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Phylogenomic analysis, reclassification, and evolution of South American nemesioid burrowing mygalomorph spiders

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ABSTRACT

The family Nemesiidae was once among the most species-rich of mygalomorph spider families. However, over the past few decades both morphological and molecular studies focusing on mygalomorph phylogeny have recovered the group as paraphyletic. Hence, the systematics of the family Nemesiidae has more recently been controversial, with numerous changes at the family-group level and the recognition of the supra-familial clade Nemesioidina. Indeed, in a recent study by Opatova and collaborators, six nemesiid genera were transferred to the newly re-established family Pycnothelidae. Despite these changes, 12 South American nemesiid genera remained unplaced, and classified as *incertae sedis* due to shortcomings in taxon sampling. Accordingly, we evaluate the phylogenetic relationships of South American nemesioid species and genera with the principle aim of resolving their family level placement. Our work represents the most exhaustive phylogenomic sampling for South American Nemesiidae by including nine of the 12 genera described for the continent. Phylogenetic relationships were reconstructed using 457 loci obtained using the spider Anchored Hybrid Enrichment probe set. Based on these results Nemesiidae, Pycnothelidae, Microstigmatidae and Cyrtaucheniidae are not considered monophyletic. Our study also indicates that the lineage including the genus *Fufius* requires elevation to the family level (Rhytidicolidae Simon, 1903 (NEW RANK)). In Pycnothelidae, we recognize/delimit five subfamilies (Diplothelopsinae, Pionothelinae (NEW SUBFAMILY), Prorachiinae (NEW SUBFAMILY), Pselligminae (NEW RANK), Pycnothelinae). We also transfer all the 12 South American nemesiid genera to Pycnothelidae: *Chaco*, *Chilelopsis*, *Diplothelopsis*, *Flamencopsis*, *Hermachura*, *Longistylus*, *Lycinus*, *Neostothis*, *Prorachias*, *Psalistopoides*, *Pselligmus*, *Rachias*. Additionally, we transferred the microstigmatid genus *Xenonemesia* to Pycnothelidae, and we propose the following generic synonymies and species transfers: *Neostothis* and *Bayana* are junior synonyms of *Pycnothele* (NEW SYNONYMY), as *P. gigas* and *P. labordai*, respectively (NEW COMBINATIONS); *Hermachura* is a junior synonym of *Stenoterommata* (NEW SYNONYMY), as *S. luederwaldti* (NEW COMBINATION); *Flamencopsis* is a junior synonym of *Chilelopsis* (NEW SYNONYMY), as *C. minima* (NEW COMBINATION); and *Diplothelopsis* is a junior synonym of *Lycinus* (NEW SYNONYMY), as *L. ornatus* and *L. bonariensis* (NEW COMBINATIONS). Considering the transferred genera and synonymies, Pycnothelidae now includes 15 described genera and 137 species. Finally, these results provide a robust phylogenetic framework that includes enhanced taxonomic sampling, for further resolving the biogeography and evolutionary time scale for the family Pycnothelidae.

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1. Introduction

The infraorder Mygalomorphae is an ancient lineage of spiders that includes tarantulas, trapdoor, funnel and sheet-web spiders, among others. With a fossil record extending back to the Middle Triassic (Selden and Gall 1992), they diverged approximately 300 Mya (Ayoub and Hayashi 2009, Garrison et al. 2016). Mygalomorphs currently comprise 30 families (Opatova et al. 2020), 367 genera and 3276 species (World Spider Catalog, 2021; WSC). The systematics of this group has generally been perceived as a challenge due to their remarkably homogeneous morphology (Goloboff 1995, Hedin and Bond 2006). The first exhaustive cladistic assessment of the infraorder was conducted by Raven (1985), using morphological data; Eskov and Zonstein (1990) disputed some of the hypotheses proposed by Raven (e.g., Atypoidina). Goloboff (1993) implemented a cladistic computational-based analysis also using morphological data that indicated many of the families may be para or polyphyletic. Subsequently, the first molecular studies using Sanger-sequencing approaches made some advances but lacked the taxon sampling necessary to resolve a number of newly identified and long-standing issues in mygalomorph classification (Hedin and Bond 2006, Ayoub et al. 2007, Bond et al. 2012). Owing to the new genomic technologies now readily available in non-model organismal groups like spiders, a recent study by Opatova et al. (2020) using > 400 loci, established a revised and well-supported classification for mygalomorph families. Nevertheless, there are still a number of longstanding issues that remain unresolved.

Nemesiidae Simon, 1889a is currently defined as a family of mygalomorph spiders comprising 22 genera with 187 nominal species (WSC). Even before its establishment (Raven 1985) Nemesiidae *sensu lato* has had a tumultuous history. Many species included in this family have been synonymized (i.e., Pérez de San Román and Ruiz de Zárate 1947, Denis 1960, Loksa 1966, Gerschman and Schiapelli 1966, Schiapelli and Gerschman 1973, Raven 1985, 1990, Blasco 1986, Goloboff 1995, Decae et al. 2007, Zonstein 2016b); some were transferred to other genera or families (i.e., Gerschman and Schiapelli 1965, Raven 1985, Goloboff 1995, Lucas et al. 2008, Passanha et al. 2014, Leavitt et al. 2015, Opatova et al. 2020). Finally, some species were placed in a number of other families such as Dipluridae Simon, 1889a, Ctenizidae Thorell, 1887, Pycnothelidae Chamberlin, 1917 and Migidae Simon, 1889a (i.e., Chamberlin and Ivie 1939, Piza, 1939, Gerschman and Schiapelli 1965, 1967, Lucas and Bücherl 1973, Raven 1985). The type genus *Nemesia* Audouin (1826) itself, was first placed in the family Aviculariidae Simon, 1874. Simon proposed the tribe Nemesiae Simon, 1889a, originally described within Ctenizinae Thorell, 1887, including the Ethiopian, Palearctic and Australasian genera *Genysa* Simon, 1889b, *Nemesia, Arbanitis* L. Koch, 1874, *Hermacha* Simon, 1889c, *Spiroctenus* Simon, 1889c, *Misgolas* Karsch, 1878 and *Hermeas* Karsch, 1878. *Hermeas* and *Misgolas* were later synonymized with *Arbanitis* and then transferred along with *Genysa* to Idiopidae Simon, 1889a by Raven (1985).

The first taxonomic revision carried out indirectly in Pycnothelidae (before Nemesiidae was recognized), was undertaken by Schiapelli and Gerschman (1967) which included six species drawn from various South American genera. They also revised Pycnothelinae Chamberlin, 1917 which included *Lycinus* Thorell, 1894, *Pycnothele* Chamberlin, 1917, *Pycnothelopsis* Schiapelli & Gerschman, 1942 (currently a junior synonym of *Pycnothele*); and proposed the subfamily Diplothelopsinae Schiapelli & Gerschman, 1967 including *Diplothelopsis* Tullgren, 1905 (transferred at the time from Barychelidae Simon, 1889a). Raven's (1985) cladistic evaluation of mygalomorph spiders united Pycnothelidae and Nemesiidae, elevating Nemesiidae to family status, relimiting and considering it as a senior synonym of Pycnothelidae. He hypothesized the monophyly of Nemesiidae based on three synapomorphies: presence of two rows of teeth on the superior tarsal claw (STC), STC wide, and female palpal claw with teeth on the promargin, of which all three are largely homoplasic features when considered within the context of the entire infraorder. Raven (1985) recognized six subfamilies: Anaminae Simon, 1889a, Bemmerinae Simon, 1903, Diplothelopsinae, Ixamatinae Raven, 1985, Nemesiinae Simon, 1889a, and Pycnothelinae and considered South American Nemesiidae paraphyletic (Fig. 1A). The subsequent infraordinal level cladistic analysis performed by Goloboff (1993), which included only a few nemesiid genera (*Acanthogonatus* Karsch, 1880, *Stenoterommata* Holmberg, 1881 (Neotropical region), *Ixamatus* Simon, 1887b (Australasian region) and *Nemesia* (Palearctic region)), did not recover the family as monophyletic, but instead paraphyletic with respect to Microstigmatidae Roewer, 1942.

In 1995, Goloboff revised and reconstructed the relationships of South American nemesiid species (excepting Brazil) using morphological data including 12 of the 13 genera described at the time. The family was recovered as paraphyletic with respect to Theraphosoidina + Microstigmatidae and Goloboff (1995) suggested that the three characters proposed by Raven (1985) as synapomorphies of Nemesiidae actually represent one character, described in a different way. Also, South American Nemesiidae were recovered as paraphyletic constituting three different lineages (Fig. 1B). Subsequent infraordinal level works, incorporating a few molecular markers (Hedin and Bond 2006, Bond et al. 2012) re-confirmed the paraphyly of Nemesiidae but chose not to make any taxonomic changes. Both analyses included the South American genera *Acanthogonatus* and *Stenoterommata* which were recovered as paraphyletic with respect to other nemesiids, sharing a clade with the Australian genus *Stanwellia* Rainbow and Pulleine, 1918 (Fig. 1C). Indeed, a recent more exhaustive study conducted by Opatova et al. (2020) employing 472 loci scattered members of the family Nemesiidae among a number of other families, and relimited the spider family Nemesiidae to just five genera (*Mexentypesa* Raven, 1987, *Calisoga* Chamberlin, 1937, *Amblyocarenum* Simon, 1892b, *Iberesia* Decae & Cardoso, 2006 and *Nemesia*). The four South American nemesiid genera included in the study (*Acanthogonatus*, *Bayana* Pérez-Miles, Costa & Montes de Oca, 2014, *Stenoterommata*, *Pycnothele*) were transferred to the revalidated family Pycnothelidae (Fig. 1D). Pycnothelidae now comprises six genera with *Pionothele* Purcell, 1902 (from Africa) as the sister group to the remaining taxa; notably the three South American Pycnothelidae genera were recovered as paraphyletic clade which also included the genus *Stanwellia* from Australia (Fig. 1D).

As Nemesiidae currently stands, there are 12 South American genera which remain *incertae sedis* (*Chaco* Tullgren, 1905, *Chilelopsis* Goloboff, 1995, *Diplothelopsis*, *Flamencopsis* Goloboff, 1995, *Hermachura* Mello-Leitão, 1923, *Longistylus* Indicatti & Lucas, 2005, *Lycinus*, *Neostothis* Vellard, 1925, *Prorachias* Mello-Leitão, 1924, *Psalistopoides* Mello-Leitão, 1934, *Pselligmus* Simon, 1892a, *Rachias* Simon, 1892b) with 48 species (WSC) (Opatova et al. 2020). Nemesiidae *sensu lato* are tiny to medium-sized spiders (3.8–38.7 mm) possessing a transverse foveal groove; eyes grouped on a tubercle; 2–4 short spinnerets; anterior tarsus without spines; scopula on tarsus III and IV light or absent; are without claw tufts; and the superior tarsal claws are bipectinate with numerous teeth. They are generally nocturnal and fossorial. Their burrows are J- or Y-shaped tubes with one or two entrances, usually covered by silk (Goloboff 1995, Nascimento et al. 2021). They are found under stones, logs (some *Acanthogonatus* and *Stenoterommata*), or trunks and upper branches of the trees (*Stenoterommata*); in open or closed burrows under the soil (*Stenoterommata*, *Rachias*, *Pycnothele*) or equipped with a trapdoor or flap-door (*Chaco*, *Prorachias*, some *Rachias*) (Fig. 2) (Goloboff 1995, Lucas et al. 2005, Montes de Oca and Pérez-Miles 2013, Indicatti, 2013, Ghirotto et al. 2021, Figs. 8, 9, Nascimento et al. 2021).

