WILEY

Cladistics

Cladistics 39 (2023) 18–42

doi:10.1111/cla.12518

Molecular phylogeny of the tropical wandering spiders (Araneae, Ctenidae) and the evolution of eye conformation in the RTA clade

Nicolas A. Hazzi[a,b]* and Gustavo Hormiga[a]

[a]*Department of Biological Sciences, The George Washington University, 2029 G St. NW, Washington, DC, 20052, USA;* [b]*Fundación Ecotonos, Cra 72 No. 13[a]-56, Cali, Colombia*

Accepted 25 August 2022

Abstract

Tropical wandering spiders (Ctenidae) are a diverse group of cursorial predators with its greatest species richness in the tropics. Traditionally, Ctenidae are diagnosed based on the presence of eight eyes arranged in three rows (a 2–4–2 pattern). We present a molecular phylogeny of Ctenidae, including for the first time representatives of all of its subfamilies. The molecular phylogeny was inferred using five nuclear (histone H3, 28S, 18S, Actin and ITS-2) and four mitochondrial (NADH, COI, 12S and 16S) markers. The final matrix includes 259 terminals, 103 of which belong to Ctenidae and represent 28 of the current 49 described genera. We estimated divergence times by including fossils as calibration points and biogeographic events, and used the phylogenetic hypothesis obtained to reconstruct the evolution of the eye conformation in the retrolateral tibial apophysis (RTA) clade. Ctenidae and its main lineages originated during the Paleocene–Eocene and have diversified in the tropics since then. However, in some analyses Ctenidae was recovered as polyphyletic as the genus *Ancylometes* Bertkau, 1880 was placed as sister to Oxyopidae. Except for Acantheinae, in which the type genus *Acantheis* Thorell, 1891 is placed inside Cteninae, the four recognized subfamilies of Ctenidae are monophyletic in most analyses. The ancestral reconstruction of the ocular conformation in the retrolateral tibial apophysis clade suggests that the ocular pattern of Ctenidae has evolved convergently seven times and that it has originated from ocular conformations of two rows of four eyes (4–4) and the ocular pattern of lycosids (4–2–2). We also synonymize the monotypic genus *Parabatinga* Polotov & Brescovit, 2009 with *Centroctenus* Mello-Leitão, 1929. We discuss some of the putative morphological synapomorphies of the main ctenid lineages within the phylogenetic framework offered by the molecular phylogenetic results of the study.

Introduction

Wandering spiders (Ctenidae) are a diverse group that is distributed worldwide, with more than 500 species in 48 genera (World Spider Catalog, 2022), having its highest species richness in the tropics. Ctenids are medium to large (5–50 mm) wandering spiders that usually inhabit the forest floor and low vegetation, although a few species are arboreal (Figs 1–3; Gasnier et al., 2009). Wandering spiders are nocturnal, cursorial predators that do not build webs to catch prey (Polotow and Brescovit, 2014). Some species of ctenids are restricted to forests and their population densities decrease significantly when forested habitats suffer fragmentation and disturbance (Jocqué et al., 2005; Rego et al., 2005, Rego et al., 2007; Hazzi, 2020). Their large size and predominant abundance in most tropical forests suggest that ctenids play an important role in tropical ecosystems as top generalist predators of invertebrates and small vertebrates (Gasnier and Hofer, 2001; Menin et al., 2005; Mestre and Gasnier, 2008; Torres-Sanchez and Gasnier, 2010; Hazzi, 2014; Folt and Lapinski, 2017), thus, ctenids are promising models for ecology and conservation studies (Hazzi et al., 2020; Lapinski and Tschapka, 2013, 2014). Furthermore, most species of Ctenidae are narrowly distributed geographically, coinciding with well-known biogeographic regions, making this family a good candidate to test biogeographic

*Corresponding author:
E-mail address: nicolashazzi@gwmail.gwu.edu

hypotheses of diversification in the tropics (Hazzi et al., 2018; Hazzi and Silva, 2012). The highly venomous species of the genus *Phoneutria* Perty, 1833 are some of the best-known representatives of this family, commonly referred to as "banana spiders" because they often inhabit this crop (Simó and Brescovit, 2001; Martins and Bertani, 2007; Hazzi, 2014). These aggressive ctenid species are among the most medically important spiders (Bucaretchi et al., 2018). Their venom is neurotoxic, and many researchers have studied its components and the epidemiology of bites (Gomez et al., 2002; Bucaretchi et al., 2008, 2018; Estrada-Gomez et al., 2015; Diniz et al., 2018; Valenzuela-Rojas et al., 2019).

Ctenids belong to the superfamily Lycosoidea, which comprises the families Lycosidae, Pisauridae, Ctenidae, Psechridae, Thomisidae, Oxyopidae, Senoculidae and Trechaleidae, and they are placed in the retrolateral tibial apophysis (RTA) clade, the most speciose lineage of spiders (Wheeler et al., 2017; Fernández et al., 2018; Kallal et al., 2021). The majority of RTA clade spiders have eight eyes, arranged roughly in two rows (but not Ctenidae, see below), where the anterior row contains the anteromedian (AME) and anterolateral eyes (ALE), and the posterior contains the posteromedian (PME) and the posterolateral eyes (PLE; Griswold, 1993; Ramírez, 2014). The AME pair is usually referred to as the main eyes, which differ from the secondary eyes in having the rhabdomeres arranged distally, without a reflecting layer (tapetum; Homann, 1971; Land, 1985; Morehouse, 2020). The secondary eyes usually have a tapetum that is composed of several layers of guanine crystals and acts as a colour-selective interference reflector with the rhabdomeres pointing away from the light (Homann, 1971; Barth, 2002). Traditionally, the family Ctenidae is diagnosed based on the presence of eight eyes arranged in three rows (2–4–2), with the AME in the first row, the PME and ALE in the second row, and the PLE in the third row, resulting in two strongly recurved rows (Silva, 2003; Polotow and Brescovit, 2014). This ocular conformation is shared across a great diversity of morphotypes that specialized in different habitats (e.g. litter, low vegetation, arboreal and aquatic), suggesting that Ctenidae is not

Fig. 1. Habitus of Ctenidae species of the subfamily Cteninae. (a) *Centroctenus varzea* Brescovit et al., 2020, female from Iquitos, Peru; (b) *Phoneutria fera* Perty, 1833, female from Yasuní National Park, Ecuador; (c) *Ctenus datus* Strand, 1909, female from Gamboa, Panama; (d) *Centroctenus alinahui* Brescovit et al., 2020, female from Putumayo, Colombia; (e) *Spinoctenus flammigerus* Hazzi et al., 2018, female from Barbacoas, Colombia; (f) *Kiekie griswoldi* Polotow & Brescovit, 2018, female from Las Alturas Station, Costa Rica. Photos: N. Hazzi (a, c, d, e, f); G. Hormiga (b).

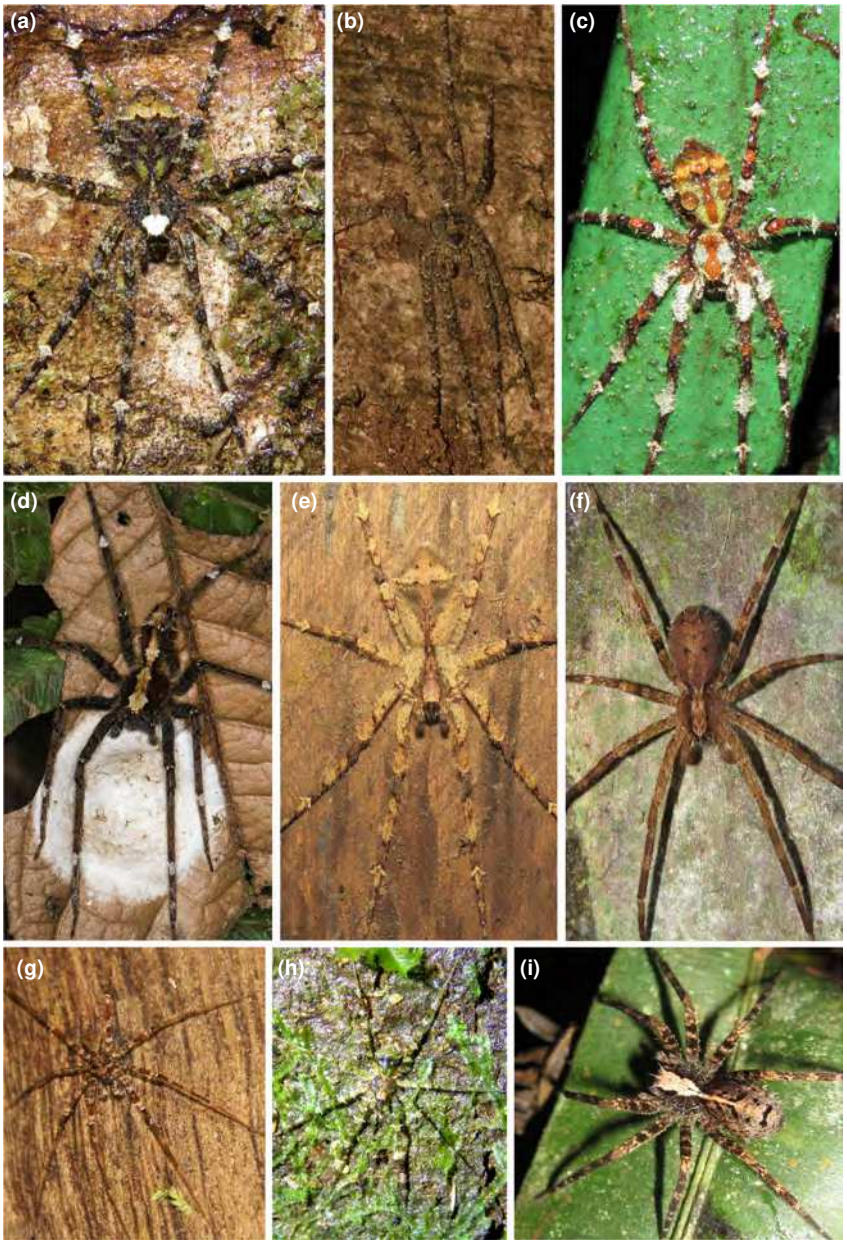


Fig. 2. Habitus of Ctenidae species of the subfamilies Acantheinae, Acanthocteninae and Calocteninae. (a) *Phymatoctenus* sp., female from Tortuguero, Costa Rica; (b) *Enoploctenus* sp., female from Iquitos, Peru; (c) *Phymatoctenus* cf. *sassi*, female from Tirimbina Station, Costa Rica; (d, e) *Enoploctenus* sp., female from Fin del Mundo, Putumayo, Colombia; (f) *Acanthoctenus* sp., female from Tirimbina Station, Costa Rica; (g, h) *Gephyroctenus* sp., from Iquitos, Peru, and Vaupes, Colombia; *Chococtenus miserabilis* (Strand, 1916), female from Pance, Colombia. Photos: N. Hazzi (a, b, c, d, e, f, h, i); E. Vargas (g).

a monophyletic group. Although to date, molecular phylogenies have included few representatives of Ctenidae (Polotow et al., 2015; Henrard and Jocqué, 2017; Wheeler et al., 2017), these hypotheses suggest that the characteristic ocular pattern of ctenids has evolved independently in other families of the RTA clade, such as Cycloctenidae, Miturgidae, Senoculidae, Xenoctenidae and Viridasiidae.

Morphological phylogenies (Silva, 2003; Polotow and Brescovit, 2014; Hazzi et al., 2018) support five main lineages of Ctenidae corresponding to subfamilial groups: Acantheinae Simon, 1897; Acanthocteninae Simon, 1897; Calocteninae Simon, 1897; Cteninae Simon, 1897; and Viridasiinae Lehtinen, 1967. The most recent molecular phylogenies suggest that the family Ctenidae is not monophyletic (Polotow et al., 2015; Wheeler et al., 2017). For instance, molecular studies have raised Viridasiinae from subfamily to family rank and have transferred this group from Lycosoidea to Dionycha (Polotow et al., 2015). In addition, molecular

Fig. 3. (a) Habitus of *Caloctenus aculeatus* Keyserling, 1877 female from Los Tunos, Colombia; *Cupiennius coccineus*, F. O. Pickard-Cambridge, 1901 female from La Selva Biological Station, Costa Rica (b); *Ancylometes amazonicus* Simon, 1898, female (c) and male (d), both specimens from Iquitos, Peru; (e) *Ancylometes* sp. next to the burrow (red arrow) with soil recently removed from the burrow presenting a lighter colour (black arrow), female from Madre de Dios, Peru; (e) close up showing the carapace covered with soil (photos: N. Hazzi (a, e, f); G. Hormiga (b); G. Gagliardi (c, d).

phylogenies have shown that *Cupiennius* Simon, 1890, one of the most intensively studied spider genera (Barth, 2002), does not belong to Ctenidae, and in a recent study this Neotropical genus was transferred to Trechaleidae (Piacentini and Ramírez, 2019). The semi-aquatic spider genus *Ancylometes* has been considered as pisaurids (Sierwald, 1997) prior to its current placement in Ctenidae (Silva, 2003). Molecular studies have failed to robustly place *Ancylometes* in Ctenidae or in any other family (Polotow et al., 2015; Wheeler et al., 2017).

