J. M. (2023). Two new species of *Neischnocolus* Petrunkevitch, 1925 (Araneae: Theraphosidae) from eastern and western Ecuador. *Zootaxa* 5351(4): 483-493. <http://dx.doi.org/10.11646/zootaxa.5351.4.6>

- Perafán, C. & Valencia-Cuéllar, D. (2018). *Proshapalopus marimbai*, a new tarantula species (Mygalomorphae, Theraphosidae) and first genus record from Colombia. *Tropical Zoology* 31(4): 200-213. <http://dx.doi.org/10.1080/03946975.2018.1493181>
- Perafán, C. (2017). Distribución actual e histórica del infraorden Mygalomorphae (Araneae) en los Andes del Norte. PhD Thesis, Universidad de los andes, Colombia.
- Pérez-Miles, F., Gabriel, R., Miglio, L., Bonaldo, A., Gallon, R., Jimenez, J. J. & Bertani, R. (2008). *Ami*, a new theraphosid genus from Central and South America, with the description of six new species (Araneae: Mygalomorphae). *Zootaxa* 1915: 54-68. <http://dx.doi.org/10.11646/zootaxa.1915.1.3>
- Pérez-Miles, F., Lucas, S. M., Silva jr., P. I. da & Bertani, R. (1996). Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). *Mygalomorph* 1: 33–68.
- Rudloff, J.-P. (2008). Zur Kenntnis der Gattung *Phormictopus* Pocock, 1901 - einem Faunenelement der Grossen Antillen (Mygalomorphae: Theraphosidae: Theraphosinae). *Arthropoda* 15(4): 2-51.
- Schmidt, G. (1986). Vogelspinnen: Lebensweise, bestimmungsschlüssel, haltung und zucht. albrecht philler, minden.
- Schmidt, G. (1993). Vogelspinnen: Vorkommen, lebensweise, haltung und zucht, mit bestimmungsschlüsseln für alle gattungen, vierte auflage. landbuch, hannover, 151 pp.
- Sherwood, D. & Gabriel, R. (2023). *Cymbiapophysa seldeni*, a new theraphosine species from Ecuador (Araneae: Theraphosidae). *Arachnology* 19(5): 777-779. <http://dx.doi.org/10.13156/arac.2023.19.5.777>
- Sherwood, D., Gabriel, R., Brescovit, A. D. & Lucas, S. M. (2021a). A new species of *Cymbiapophysa* Gabriel & Sherwood, 2020 from Colombia and a transfer from *Proshapalopus* Mello-Leitão, 1923 (Araneae: Theraphosidae). *Arachnology* 18(8): 838-843. <http://dx.doi.org/10.13156/arac.2021.18.8.838>
- Sherwood, D., Gabriel, R., Kaderka, R., Lucas, S. M. & Brescovit, A. D. (2021b). Stabilizing a chaotic taxonomy: redescription and redefinition of the genera *Lasiodorides* Schmidt & Bischoff, 1997 and *Thrixopelma* Schmidt, 1994 (Araneae: Theraphosidae). *Arachnology* 18(8): 893–917. <http://dx.doi.org/10.13156/arac.2021.18.8.893>
- Sherwood, D., Gabriel, R., Peñaherrera-R., P., Brescovit, A. D. & Lucas, S. M. (2023). On the tarantula genus *Xenesthis* Simon, 1891, with description of a new species from Venezuela (Araneae: Theraphosidae). *Taxonomy* 3: 509–527.
- Tarasov, S., Vaz-de-Mello, F. Z., Krell, F. T., & Dimitrov, D. (2016). A review and phylogeny of Scarabaeine dung beetle fossils (Coleoptera: Scarabaeidae: Scarabaeinae), with the description of two *Canthochilum* species from Dominican amber. *PeerJ*, 4: e1988.