The aim of this study was to infer the placement of the 12 South American Nemesiidae genera by reconstructing the phylogenetic relationships of South American Nemesioidina, using a target enriched genomic approach via Anchored Hybrid Enrichment. Our newly derived phylogenetic framework which includes many field-sampled taxa allows us to revise the classification of Nemesiidae; affinities with other groups are evaluated providing a substantive contribution to resolving some long-neglected branches on the Spider Tree of Life.

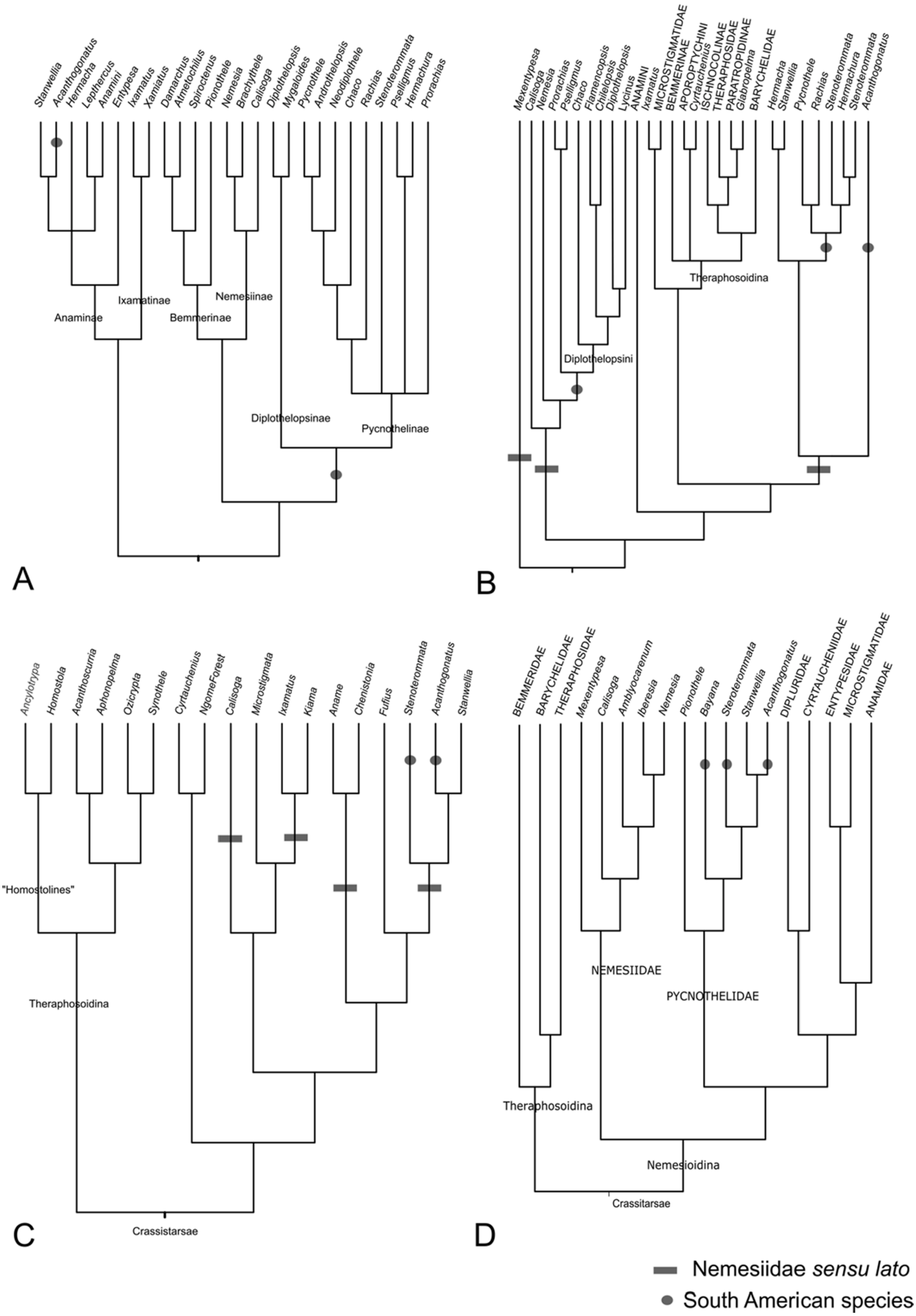

Fig. 1. Phylogenetic relationships of the family Nemesiidae. A. Raven 1985, morphological characters; B. Goloboff 1995, morphological characters; C. Bond et al. 2012, morphological and molecular data (Sanger); D. Opatova et al. 2020, molecular data (Anchored Hybrid Enrichment). Bar indicates Nemesiidae species; circle indicates South American Nemesiidae/Pycnothelidae species.

Fig. 2. A-F. Types of burrows. A. Open burrow (*Bayana labordai*); B. Silk tube (*Acanthogonatus tacuariensis*); C. Trapdoor (*Lycinus* sp.); D. Flap-door (*Chaco costai*); E. Trapdoor (*Prorachias* sp.); F. Open burrow/silk tube (*Fufius lucasae*). Photo credit: A: Pérez-Miles et al. 2014; B: L. Montes de Oca; C: L.S. Espinoza; D: Montes de Oca et al. 2013; E, F: R.P. Indicatti. Scale bars = 10 mm.

2. Material and methods

Specimen sampling and DNA extraction. We included nine of 12 Nemesiidae genera described for South America (WSC) (*Chaco*, *Chilelopsis*, *Diplothelopsis*, *Flamencopsis*, *Hermachura*, *Lycinus*, *Neostothis*, *Prorachias*, *Rachias*) and six Pycnothelidae genera (*Acanthogonatus*, *Bayana*, *Pionothele*, *Pycnothele*, *Stanwellia*, *Stenoterommata*). We used representatives of 16 and 14 species, respectively. For outgroups, we incorporated non-South American Nemesiidae *sensu stricto* samples, as well as other samples representative of the Crassitarsae clade (*sensu* Opatova et al. 2020) such as Anamidae Simon, 1889a, Barychelidae, Bemmeridae Simon, 1903, Cyrtaucheniidae Simon, 1889a, Dipluridae, Entypesidae Bond, Opatova & Hedin, 2020, Microstigmatidae and Theraphosidae Thorell, 1869 providing a robust evolutionary framework totaling a sample of 101 taxa (Table S1). In this study, we incorporate 87% new samples of Nemesiidae *sensu lato*, whereas 40% of the total data set was obtained from previous works (Hamilton et al. 2016, Godwin et al. 2018, Opatova et al. 2020). Newly obtained samples were collected in the field or obtained from museum collections; all samples were stored in 100% ethanol (Fig. 3, Table S1). DNA was extracted using DNeasy blood and tissue kit (Qiagen) following manufacture's protocol. RNase A was added to each sample following the lysis step. Library preparation, enrichment and sequencing were carried out at the Center of Anchored Phylogenomics, Florida State University following the methodology

Fig. 3. Sampling locations of Neotropical taxa used in this study.

described in Lemmon et al. (2012) and Hamilton et al. (2016). The 585 loci Spider Probe kit v1 (Hamilton et al. 2016) was used for the targeted capture through Anchored Hybrid Enrichment (AHE). Stereomicroscope and scanning electron microscopy (SEM) images were prepared and taken as in Indicatti et al. (2015). Institutions of the additional material examined used for the figures of morphological features or for the discussions: Coleção Aracnológica Diamantina, Universidade Estadual Paulista, Rio Claro, Brazil (CAD); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN); Instituto Butantan, São Paulo, Brazil (IBSP); Musée Royal de L'Afrique Centrale, Tervuren, Belgique (MRAC); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP); Instituto Nacional de Pesquisas da Amazônia (INPA); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Phylogenomic analyses. Loci were aligned using MAFFT v7.023b (Katoh 2013) implementing L-INS-I method (–localpair –maxiterate 1000). Aliscore and Alicut (Misof and Misof 2009, Kück, 2009) were used to score and remove ambiguous or random similar sites within the multiple sequence alignment. Alignments were further examined by eye in Geneious Pro v5.6 (Kearse et al. 2012) for consistency and, for removing short sequences or obvious paralogs. Loci were then concatenated using FASconCAT (Kück and Meusemann 2010). For the DNA matrix, partition scheme and substitution models were defined using PartitionFinder 2 (Lanfear et al., 2017) under the Akaike Information Criterion (AIC) with rcluster algorithm (Lanfear et al. 2014) with RAxML implementation (Stamatakis 2014). Maximum likelihood (ML) analyses were conducted using RAxML v8 (Stamatakis 2014) selecting the best tree using the parameters -m GTRGAMMA, -N 1000, and the partitions scheme for each locus. Bootstrap support values were inferred from $>$ 50 replicates computed via autoMRE (Pattengale et al. 2010). The tree was rooted with *Hebestatis theveneti* (Simon, 1891b) (Halonoproctidae Pocock, 1901). Genealogical and sites concordance factors (gCF and sCF, respectively) were also calculated using IQ-TREE (Nguyen et al. 2015, Minh et al. 2020); gCF and sCF analyses are alternative measures of topological support and calculate the proportion of loci or sites from which a particular node in the preferred tree is inferred (Ané et al., 2007). Bayesian (BI) analyses were inferred using Exabayes version 1.4.1 (Aberer et al. 2014) with two independent runs of 20 million generations, four coupled chains each, starting from a parsimony tree resampling every 1000 generations with 0.33 burn in proportion discarded.

Species tree estimation was inferred from 454 gene trees in ASTRAL v. 4.11.2 (Mirarab and Warnow 2015). Individual gene trees were first inferred from AHE nucleotide alignments implementing GTR + G model in RAxML, selecting the best ML tree from 1000 independent iterations for each locus individually. Node support was estimated using ASTRAL's local posterior probabilities.

Divergence times. Node divergences were estimated using penalized likelihood method (Sanderson, 2002) implemented in treePL (Smith and O'Meara, 2012) with the tree topology obtained in RAxML. The setting for the analysis was determined with the following smoothing values = 0.01, 0.1, 1, 10, and 100. Because there are no relevant fossil calibration points for the Crassitarsae clade, we used the divergence times estimates and their 95% confidence intervals (Opatova et al. 2020) inferred among Mygalomorphae lineages represented in both data sets. Calibration was as follows (Fig. 4): (1) Most recent common ancestor (MRCA) of Idiopidae and Bemmeridae: 123 Mya (corresponding to the minimum bound of the Idiopidae clade node) as a minimum bound and 163 Mya (maximum bound from the MRCA between *Idiops* Perty, 1833 and *Spiroctenus*) as a maximum bound; (2) Theraphosoidina clade, MRCA between Bemmeridae and Barychelidae: 125 – 160 Mya (minimum bound corresponding to MRCA between *Spiroctenus* and *Atrophothele* Pocock, 1903 and maximum bound to the Crassitarsae node); (3) MRCA of *Atrophothele* and *Ozicrypta* Raven, 1994: 82 – 94 Mya (corresponding to the MRCA between the same pair of samples); (4) Nemesioidina clade, MRCA of *Mexentypesa* and *Calisoga*: 94 – 106 Mya (corresponding to the MRCA between the same pair of samples); and (5) MRCA of *Kiama* and *Kwonkan* Main, 1983: 81 – 92 Mya (corresponding to the same pair of samples). All phylogenetic analyses were run on the Hopper Community Cluster at Auburn University and the Farm Community Cluster at UC Davis. All supplementary material is uploaded in Figshare Repository https://doi.org/10.6084/m9.figshare.16622284.