The aim of this study was to test the monophyly of the family Ctenidae and to infer the phylogenetic relationships of the ctenid subfamilies based on nucleotide sequence data, including for the first time a dense taxon sampling of representatives of all ctenid subfamilies (Acantheinae, Cteninae, Acanthocteninae and Calocteninae). Our molecular phylogeny was inferred using five nuclear (histone H3, 28S, 18S, Actin and ITS-2) and four mitochondrial (NADH, COI, 12S and 16S) markers for a total of 9123 base pairs. In addition, we inferred a dated phylogenetic tree in order to estimate the diversification times of Ctenidae and its main clades. Ocular arrangement has been an important diagnostic feature of several families, including Ctenidae, although its phylogenetic distribution across families suggests that this pattern (2–4–2) may have evolved more than once. To test this hypothesis and to explore the evolution of the ocular conformation in the RTA clade we included representatives of major groups of the RTA clade (see below) and of the UDOH grade (Uloboridae, Deinopidae, Oecobidae and Hersiliidae; Fernández et al., 2018).

Material and methods

Taxon sampling

We sequenced a total of 85 taxa of which 80 belong to the ingroup (Ctenidae). To further complement the Ctenidae taxon

sample, we included DNA sequences from published phylogenetic studies of Lycosoidea and the RTA clade (Polotow et al., 2015; Wheeler et al., 2017; Piacentini and Ramírez, 2019) that are available in GenBank. The final matrix includes 259 terminals, 103 of which belong to Ctenidae and represent 28 of the 49 described genera and, as implied by the results of this analysis, at least six additional genera that remain to be described. Each subfamily of Ctenidae is represented in this study by several terminals, including the type genus. Moreover, outgroup taxa included at least one species per RTA clade family that was available in GenBank, two representatives of the UDOH grade and the araneoid *Leucauge venusta* (Walckenaer, 1841; Tetragnathidae) to root the tree.

DNA methods

Specimens in this study were collected in several expeditions in Central and South America (2018–2019) and were preserved in 95% ethanol. Tissue from coxae and femora was used for DNA extraction using the Qiagen DNEasy kit and the rest of the specimen was preserved as a voucher. Seven markers were amplified for analyses. These are mitochondrial ribosomal markers 12S rRNA (~400 bp) and 16S rRNA (~550 bp), cytoplasmic ribosomal markers 18S rRNA (~1800 bp), 28S rRNA (~2200 bp) and ITS-2 (~350 bp), nuclear protein-coding gene histone H3 (~320 bp) and mitochondrial protein-coding gene cytochrome c oxidase subunit I or COI (~800 bp). PCR was achieved with the Promega GoTaq kit, using the primers listed in the Supporting Information and the thermocycle conditions reported in Ballesteros and Hormiga (2018) for ITS-2 and Kallal and Hormiga (2018) for the six remaining markers. Sequence contigs were formed using GENEIOUS 6.0.6 (http://www.geneious.com; Kearse et al., 2012) and protein coding gene sequences were checked for stop codons, then queried against the NCBI BLAST nucleotide database to check for contamination. In addition, we incorporated sequences for two additional genes from GenBank: the mitochondrial NADH (~350 bp) and the nuclear Actin (~320 bp). We were also able to obtain several of these genes from transcriptome data for families or genera with few or no representation of the genes used on GenBank. We downloaded transcriptome data from the Sequence Read Archive and assembled them using Trinity (Grabherr et al., 2011). We then used "map to reference gene" as implemented in GENEIOUS and selected the assembly with the highest percentage of identity. The gene used as a reference was always from the same genus or family of the transcriptome taxon. Multiple sequence alignments were completed using MAFFT (https://mafft.cbrc.jp/alignment/server/) with the "Auto" option to find the best alignment strategy.

Phylogenetic analyses

Phylogenetic analyses were performed using equal weights parsimony and maximum likelihood. Gaps were treated as "missing data" in the phylogenetic analyses. The parsimony analysis was carried out in TNT v. 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016) using the "New Technology Search" options. Driven searches were performed setting the initial level at 100 and 15 replicates. Sectorial searches, tree-drifting and fusing options were performed. This aggressive search ensured that the minimum length tree was found five times. All trees found during searches were collapsed under "rule 1" (the minimum possible length is zero; Coddington and Scharff, 1994). Owing to the high number of polytomies in the strict consensus tree, we also report a majority (50% cutoff) consensus tree. Branch support was assessed using 1000 replicates of jackknife resampling presented as group frequency difference (GC) with a 36% elimination probability (Farris et al., 1996; Goloboff et al., 2003). Replicates were achieved using the same search parameters described above but setting the initial level search at 10 (a less aggressive search). For the model-based analysis, the best partitioning scheme and substitution models were explored using ModelFinder implemented in IQTREE (Nguyen et al., 2015; Kalyaanamoorthy et al., 2017), selecting partition merging and the corrected Akaike information criterion (AICc). Seventeen partition schemes were used as input data: first, second and third codon position for protein coding genes (histone H3, COI, NADH and Actin), and each ribosomal gene as a whole (ITS-2, 28S, 12S, 16S and 18S). We ran two likelihood analyses considering different approaches to deal with site specific heterogeneity: (1) the classic Gamma + Invariant sites; and (2) The FreeRate model (Yang, 1995). The second approach relaxes the assumption of gamma distributed rates across sites and it has been shown to fit data better than the classic +Gamma model (Yang, 1995; Kalyaanamoorthy et al., 2017). Furthermore, we did a third likelihood analysis with a GTR+ FreeRate model for each of the 17 partitions, in order to have a fourth phylogenetic hypothesis and to explore the different positions of unstable taxa. Maximum likelihood was performed with IQ-TREE 1.4.2 (Nguyen et al., 2015) running 100 independent analyses using default parameters. Ultrafast bootstrap (UFBoot; Minh et al., 2013) and SH-aLRT (Shimodaira–Hasegawa approximate likelihood-ratio test; Guindon et al., 2010) were estimated from 1000 pseudoreplicates as support metrics.

A Bayesian inference analysis was carried out to estimate a dated phylogeny using BEAST version 2.5.2. (Bouckaert et al., 2014). The analysis was run with linked trees, an uncorrelated lognormal clock and a birth–death model for the tree prior. All markers were unlinked for site and clock models with the exception of mitochondrial rRNA genes 16S and 12S which ModelFinder indicated that these two markers can be treated as a single partition. All of the remaining markers were unlinked for site and clock models. Based on previous transcriptomes and ultraconserved elements (UCE; Cheng and Piel, 2018; Fernández et al., 2018; Kulkarni et al., 2021) studies, the tree topology for Lycosoidea was constrained with Ctenidae and Psechridae as sister groups. Because the position of *Ancylometes* in the likelihood and parsimony analyses was unstable, sometimes falling outside of Ctenidae, we did not include it in the dated phylogeny. We estimated a likelihood tree in IQ-TREE with the topological constraints mentioned above and converted it into an ultrametric tree using a penalized likelihood method with the chronos function in R (ape v5.3; Paradis et al., 2019). This likelihood tree was then used as a fixed tree topology for the BEAST analysis, and three independent runs of 200 million generations each from four Markov Chain Monte Carlo chains were performed and combined with Logcombiner 2.5.1 (Bouckaert et al., 2014) for a total of 600 million generations. Trees and parameters were sampled every 10 000 generations, 25% of the generations were discarded as burn-in and the remainder were used to calculate posterior parameters. We used Tracer v. 1.7 (Rambaut et al., 2018) to examine chains to convergence (ESS > 200). Trees were summarized with TreeAnnotator, which is distributed as part of the BEAST package. Analyses were run in the CIPRES Science Gateway platform (Miller et al., 2011).

In time-calibrated analyses, uncertainties around the calibrations can greatly impact the estimates of divergence times and rate variation (Smith, 2009). Unfortunately, the only fossil specimen of Ctenidae (*Nanoctenus longipes* Wunderlich, 1988) was not found in the Geological–Paleontological Institute and Museum of the University of Hamburg (U. Kotthoff, personal communication) and the original description does not allow placement of this fossil with certainty in Ctenidae. Thus, owing to the lack of ctenid fossils, two different approaches were used to assess how inferred divergence dates vary across different sets of calibrations. In the first approach, eight divergence estimates were inferred by incorporating only fossil calibration points for outgroup taxa selected from the most recent revision of spider fossils (Magalhaes et al., 2020): Sparassidae stem minimum age of 43 Ma based on *Eusparassus crassipes* Koch & Berendt, 1894

from Baltic amber; Oxyopidae stem minimum age based on *Oxyopes succini* Petrunkevitch, 1958 from Baltic amber (Ritzkowski, 1997); Thomisidae stem age of 43 Ma based on *Syphax microcephalus* & Berendt, 1894 from Baltic amber; Lycosidae stem age of 15 Ma from Dominican amber (Iturralde-Vinent and MacPhee, 1996), based on an unidentified immature Lycosidae (Penney, 2001); Salticidae crown minimum age of 43 Ma from Baltic amber, based on *Almolinus ligula* Wunderlich, 2004; Anyphaenidae crown minimum age of 43 Ma from Baltic amber, based on *"Anyphaena" fuscata* C. L. Koch & Berendt 1894; Thomisidae stem of 43 Ma based on *Syphax macrocephalus* Kock & Berendt 1854 from Baltic Amber; and Selenopidae stem minimum age of 53 Ma from Le Quesnoy amber, based on *Selenops* sp. (Penny, 2006). Finally, for the root of the tree we set a minimum age of 133 Ma based on *Eocoddingtonia eskovi* Selden, 2010 (Theridiosomatidae) from the early Cretaceous of Russia, which corresponds to the oldest known fossil of Entelegynae (Magalhaes et al., 2020).

While there is a disproportionate diversity of Synspermiata and Palpimanoidea families in Mesozoic amber deposits, there is no unambiguous fossil evidence of current RTA clade families in the Mesozoic (Magalhaes et al., 2020). Therefore, for the calibration of RTA points described above, we used a uniform distribution with the minimum age of the fossil (thus ensuring that the clade has zero probability of being younger), and maximum age 100 Ma, where there is no evidence of these RTA families in the rich Myanmar deposits. Finally, we used a uniform prior for the root of the tree from 133 to 280 Ma based on recent age estimations for Entelegynae (Magalhaes et al., 2020).

Biogeographic dating has been used as an alternative or complementary method for dating phylogenies because incomplete or absent fossil record data can provide imprecise divergence time estimations (Landis, 2017). In the case of South America, where major palaeogeographical events have been dated (Hoorn et al., 2010) and biogeographic events depend on palaeogeographic processes, biogeographic dating can be used as a complementary approach to only fossil dating (Ho et al., 2015; Landis, 2017). In absence of a ctenid fossil record, we used biogeographic dating in combination with fossil calibrations to infer the divergence times of ctenids. We incorporated two calibration points within Ctenidae based on biogeographic events related to biome formation in the Tropical Andes (Jaramillo, 2019). We set a maximum crown age of 10 Ma with a uniform distribution for each of the following genera: *Spinoctenus* Hazzi et al., 2018 and *Caloctenus* keyserling, 1877. The genus *Spinoctenus* is composed of 12 species distributed in the tropical Andes and Chocó biogeographical regions (Hazzi et al., 2018; Hazzi and Silva, 2012). Most *Spinoctenus* diversity is found in the Andes (eight species) and using event-based biogeographic analyses on a morphological phylogeny, Hazzi et al. (2018) inferred an Andean origin for this genus. Both our molecular phylogeny (see Results section) and the morphological phylogeny of Hazzi et al. (2018) indicate that the Andean species *Spinoctenus eberhardi* Hazzi et al., 2018 and *S. stephaniae* Hazzi et al., 2018 diverged early within the genus. These two species are endemic to cloud forest ecosystems above 2000 m, a biome that was completely absent from the north of South America before 10 Ma (Hoorn et al., 2010; Jaramillo, 2019). Moreover, *Caloctenus* species are also endemic to high elevation ecosystems in the tropical Andes from cloud forests to paramos (1800–3200 m). Although the Amazonian genus *Gephyroctenus* Keyserling, 1977 is nested within *Caloctenus*, its more distal position indicates an Andean origin for the *Caloctenus* + *Gephyroctenus* clade that is related to montane ecosystems. Biogeographic dating has been heavily criticized when this approach assumes *a priori* that a biogeographic process (e.g. vicariance or dispersal) is related to a geological event (Forest, 2009). For instance, nodes that are calibrated with the timing of geological events assume that the divergence of that given node is the result of a new geographical barrier, through either vicariance (e.g. continental split) or dispersal (e.g. oceanic islands) events (Forest, 2009). In our study, we are not assuming any biogeographic process, but rather we are assuming that two lineages that originated in the cloud forest biome of the tropical Andes could not have originated before the formation of this biome. To test for statistically significant differences in the substitution rates among the two dating strategies, a paired sample *t*-test was carried out in R (R Core Team, 2021), using the package rstatix (Kassambara, 2020).

Eye conformation evolution

We coded the ocular pattern diversity of our study taxa (Fig. 6) into a discrete unordered multistate character as follows: two rows (0); Deinopidae type (1); Ctenidae type (2); *Agelenopsis* type (3); Selenopidae type (4); Oxyopidae type (5); Salticidae type (6); and Lycosidae type (7).