Turner, S. P., Longhorn, S. J., Hamilton, C. A., Gabriel, R., Pérez-Miles, F. & Vogler, A. P. (2018). Re-evaluating conservation priorities of New World tarantulas (Araneae: Theraphosidae) in a molecular framework indicates nonmonophyly of the genera, *Aphonopelma* and *Brachypelma*. *Systematics and Biodiversity* 16(1): 89–107.

Wheeler, W. C. (1995). Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology* 44, 321–331. <https://doi.org/10.2307/2413595>
WSC (2023) World Spider Catalog. Version 24. Natural History Museum Bern, Bern. Available from: <http://wsc.nmbe.ch> (accessed 29 August 2023) <https://doi.org/10.24436/2>

APPENDIX

Appendix A: Character list used for general Theraphosinae phylogeny

(1) Apical region of palpal bulb: subcylindrical = 0; subconical = 1; concave-convex = 2. (2) Relative width of sclerites II + III of bulb: narrow (less than 10% of length) = 0; wide = 1. (3) Paraembolic apophysis: absent = 0; present = 1. (4) Subtegulum: not extended = 0; large extended = 1. (5) Male tibial apophysis (leg I): double = 0; one = 1; absent = 2. (6) Digitiform apophysis of bulb: absent = 0; present = 1. (7) Metatarsus I of male: without basal process = 0; with basal process = 1. (8) Male palpal tibia: without retrolateral process = 0; with retrolateral process = 1. (9) Male palpal tibia: without retrolateral cluster of spines = 0; with retrolateral cluster of spines = 1. (10) Male palpal tibia: without prolateral process = 0; with prolateral process = 1. (11) Flexion of metatarsus I on males: on outer side of tibial spurs = 0; between tibial spurs = 1. (12) Spermathecae: two separated longitudinal seminal receptacles = 0; two separated transversal seminal receptacles = 1; four separated longitudinal seminal receptacles = 2; two seminal receptacles widely fused = 3; single semicircular receptacle = 4; single oval receptacle = 5. (13) Spermathecae: multilobular in each side = 0; unilobular at least in each side = 1. (14) Femur III: not incrassate = 0; incrassate = 1. (15) Tibia IV: not incrassate = 0; incrassate = 1. (16) Femur IV: without retrolateral scopula = 0; with retrolateral scopula = 1. (17) Urticating setae type I: absent = 0; present = 1. (18) Urticating setae type III: absent = 0; present = 1. (19) Urticating setae type IV: absent = 0; present = 1. (20) Well-developed coxal spinules (pro- or retrolateral): absent = 0; present = 1. (21) Weakly developed coxal spinules: absent = 0; present = 1. (22) Labial cuspules: numerous (more than 15) = 0; few or none = 1. (23) Fovea: normal = 0; with spheroid process = 1. (24) Metatarsus I of males: normal = 0; strongly curved = 1. (25) Urticating hairs on prolateral palpal femur: absent = 0; present = 1. (26) Urticating setae type VI:

absent = 0; present = 1. (27) Coxae: normal = 0; retrolaterally extend = 1. (28) Apical keel: absent = 0; small = 1; intermediated = 2; very long = 3. (29) Retrolateral keel: absent = 0; present, not pronounced = 1; present, pronounced = 2. (30) Subapical keel: absent = 0; present, not serrated = 1; present, serrated = 2. (31) Prolateral accessory keel, under the prolateral inferior keel: absent = 0; present = 1. (32) Prolateral inferior keel: absent = 0; present = 1. (33) Denticulate row in the prolateral inferior keel: absent = 0; present = 1. (34) Prolateral superior keel: absent = 0; present = 1. (35) Embolus direction: directed ventrolaterally = 0; directed retrolaterally = 1; straight = 2. (36) Urticating setae type VII: absent = 0; present = 1. (37) Coarse and densely grouped Spiniform setae on ventral maxillae: absent = 0; present = 1. (38) Thin and dispersed spiniform setae on ventral maxillae: absent = 0; present = 1. (39) Urticating setae patch: absent = 0, one dorsal patch = 1, two dorsolateral patches = 2. (40) Median dorsal granular area: absent = 0; present = 1. (41) Ventral medial depression: absent = 0; present = 1. (42) Retrolateral cymbial apophysis: absent = 0; present = 1. (43) Spermathecal guard plates: absent = 0; present = 1. (44) Receptacle sclerotisation: normal = 0; partial hypersclerotized (rigid but considerably translucent) = 1; hypersclerotized = 2. (45) Stridulatory plumose setae on the coxae: absent = 0; present = 1. (46) Stridulatory plumose setae on the trochanters: absent = 0; present = 1. (47) Stridulatory claviform setae on the coxae: absent = 0; present = 1. (48) Stridulatory claviform setae on the trochanters: absent = 0; present = 1. (49) Stridulatory velvet setae on the coxae: absent = 0; present = 1. (50) Stridulatory spiniform setae on the coxae: absent = 0; present = 1. (51) Stridulatory spiniform setae on the trochanters: absent = 0; present = 1. (52) Stridulatory rough setae in the coxae: absent = 0; present = 1. (53) Stridulatory sectioned setae in the coxae: absent = 0; present = 1. (54) Stridulatory spatuliform setae in the coxae: absent = 0; present = 1. (55) Stridulatory spatuliform setae in the trochanters: absent = 0; present = 1. (56)

Stridulatory velvet setae in the coxae: absent = 0; present = 1. (57) Stridulatory sectioned setae in the coxae: absent = 0; present = 1. (58) Stridulatory sectioned setae in the trochanters: absent = 0; present = 1. (59) Stridulatory pilose setae in the coxae: absent = 0; present = 1. (60) Stridulatory pilose setae in the trochanters: absent = 0; present = 1. (61) Females with urticating setae I subtype d: absent = 0; present = 1.

Appendix B: Characters for cladistics within Cycloformis and Lasiodoriformis

(1)—Embolus length: 0, long, embolus 2.5 times longer than its width. 1, short, embolus length less than 2.5 times its width. (2) —Apical keel (A): 0, small, restricted to the embolus apex. 1, intermediate, extending slightly backwards, reaching or not the subapical keel. 2, very long, extending backwards by almost all ventral embolus edge. (3)—Embolus apex diameter: 0, slender. 1, thick. (4)—Retrolateral keel: 0, absent. 1, present, not pronounced, slightly rounded. 2; present, pronounced, sharp. (5) —Subapical keel (SA): 0, absent. 1, present. (6)—Prolateral accessory keel, under prolateral inferior keel: 0, absent. 1, present. (7) —Denticulate row in the prolateral inferior keel: 0, absent. 1, present. (8)—Distal embolus shape: 0, embolus apex conical, retrolateral region slightly convex. 1, embolus apex slightly laterally flattened, retrolateral region slightly concave under and above retrolateral keel. 2, embolus apex very flattened laterally, giving it a concave/convex general appearance; retrolateral side very concave under and above retrolateral keel, or only one concave region when retrolateral keel absent. (9)—Prolateral inferior keel: 0, present. 1, absent. (10)—Male palpal bulb ventral median area: 0, normal, or with slight depression at ventral median area. 1, male palpal bulb with pronounced depression at ventral median area. (11)—Male palpal bulb with long subapical row of denticles (SA), reaching more than half of embolus length: 0, absent. 1, present. (12)—Male palpal bulb with prolateral superior keel and apical keel apically fused: 0, prolateral superior keel and apical

keel not completely fused. 1, prolateral superior keel and apical keel completely fused. (13)—

Male tibial apophysis shape: 0, two straight branches originated from common base, retrolateral branch slightly narrow in its median region. 1, two convergent branches originated from common base, tapering distally, prolateral branch is thickened. 2, two straight branches originated from common base, retrolateral lacks median narrowing. 3, two convergent branches which do not originate from common base, retrolateral with median narrowing. (14)—Male tibial apophysis: 0, present, normal size. 1, present, very reduced. 2, absent. (15)—Flexion of metatarsus I of males: 0, touching side of retrolateral branch. 1, touching apex of retrolateral branch. 2, closing between two branches, thus contacting inner face of both branches. (16)—