3. Results

Concatenated analyses. The total data set comprised 456 loci (of 85,374 nucleotides) for 101 terminals (https://doi.org/10.6084/m9.figshare.16622284) with a 13.2% proportion of missing data. We recovered similar tree topologies from the ML (-ln 940239.669658) and BI analyses. In general, nodes on all trees have high support. At the family level all clades are fully supported (bootstrap = 100, pp = 1.0) (Fig. 5, Supplementary Fig. S1-2). Maximum likelihood analysis performed with IQ-tree recovered the same topology (Fig. S3). The Crassitarsae clade was recovered with two main clades (Theraphosoidina and Nemesioidina), with both clades strongly supported (bootstrap = 100, pp = 1.0). The Theraphosoidina clade (including Bemmeridae as the sister-group of Barychelidae plus Theraphosidae) was recovered as the sister-group to the Nemesioidina clade. The Nemesioidina comprises the family Nemesiidae as sister-group to a clade which includes the families Pycnothelidae, Microstigmatidae, Entypesidae, Anamidae, Cyrtaucheniidae, Dipluridae plus Rhytidicolidae Simon, 1903 (NEW RANK). The family Nemesiidae is here represented by a clade including *Mexentypesa* as the sister-group to a clade comprising (*Calisoga* (*Nemesia, Iberesia*)); all nodes are strongly supported (bootstrap = 100, pp = 1.0) (Fig. 5). In Pycnothelidae five major lineages (Fig. 6) are recovered (each one with pp = 1.0, bootstrap = 100) (Fig. 5). The monogeneric Pionothelinae (NEW SUBFAMILY) represented by *Pionothele* from Africa is recovered as sister-group of Pycnothelinae (including *Pycnothele*, *Bayana*, *Neostothis, Xenonemesia* Goloboff, 1988) (Fig. 6); Prorachiinae (NEW SUBFAMILY), including only the genus *Prorachias* (Fig. 6); and Pselligminae Mello-Leitão, 1923 (NEW RANK), including *Stenoterommata*, *Hermachura*, *Rachias* and two new genera (one from Peru and one from Brazil) (Fig. 6). The genera *Pycnothele*, *Diplothelopsis*, *Lycinus*, and *Chilelopsis* are recovered as paraphyletic, whereas *Prorachias* and *Rachias* are recovered as monophyletic, and *Acanthogonatus* and *Stenoterommata* polyphyletic (Figs. 5, 6). Anamidae is the sister-group to Entypesidae + Microstigmatidae, all of which are recovered with high support (bootstrap = 100, pp = 1.0) (Fig. 5). Cyrtaucheniidae was recovered as sister-group to a clade with two lineages comprising Dipluridae and Rhytidicolidae (NEW RANK) (Fig. 5).

Species tree analysis. Multi-species coalescent analysis produced a species tree from 454 input gene trees obtained using RAxML. The resulting quartet-based super tree estimated in ASTRAL (Supplementary Fig. S4) comprises 990,021,192 induced quartet trees from the input gene trees, representing 74.6% of all quartets present in the species tree. ASTRAL produced a slightly different topology than the concatenated analyses (the white boxes in the third position on Fig. 5). This is congruent with the low percentage of gene trees containing a specific branch in the species tree (i.e. the red boxes in the fourth position on Fig. 5). The major differences are the inclusion of Idiopidae in the Crassitarsae clade (pp = 0.65) and the Cyrtaucheniidae clade is recovered as a sister group of (((Microstigmatidae, Entypesidae), Anamidae), (Dipluridae, Rhytidicolidae)) with a low support (pp = 0.55). The Theraphosoidina and Nemesioidina clades are recovered highly supported (pp = 1.0) as well as all family clades.

Divergence times estimation. The dated topology infers the origin of Pycnothelidae ~ 84 Mya during the Cretaceous (Mesozoic era), but South American pycnothelids started to diverge ~ 60 Mya in the Paleogene (Cenozoic era) similar to most South American taxa sampled in this study (Cyrtaucheniidae ~ 63 Mya, Theraphosinae ~ 55 Mya, Dipluridae ~ 50 Mya, Barychelidae ~ 23 Mya). The origin of Rhytidicolidae NEW RANK dates back to the late Cretaceous ~ 70 Mya but its diversification, according to our sample, occured in the Cenozoic during the Neogene and Quaternary periods. Likewise, the Theraphosidae clade in our dated topology split ~ 75 Mya during the Cretaceous between the Ischnocolinae (including the South American genus *Catumiri* Guadanucci, 2004) and the other lineages.

4. Discussion

Pycnothelidae and Nemesiidae. Our results closely resemble the classification proposed by Schiapelli and Gerschman (1967) where they classified the family Pycnothelidae as containing five South American species from the genera *Lycinus, Pycnothele*, and *Diplothelopsis*. In contrast, Raven (1985) united them within the tribe Nemesiae, elevating that group to family level (Nemesiidae). Our results alternatively infer the non-monophyly of South American Nemesiidae. Indeed, all South American Nemesiidae *sensu lato* included in our analysis are recovered within the family Pycnothelidae as a robustly supported clade. Furthermore, South American Pycnothelidae are recovered paraphyletic as in Opatova et al. (2020) including the genus *Stanwellia* (found in Australia and New Zealand).

Based on the Nemesiidae subfamilies proposed by Raven (1985) and following the reclassification scheme proposed by Opatova et al. (2020), the available pycnothelid subfamilial names are Pycnothelinae and Diplothelopsinae. Our results further support the circumscription of three additional family-group taxa as subfamilies: Pionothelinae (NEW SUBFAMILY), Prorachiinae (NEW SUBFAMILY) and Pselligminae Mello-Leitão, 1923 (NEW RANK) (see below). The subfamily Pycnothelinae is relimited to include the genera *Xenonemesia* and *Pycnothele*.

It is noteworthy that the genus *Xenonemesia* currently belongs to the family Microstigmatidae and is transferred herein to Pycnothelidae. *Xenonemesia* was originally described as a nemesiid genus by Goloboff (1988) based on *X. platensis* Goloboff, 1988 specimens from Argentina and Uruguay. Goloboff (1993) suggested that *Xenonemesia* be transferred to Microstigmatidae or alternatively that microstigmatids be considered as a subfamily of Nemesiidae. Goloboff (1995) transferred *Xenonemesia* to Microstigmatidae, a family diagnosed as having round book lungs openings, extremely short posterior lateral spinnerets (PLS), glabrous tegument and anterior tarsi with absent (or very light) scopula. According to Goloboff (1993), the book lung openings of *Xenonemesia* were coded as for *Microstigmata*, *Pseudonemesia*, and *Micromygale* despite some apparent differences. The book-lung openings are not as small, and the posterior margin is not as sclerotized as in *Microstigmata* and *Pseudonemesia*. All of them, however, seem to share a common type of modification (much more pronounced in *Microstigmata* and *Pseudonemesia*), and are therefore coded as having the derived state as being small and rounded (state "1" in Goloboff's character scoring scheme as opposed to "Book-lung openings normal = 0"), whereas *Xenonemesia* should be coded as having normal openings (see Indicatti et al. 2007 fig. 27, Indicatti et al. 2008 fig. 12). On the other hand, *Xenonemesia* has several characteristics that distinguish it from all other microstigmatid

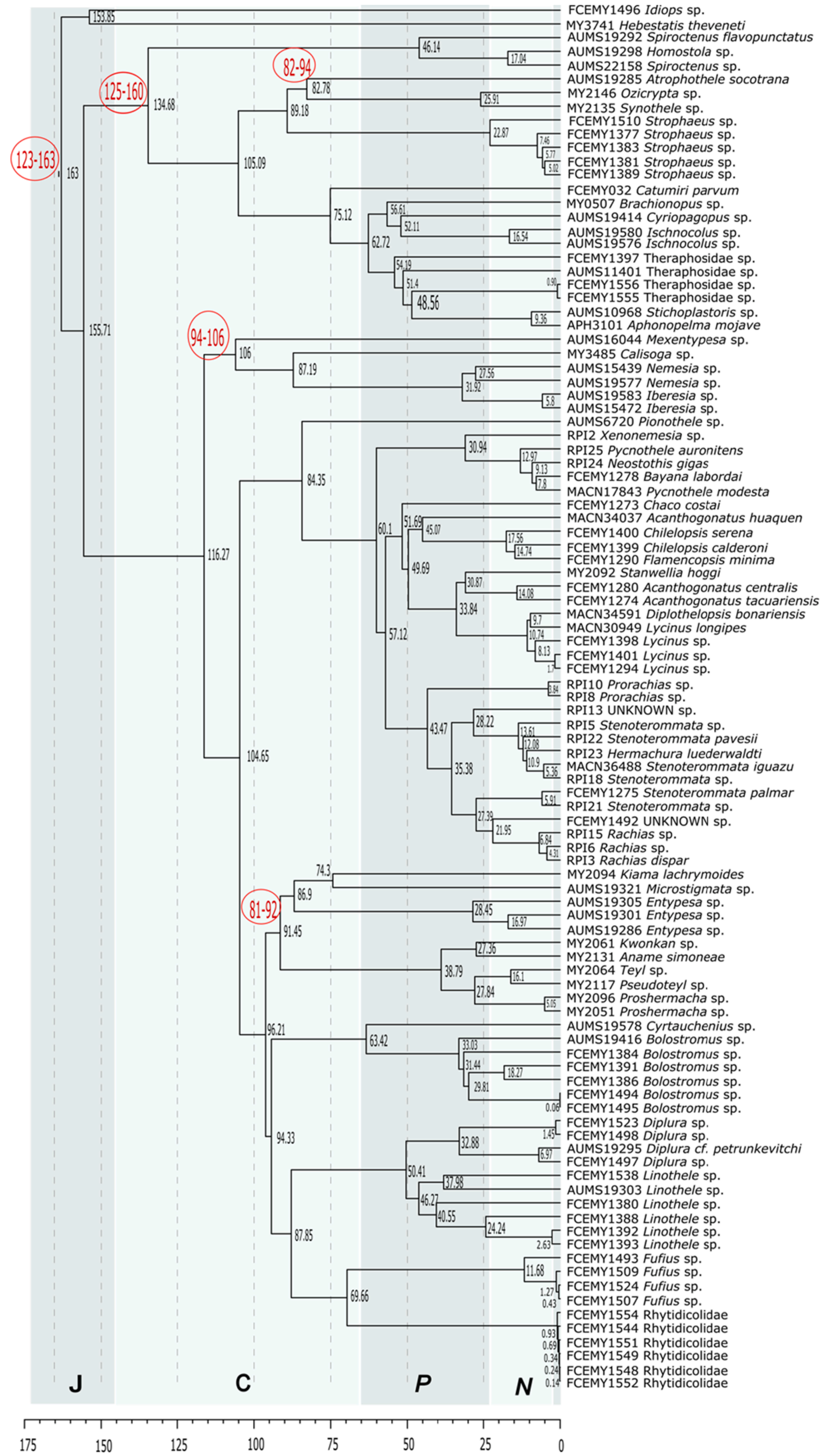

Fig. 4. Divergence time estimates inferred by treePL on a topology obtained in RAxML. Calibration points are marked in red circles. The × axis represents the time in million years. Geologic time abbreviations: (J) Jurassic, (C) Cretaceous, (P) Paleogene, (N) Neogene. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