State 0 refers to two well-defined ocular rows and is the most common pattern found in RTA clade taxa (e.g. Anyphaenidae and Sparassidae). State 1 refers to the Deinopidae eye pattern, where the eight eyes are arranged in three rows, with the PME enlarged and ALE on small tubercles. State 2 refers to three eye rows in a 2–4–2 arrangement, the so-called "ctenid ocular pattern": the AME stand alone in the first row, the ALE are below the PLE, the PME are sitting at the behaviour and the ALE are reduced. Silva (2003) scored the ctenid eye pattern found in both ctenids and non-ctenid families (e.g. *Cycloctenus* L. Koch, 1878 and Senoculidae) as different states, based on prior expectations of the phylogenetic placement of the non-ctenid families. However, she acknowledged that these groups present a 2–4–2 eye arrangement, and therefore we considered both these non-ctenid families as having the ctenid eye pattern. State 3 refers to the *Agelenopsis* Giebel, 1869 eye pattern, where the eyes are arranged in two strongly procurved rows. State 4 refers to the eye conformation found in selenopids: an anterior row with six eyes near the front edge of the carapace and a posterior row with two large eyes. State 5 refers to the Oxyopidae eye pattern where the eyes form a hexagon with the posterior row slightly procurved and the anterior row strongly recurved. State 6 refers to the eye pattern found in jumping spiders (Salticidae), which can be arranged in three or four rows (e.g. *Lyssomanes*), with the AME being very large and the ALE slightly smaller; both pairs are directed forward. Finally, state 7 refers to a 4–2–2 eye pattern, a condition that is found in Pisauridae, Lycosidae and Trechaleidae. Some authors have suggested that the lycosid eye pattern is a synapomorphy of Lycosidae (Dondale, 1986), and Sierwald (1993) suggested differences to distinguish the eye patterns of Lycosidae, Pisauridae and Trechaleidae. However, owing to the large amount of variation of the ocular arrangement of some genera in these families, they cannot be distinguished by this character. We have treated Pisauridae and Trechaleidae as having a 4–2–2 eye pattern because the goal of our study is to infer the history of changes in the general ocular pattern, and not the evolution of the minor and somewhat subjective differences between these three families.

Ancestral ocular arrangements were inferred using both model-based and parsimony methods. We used the maximum clade credibility dated tree resulting from the BEAST analysis calibrated with fossils + biogeography and the R packages ape (Paradis et al., 2004) and phytools (Revell, 2012) for likelihood ancestral reconstructions. Likelihood ancestral character estimations were estimated using the function "ace" of the ape package. To facilitate the visualization of the ancestral reconstruction figure, we randomly pruned the dated tree leaving just four taxa of Ctenidae. The removal of Ctenidae taxa did not change the likelihood of ancestral states nor the selected model of character evolution. Three likelihood models for discrete characters were fitted to our data: (1) there are equal rates of transition between states (ER); (2) forward and reverse rates of transition between two states are equal but other rates may vary (SYM); and (3) all rates are different (ARD), the latter being the most

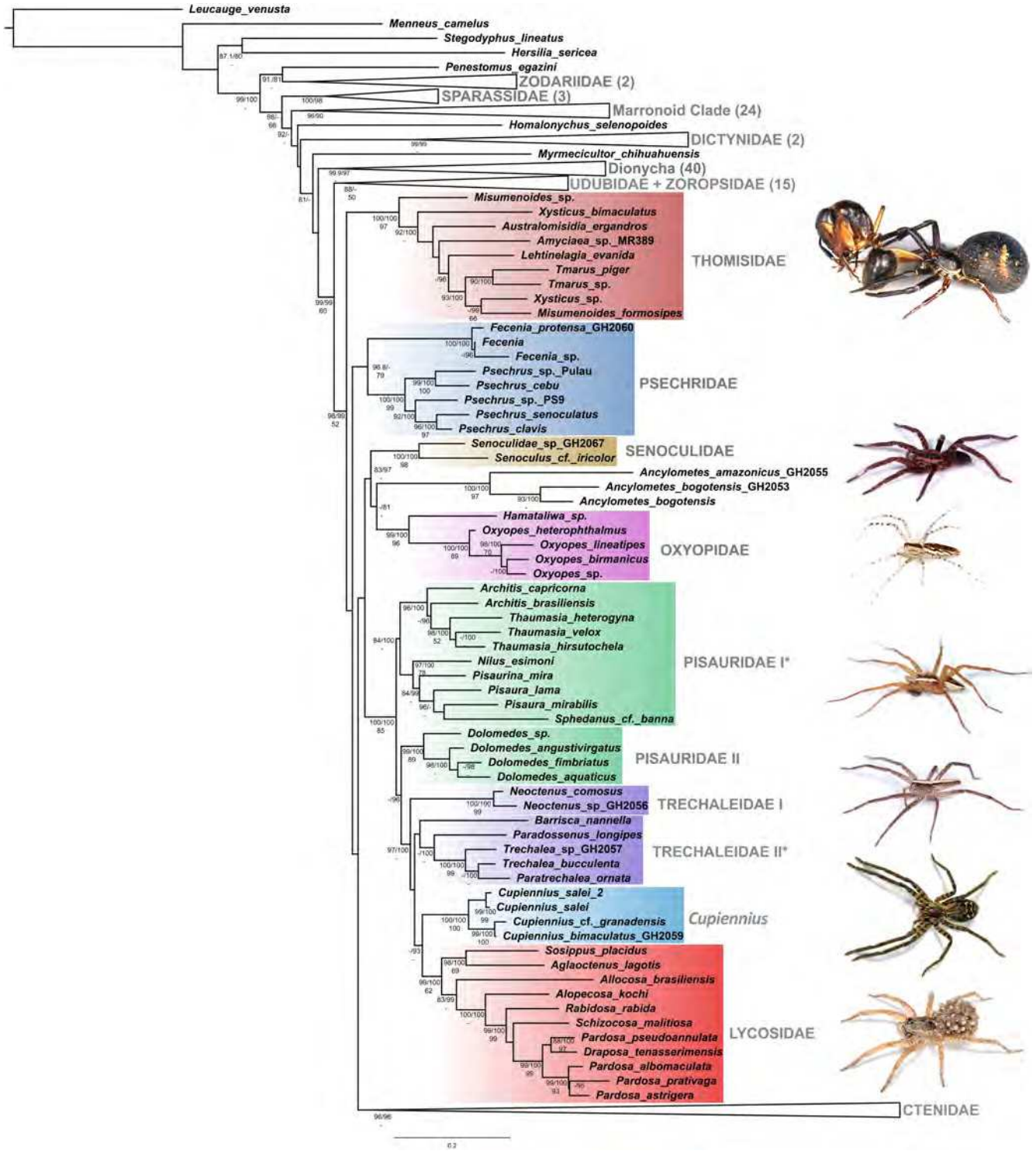


Fig. 4. Maximum likelihood phylogenetic tree with GTR+ FreeRate model for each partition depicting the main phylogenetic relationships. UB, ultrafast bootstrap; SH_aLRT, Shimodaira–Hasegawa approximate likelihood-ratio test; and JAC, jackknife (derived from the parsimony tree). Support metrics for nodes with low support (UB < 95, SH_aLRT < 080 and Jac < 50) are not shown. Numbers in parentheses next to collapsed clades indicate the number of taxa. Photo credits (from top to the bottom): Thomisidae (A. Pérez), *Ancylometes* sp. (M. Ramírez), Oxyopidae and Pisauridae (I. Magalhães), *Neoctenus* sp. (M. Ramírez), *Cupiennius salei* Simon, 1891 (Benny Trapp) and Lycosidae (A. Arroyave).

parameterized model. We selected the model with lowest AICc as the best fitting model and used it to optimize ocular arrangements on the tree. In addition, we also carried out an unordered parsimony state reconstruction in Mesquite 2.74 (Maddison and Maddison, 2010). Evolution transformation paths are represented using directional unipartite networks.

Results

Phylogenetic analyses

The concatenated matrix had a maximum of 9123 bp per taxon, with 36.3% missing data, 3343 parsimony informative sites, 1300 singleton sites and 4479 constant sites. The three likelihood analyses: GTR+ FreeRate (GFR) model for each partition, FreeRate model (FR) for best partition scheme, and GTR + Gamma + Invariant sites (GI) resulted in similar topologies (Figs S1–S3). The parsimony analysis under equal weights resulted in 13 trees of 46 890 steps (CI = 0.23; RI = 0.36). The majority rule and the strict consensus of the optimal parsimony trees are depicted in Figs S4 and S5, respectively. Except for the marronoid clade (Wheeler et al., 2017), which was recovered only in the likelihood analyses, both likelihood and parsimony analyses recover the monophyly of well-known clades such as Dionycha, the oval calamistrum clade and Lycosoidea. Although not well supported, the likelihood analyses indicated a paraphyletic relationship between *Neoctenus* Simon, 1897 and the remaining trechaleids. In the three likelihood analyses the intensively studied genus *Cupiennius*, which was recently transferred from Ctenidae to Trechaleidae, is placed with low support as sister to Lycosidae (Fig. 4). In the parsimony analysis Trechaleidae is monophyletic and *Cupiennius* is its sister lineage, but with low support.

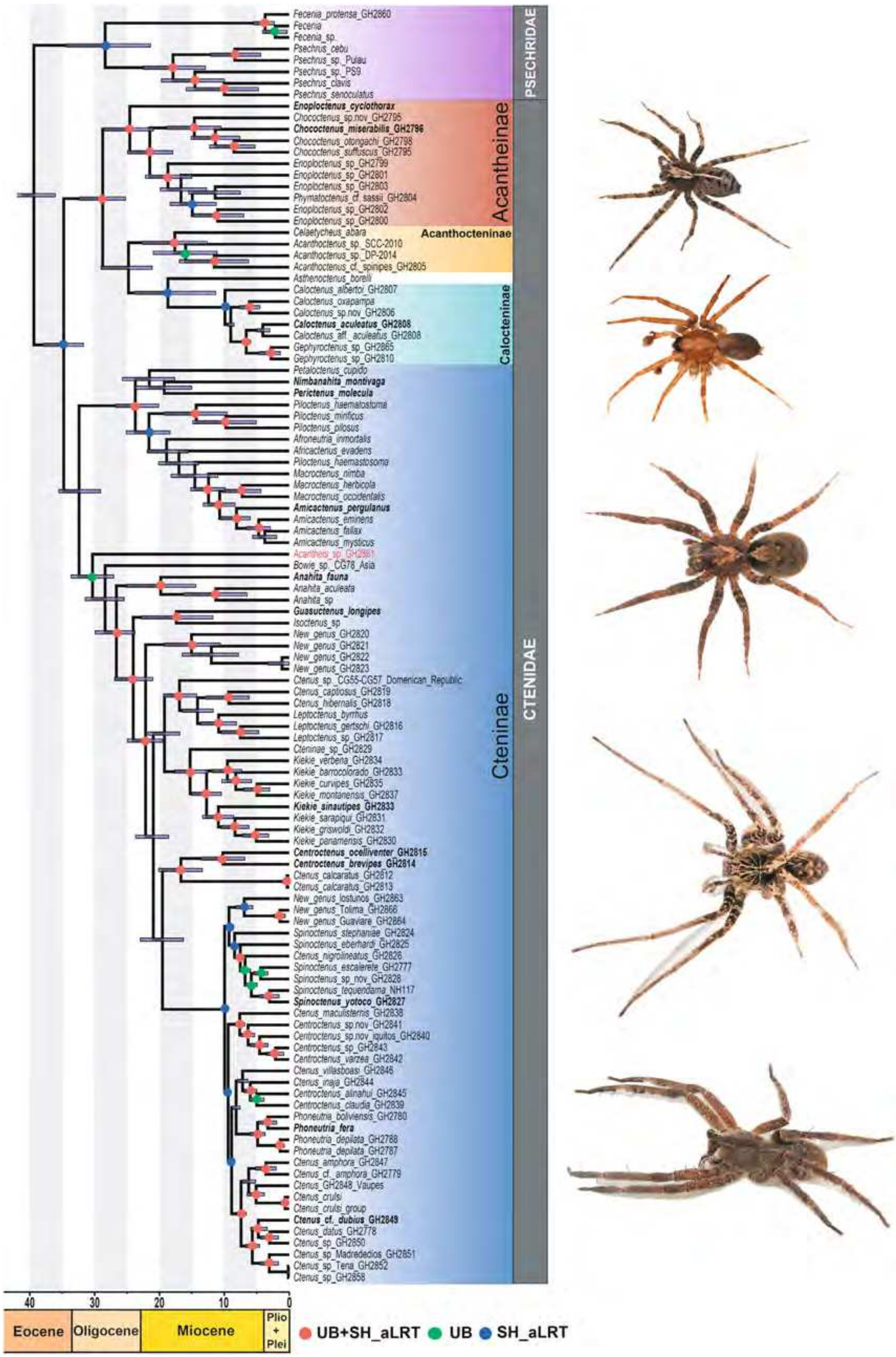
Two of three likelihood analyses (GFR and GI) indicated that Ctenidae is not monophyletic (Figs S1 and S3). In the GFR tree, *Ancylometes* was more closely related to other Lycosoidea families than to the remaining ctenids (Figs 4 and S1). The GI analysis placed both *Ancylometes* and Calocteninae outside of Ctenidae, as sisters to Senoculidae with low support (Fig. S3). The family Ctenidae is monophyletic in both the maximum likelihood with the FR model and in the parsimony analysis, placing *Ancylometes* within Ctenidae, closely related to Calocteninae (Figs S2 and S4). The phylogenetic position of *Ancylometes* within Lycosoidea varied across the four analyses, always with low support, and thus it was not possible to find a robust phylogenetic placement for *Ancylometes*. The support for the monophyly of Ctenidae *sensu stricto* (Fig. 4) varied from moderate to high in the three likelihood analyses and was low for the parsimony analysis. Except for the *Ancylometes* placement, two of the three likelihood analyses plus the constrained likelihood topology used to estimate divergence times in BEAST produced similar results within Ctenidae *sensu stricto*. We chose the GRF tree (Figs 4 and S1) and the time-calibrated tree (Figs 5 and S8) to summarize the results and to guide the discussion of Ctenidae systematics. Based on the UB and SH-aLRT support metrics we refer to clade support as low or weak (UB < 0.95 and SH-aLRT < 80), moderate (UB > 0.95 or SH-aLRT > 80), and high or strong (UB > 0.95 and SH-aLRT > 80).