Number of male tibial apophysis branches: 0, two branches. 1, one branch. (17) —Fusion of spermathecae: 0, spermathecae separated. 1, spermathecae fused in small area. 2, spermathecae widely fused, but still presenting vestiges of two spermathecae in the distal region. 3, spermathecae completely fused, i.e., no vestige of two spermathecae. (18)—Spermatheca shape: 0, not subspheric. 1, subspheric. (19)—Spermathecae length: 0, short. 1, long, at least twice as long as heavily sclerotized area. (20)—Spermathecae stalk: 0, stalk narrower than spermathecae bulb. 1, stalk as wide as spermathecae bulb. (21)—Trochanteral stridulatory hairs: 0, absent. 1, present. (22)—Coxal stridulatory hairs: 0, absent. 1, present. (23)—Type III urticating hair in females: 0, present. 1, absent. (24)—Type I urticating hair morphology: 0, “A” region longer or as long as the “B” region. 1, “A” region shorter than “B” region. (25)—Type I urticating hair: 0, present. 1, absent. (26)—Tibiae IV: 0, normal. 1, thickened. (27)—Color pattern: 0, variable, commonly a homogeneous black or dark brown. 1, carapace dark brown with thoracic region gradually lighter, femora black, patellae, tibiae, and metatarsi I and II laterally pinkish. (28)—

Male leg length and diameter: 0, normal legs. 1, long and narrow legs. (29) —Female carapace

marginal hairs: 0, covered with short marginal stiff hairs, pointing out. 1, covered by long marginal soft hairs, many pointing to inner carapace region. (30)—Female carapace hair cover: 0, short hairs, mainly on cephalic region. 1, very long, curly, scattered hairs, mainly on cephalic region. (31)—Male palpal tibia retrolateral process: 0, absent. 1, present. (32)—Spine row on male dorsal palpal tibia apex: 0, male dorsal palpal tibia apex without row of spines. 1, male dorsal palpal tibia apex with a row of 5 or more spines. (33)— Spines on male palpal tibia apex: 0, 1 to 3 scattered apical prolateral spines. 1, 5 or more apical prolateral closely positioned spines. (34)—Male metatarsus I: 0, straight. 1, curved. (35)—Scopulae on retrolateral femora IV face: 0, absent. 1, present, (36) Stridulatory plumose setae on the coxae: absent = 0; present = 1. (37) Stridulatory plumose setae on the trochanters: absent = 0; present = 1. (38) Stridulatory claviform setae on the coxae: absent = 0; present = 1. (39) Stridulatory claviform setae on the trochanters: absent = 0; present = 1. (40) Stridulatory velvet setae on the coxae: absent = 0; present = 1. (41) Stridulatory spiniform setae on the coxae: absent = 0; present = 1. (42) Stridulatory spiniform setae on the trochanters: absent = 0; present = 1. (43) Stridulatory rough setae in the coxae: absent = 0; present = 1. (44) Stridulatory sectioned setae in the coxae: absent = 0; present = 1. (45) Stridulatory spatuliform setae in the coxae: absent = 0; present = 1. (46) Stridulatory spatuliform setae in the trochanters: absent = 0; present = 1. (47) Stridulatory velvet setae in the coxae: absent = 0; present = 1. (48) Stridulatory sectioned setae in the coxae: absent = 0; present = 1. (49) Stridulatory sectioned setae in the trochanters: absent = 0; present = 1. (50) Stridulatory pilose setae in the coxae: absent = 0; present = 1. (51) Stridulatory pilose setae in the trochanters: absent = 0; present = 1. (52) Females with urticating setae I subtype d: absent = 0; present = 1.