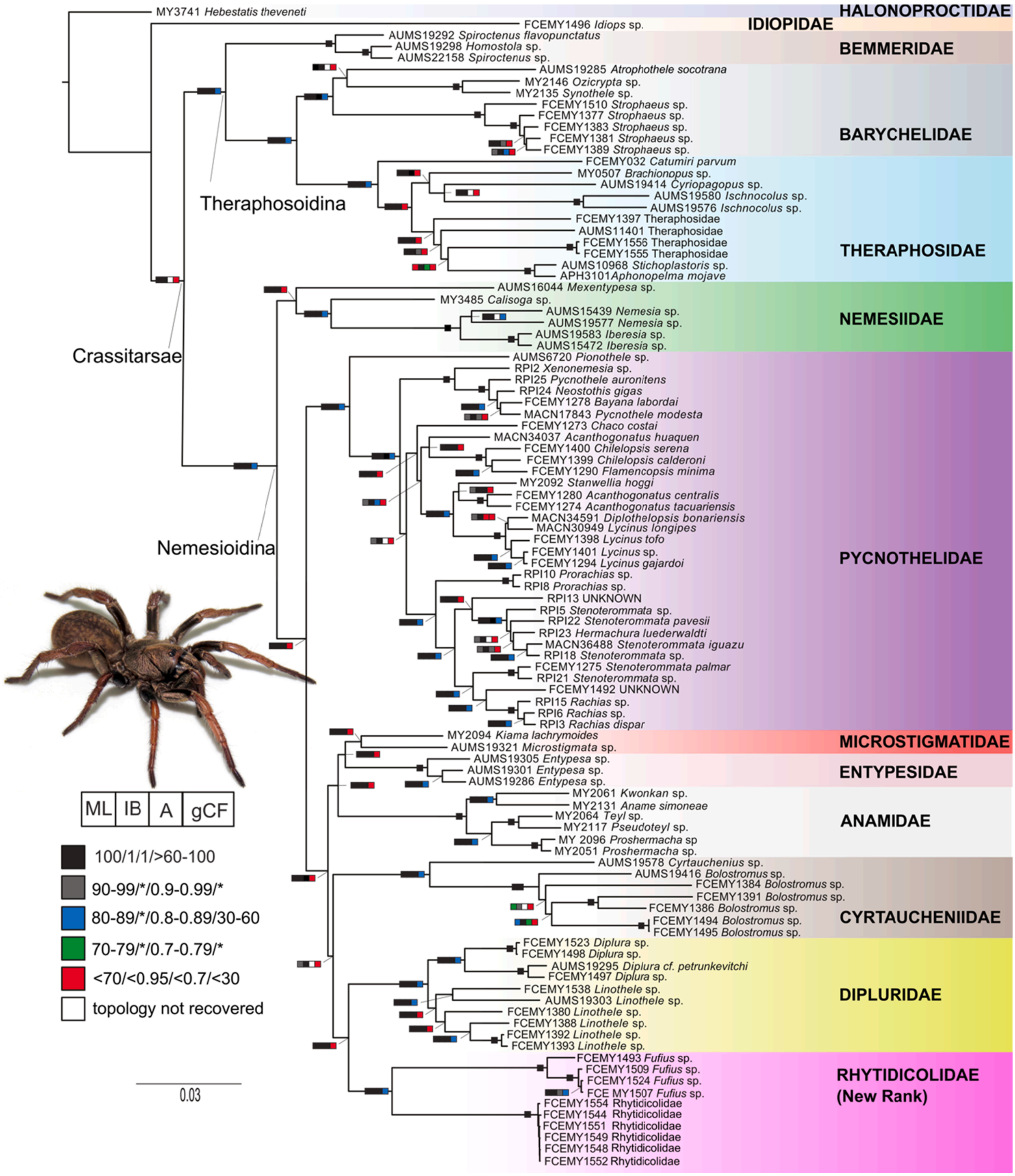

Fig. 5. Phylogenetic tree summarizing concatenated and species tree analyses. Tree topology obtained in maximum likelihood (ML) analysis conducted in RAxML. Boxes on the nodes denote support values. Left to right: ML: RAXML bootstrap support, BI: Bayesian posterior probabilities, A: ASTRAL support values, IQ-TREE gCF support values. Support levels correspond to a color scheme depicted on the left. A single box indicates a full support in all analyses; white box = topology not recovered in the species tree analysis. Taxon in picture: *Rachias dispar*, female (CAD RPI3). Photo: Rafael P. Indicatti.

genera (except *Speloctenıza* Gertsch, 1982, not examined; see proposed changes below). Based on our results and features mentioned we transfer *Xenonemesia* from Microstigmatidae to Pycnothelidae (Pycnothelinae). Furthermore, we are confident that the inclusion of more microstigmatid or nemesiid (*sensu lato*) genera in a new analysis will facilitate elevating the *Xenonemesia* lineage as a new subfamily, as first suggested by Goloboff (1993).

Indeed, more taxa are needed for future studies in order to accurately delimit many of these genera as well as create effective identification keys that employ diagnostic characters principally for *Stenoterommata* and *Acanthogonatus*, genera that remain ostensibly polyphyletic. The systematics of these two genera has been chaotic – *Stenoterommata* has been transferred from Ctenizidae to Nemesiidae by Raven (1985) and recently to Pycnothelidae by Opatova et al. (2020), and some species have been transferred to *Acanthogonatus* or synonymized (Goloboff 1995). *Acanthogonatus* was transferred from Barychelidae to Nemesiidae

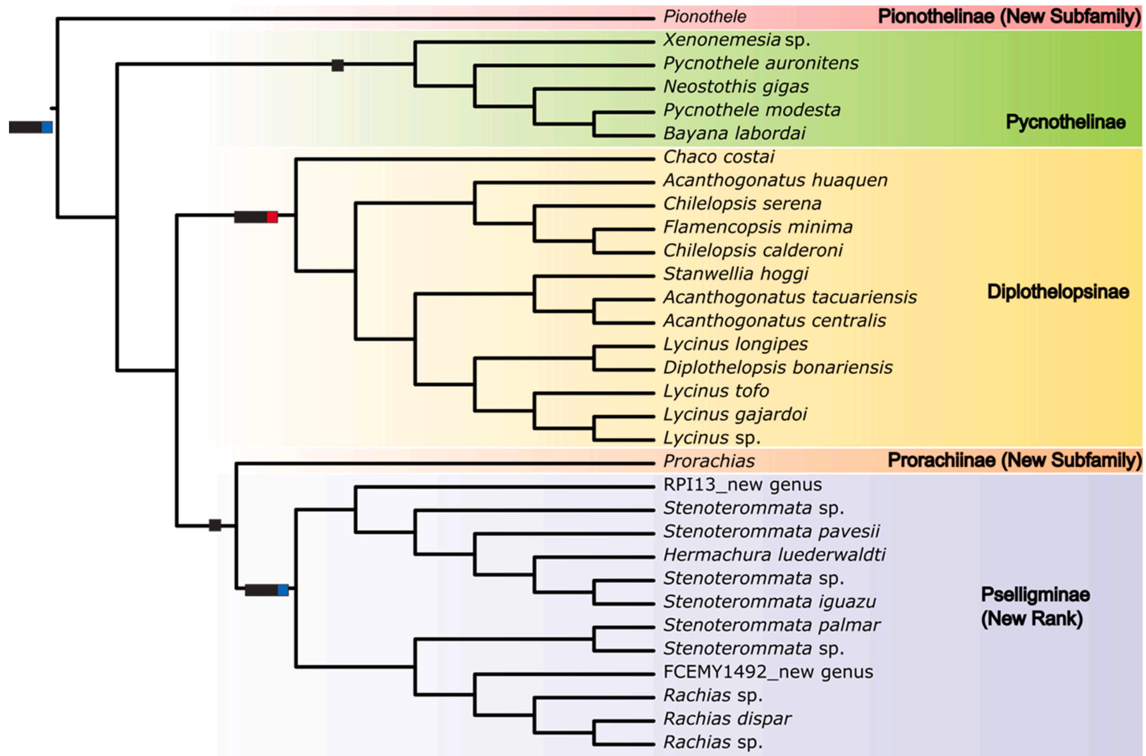

Fig. 6. Cladogram summarizing the phylogenetic relationships among Pycnothelidae subfamilies.

(Raven 1985) and recently to Pycnothelidae by Opatova et al. (2020), and some species have been transferred to the genus *Fufius* Simon, 1888 (Raven 1985) and to *Stenoterommata* (Goloboff 1995). Thus, the taxonomy of these genera clearly remains in need of a comprehensive revision.

Finally, in light of our results we propose the following generic level synonymies and transferred species: (1) *Neostothis* and *Bayana* are junior synonyms of *Pycnothele*, and their type species, *N. gigas* Vellard, 1925 and *B. labordai* Pérez-Miles et al., 2014, respectively, are transferred to *Pycnothele*; (2) *Hermachura* is a junior synonym of *Stenoterommata*, and

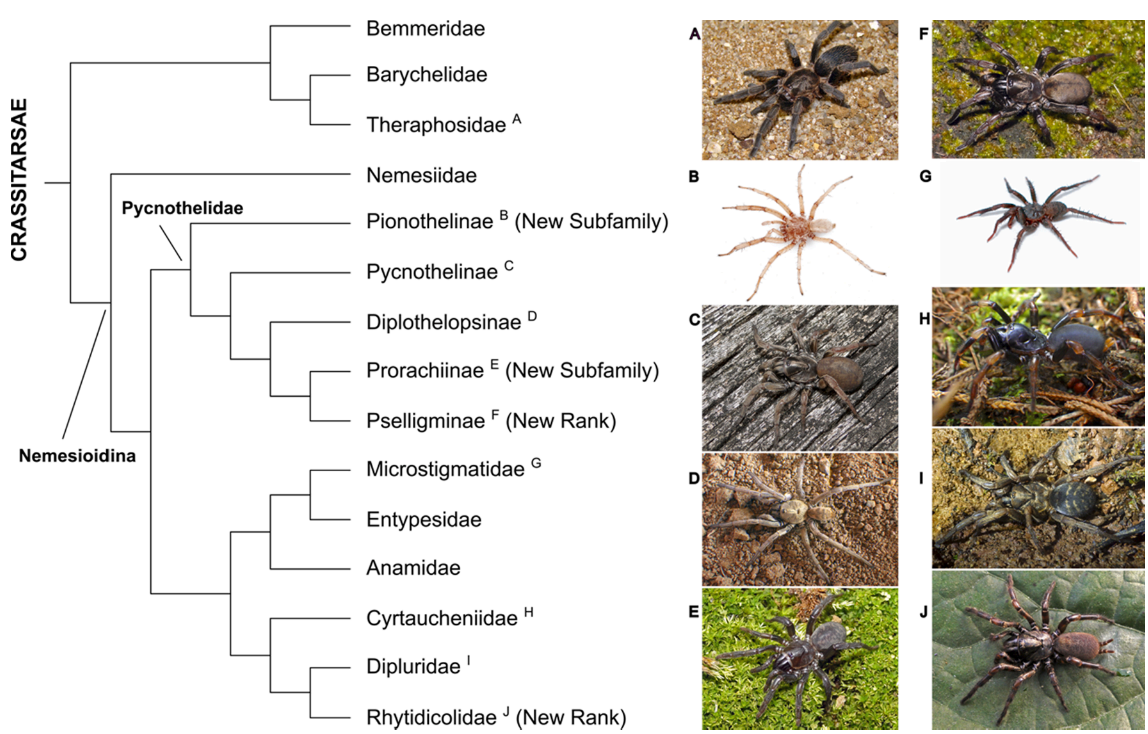

Fig. 7. Cladogram summarizing the phylogenetic relationships among the Crassitarsae families and Pycnothelidae subfamilies. Taxa in pictures are: A. *Catumiri parvum*; B. *Pionothele gobabeb*; C. *Pycnothele auronitens*; D. *Lycinus gajardoi*; E. *Prorachias* sp.; F. *Stenoterommata pavesii*; G. *Microstigmata longipes*; H. *Bolostromus* sp.; I. *Diplura* sp.; J. *Fufius lucasae*. Photo credit: A, C, E, F, J: Rafael P. Indicatti; B: Bond and Lamb 2019; D, H, I: Laura Montes de Oca. G: Dippenaar-Schoeman et al. 2010.

its type species, *H. luederwaldti* Mello-Leitão, 1923 is transferred to *Stenoterommata* (as mentioned and corroborated by Goloboff 1995, Indicatti 2013); (3) *Flamencopsis* is a junior synonym of *Chilelopsis*, and its type species, *F. minima* Goloboff, 1995 is transferred to *Chilelopsis*; and (4) *Diplothelopsis* is a junior synonym of *Lycinus*, and its included species, *D. ornata* Tullgren, 1905 and *D. bonariensis* Mello-Leitão, 1938 are transferred to *Lycinus*. See proposed taxonomic changes below.