Acanthinae was rendered as polyphyletic because *Acantheis* Thorell, 1891, the type genus, was recovered inside Cteninae in the optimal topologies of the likelihood and parsimony analyses. A clade comprising representatives of the subfamilies Acantheinae, Calocteninae and Acanthocteninae is strongly supported. The Neotropical Acantheinae genera *Chococtenus* Duperré, 2015, *Enoploctenus* Simon, 1897 and *Phymatoctenus* Simon, 1897 were recovered as strongly supported. *Enoploctenus* was not monophyletic because the type species, *Enoploctenus cyclothorax*, was recovered as the sister group of *Chococtenus*, *Enoploctenus* spp. and *Phymatoctenus*. The latter was recovered inside of a moderately supported clade of *Enoploctenus* species.

Celaetycheus abara Polotow and Brescovit, 2013 was strongly supported as the sister group of *Acanthoctenus* (the only representative of Acanthocteninae in our analysis). The clade comprising *Celaetycheus* Simon, 1897 plus Acanthocteninae was sister to *Asthenoctenus borelli* Simon, 1897 and Calocteninae with low support. *Asthenoctenus borelli* was moderately supported as sister to *Caloctenus* + *Gephyroctenus*. Calocteninae was highly supported as monophyletic and *Caloctenus aculeatus* (the type species of the genus) and a new species of *Caloctenus* are more closely related to *Gephyroctenus* than to the remaining species of *Caloctenus*.

The subfamily Cteninae was monophyletic in two of the three likelihood analyses, receiving low to moderate support. There were two strongly supported clades

Fig. 5. Close up of the constrained likelihood tree estimated in IQTREE and time calibrated in BEAST depicting the divergence times and phylogenetic relationships in Ctenidae. Bars represent the 95% highest posterior density interval. UB, Ultrafast bootstrap; SH_aLRT, Shimodaira–Hasegawa approximate likelihood ratio test. Support metrics for nodes with low support (UB < 95, SH_aLRT < 080 and Jac < 50) are not shown. Bold taxa are genus type species. Photo credits (from top to the bottom): *Chococtenus* sp. (A. Arroyave), *Caloctenus albertoi* (N. Hazzi), Cteninae sp (A. Arroyave), *Kiekie panamensis* (A. Arroyave), *Phoneutria boliviensis* (N. Hazzi).


Fecenia_protensa_GH2860
Fecenia
Fecenia_sp.
Psechrus_cebu
Psechrus_sp._Pulau
Psechrus_sp._PS9
Psechrus_clavis
Psechrus_senoculatus
Enoploctenus_cyclothorax
Chococtenus_sp.nov_GH2795
Chococtenus_miserabilis_GH2796
Chococtenus_otongachi_GH2798
Chococtenus_suffuscus_GH2795
Enoploctenus_sp_GH2799
Enoploctenus_sp_GH2801
Enoploctenus_sp_GH2803
Phymatoctenus_cf._sassii_GH2804
Enoploctenus_sp_GH2802
Enoploctenus_sp_GH2800
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp._DP-2014
Acanthoctenus_cf._spinipes_GH2805
Asthenoctenus_borelli
Caloctenus_albertoi_GH2807
Caloctenus_oxapampa
Caloctenus_sp.nov_GH2806
Caloctenus_aculeatus_GH2808
Caloctenus_aff._aculeatus_GH2808
Gephyroctenus_sp_GH2865
Gephyroctenus_sp_GH2810
Petaloctenus_cupido
Nimbanahita_montivaga
Perictenus_molecula
Piloctenus_haematostoma
Piloctenus_minficus
Piloctenus_pilosus
Afroneutria_inmortalis
Africactenus_evadens
Piloctenus_haemastosoma
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_pergulanus
Amicactenus_eminens
Amicactenus_fallax
Amicactenus_mysticus
Acantheis_sp_GH2861
Bowie_sp._CG78_Asia
Anahita_fauna
Anahita_aculeata
Anahita_sp
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2820
New_genus_GH2821
New_genus_GH2822
New_genus_GH2823
Ctenus_sp._CG55-CG57_Domenican_Republic
Ctenus_captiosus_GH2819
Ctenus_hibernalis_GH2818
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2816
Leptoctenus_sp_GH2817
Cteninae_sp_GH2829
Kiekie_verbena_GH2834
Kiekie_barrocolorado_GH2833
Kiekie_curvipes_GH2835
Kiekie_montanensis_GH2837
Kiekie_sinautipes_GH2833
Kiekie_sarapiqui_GH2831
Kiekie_griswoldi_GH2832
Kiekie_panamensis_GH2830
Centroctenus_ocelliventer_GH2815
Centroctenus_brevipes_GH2814
Ctenus_calcaratus_GH2812
Ctenus_calcaratus_GH2813
New_genus_lostunos_GH2863
New_genus_Tolima_GH2866
New_genus_Guaviare_GH2864
Spinoctenus_stephaniae_GH2824
Spinoctenus_eberhardi_GH2825
Ctenus_nigrolineatus_GH2826
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2828
Spinoctenus_tequendama_NH117
Spinoctenus_yotoco_GH2827
Ctenus_maculisternis_GH2838
Centroctenus_sp.nov_GH2841
Centroctenus_sp.nov_iquitos_GH2840
Centroctenus_sp_GH2843
Centroctenus_varzea_GH2842
Ctenus_villasboasi_GH2846
Ctenus_inaja_GH2844
Centroctenus_alinahui_GH2845
Centroctenus_claudia_GH2839
Phoneutria_boliviensis_GH2780
Phoneutria_fera
Phoneutria_depilata_GH2788
Phoneutria_depilata_GH2787
Ctenus_amphora_GH2847
Ctenus_cf._amphora_GH2779
Ctenus_GH2848_Vaupes
Ctenus_crulsi
Ctenus_crulsi_group
Ctenus_cf._dubius_GH2849
Ctenus_datus_GH2778
Ctenus_sp_GH2850
Ctenus_sp_Madrededios_GH2851
Ctenus_sp_Tena_GH2852
Ctenus_sp_GH2858
PSECHRIDAE
Acantheinae
Acanthocteninae
Calocteninae
Cteninae
CTENIDAE
40
30
20
10
0
Eocene
Oligocene
Miocene
Plio + Plei
UB+SH_aLRT
UB
SH_aLRT

of Cteninae: an African lineage and an American + *Anahita* spp. lineage. The American lineage + *Anahita* spp. lineage is composed of a strongly supported lineage of endemic American ctenines that is sister to *Anahita* Keyserling, 1877, a genus distributed in Asia, Africa and with one species in North America. In the American endemic clade most of the inferred relationships between genera received low support values, but genera such as *Kiekie* Polotow and Brescovit, 2018, *Spinoctenus* and *Phoneutria* are strongly supported as monophyletic. A clade that includes the genera *Centroctenus* Mello-Leitão, 1929, *Ctenus* Walckenaer, 1805 and *Phoneutria*, which are mostly distributed in the Cis Andean biogeographic region (the Amazon and Brazil), was highly supported. Although the genus *Ctenus* is indicated as polyphyletic, the type species of the genus, *Ctenus dubius* Walckenaer, 1805, represented in this phylogeny with a specimen probably belonging to this species and labelled as "*Ctenus* cf. *dubius*" was highly supported as grouping with other morphologically similar *Ctenus* species.

The genus *Centroctenus* is polyphyletic with three highly supported independent clades. The type species *Centroctenus ocelliventer* (Strand, 1909) was highly supported as sister to *Parabatinga brevipes* (Keyserling, 1891), the single species in the genus. Two remaining strongly supported independent clades include: (1) *Ctenus maculisternis* Strand, 1909, *Centroctenus* sp. nov. 1, 2 and 3, *Centroctenus varzea* Brescovit et al., 2020; and (2) *Ctenus inaja* Höfer et al. 1994, *Centroctenus claudia* Brescovit et al., 2020 and *Centroctenus alluhini* Brescovit et al., 2020. The Nearctic ctenid species that have been described in *Ctenus* and *Leptoctenus* L. Koch, 1878 were highly supported as monophyletic. Both North American *Leptoctenus* and *Ctenus* form reciprocal monophyletic groups with high support.

The age of Ctenidae and its main lineages

Based on the BEAST analysis that included only fossils as calibration points, the estimated dates for well-known families or clades (e.g. Lycosidae, Pisauridae, etc.) are similar to previous estimations (Fig. S7; Piacentini and Ramírez, 2019). The second dating approach that included both fossil and biogeographic calibrations inferred a younger origin for Lycosoidea families compared with previous estimations (Fig. S8). Ctenidae diverged from Psechridae during the late Cretaceous using the first calibration approach (70 Ma, highest posterior density, HPD = 66–74 Ma, Fig. S7) and during the Eocene (40 Ma, HPD = 37–43 Ma, Figs 5 and S8) in the second calibration approach. In both calibration approaches, subfamilies or main lineages of Ctenidae originated during the Paleocene–Eocene and have continued diversifying in the tropics since. Our estimates of substitution rates differ greatly between both calibration approaches, with the fossil + biogeographic calibration analysis resulting in faster rates than the fossil-only calibrated analysis ($t = -3.38$, $p = 0.012$, mean difference = 0.35, Fig. S9). Tables S1 and S2 summarize the parameter rate estimations of the markers.

Evolution of ocular patterns

The equal rates model was selected as the best fitting character evolution model (AICc: EQ = 150.87, SYM = 180.65 and ARD = 207.68). Based on this model, the ctenid eye pattern has originated independently seven times: in Cycloctenidae, Xenoctenidae I and II, Viridasiidae, *Argoctenus* (Miturgidae), Senoculidae, *Cupiennius* (Trechaleidae), and Ctenidae (Fig. 6). The unipartite directional network shows that the common two-rows eye pattern (4–4) is in the behaviour of the network and that most eye conformation states in RTA clade taxa have evolved from this 4–4 eye pattern (e.g. the Lycosidae, Oxyopidae, Salticidae, Selenopidae and *Agelenopsis* eye patterns). Six of the seven convergent events of the Ctenidae eye pattern have evolved from two rows (4–4) and one from the Lycosidae eye pattern (in *Cupiennius*). We also found a reversal in Trechaleidae from a Lycosidae eye arrangement to two rows (4–4). Ancestral state reconstructions using parsimony produced identical results, with the ctenid eye arrangement having evolved independently seven times (Fig. S10).

Discussion

This study presents the first densely sampled molecular phylogeny of Ctenidae that includes representatives of all of its subfamilies worldwide. The phylogenetic relationships of the main RTA clade lineages (Lycosoidea, Marronoidea, Dionycha and the oval calamistrum clade) are congruent with previous molecular hypotheses (Polotow et al., 2015; Fernández et al., 2018; Kallal et al., 2021; Kulkarni et al., 2021). None of our phylogenetic analyses recovered Psechridae and Ctenidae as sister groups as hypothesized in previous studies based on transcriptomes and UCE data (Cheng and Piel, 2018; Kallal et al., 2021). Our analyses indicated that neither Ctenidae nor the subfamily Acantheinae are monophyletic. Nevertheless, the generic composition of the main ctenid lineages is congruent with those reported in previous morphological phylogenies (Silva, 2003; Polotow and Brescovit, 2014). Despite increasing both the number of markers and taxa used in previous studies of Lycosoidea (Polotow et al., 2015; Piacentini and Ramírez, 2019), the placement of *Cupiennius* and *Ancylometes* remains uncertain.