Crassitarsae reclassification. Since the first cladistic assessment using morphological characters by Raven (1985) followed by a number of molecular studies (Hedin and Bond 2006, Ayoub et al. 2007, Bond et al. 2012, Garrison et al. 2016) and the more recent exhaustive genomic based analysis (Opatova et al. 2020), the number of families composing the Crassitarsae clade have been increased and the relationships among them have been shuffled. Within the context of this study (Fig. 7), we recovered the Crassitarsae lineage with high support (bootstrap = 100, pp = 1.0). The Theraphosoidina clade is recovered as in Opatova et al. (2020) comprising the family Bemmeridae as sister to Barychelidae plus Theraphosidae. However, for the clade Nemesioidina we document three noteworthy departures. First, the clade including the genus *Fufius,* although within the Nemesioidina clade, is strongly supported as an independent lineage from other cyrtaucheniids (Fig. 5). The placement of the genus has been controversial, first placed in Ctenizinae (Aviculariidae) (Simon 1888, 1891a) and then transferred to Diplurinae (Aviculariidae) (Simon 1892a, b). In 1985, Raven considered it to be a Cyrtaucheniidae (a family suggested to be paraphyletic according to Goloboff (1993, 1995)). Indeed, the phylogenetic analysis by Bond et al. (2012) recovered *Fufius* as being more closely related to genera currently included in Pycnothelidae than other cyrtaucheniids. Consequently, we propose the new family rank taxon Rhytidicolidae Simon, 1903 (NEW RANK). Secondly, the sister group of the *Fufius* clade is a second divergent lineage comprising an unknown species from Peru. The samples included here are females and juveniles and differ from all other known mygalomorph taxa described to date (L.MdeO. pers. observation). Rather than describe this lineage as a new family we believe the conservative approach is to attribute these to the family Rhytidicolidae (NEW RANK) until more material (particularly male specimens) have been collected. Third, relationships among the Nemesioidina clade are appreciably changed: Dipluridae is not the sister-group of Cyrtaucheniidae as recovered in Opatova et al. (2020), but rather the sister-group of the clade comprising Dipluridae + Rhytidicolidae (NEW RANK). Although Dipluridae and Cyrtaucheniidae were not exhaustively sampled for this study, the Nemesioidina clade is highly supported, allowing us to formulate this new phylogenetic hypothesis.

Divergence time. According to the dated topology the family Pycnothelidae diverged ~ 84.3 Mya during the Cretaceous where we observe the split between the lineage comprising *Pionothele* from the rest of the pycnothelids. *Pionothele* is an African genus and is recovered as the sister group to the South American pycnothelids. According to our results, the divergence time of these lineages coincides with the separation of the African and South American continents as a consequence of the Gondwanan break up during the Cretaceous (see also Opatova et al. 2020). In that sense the divergence of South American taxa of Pycnothelidae, as well as Dipluridae, Theraphosinae and Cyrtaucheniidae clades appears to have occurred during the Paleogene after the Cretaceous-Paleogene boundary event (~66 Ma; Vandenberghe et al., 2012). Principally they all started to diversify after the Paleocene-

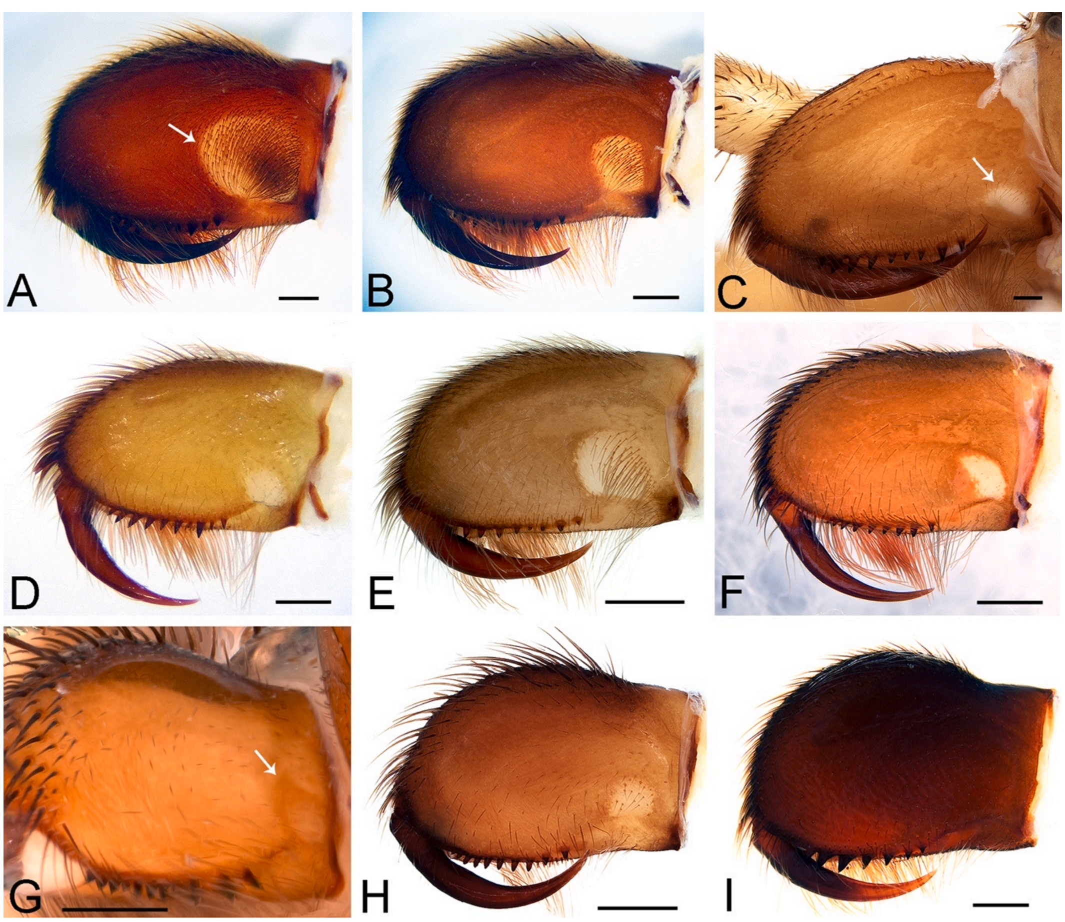

Fig. 8. A-I. Intercheliceral tumescence: A. *Pycnothele perdita* (IBSP); B. *Neostothis gigas* (IBSP); C. *Stanwellia grisea* (CAD); D. *Prorachias* sp. (CAD); E. *Stenoterommata* sp. (CAD RPI18 in this paper) (IBSP); F. *Xenonemesia* sp. (CAD); G. *Microstigmata longipes* (MRAC); H. *Ixamatus barina* (CAD); I. *Fufius* sp. (MZSP). Photos: R.P. Indicatti. Scale bars = 0.5 mm.

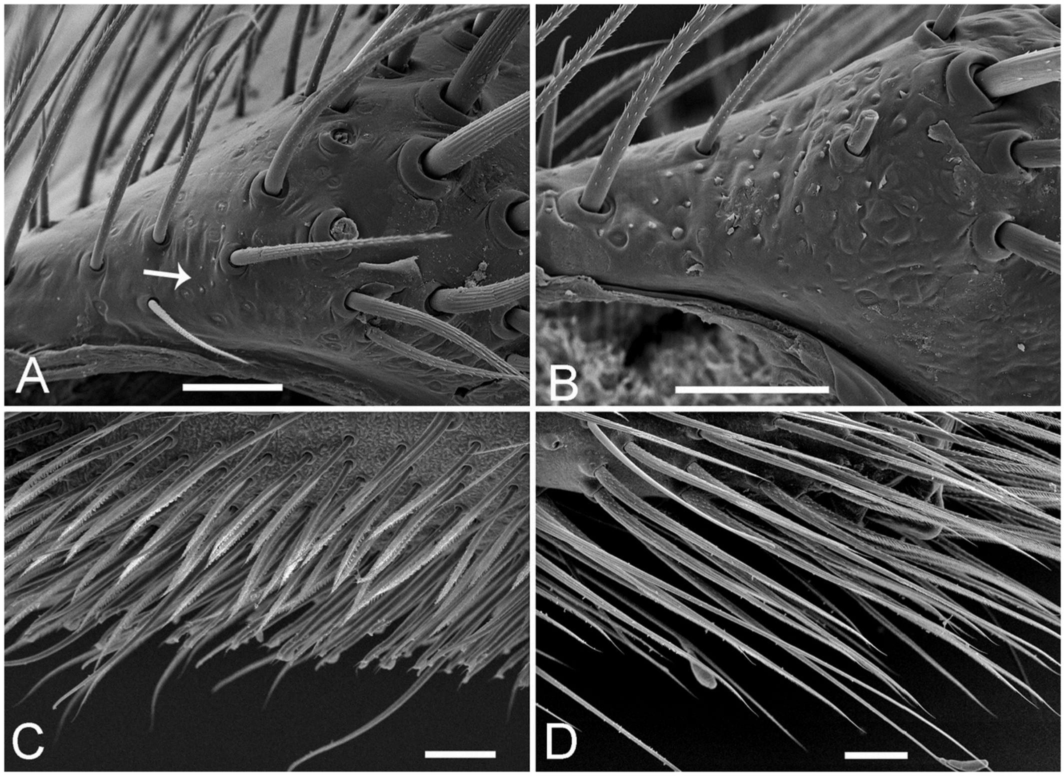

Fig. 9. A, B. Serrula, male, C, D. Adhesive setae, male: A, C. *Xenonemesia* sp. (CAD); B, D. *Xenonemesia otti* (IBSP); C. Tarsus I, retrolateral view; D. Tarsus IV, retrolateral view. Photos: B. Mauricio and R.P. Indicatti. Scale bars = 50 µm.

Eocene Thermal Maximum (~56 Ma, Vandenberghe et al., 2012). During this time frame there is evidence for diversification of terrestrial and marine lineages (Keller et al. 2018, Molina 2015). Moreover, in South America, since ~ 66 Mya the Andes Mountain range started to form, creating vicariant events which may have facilitated allopatric speciation/divergence among some of these groups. *Stanwellia* (an Australian and New Zealand genus) is recovered within the subfamily Diplothelopsinae that includes a number of South American taxa. The relationship between those clades may be explained by the divergence time of this lineages (crown age ~ 31 Mya, stem age ~ 34 Mya) which coincides with the last connection between Australia and South America via Antarctica which occurred 30 Mya (San Martín & Ronquist 2004, see also Opatova et al. 2020). Our work can not be compared to the results obtained by Harvey et al (2018, Fig. 4, Table 3) due to their only including the Australian species in their rate calibration dating analysis. We believe that the divergence dates accuracy could be improved if we increase the number of samples to include both Australian and African species. Also, from the dated topology we infer that the split between cyrtaucheniids and rhytidicolids occurred during the Cretaceous, ~ 88 Mya. Most significantly, according to our sample, Rhytidicolidae diversification started ~ 70 Mya during the Cretaceous but the species in the clade at the present day are dated since ~ 11 Mya during the Neogene. On the other hand, Cyrtaucheniidae family-level diversification started during the Eocene (~50 Mya).