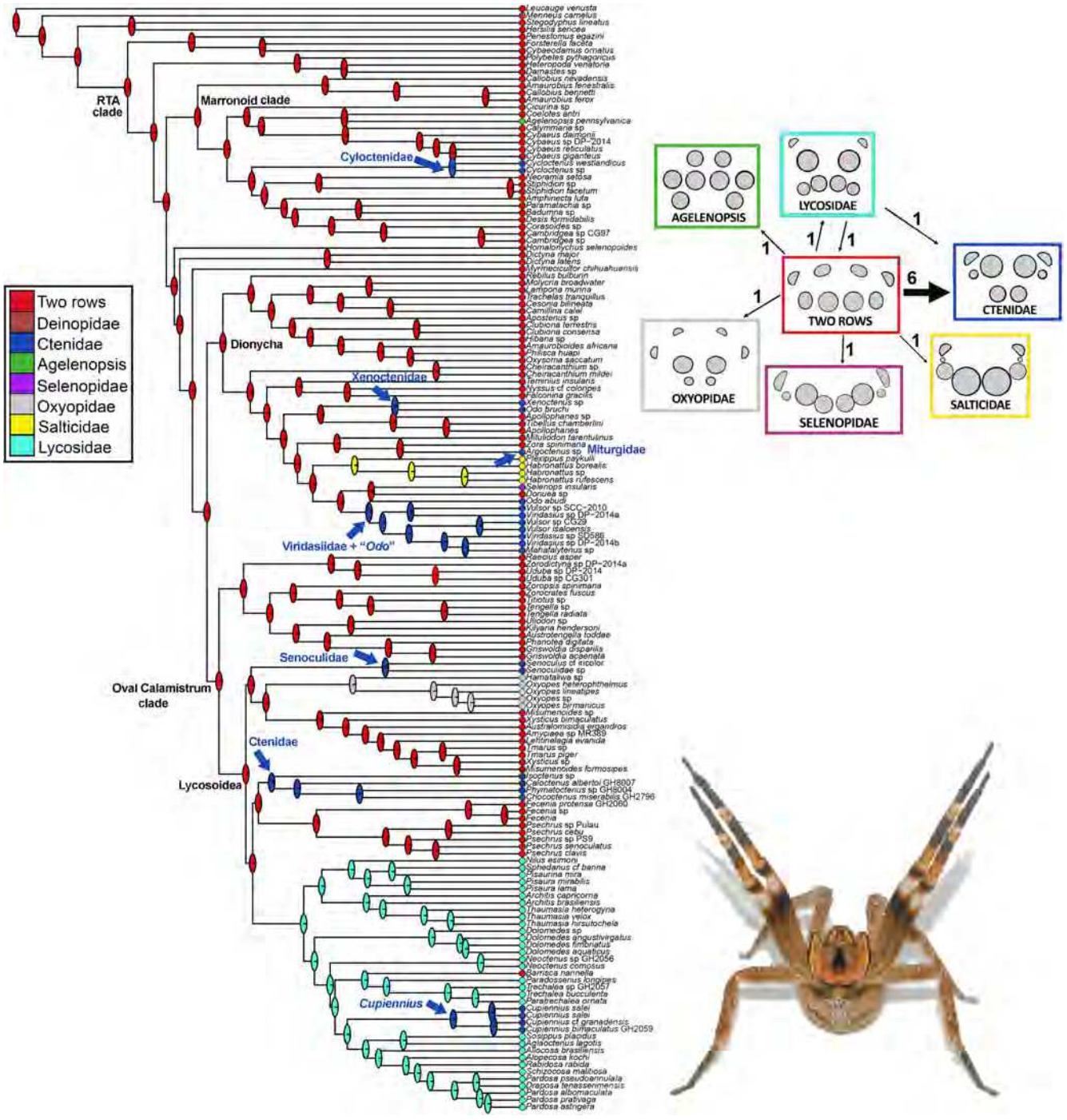


Fig. 6. Likelihood equal rate ancestral state reconstruction and directional unipartite network of the eye pattern in the RTA families. Arrows indicate the direction and number of evolution transformations, with line thickness proportional to the number of events. Lines without direction and question mark indicate high uncertainty in the ancestral state reconstruction. Arrows on the phylogenetic tree indicate Ctenidae eye pattern transformations.

Cupiennius, one of the most studied genus of spiders, considered a model organism in arachnology (e.g. see Barth, 2002), is sister to Lycosidae with low to moderate support in our three likelihood analyses, contradicting its current placement in Trechaleidae. In the parsimony analysis, *Cupiennius* is sister to the remaining trechaleid genera. The unstable phylogenetic position of *Cupiennius* as the sister group of either Lycosidae or Trechaleidae was also found in the most recent molecular phylogeny of Lycosidae (Piacentini

and Ramírez, 2019), which reports the same contradictory relationships in the two Bayesian analyses performed (MrBayes and BEAST). Unfortunately, to our knowledge, there are no putative morphological synapomorphies that would support either of these two hypotheses.

The Neotropical and semiaquatic genus *Ancylometes* comprises 11 species (WSC, 2022) and has a long taxonomic history. *Ancylometes* was originally placed in Pisauridae (Bertkau, 1880; Sierwald, 1997) and later transferred to Ctenidae (Silva, 2003). It has been hypothesized to be closely related to *Cupiennius* based on homoplastic characters such as the presence of a third tarsal claw and four pairs of ventral macrosetae on tibiae I–II (Silva, 2003). Because *Ancylometes* is a semiaquatic genus, it has morphological features unique from other Ctenidae genera such as the lack of scopulae, claw tufts and the presence of numerous spines on the third and fourth tarsi (Höfer and Brescovit, 2000). Two species of *Ancylometes*, *A. bogotensinsis* (Keyserling, 1877) and *A. cf. rufus* (Walckenaer, 1837), dig burrows close to streams where they remain during the dry season (N. Hazzi, unpubl.), perhaps to avoid desiccation, a behaviour that to our knowledge is unique among ctenids. We concluded that these two species dig their own burrows, because we found several specimens next to freshly dug burrows, and the *Ancylometes* specimens had traces of soil on their carapace and abdomen (Fig. 3e,f). The lack of scopulae and claw tufts has been associated with morphological adaptations to aquatic environments in Ctenidae and Trechaleidae (Lapinski et al., 2015), and the third and fourth tarsal macrosetae may be used for digging burrows. The nucleotide data used in our phylogenetic analyses cannot robustly place *Ancylometes*. However, it is still likely that this genus belongs to Ctenidae because in the parsimony (Fig. S4) and in one of the likelihood (Fig. S2) hypotheses *Ancylometes* is nested in Ctenidae, closely related to *Caloctenus*.

The phylogenetic relationships of Ctenidae inferred in this study suggest several putative morphological synapomorphies of the family, such as the presence of five and three pairs of ventral macrosetae on tibiae and metatarsi I–II, respectively, the epigynal lateral processes and the sternum base not extended between the fourth coxae (Silva, 2003; Polotow and Brescovit, 2014). Our results indicate that the first two characters were subsequently lost in Calocteninae and Acanthocteninae. The subfamily Cteninae is the most diverse lineage of ctenids, and it is mainly composed of ground-dwelling species. Cteninae monophyly has been supported by all morphological analyses (Polotow and Brescovit, 2009a,b, 2014; Silva, 2003). Our molecular results corroborate the monophyly of Cteninae, although with low support. Synapomorphies of the subfamily have a protuberant median sector of the epigynum, an embolus fixed by a membranous region and a cup-shaped median apophysis (Polotow and Brescovit, 2014).

Almost half of all Ctenidae species have been classified in the genus *Ctenus*, which includes more than 210 species distributed worldwide (World Spider Catalog, 2022). The results of our molecular phylogenetic analyses are congruent with the hypothesis of a polyphyletic *Ctenus* as currently delimited, reported in previous morphological analyses (Polotow and Brescovit, 2014; Silva, 2003). *Ctenus dubius* Walckenaer, 1805, from French Guiana, is the type species of the genus, and in our phylogenetic hypothesis *Ctenus* cf. *dubius* groups with 11 other Neotropical species with morphological affinities to one another and this relationship is strongly supported (Fig. 5). The group that includes *Ctenus* cf. *dubius* comprises ground-dwelling spiders that have a basal projection at the embolus, a median sector of the epigynum with protruding ovoid lobes at the copulatory opening area, and lobed copulatory openings (Brescovit and Simó, 2007; Polotow and Brescovit, 2014). Brescovit and Simó (2007) redescribed *Ctenus dubius* and provided a diagnosis for the genus. Our results corroborated Brescovit and Simó's delimitation and provide a reference framework for a phylogenetic circumscription of the genus to transfer misplaced *Ctenus* species and to place new species. The results of our phylogenetic analysis suggest that several species described in *Ctenus* represent new genera. For example, a new genus is required to classify the North American species of *Ctenus* that were revised by Peck (1981): *Ctenus hibernalis*, *Ct. captiosus*, *Ct. exlineae* and *Ct. valverdiensis*. These species form a clade separated from the *Ctenus dubius* group. The morphological phylogeny of Polotow and Brescovit (2014) has promoted subsequent studies that have erected new genera to accommodate species previously described in *Ctenus* (e.g. *Kiekie*, *Afroneutria*, *Amicactenus* and *Macroctenus*; Polotow & Brescovit, 2018; Polotow & Jocqué, 2015); our molecular phylogeny also provides a framework to advance in the systematics and classification of *Ctenus*.

Our results suggest that most of the recently revised Cteninae genera (such as *Kiekie*, *Spinoctenus* and *Phoneutria*) are strongly supported as monophyletic. Moreover, in our hypothesis the North American species of *Leptoctenus* (three species) and *Ctenus* (two species) that were revised by Peck (1981) form a highly supported clade. Although we are unaware of any morphological synapomorphies that would group North American *Leptoctenus* and *Ctenus* species, both are distributed in the Nearctic region. In North America, *Leptoctenus* species are smaller than those of *Ctenus*, they have three retromarginal teeth and the RTAs are medially or basally positioned (Peck, 1981).

Leptoctenus comprises the type species, *L. agalenoides* Koch, 1878, from Australia, and morphological phylogenies have indicated that this latter species is closely related to *Anahita*, a relationship supported by morphological synapomorphies that are all absent in the North American *Leptoctenus* (Polotow and Brescovit, 2014). Therefore, *Leptoctenus* is not monophyletic as currently delimited, and the North American species should be transferred to a new genus. Although North American *Ctenus* should be transferred to a new genus, these species do not present clear morphological synapomorphies or a combination of characters that distinguish them from other Cteninae genera. A revision of the North American *Ctenus* species is required to circumscribe, describe and properly diagnose this putative new genus.

The Neotropical genus *Centroctenus* is polyphyletic. This genus was recently diagnosed by Brescovit et al. (2020) based primarily on the elongated tibia of the male palp. However, as shown in a morphological phylogenetic analysis (Polotow and Brescovit, 2011), this character is highly homoplasious and species previously described in *Centroctenus* based on this character have now been transferred to a different family (*Itatiaya*, Zoropsidae; Brescovit, 1996; Polotow and Brescovit, 2011). In our molecular phylogenetic hypothesis (Fig. 5) a long male palpal tibia is present in three robustly supported independent lineages (except for *Ctenus inaja*). In all the phylogenetic analyses, the type species, *Centroctenus ocelliventer*, is sister to *Parabatinga brevipes* (Keyserling, 1891), a monotypic genus described by Polotow and Brescovit (2009a) and Polotow and Brescovit (2009b) within the framework of a morphological cladistic analysis. Both genera share a unique coloration pattern on the ventral surface of the abdomen and a distal laminar process on the median apophysis. We here transfer *Parabatinga brevipes* to *Centroctenus*, and thus synonymize the former under the latter genus. We provide a new diagnosis for the genus (see the section "Systematics" below). Two additional and well supported lineages were found: (1) *Ctenus maculisternis*, *Centroctenus varzea* and three new species; and (2) *Ctenus inaja*, *Centroctenus claudia* and *Centroctenus alluhini*. The first clade comprises ground-dwelling species with white-yellow longitudinal bands on the carapace and a wide posterior medial epigynal projection. The second clade is composed of species that are not strictly ground dwelling, but are usually found on the bases of trees, in low vegetation or on steep slopes (Gasnier et al., 2009; N. Hazzi unpl.). The species of the second clade have long and slender legs relative to their carapace (possibly because they live above the ground) and share the presence of a wide median epigynal field with a narrow anterior projection. Except for *Ctenus inaja*, the remaining male species of the second clade have a palpal tibia that is twice as long as the cymbium. A taxonomic study is underway (N. Hazzi and G. Hormiga in prep.) to erect and describe two new genera to accommodate these species.

Based on the results of the likelihood analysis, the sister lineage of Cteninae comprises the subfamilies Acantheinae, Calocteninae and Acanthocteninae and the genus *Asthenoctenus*. The Neotropical Acantheinae genera *Chococtenus*, *Enoploctenus* and *Phymatoctenus* were recovered as a highly supported monophyletic group. Acantheinae includes ctenids that have iridescent scales and sparse plumose setae on the carapace, abdomen and sometimes legs. In addition, this clade presents overlapping elongated spines on the first and second tibiae and metatarsi (Silva, 2003; Polotow and Brescovit, 2014). Acantheines are mostly arboreal, except for *Chococtenus* species, which are ground-dwellers. All three acantheine genera have four retromarginal cheliceral teeth, the basal one distant from the remaining three teeth, a membranous tegular process and a V-shaped depression between the pars thoracica and the pars cephalica (Silva, 2003; Polotow and Brescovit, 2014). Although Polotow and Brescovit (2014) and Dupérré (2015) indicated that the male tibial retroapical notch is a synapomorphy of *Enoploctenus*, we note that *Phymatoctenus* and *Chococtenus* also exhibit this character. In *Phymatoctenus* this notch is very conspicuous, whereas in *Chocotenus* it is less evident because it is a concealed by a ventral tibial apophysis.