4.1. *Proposed taxonomic changes*

4.1.1. *Relimitation of Pycnothelidae Chamberlin, 1917*

4.1.1.1. Pycnothelidae Chamberlin, 1917 (New Circumscription). ***Type genus***: *Pycnothele* Chamberlin, 1917 (type species *Pycnothele perdita* Chamberlin, 1917)

Diagnosis and remarks. Pycnothelidae was re-established to the family level by Opatova et al. (2020). Based on our results and the inclusion of 13 Neotropical genera, we can reorganize the family classification and propose diagnostic characters. In that sense, Pycnothelidae can be recognized by the following unique combination of characters: (1) presence of small to large, yellow pallid, soft, developed intercheliceral tumescence covered with few to many setae (Fig. 7A-F) (not evident/absent in *Pionothele* and *Afromygale* Zonstein, 2020 (Raven 1985, Zonstein 2016a, 2020)); (2) cymbium lacking dorsal spines; (3) patella III with 1–1–1 prolateral spines or more in same three positions (except *Pionothele straminea* Purcell, 1902 and *Afromygale rukanga* Zonstein, 2020 with 1–1); (4) male tarsi flexible (one or more legs) (except *Pionothele, Afromygale, Xenonemesia* and new genus from Brazil); (5) tarsal organ located on apical central region (Fig. 11A); (6) absence of claw tufts. Additionally, all Pycnothelidae genera, except *Pionothele* (not examined), have the palpal bulb with very low ridges to high keels (Main 1972, fig. 18, Raven 1985, Goloboff 1995, R.P. Indicatti pers. observation examined under SEM or light microscope). We also consider these ridges homologous to keels as in Goloboff (1995).

4.1.1.2. Transferred genera and synonymies. Based on our results, 13 Neotropical genera are transferred to Pycnothelidae, 12 from Nemesiidae (*Chaco*, *Chilelopsis*, *Diplothelopsis*, *Flamencopsis*, *Hermachura*, *Longistylus*, *Lycinus*, *Neostothis*, *Prorachias*, *Psalistopoides*, *Pselligmus*, *Rachias*) and one from Microstigmatidae (*Xenonemesia* Goloboff, 1988). They are transferred on the basis of their phylogenetic position and/or by sharing features of the family diagnosis here proposed. Five new generic synonymies are proposed: *Neostothis* and *Bayana* are junior synonyms of *Pycnothele* by sharing wide clypeus, chelicerae projected at the apex (Fig. 10A, G), tibial spur on male leg I absent, metatarsal preening combs absent, inferior tarsal claws (ITC) I-IV absent, large and deep ventral excavation on palpal tibia (Passanha et al. 2014, figs. 3, 8) less developed in *Neostothis* and *Bayana*, and presence of a supraspermathecal chamber (Goloboff 1995, fig. 115g, h, Lucas et al. 2008, fig. 2e, f, Pérez-Miles et al. 2014, fig. 6, Passanha et al. 2014, figs. 7, 12). *Flamencopsis* is a junior synonym of *Chilelopsis* by sharing a flattened

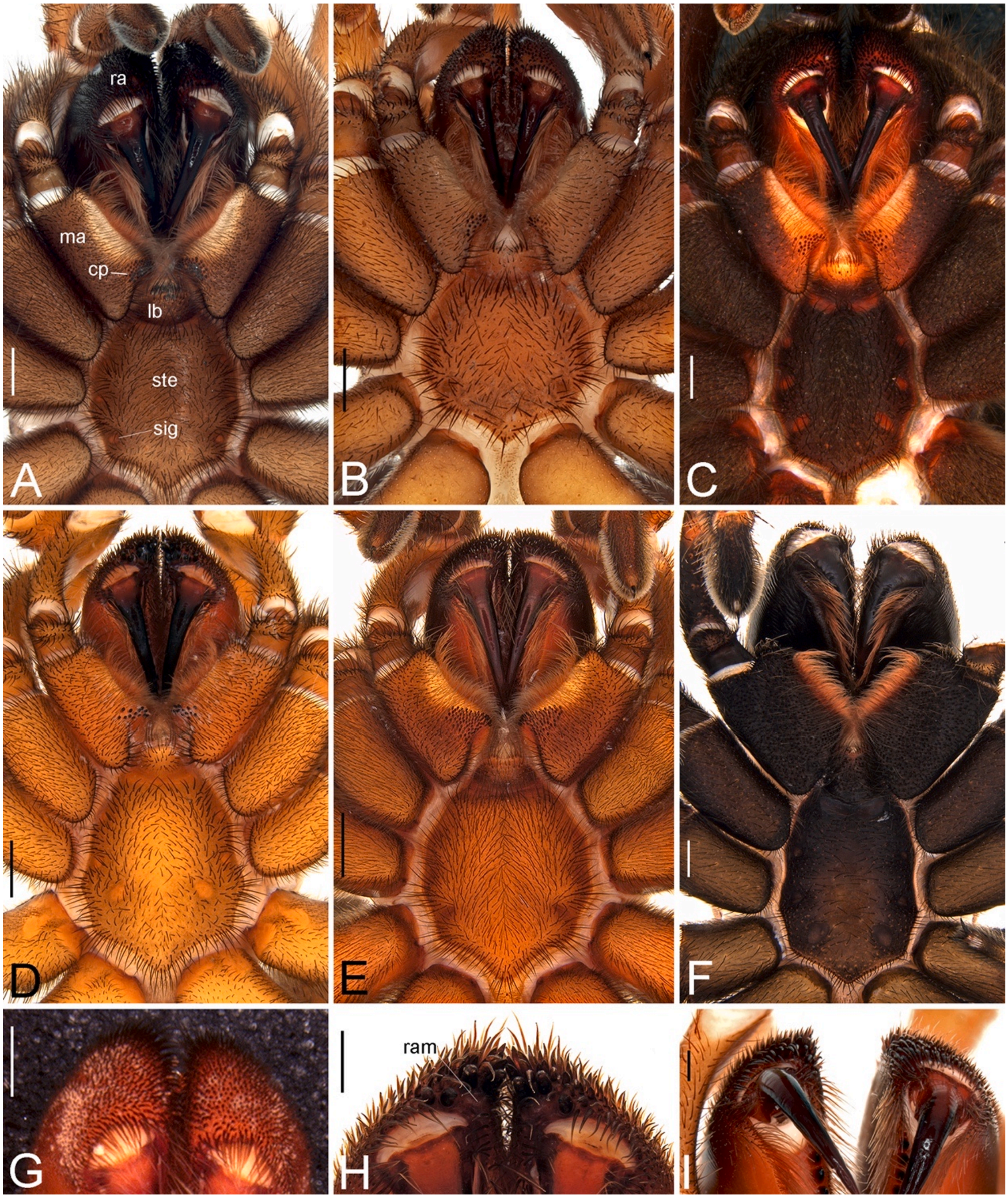

Fig. 10. A-F. Cephalothorax and rastellum, female, ventral view: A. *Pycnothele auronitens* (IBSP); B. *Xenonemesia* sp. (CAD); C. *Chaco obscura* (MACN); D. *Prorachias* sp. (CAD); E. *Stenoterommata iguazu* (CAD); F. *Fufius lucasae* (CAD); G-I. Rastellum; G. *Pycnothele modesta* (MACN); H. *Prorachias* sp. (CAD); I. *Rachias timbo* (MACN). Abbreviations: ra, rastellum; ma, maxilla; cb, maxillary cuspules; lb, labium; ste, sternum; sig, posterior sigillum; ram, rastellum on raised mound. Photos: R.P. Indicatti. Scale bars: A-F = 1 mm, G-I = 0.5 mm.

basal bothrial plate and with deeper ridges (see Goloboff 1995, figs. 10-12). *Diplothelopsis* is a junior synonym of *Lycinus* by sharing few maxillary cuspules (0–10), trichobothria on male cymbium occurring only on the basal half, and few spines (0–3) on dorsal posterior tibia of males (Goloboff 1995); moreover, despite the absence of posterior median spinnerets (PMS) in *Diplothelopsis* this characteristic is not enough to differenciate the genus from *Lycinus*, in which all species have the four spinnerets (PMS, PLS). Finally, *Hermachura* is a junior synonym of *Stenoterommata* by having a male palpal embolus with rigid and smooth parallel keels (as in Indicatti et al. 2017, figs. 19, 21, 22, 2008, fig. 27), male tibia I with a sessile apical retrolateral megaspine (as in Indicatti et al. 2017, figs. 32, 61; Goloboff 1995, figs. 72K, 73F), and females lacking scopulae on tibia I and II, PLS with triangular apical segment, enlarged pumpkiniform spigots (as in Indicatti et al. 2017, fig. 40) along of the PLS spinning field, preening combs on the female metatarsi II, and numerous maxillary cuspules (*ca.* 45 in males and 60 in females, R.P. Indicatti pers. observation). In his phylogenetic analysis, Goloboff (1995) showed that the genus can be synonymized with *Stenoterommata* but he postponed the action to be carried out in future work with the Brazilian species of Nemesiidae. Considering the transferred genera and synonymies, Pycnothelidae now includes 15 described genera and 137 species.