A clade comprising Acanthocteninae, Calocteninae and *Asthenoctenus borellii* is sister to the Neotropical Acantheinae, but this node lacks high support. Both ground-dwelling and arboreal spiders with a great variety of morphologies compose this heterogeneous clade. The monophyly of this group is supported by the presence of a hook-shaped median apophysis (as opposed to the typical cup-shaped apophysis found in Cteninae) with a small apical peak and by the loss of the apical reduced spine on tibia I and II (Silva, 2003). *Asthenoctenus* Simon, 1897 is an enigmatic genus composed of two species distributed in South America, and different morphological phylogenies disagree about their placement. Silva (2003) hypothesized that *Asthenoctenus* was sister to a clade of Acantheinae + Cteninae, noting that "further studies might prove that indeed it belongs to Acantheinae". The cladistic analysis of Polotow and Brescovit (2014) placed *Asthenoctenus* in the subfamily Viridasiinae, which is composed of Malagasy taxa. Subsequently, in a total evidence analysis that only included the Malagasy taxa, Polotow and Griswold (2015) placed viridasiines in Dionycha and ranked them as a family (Viridasiidae). Our phylogenetic analyses show that *Asthenoctenus borellii*, the type species of the genus, falls within Ctenidae, with the likelihood analyses

placing it as the sister group of Calocteninae and the equal weight parsimony analysis placing it as sister group to Acanthocteninae. The swollen male palpal patella, a character state considered a synapomorphy of Acanthocteninae, and misinterpreted in former morphological phylogenies (Silva, 2003; Polotow and Brescovit, 2014), supports the placement of *Asthenoctenus* as sister to Acanthocteninae.

The placement of *Celaetycheus* Simon, 1897 is another genus in which morphological phylogenies disagree about its placement. This genus comprises 10 species from Brazil and has been placed as sister to Calocteninae and Acanthocteninae (Silva, 2003), in Cteninae (Polotow and Brescovit, 2013) and most recently in Calocteninae (Polotow and Brescovit, 2014, 2015). Our molecular hypothesis suggests that *Celaetycheus* does not belong in Calocteninae, but instead it is the sister group of Acanthocteninae, and this result is strongly supported. The *Celaetycheus* + Acanthocteninae lineage is supported by the presence of a retrolateral cymbial process (also present in other acanthoctenines, such as *Viracucha* and *Nothroctenus*, that were not included in our taxon sample).

The subfamily Calocteninae is composed of four genera of small ctenids that inhabit the leaf litter (e.g. *Caloctenus*) and trees (e.g. *Gephyroctenus*) of tropical forests. In our molecular phylogeny, Calocteninae is represented by the genera *Gephyroctenus* and *Caloctenus*, and the subfamily was moderately supported as monophyletic. These two genera share a ventral tibial apophysis (absent in *Caloctenus albertoi* Hazzi and Silva, 2012), reduced anterior lateral eyes, the presence of three or more prolateral spines on the first femur and leaf-shaped setae on the abdomen (Silva, 2003, 2004). In addition, our molecular hypothesis suggests that *Caloctenus* Keyserling, 1877, endemic to the tropical Andes, is not monophyletic because the type species *Caloctenus aculeatus* Keyserling, 1877 and a new species of *Caloctenus* are more closely related to *Gephyroctenus* Mello-Leitão, 1936 than to the remaining species of *Caloctenus* (Fig. 5). Although there are no evident morphological synapomorphies supporting the placement of *Gephyroctenus* in *Caloctenus*, *Caloctenus* harbours a large amount of morphological interspecific diversity in both male and female genitalia. For example, *Caloctenus* females can have well-defined epigynal folds, sometimes fused in part or entirely (Silva, 2004; Hazzi and Silva, 2012), while different ctenid genera, even from different subfamilies, have a similar epigynal conformation (median sector and two lateral lobes). A revision of *Caloctenus* using both morphological and molecular data is needed to more accurately circumscribe this genus.

In the absence of a fossil record or well supported vicariant events, nucleotide substitution rates may provide the necessary information to date phylogenies. Our rate estimates (Tables S1 and S2) are considerably lower for mitochondrial genes than those previously reported for other spider groups (Bidegaray-Batista and Arnedo, 2011; Zhang and Li, 2013; Piacentini and Ramírez, 2019). The average divergence rate for the mitochondrial genes estimated in the combined fossil and biogeography calibration approach (0.91% My^{-1}) is faster than the rates resulting from the analysis using only fossil calibration and is still more than two times slower than that reported for arthropod mitochondrial DNA (2.3% My^{-1}; Brower, 1994) or than what has been previously estimated for Lycosidae (2.44% My^{-1}; Piacentini and Ramírez, 2019) or Dysderidae (2.25%; Bidegaray-Batista and Arnedo, 2011). The substitution rates estimated for nuclear genes, such as 28S and histone H3 were slightly higher in the fossil and biogeography calibrated analysis than those in previous analyses (Bidegaray-Batista and Arnedo, 2011; Piacentini and Ramírez, 2019). In addition, we also report for the first time the estimated rates for the Actin and ITS-2 markers for members of the RTA clade. The large discrepancies in the estimation of the substitution rates for mitochondrial genes in this study and those mentioned above could be attributed to mitochondrial genome saturation (multiple substitutions at the same nucleotide position; Nabholz et al., 2008; Saclier et al., 2018). Mitochondrial genomes evolve faster than nuclear genomes, and our study includes a larger number of distantly related taxa with older divergence dates compared with previous studies that focused on a specific genus or family. Therefore, our mitochondrial substitution rate estimates could be more prone to be biased by saturation, resulting in lower substitution rates compared with previous studies. A similar explanation has been provided for the observed estimation of divergence times and substitution rates when fossil constrains on deeper nodes are applied (Jansa et al., 2006; Lukoschek et al., 2012; Dornburg et al., 2014; van Tuinen and Torres, 2015).

Although the two calibration approaches resulted in different time origins of Ctenidae, both analyses somewhat agree in that the main ctenid lineages appeared around the Paleocene–Eocene (Figs 5 and S7), and that the family has been diversifying in the tropics since. During the Paleocene–Eocene, temperatures increased globally between 4 and 8°C and lasted for several thousand years, and then at the end of the Eocene, global temperature gradually decreased (Gingerich, 2006). During the Paleocene and Eocene, there was a plant composition turnover from open canopy forests composed mainly of conifers, cycadophytes, angiosperms and pteridophytes to a modern closed canopy tropical forest dominated mainly by angiosperms (Crane and Lidgard, 1990; Currano et al., 2008; Jaramillo et al., 2010; Leebens-Mack et al., 2019). In

addition, the fossil insect plant damage diversity in the Neotropics only became similar to the current diversity levels during the Paleocene and early Eocene (Carvalho et al., 2021), indicating that modern tropical rainforest ecosystems originated during that period. Thus, the plant species turnover and the change in forest structure (open vs. closed canopy) may have promoted the diversification and success of Ctenidae, especially for the subfamily Cteninae, the most diverse ctenid lineage. Cteninae species inhabit the leaf litter of tropical forests (Gasnier et al., 2009) and, as in other soil arthropods, their presence and abundance are affected by the depth, chemical composition and structure of the leaf litter, which also vary depending on the taxonomic plant composition and canopy density (Rego et al., 2007; Torres-Sanchez and Gasnier, 2010; Hazzi et al., 2020).

Ctenidae have a pantropical distribution, with few representatives distributed in the Holarctic and Austral regions. The estimated dates for the origin and diversification of Ctenidae and its main lineages largely postdate continental breakup, and therefore the current Pantropical distribution of Ctenidae would be explained by long-distance dispersal events rather than by vicariance and continental drift. As in other lycosoids, ctenid spiderlings can perform aerial dispersal by "ballooning" (Richter, 1970; Woolley et al., 2016; Carlozzi et al., 2018). Ballooning refers to the ability of many young spiders to float through the air on their own silk lines (Foelix, 2011). Wind-induced drag and electrostatic forces make it possible for the spiders to become airborne with their silk "kites". This dispersal strategy may explain the presence of Ctenidae on oceanic islands far from the mainland, such as Cocos Island (about 550 km southwest of continental Costa Rica; Polotow and Brescovit, 2009a; Polotow and Brescovit, 2009b; Hazzi et al., 2013; Víquez, 2020) as well as their post-Gondwana Pantropical distribution. Worldwide distribution patterns of Ctenidae driven by long-distance dispersal are also congruent with those of other lycosoids, such as wolf spiders (Piacentini and Ramírez, 2019). It is well known that species or lineages adapted to disturbed environments, such as wolf spiders (Lycosidae), have higher dispersal capacities compared with groups that are more restricted to natural environments (Jocqué and Alderweireldt, 2005; Samu and Szinetár, 2002). With some exceptions (e.g. *Phoneutria*, *Asthenoctenus* and *Centroctenus*), ctenids are restricted to forest habitats, and their abundance decreases when the habitats are altered (Jocqué and Alderweireldt, 2005; Rego et al., 2006, 2007; Hazzi et al., 2020). The presence of some ctenid lineages that are endemic to continental or biogeographic regions (e.g. American, African and Amazonian lineages) together with their environmental restrictions to forest habitats indicate that they will have lower dispersal capabilities relative to lycosids (Piacentini and Ramírez, 2019), and that their distribution patterns could be explained by a combination of rare continental dispersal events and vicariance/dispersion within continental regions. However, owing to the low nodal support values in the intrafamilial relationships, it is not possible to achieve a detailed historical biogeographic reconstruction of the family.

The likelihood and parsimony ancestral reconstructions of the evolution of the ctenid eye configuration suggest that the 2–4–2 pattern has evolved seven times independently in the RTA clade (Figs 6 and S9). In addition, the ancestral reconstruction and the unipartite directional network suggest that most of the ocular conformation states in the RTA clade originated from an ancestral ocular pattern of two rows of eyes. Such is the case of Lycosoidea, where the most likely ancestral state is also two eye rows, and the ocular conformations of Oxyopidae, Ctenidae and Lycosidae also originated from a two-rows eye pattern. The inference of two eye rows as plesiomorphic for Lycosidae is congruent with ontogenetic changes in Lycosidae in which the size and conformation of the eyes change from two rows to three rows, and the optic axis turns from the vertical to the horizontal (Homann, 1971). Our results also imply that the eye pattern of Selenopidae has evolved from a two-eye-row pattern based on the position of *Donuea* sp. as its sister group with low support. However, previous molecular studies using Sanger (Wheeler et al., 2017) and UCE data combined with morphology (Azevedo et al., 2022) indicate with strong support that *Donuea* sp. belongs to Corinnidae, and Selenopidae is the sister group of Viridasiidae. Therefore, the topologies of these studies that the selenopid eye pattern has evolved from the ctenid eye pattern or vice versa.

Treating complex phenotypic structures, such as variation of the ocular arrangement of spiders, as a discrete multistate character to be reconstructed on a phylogenetic tree can be considered questionable if the character coding method is not closely linked to homology statements. The premise of ancestral character reconstruction is that the phenotypic feature whose history of changes is being reconstructed is a character itself, and thus, the alternative conditions (states) are deemed to be part of a single transformation series, that is, a hypothesis of homology (e.g. in the sense of De Pinna (1991) "primary homology"). As such, the transformations of the states represented at the terminals can be optimized on a cladogram. In phylogenetic analysis, when coding the phenotypic variation of complex structures, the "complexity" is broken down into as many independent propositions of homology as is allowed with the systematic context, and each is treated as a character (Brazeau, 2011). In general, variation in the ocular pattern of spiders can be

separated into several discrete arrangements defined by the relative positions of the eyes (Fig. 6). Taxonomists have traditionally used such ocular arrangements to diagnose higher taxa, such as families (e.g. the "salticid eye pattern"). Ideally, one would study evolutionary changes in the arrangement of the eyes by reconstructing the changes of its various homologous components (i.e. the eyes), for example, by homologizing each pair of eyes (such as the AME) across species, rather than treating the arrangement of all the eyes as a single character. However, it is not a simple task to define if the coding of the different eyes should be based on their relative position to a specific eye, all the remaining eyes and/or the carapace. Treating the interspecific variation of the ocular arrangement as a single multistate character with the various alternative conformations as its states divorces to some extent this putative character from the concept of homology because different ocular patterns are not homologous conditions of a single transformation series. Coding ocular arrangements rather than stricter hypotheses of homology also imposes limitations in the understanding of the evolution of the ocular patterns because such a character coding approach does not discriminate among the multiple possible evolutionary pathways that can result in a specific ocular arrangement. For example, different pathways of change in the location of the eyes may result in the same type of ocular arrangement, and thus coding the pattern, rather than the various components that produce a pattern, may not necessarily elucidate the actual evolutionary transformations, which can remain hidden under such a coding scheme. In the spider literature, similar coding and ancestral state reconstruction problems have been discussed for sexual size dimorphism and the evolution of web architecture (e.g. Hormiga et al., 2000; Kallal et al., 2021). Reconstructing sexual size dimorphism as a ratio (e.g. male to female body length), as opposed to reconstructing the size of each sex independently, can potentially mask the diversity of evolutionary pathways that result in similar ratios (Hormiga et al., 2000). For example, male dwarfism (small males relative to female size) can evolve by a reduction of male size relative to female size, by an increase of the female size or by a combination of the two.

Variation in foraging webs presents a more complex problem that has also been treated in an overly simplistic fashion, coding different web architectures as states of a single character (e.g. Blackledge et al., 2009). In some foraging webs, such as orb webs, it is possible to homologize components of the final web architecture and the stereotypical behaviours used to build such components (e.g. the radii; see Eberhard, 1982), but it has not been possible to find the corresponding homologous behaviours (or structures) in non-orbicular webs, even in cases where the web architecture is inferred to have evolved at some point from an orb (e.g. in the sheet webs of the family Linyphiidae; Eberhard, 2020). Despite this circumvention of the concept of homology (characterized as "a quantum leap in the concept of homology" by Dimitrov and Hormiga, 2021), this admittedly flawed coding method has been often used to study the evolution and diversification of spider webs (Kallal et al., 2021 and references therein), in part because a pragmatic but epistemologically superior option is not available. Similarly, we have coded the different ocular patterns of our study taxa as alternative states of a single multistate character, recognizing that while this approach also circumvents the equivalence character—homology—it does provide a coarse starting point to explore the evolution of ocular arrangements. Although in general, it does not seem possible to implement a strict concept of homology in coding the ocular arrangements of our taxa, in the case of the convergently evolved ctenid arrangement of *Cupiennius* (Trechaleidae), it seems logical to infer that the ALE have migrated from an anterior to a more posterior position (that is, a transition from the lycosid to the ctenid ocular pattern). This particular inference is possible because both Lycosidae and Ctenidae have similar eye patterns and carapace shapes. An alternative approach to reconstruct the ocular conformation would be to use geometric morphometrics methods on phylogenetic trees (Catalano et al., 2010). This method could trace the position of each eye independently (coded as a landmark) on the phylogeny and at the same time reconstruct the ocular arrangement. In addition, the implementation of 3D geometric morphometrics could properly manage that the position of the eyes is also affected by the evolutionary changes in carapace shape. For instance, it would be challenging to find a standard orientation of the prosoma that would be suitable to assess eye placements across all spider groups because of the great morphological variation in carapace shape.

In conclusion, our study presents for the first time a molecular corroboration of the main ctenid lineages and the monophyly of several genera of Ctenidae which had been previously hypothesized based on morphological analyses or on molecular analyses with modest taxon samples. In addition, we propose new relationships and taxonomic changes that will contribute to future systematic studies of Lycosoidea. Our study indicates that at least six new genera should be described to accommodate both new species and species misplaced in the phylogenetically circumscribed genera *Ctenus*, *Leptoctenus* and *Centroctenus*. Despite more molecular data and denser taxon sampling, relative to other lycosoids studies, the empirical support for the monophyly of Ctenidae remains elusive and many of the intrafamilial phylogenetic relationships

receive low nodal support, preventing reliable ancestral character reconstructions or other comparative analyses (e.g. biogeographic reconstructions). A phylogenetic study combining hundreds of UCEs and the Sanger data generated in this work is underway (N. Hazzi, H. Wood and G. Hormiga, in prep.) to test biogeographic and ecomorphological evolutionary hypotheses that explain the current distribution patterns and habitat specializations of this diverse Pantropical family.

Systematics

Centroctenus Mello-Leitão, 1929

Type: *Centroctenus longimanus* Mello-Leitão, 1929 (= *Centroctenus ocelliventer* (Strand, 1909))

Parabatinga Polotow and Brescovit, 2009: 603–607 (type species by monotypy: *Parabatinga brevipes* Polotow & Brescovit, 2009). **New synonymy.**

Diagnosis. *Centroctenus* resemble *Isoctenus* Bertkau, 1880 and *Guasuctenus* Polotow and Brescovit, 2009 by the presence of ventral cymbial process and prolateral tegular process at the embolus base (Polotow and Brescovit, 2014), but it can be distinguished by the presence of a prolateral laminar process on the median apophysis (Fig. 8c,e), a tegular pointed projection at the embolus base (Fig. 9a,c) and by having the embolus with a deep dividing suture (Fig. 10a,c), which are both absent in *Isoctenus* and *Guasuctenus*. Both females and males of *Centroctenus* have a wide black area with white ventral abdominal spots (Fig. 7b,d).

Composition. Two species, *Centroctenus ocelliventer* and *Ce. brevipes*

Distribution. South America.

Phylogenetics. The following putative morphological synapomorphies of the male palp support the monophyly of *Centroctenus*: prolateral laminar process in the median apophysis (Polotow and Brescovit, 2014), tegular pointed projection at the embolus base and the embolus with a deep dividing suture. The black coloration with white ventral abdominal spots could be a synapomorphy.

Taxonomic remarks. Our molecular phylogenetic hypothesis using four of the eleven described species, plus three new species indicated that *Centroctenus* as currently circumscribed is not monophyletic, and that the type species (*C. ocelliventer*) is not closely related to any of the remaining species currently placed in *Centroctenus*, but instead *C. ocelliventer* is sister to the monotypic genus *Parabatinga* (Fig. 5). The main diagnostic character that was proposed in the first taxonomic revision of *Centroctenus* had a tibia twice as long as the cymbium (Brescovit, 1996). Previous morphological phylogenetic studies including only one species showed that this character was unique to *Centroctenus* (Simó and Brescovit, 2001; Polotow and Brescovit, 2009a,b). However, as shown in a subsequent morphological phylogenetic analysis (Polotow and Brescovit, 2011), this tibial character is highly homoplasious and species that do not even belong to

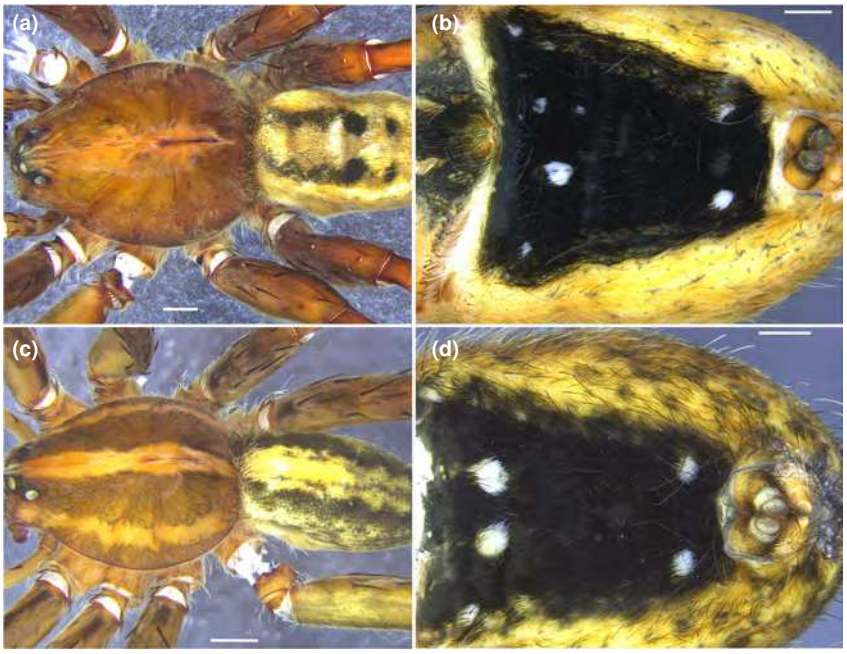


Fig. 7. (a, b) Dorsal and ventral views of the abdomen of *Centroctenus brevipes* (Keyserling, 1891); (c, d) dorsal view of the carapace and ventral view of the abdomen of *Centroctenus ocelliventer* (Strand, 1909). Scale bars: 1.3 mm (a), 0.5 mm (b), 1.00 mm (c) and 0.5 mm (d).

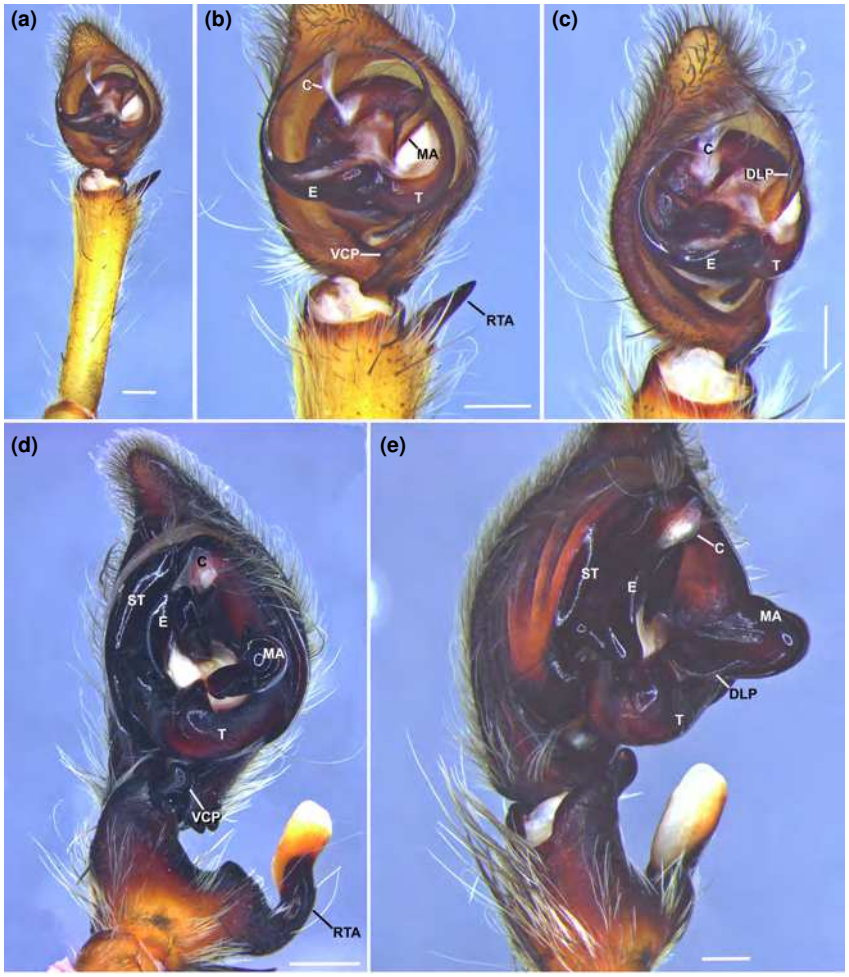


Fig. 8. (a–c) Left male palp of *Centroctenus ocelliventer* (Strand, 1909). (a) Ventral view; (b) close up; (c) prolateral view. (d, e) Left male palp of *Centroctenus brevipes* (Keyserling, 1891). (d) Ventral view; (e) prolateral view. Scale bars: 0.3 mm (a), 0.3 mm (b, c), 0.5 mm (d) and 0.3 mm (e). C, conductor; DLP, distal laminar process; E, embolus; LL, locking lobes; ST, subtegulum; VCP, ventral cymbial process.

Ctenidae (e.g. *Itatiaya*, Zoropsidae) have been described in *Centroctenus* based on the tibial length (Brescovit, 1996). In the most comprehensive morphological phylogeny of Ctenidae to date, *Centroctenus* (represented by *C. ocelliventer* and *C. acara* Brescovit, 1996) was recovered as monophyletic (Polotow and Brescovit, 2014). Recently, Brescovit et al. (2020) described six new *Centroctenus* species and updated the genus diagnosis. Based on a morphological phylogeny, Polotow and Brescovit (2009a) and Polotow and Brescovit (2009b) described the monotypic genus *Parabatinga* to accommodate the species *Ctenus brevipes* Keyserling, 1891 that was placed as sister to *Isoctenus*. Our molecular phylogenetic analyses show that *Isoctenus* is not closely related to *Parabatinga*, but to *Guasuctenus* Polotow and Brescovit, 2019, with high nodal support. In addition, our phylogenetic analysis implies three highly supported independent lineages with a long male palpal tibia: (1) *Parabatinga brevipes* and *C. ocelliventer*; (2) *Ctenus maculisternis*, *Centroctenus varzea* and three new species; and (3) *Centroctenus claudia* and *Centroctenus alluhini*.

Differences in the genitalia of *P. brevipes* and *C. ocelliventer* make grouping these two species in the same genus questionable despite their sister group relationship. For instance, *C. ocelliventer* has a tibia twice as long as the cymbium, a long flagelliform embolus, and a short, bifurcated RTA. In contrast, *P. brevipes* has both a short tibia and embolus, and the RTA is large with a laminar tip. However, both species also share some unique characters that could be considered synapomorphies such as a prolateral laminar process in the median apophysis, a tegular pointed projection at the embolus base and a wide dark black area with white spots ventrally on the abdomen. Based on the latter two characters and on the strongly supported sister group relationship suggested by our analyses, we

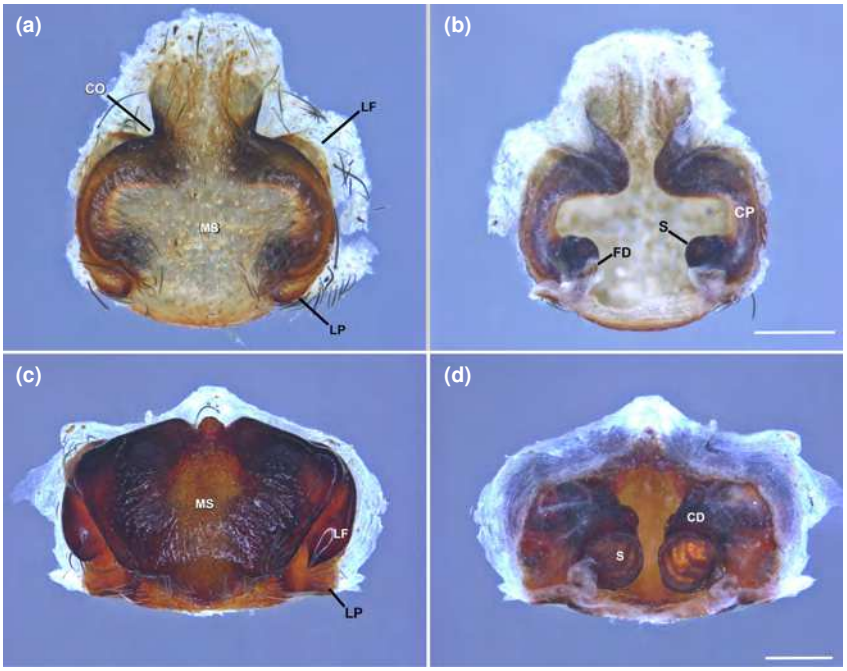


Fig. 9. (a, b) Female genitalia of *Centroctenus ocelliventer* (Strand, 1909). (a) Epigynum, ventral view; (b) vulva, dorsal view. (c, d) Female genitalia of *Centroctenus brevipes*. (c) Epigynum, ventral view; (d) vulva, dorsal view. Scale bars: 0.25 mm (a, b) and 0.35 mm (d, e). CD, Conductor; CO, copulatory opening; FD, fertilization ducts; LP, lateral process; MS, median sector.