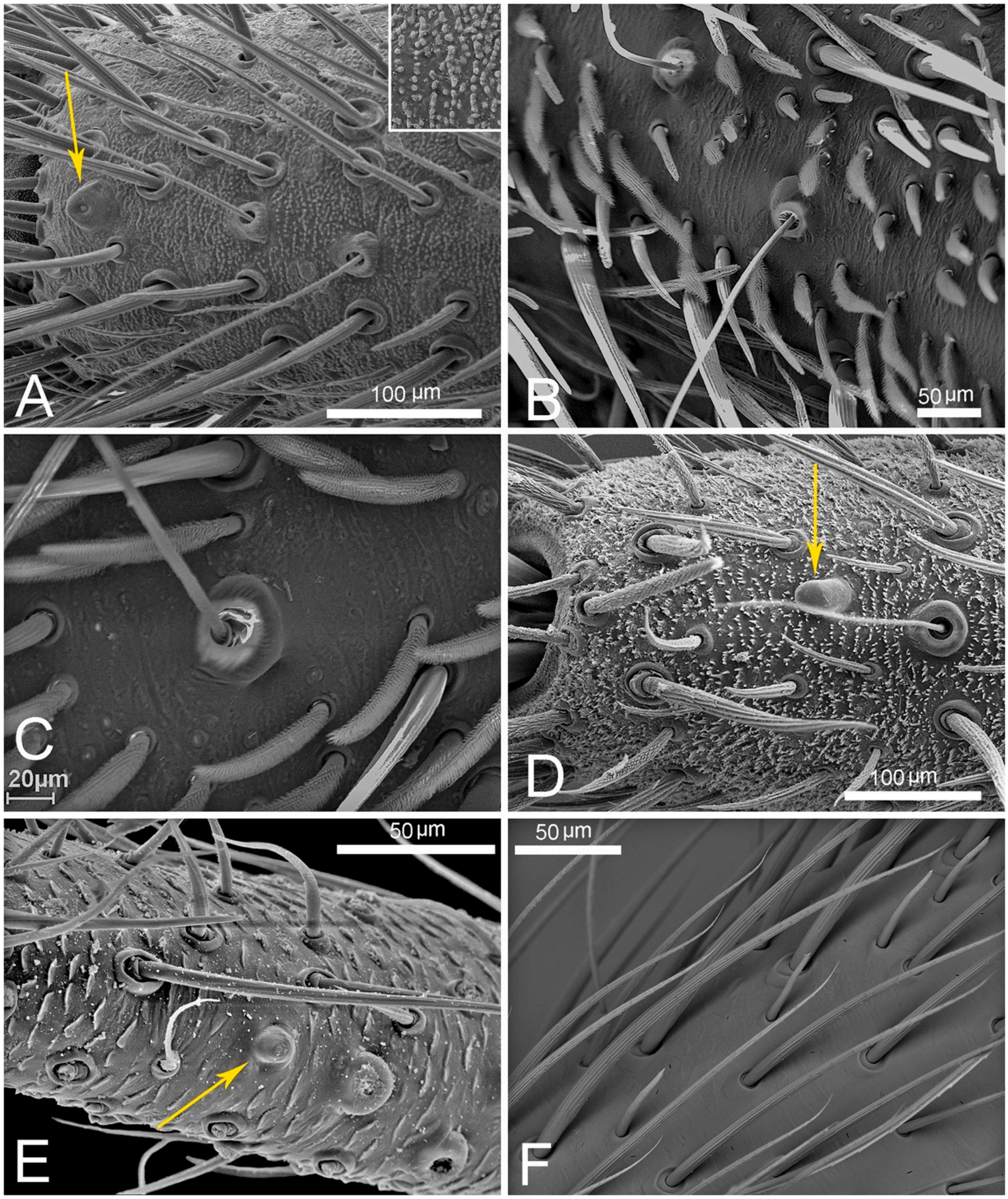

Fig. 11. A-F. Integument and tarsal organ (arrows), dorsal view: A. *Xenonemesia* sp. (CAD); B. *Pycnothele perdita* (IBSP); C. *Neostothis gigas* (IBSP); D. *Microstigmata longipes* (MRAC); E. *Pseudonemesia tabiskey* (IBSP); F. *Fufius* sp. (CAD). Photos: A, D: B. Mauricio and R.P. Indicatti; B: Passanha et al. 2014; C: D.F. Candiani and R.P. Indicatti; E: Indicatti and Villarreal 2016; F: J.P.L. Guadanucci and R.P. Indicatti.

List of included genera for Pycnothelidae (* indicates taxa included in our analysis):

**Acanthogonatus* Karsch, 1880
Afromygale Zonstein, 2020
**Chaco* Tullgren, 1905
**Chilelopsis* Goloboff, 1995
Longistylus Indicatti and Lucas, 2005
**Lycinus* Thorell, 1894
**Pionothele* Purcell, 1902
**Prorachias* Mello-Leitão, 1924
Psalistopoides Mello-Leitão, 1934
Pselligmus Simon, 1892a
**Pycnothele* Chamberlin, 1917
**Rachias* Simon, 1892b
**Stanwellia* Rainbow & Paulleine, 1918
**Stenoterommata* Holmberg, 1881
**Xenonemesia* Goloboff, 1988

Transferred species (on the basis of their phylogenetic position and morphological features)

Chilelopsis minima (Goloboff, 1995) NEW COMBINATION
Lycinus bonariensis (Mello-Leitão, 1938) NEW COMBINATION
Lycinus ornatus (Tullgren, 1905) NEW COMBINATION
Pycnothele gigas (Vellard, 1925) NEW COMBINATION

Pycnothele labordai (Pérez-Miles et al. 2014) NEW COMBINATION
Stenoterommata luederwaldti (Mello-Leitão, 1923) NEW COMBINATION

4.1.2. *Relimitation of Pycnothelidae subfamilies*

4.1.2.1. Pycnothelinae Chamberlin, 1917 (New Circumscription). ***Type genus:*** *Pycnothele* Chamberlin, 1917 (type species by monotypy *Pycnothele perdita* Chamberlin, 1917)

Genera included: *Pycnothele* Chamberlin, 1917; *Xenonemesia* Goloboff, 1988; *Longistylus* Indicatti & Lucas, 2005

Distribution: Argentina, Brazil, Uruguay

Remarks and diagnosis. The genera *Xenonemesia* and *Longistylus* do not share most of the diagnostic morphological characters of *Pycnothele*, *Neostothis*, *Bayana*, making it difficult to find features that unite them as a subfamily. *Longistylus* shares features present in *Diplothelopsinae* and *Pycnothelinae* genera, however, it is tentatively assigned in *Pycnothelinae* by the chelicerae with weak rastellum composed of thin setae, tibial spur on male leg I absent, metatarsal preening combs absent, ITC I-IV absent, PLS with domed apical article (Indicatti & Lucas 2005), and low ridges on the palpal bulb. The subfamilial placement of *Longistylus* was discussed by Harvey et al. (2018) and Opatova et al. (2020) but both studies maintained it in Nemesiidae. There is the possibility of *Longistylus* belonging to a new subfamily by having a singular male palpal bulb with a very long (at least twice as long as the palpal tibia) styliform embolus, reflexed embolus insertion (Indicatti & Lucas 2005), longitudinal grooves along of the entire embolus, prolateral lobe of cymbium slightly more projected anteriorly, and no pumpkiniform spigots (R.P. Indicatti pers. observation). Even so, we highlight some characteristics that combined distinguish Pycnothelinae from other subfamilies: (1) chelicerae with weak rastellum composed of thickened setae (Fig. 10A, B, G), (2) chelicerae projected at the apex (Fig. 10A, B, G) (except on Longistylus), (3) maxillary serrula found only in males, (4) tibial spur on male leg I absent, (5) metatarsal preening combs absent, (6) female scopulae on legs I and II symmetric, (7) ITC I-IV absent (Fig. 9D, for leg IV), and (8) PLS with domed apical article.

4.1.2.2. Diplothelopsinae Schiapelli & Gerschman, 1967 (new circumscription). ***Type genus:*** *Diplothelopsis* Tullgren, 1905 (here considered a junior synonymy of *Lycinus*) (type species by monotypy *Diplothelopsis ornata* Tullgren, 1905)

Genera included: *Chaco* Tullgren, 1905*; Acanthogonatus* Karsch, 1880*; Chilelopsis* Goloboff, 1995*; Stanwellia* Rainbow & Pulleine, 1918*; Lycinus* Thorell, 1894

Distribution: Argentina, Australia, Brazil, Chile, New Zealand, Uruguay

Diagnosis and remarks. Diplothelopsinae can be recognized by the combination of the following characters: (1) male tarsi flexible; (2) female scopulae on legs I, II symmetric; (3) ITC on tarsi IV or absent. Even though not recognizing the subfamily Diplothelopsinae in his phylogeny, Goloboff (1995) proposed the tribe Diplothelopsini, comprising *Chilelopsis*, *Flamencopsis, Diplothelopsis* and *Lycinus.* It can be recognized by having the anterior median eyes much larger than the minute posterior median eyes; posterior eye row slightly procurved (Goloboff 1995 figs. 118A, 119A, 123A); and by the short, wide caput of females (Goloboff 1995). However, these characters cannot be applied to *Chaco* (Goloboff 1995) and recently, to Brazilian species of *Lycinus* with posterior eyes row slight recurved (Lucas and Indicatti 2010 figs. 5, 12). Moreover, the inclusion of *Acanthogonatus* and *Stanwellia* in Diplothelopsinae make it difficult to find features that diagnose the subfamily.

4.1.2.3. ***Pionothelinae*** *Indicatti, Montes de Oca, Opatova, Almeida, Pérez-Miles, Bond* ***NEW SUBFAMILY***. urn:lsid:zoobank.org:act:D17AE268-4AEF-4EEF-908B-3AC47AF24615

Type genus: *Pionothele* Purcell, 1902 (type species by monotypy *Pionothele straminea* Purcell, 1902)

Genera included: *Pionothele* Purcell, 1902; *Afromygale* Zonstein, 2020

Distribution: Namibia, South Africa

Diagnosis and remarks. *Pionothele* was first described by Purcell (1902) as a ctenizid. The new subfamily Pionothelinae proposed here can be diagnosed by the genus and species descriptions following Purcell (1902), Tucker (1917), Raven (1985, figs. 73–78) and Zonstein (2016a, figs. 1-7): (1) rastellum weak, composed by slightly thickened setae; (2) clypeus narrow; (3) thoracic fovea short, more or less straight in males and females; (4) sternum broad posteriorly, narrowing anteriorly (as in Prorachiinae); (5) posterior sternal sigilla oval, very small, away from margin *ca*. three times length (as in Prorachiinae); (6) male tibia I with one sessile retroventral megaspine (except on *Afromygale*); (7) metatarsal preening combs absent; (8) male tarsi I, II swollen in the middle or distal region (except on *Afromygale*); (9) tarsi I-IV not flexible; (10) ITC very small. *Afromygale* is tentatively assigned in Pionothelinae (NEW SUBFAMILY) because the genus has eight of ten subfamily diagnostic features, as indicated above. Actually, *Pionothele* and *Afromygale* do not share most of the morphological characters existing in Pycnothelidae, e. g. presence of intercheliceral tumescence. Moreover, *Pionothele* probably has the palpal bulb with low ridges on embolus (homologous to keels). Indeed, the inclusion of more genera in future studies would probably indicate elevating Pionothelinae as a new family.

4.1.2.4. ***Prorachiinae*** *Indicatti, Montes de Oca, Opatova, Almeida, Pérez-Miles, Bond* ***NEW SUBFAMILY***. urn:lsid:zoobank.org:act:85E2C410-BEEA-4724-A4DB-C52532EF2967

Type genus: *Prorachias* Mello-Leitão, 1924 (type species by monotypy *Prorachias bristowei* Mello-Leitão, 1924)

Genus included: *Prorachias* Mello-Leitão, 1924

Distribution: Brazil

Remarks and diagnosis. Prorachias was first described by Mello-Leitão (1924) as a ctenizid. The genus was redescribed by Lucas et al. (2005) based on the type species, *Prorachias bristowei* Mello-Leitão, 1924 and additional characteristics from Raven (1985) and Goloboff (1995). The subfamily can be diagnosed by the combination of the following characters: (1) chelicerae with very strong rastellum, composed of 5–9 stout coniform spines of wich 2–3 on raised mound (Figs. 7G, 9H); (2) projected chelicerae on apical region (Fig. 10D, H); (3) clypeus wide; (4) sternum broad posteriorly, narrowing anteriorly, triangular-shaped (Fig. 10D) (as in *Pionothele straminea*); (5) posterior sternal sigilla small, oval, away from margin *ca.* three times their length (Fig. 10D); (6) tibial spur or megaspine on male leg I absent*;* (7) female scopulae on legs I, II more developed on prolateral side, asymmetric (usually more developed than on *Pselligmus*); (8) female tibiae I, II densely scopulate (usually more densely than on *Pselligmus*); (9) ITC on all legs; (10) PLS with domed apical article.

4.1.2.5. ***Pselligminae*** *Mello-Leitão, 1923* ***NEW RANK***. urn:lsid:zoobank.org:act:3BB3CCE6-B13F-468F-A6AA-C56C832ACA6F

Type genus: *Pselligmus* Simon, 1892a (type species by monotypy *Pselligmus infaustus* Simon, 1892a)

Genera included*: Stenoterommata* Holmberg, 1881*; Rachias* Simon, 1892b, *Pselligmus* Simon, 1892a, *Psalistopoides* Mello-Leitão, 1934

Distribution: Argentina, Brazil, Peru, Uruguay

Remarks and diagnosis. The subfamily name is derived from the available subfamily-level taxon *Pselligmeae* Mello-Leitão, 1923. The tribe Pselligmeae was established by Mello-Leitão (1923) to group the genera *Pselligmus* and *Ctenochelus* Mello-Leitão, 1923 (currently a junior synonymy of *Stenoterommata*) in Ctenizinae, Ctenizidae. Six decades later, Raven (1985) considered Pselligmeae a junior synonym of the subfamily Pycnothelinae (Nemesiidae) by lacking the features that diagnosed this agrupament. We revalidated the tribe Pselligmeae and elevated this taxon to the subfamily status, Pselligminae Mello-Leitão, 1923 (NEW RANK). Although *Pselligmus* and *Psalistopoides* were not included in our analysis, they were recovered in a lineage closely related to *Rachias* and *Stenoterommata* (R.P. Indicatti unpublished data) sharing the features of the family diagnosis. Due to this, *Pselligmus* and *Psalistopoides* are here transferred from Nemesiidae to Pycnothelidae, and included in Pselligminae (NEW RANK). The Pselligmus transfer also was carried out in order to maintain the taxonomic stability, avoiding the proposal of a new subfamily rank name (e.g. "Stenoterommatinae"), which will be synonymized at a later time. *Pselligmus, Psalistopoides*, *Rachias* and *Stenoterommata* share a continuos history of changes with generic synonymies, transfers, and removals of species (Raven 1985, Goloboff 1995, Guadanucci and Indicatti 2004, Lucas and Indicatti 2006). Currently, *Pselligmus* is a monotypic genus, *Psalistopoides* has two species (Lucas and Indicatti 2006), and *Rachias* and *Stenoterommata* have 11 and 24 species, respectively (Indicatti et al. 2017). Based on the examination of specimens, diagnoses and descriptions of Raven (1985), Goloboff (1995), Lucas and Indicatti (2006), and Indicatti et al. (2017) Pselligminae can be diagnosed by the combination of the following characters: (1) chelicerae with weak (Fig. 10E, I) to strong rastellum, composed of short to long thickened setae or long coniform spines not on raised mound (Fig. 10E,I), (2) clypeus narrow, (3) posterior sternal sigilla small, oval, away from margin ca. one (Fig. 10E) or two times their length, (4) female scopulae on legs I and II symmetric (except on *Pselligmus*), (5) metatarsal preening combs present (except on *Pselligmus*, which have pseudocombs), (6) narrow to wide band of pumpkiniform spigots on inner edge of the spinning field of the PLS articles (except on a new genus from Brazil), and (7) enlarged pumpkiniform spigots present (except on a new genus from Brazil).

4.1.3. Relimitation of Nemesiidae Simon, 1889

*4.1.3.1. Nemesiidae Simon, 1889 (New Circumscription). **Type genus:** Nemesia* Audouin, 1826 (type species *Nemesia cellicola* Audouin (1826))

Remarks. Since Opatova et al. (2020) relimited the family Nemesiidae many taxa remain as incertae sedis. In light of our results, we were able to transfer all the South American taxa to Pycnothelidae. Much work still remains to clarify the correct position for many of these taxa.

List of included genera (* indicates taxa included in our analysis):

**Nemesia* Audouin, 1826
Amblyocarenum Simon, 1892b
**Calisoga* Chamberlin, 1937
**Iberesia* Decae and Cardoso, 2006
**Mexentypesa* Raven, 1987

Incertae sedis

Atmetochilus Simon, 1887a
Brachythele Ausserer, 1871
Damarchilus Siliwal, Molur and Raven, 2015
Damarchus Thorell, 1891
Gravelyia Mirza and Mondal, 2018
Raveniola Zonstein, 1987
Sinopesa Raven and Schwendinger, 1995

4.1.3.2. Rhytidicolidae Simon, 1903 NEW RANK. urn:lsid:zoobank.org:act:30447466-F995-4EC0-BE45-D022C8360228

***Type genus**: Rhytidicolus* Simon, 1889a (type species by monotypy *Rhytidicolus structor* Simon, 1889a)

***Distribution**:* Argentina, Bolivia, Brazil, Colombia, Ecuador, Guatemala, Peru, Trinidad, Venezuela

Remarks and diagnosis: The family name is derived from the available subfamily-level taxon Rhytidicoleae Simon, 1903. The tribe Rhytidicoleae was established by Simon (1903) in Ctenizinae, Aviculariidae, to include only the genus *Rhytidicolus* Simon, 1889a. Six decades later, Raven (1985) considered Rhytidicoleae a junior synonym of subfamily Aporoptychinae Simon, 1889a (Cyrtaucheniidae) by serving no grouping function and the genus shares the broad maxillae, long labium, and short diagonal fang with all other Aporoptychini Simon, 1889a. Here we revalidated the tribe Rhytidicoleae and elevated this taxon to the family status, Rhytidicolidae (NEW RANK), which is proposed on the basis of phylogenetic position (Fig. 5) and morphological features. Although *Rhytidicolus* was not included in our phylogenomic analysis, it was recovered in a lineage closely related to *Fufius* (M. Almeida unpublished data). For this reason, *Rhytidicolus* is here transferred from Cyrtaucheniidae to Rhytidicolidae Simon, 1903 (NEW RANK). This transfer was carried out in order to maintain the taxonomic stability, avoiding the proposal of a new family rank name (e.g. "Fufiidae") which will be synonymized at a later time. Based on the examination of the specimens from several zoological collections, descriptions of Raven (1985), Guadanucci and Indicatti (2004), Ortega et al. (2013), Indicatti and Almeida (2020) and Raven's pers. observations of the type-specimen *R. structor*, Rhytidicolidae (NEW RANK) can be diagnosed on the basis of the following unique combination of characters: (1) intercheliceral tumescence absent (Fig. 7I), (2) short diagonal fang (Fig. 10F), (3) low eye tubercle, (4) anterior eye row recurved, (5) male tibia I with short retroventral apical spur and megaspine, (6) PLS with digitiform apical article, (7) clavate trichobothria only on male cymbium and female palpal tarsus (absent or broken on some *Fufius* specimens), and (8) bulb with low ridges and thin, long embolus.

List of included genera (* indicates taxa included in our analysis):

**Fufius* Simon, 1888
Rhytidicolus Simon, 1889a

4.1.4. Relimitation of Cyrtaucheniidae Simon, 1889

*4.1.4.1. Cyrtaucheniidae Simon, 1889 (New Circumscription). **Type genus:** Cyrtauchenius* Thorell, 1869 (type species by original designation *Cyrtauchenius terricola* (Lucas, 1846)).

Remarks. Our study allows us to confirm the placement of *Bolostromus* Ausserer, 1875 in the family Cyrtaucheniidae and transfer *Fufius* and *Rhytidicolus* to Rhytidicolidae (NEW RANK). Nonetheless, more work still remains to clarify the position of the incertae sedis genera.

List of included genera (* indicates taxa included in our analysis):

**Cyrtauchenius* Thorell, 1869
Ancylotrypa Simon, 1889c
**Bolostromus* Ausserer, 1875

Incertae sedis

Acontius Karsch, 1879
Anemesia Pocock, 1875
Bolostromoides Schiapelli and Gerschman, 1945

4.1.5. Relimitation of Microstigmatidae Roewer, 1942

*4.1.5.1. Microstigmatidae Roewer, 1942 (New Circumscription). **Type genus:** Microstigmata* Strand, 1932 (type species by original designation *Microstigmata geophila* (Hewitt, 1916)).

Remarks. Based on our phylogenetic and morphological analysis, *Xenonemesia* is transferred here to Pycnothelidae. The taxon included in our analysis corresponds to a new species from Brazil which was diagnosed as *Xenonemesia* by the combination of following features: carapace color pattern (three longitudinal yellowish light brown bands); wide sternum; keelless palpal bulb; slightly raised tarsal organ; absence of male tibia I spur; absence of thickened setae on cymbium; absence of inferior tarsal claw (Goloboff 1988, Indicatti et al. 2007); presence of black markings on legs and abdomen (wide and narrow intercalated marks on a central longitudinal band) (Indicatti et al. 2007 figs. 10, 13, 18, 23, 2008 figs. 30, 31). On the other hand, *Xenonemesia* has several characteristics that distinguish it from all microstigmatid genera (except *Speleocteniza* Gertsch, 1982, not examined): (1) body color pattern; (2) patella III with 1–1–1 prolateral spines or more in same positions (instead of 1–1 or absent); (3) only thin setae on cymbium (lacking spines); (4) inferior tarsal claw absent; (5) well developed, pallid and soft intercheliceral tumescence covered with few setae (Fig. 7F) (instead of almost inconspicuous, not soft, asetose in *Microstigmata* Strand, 1932 (Fig. 7G) or similar as in *Ixamatus* (Raven, 1981, Fig. 7H)); (6) wide and flattened book lungs openings (Indicatti et al. 2007 fig. 27, Indicatti et al. 2008 fig. 12), intermediate width among *Microstigmata* and *Ixamatus*, *Xamiatus* Raven, 1981, *Kiama* Main and Mascord, 1969 that are wider; (7) posterior margin of the book-lung openings is not as sclerotized as *Microstigmata*, *Pseudonemesia* Caporiacco, 1955 (Goloboff 1995, Indicatti and Villarreal 2016 Fig. 6C, 9A), and other *Microstigmatinae* or *Micromygalinae* genera; (8) absence of clavate setae on legs, abdomen and spinnerets (Indicatti et al. 2007 figs. 18, 20, 23); (9) weak serrula with 5–35 isolated cuticular thorns in males (Fig. 9A, B) (absent in *Xamiatus* and *Kiama* (Raven 1981, 1985)); (10) slightly raised tarsal organ (Fig. 11A), located on apical central position (Fig. 11A); (11) adhesive setae on ventral tarsi of all legs (Fig. 9C, D); (12) integument with rounded ridges (Fig. 11A) (more closely related to *Pycnothele* (Fig. 11B) and *Neostothis* (Fig. 11C) (differing in the density) than in all Microstigmatidae genera, not presenting digitiform cuticular pustules (Fig. 11D) or flattened scaly cuticle (Fig. 11D)). Microstigmatidae probably remains as non-monophyletic, mainly in the Neotropical genera.

List of included genera (* indicates taxa included in our analysis):

**Microstigmata* Strand, 1932
Angka Raven and Schwendinger, 1995
Envia Ott and Höfer, 2003
Ixamatus Simon, 1887b
**Kiama* Main and Mascord, 1969
Micromygale Platnick and Forster, 1982
Ministigmata Raven and Platnick, 1981
Pseudonemesia Caporiacco, 1955
Speleocteniza Gertsch, 1982
Tonton Passanha, Cizauskas and Brescovit, 2019
Xamiatus Raven, 1981

5. Conclusion

The lack of consensus in how morphological characters are assessed and putative widespread homoplasy coupled with phenotypic homogeneity has long complicated efforts to formulate a stable and accurate mygalomorph spider classification. The use of genomic scale data has contributed to a more comprehensive and well supported framework of phylogenetic relationships. We present the most complete sampling of the family Nemesiidae *sensu lato* since Goloboff's treatment of the group in 1995, over a quarter of a century ago. Based on extensive fieldwork throughout South America (previously undersampled in molecular studies) and the inclusion of a broader sampling scheme, we are able to delimit the families Nemesiidae and Pycnothelidae along with the composition of the Crassitarsae clade. Further studies, including more taxa, are necessary to obtain a more accurate hypothesis about the evolution of some unresolved lineages (e.g., *Acanthogonatus*, *Stenoterommata*).

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CRediT authorship contribution statement

Laura Montes de Oca: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.. **Rafael P. Indicatti:** Conceptualization, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Vera Opatova:** Methodology, Validation, Formal analysis, Investigation, Writing – review & editing. **Marlus Almeida:** Formal analysis, Resources, Writing – review & editing. **Fernando Pérez-Miles:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition. **Jason E. Bond:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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