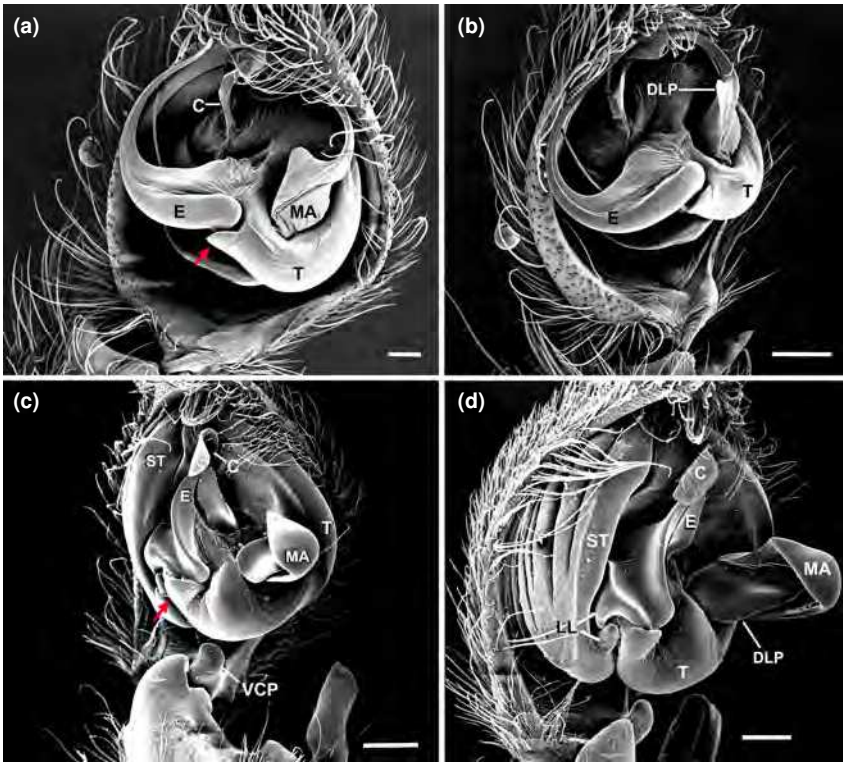


Fig. 10. (a–c) Left male palp of *Centroctenus ocelliventer* (Strand, 1909). (a) Ventral view; (b) prolateral view; (d, e) left male palp of *Centroctenus brevipes*. (d) Ventral view; (e) prolateral view. Scale bars: 0.1 mm (a), 0.2 mm (b), 0.4 mm (c) and 0.3 mm (d). C, conductor; DLP, distal laminar process; E, embolus; LL, locking lobes; ST, subtegulum; VCP, ventral cymbial process. Red arrows indicate tegular pointed projection.

synonymize the monotypic genus *Parabatinga* with *Centroctenus*. Interestingly, we have found that these two species inhabit open areas of grass, similar to wolf spiders (Lycosidae), and we have never found them in forest areas, where most ctenids can be found.

Misplaced species. The molecular phylogenetic analyses indicated that *Centroctenus alinahui* Brescovit et al., 2020 and *Ce. claudia* Brescovit et al., 2020 are not congeneric with the type species of *Centroctenus* (i.e. they should be classified in another genus). Morphological examination of the two species mentioned above, plus the published illustrations and images of *Ce. acara* Brescovit, 1996; *Ce. auberti* Brescovit, 1996; *Ce. chalkidisi* Brescovit et al., 2020, *Ce. coloso* Brescovit et al., 2020, *Ce. dourados* Brescovit et al., 2020, *Ce. irupana* Brescovit et al., 2020, and *Ce. miriuma* Brescovit et al., 2020, suggest that the species that were not included in our molecular analysis may belong to the clade of *Ce. claudia* and *Ce. alinahui*. In addition, *Centroctenus varzea* Brescovit et al., 2020 belongs to a different genus with two more undescribed species.

Acknowledgements

We thank the Department of Biological Sciences of The George Washington University, the Harlan Fellowship, the Explorers Club Washington, DC group and The Early Career Grants of National Geographic for financial support. We also thank the Ernst Mayr Travel Grants (MCZ, Harvard University) for their travel support to examine the ctenid specimens of the Museo de Zoología (MZUC), Universidad de Costa Rica. N. Hazzi was supported by a Fulbright-Colciencias scholarship and the Office of Graduate Student Assistantships and Fellowships of The George Washington University. Additional support was provided by a US National Science Foundation grants (DEB 1754289, DEB 1754289) to GH. We are also deeply grateful to Diana Silva-Dávila, Gilbert Barrantes, Diego F. Cisneros-Heredia, Jimmy Cabra, the late Juan Bernal and the Organization of Tropical Studies for their valuable help in getting the research and export permits. We also thank Bernal Rodríguez-Herrera, Gilbert Barrantes, Natalia Conejo, Diego F. Cisneros-Heredia, Juan Bernal, Tomas Alberto Rios and Diana Silva for their fieldwork and logistics support. We thank Antonio Brescovit, Arnaud Henrard, Peter Jaeger, Fernando Alvarez Padilla and Oscar Francke for sending specimens or tissue for the molecular work. N. Hazzi is grateful to Julio Monzón from ACP Panguana (Pucallpa) and Geoff Gallice and Johana Reyes Quintero from "Finca las Piedras" for their great hospitality in each biological station. N. Hazzi thanks Giussepe Gagliardi-Urrutia and Eryk Vargas for the valuable help in logistics and field company in Iquitos, Peru. We thank Alejandra Arroyave, Eryk Vargas, Guissepe Gagliardi-Urrutia, Abel Pérez, Martín J. Ramírez and Iván Magalhaes for providing really nice white background spider images. N. Hazzi is grateful to Felipe Across-Valencia, Liliam C. Perdomo and Leonel Martínez for their field assistance, logistics and great hospitality in Caquetá, Colombia. We are grateful to Paula Torres and Siddharth Kulkarni for their valuable help and advice with the transcriptome assemblies. Collecting in Costa Rica and exporting the specimens out of the country were permitted by Sistema Nacional de Areas de Conservación (SINAC) and Ministerio de Ambiente de Energia (SINAC-ACC-PI-R-045-2019 and PE-DCUSBSE-SE325-2019). Collecting in Panama and exporting the specimens out of the country were permitted by Ministerio de Ambiente (SEX/A-79-18). Collecting in Peru and exporting the specimens out of the country were permitted by Ministerio de Agricultura y Riego (3521-SERFOR, 328-2019-MINAGRI-SERFOR-DGGSPFFS and AUT-IFS-2019-059). Collecting in Ecuador and exporting the specimens out the country were permitted by Ministerio del Ambiente 001-2020-EXP-CM-FAU-DNB/MA. Collecting in Colombia and exporting the specimens out the country were permitted by Autoridad Nacional de Licencias Ambientales (ANLA) 02125. We are grateful to the Associate Editor Martín J. Ramírez, three anonymous reviewers and Hannah Wood for their helpful comments and suggestions on an earlier version of this manuscript.

Conflict of interest

None declared.

Data availability statement

The concatenation file of the sequences data are avaliable in the Supporting Information section.

REFERENCES

Azevedo, G.H., Bougie, T., Carboni, M., Hedin, M. and Ramírez, M.J., 2022. Combining genomic, phenotypic and Sanger sequencing data to elucidate the phylogeny of the two-clawed spiders (Dionycha). Mol. Phylogenet. Evol. 166, 107327.

Ballesteros, J.A. and Hormiga, G., 2018. Species delimitation of the North American orchard-spider *Leucauge venusta* (Walckenaer, 1841) (Araneae, Tetragnathidae). Mol. Phylogenet. Evol. 121, 183–197. https://doi.org/10.1016/j.ympev.2018.01.002.

Barth, F.G., 2002. A spider's world: senses and behavior. Springer Science & Business Media, Berlin, Heidelberg.

Bertkau, P., 1880. Verzeichniss der von Prof. E. van Beneden auf seiner im Auftrage der belgischen Regierung unternommenen wissenschaftlichen Reise nach Brasilien und La Plata in Jahren 1872-5 gesammelten Arachniden.

Bidegaray-Batista, L. and Arnedo, M.A., 2011. Gone with the plate: the opening of the Western Mediterranean basin drove the diversification of ground-dweller spiders. BMC Evol. Biol. 11(1), 1–15. https://doi.org/10.1186/1471-2148-11-317.

Blackledge, T.A., Scharff, N., Coddington, J.A., Szüts, T., Wenzel, J.W., Hayashi, C.Y. and Agnarsson, I., 2009. Reconstructing web evolution and spider diversification in the molecular era. Proc. Natl Acad. Sci. 106(13), 5229–5234.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A., Rambaut, A. and Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10(4), e1003537. https://doi.org/10.1371/journal.pcbi.1003537.

Brazeau, M.D., 2011. Problematic character coding methods in morphology and their effects. Biol. J. Linnean Soc. 104(3), 489–498.

Brescovit, A.D., 1996. Revisão do gênero *Centroctenus* Mello-Leitão (Araneae, Ctenidae, Cteninae). Rev. Brasil. Entomol. 40, 301–313.

Brescovit, A.D. and Simó, M., 2007. On the Brazilian Atlantic Forest Species of the Spider Genus *Ctenus* Walckenaer, with the Description of a neotype for *C. dubius* Walckenaer (Araneae, Ctenidae, Cteninae). Arachnology 14, 1–17. https://doi.org/10.13156/arac.2007.14.1.1.

Brescovit, A.D., Torres, R.A., Rego, F.N. and Polotow, D., 2020. Six new species of the spider genus Centroctenus Mello-Leitão from the Neotropical region (Ctenidae, Cteninae). Zootaxa 4877 (2), zootaxa-4877. https://doi.org/10.11646/zootaxa.4877.2.5.

Brower, A.V., 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. Proc. Natl Acad. Sci. 91(14), 6491–6495.

Bucaretchi, F., Bertani, R., De Capitani, E.M. and Hyslop, S., 2018. Envenomation by Wandering Spiders (Genus *Phoneutria*). In: Vogel, C.-W., Seifert, S.A. and Tambourgi, D.V. (Eds.), Clinical Toxinology in Australia, Europe, and Americas. Springer, Netherlands, Dordrecht, pp. 101–154. https://doi.org/10.1007/978-94-017-7438-3_63.

Bucaretchi, F., Mello, S.M., Vieira, R.J., Mamoni, R.L., Blotta, M.H.S.L., Antunes, E. and Hyslop, S., 2008. Systemic envenomation caused by the wandering spider *Phoneutria nigriventer*, with quantification of circulating venom. Clin. Toxicol. 46, 885–889. https://doi.org/10.1080/15563650802258524.

Carlozzi, A., Bidegaray-Batista, L., González-Bergonzoni, I. and Aisenberg, A., 2018. Flying sand-dwelling spiders: aerial dispersal in *Allocosa marindia* and *Allocosa senex* (Araneae: Lycosidae). J. Arachnol. 46(1), 7–12. https://doi.org/10.1636/JoA-S-17-026.1.

Carvalho, M.R., Jaramillo, C., de la Parra, F., Caballero-Rodríguez, D., Herrera, F., Wing, S., Turner, B.L., D'Apolito, C., Romero-Báez, M., Narváez, P. and Martínez, C., 2021. Extinction at the end-Cretaceous and the origin of modern Neotropical rainforests. Science 372(6537), 63–68. https://doi.org/10.1126/science.abf1969.

Catalano, S.A., Goloboff, P.A. and Giannini, N.P., 2010. Phylogenetic morphometrics (I): the use of landmark data in a phylogenetic framework. Cladistics 26(5), 539–549.

Cheng, D.Q. and Piel, W.H., 2018. The origins of the Psechridae: web-building lycosoid spiders. Mol. Phylogenet. Evol. 125, 213–219. https://doi.org/10.1016/j.ympev.2018.03.035.

Coddington, J.A. and Scharff, N., 1994. Problems with zero-length branches. Cladistics. https://doi.org/10.1111/j.1096-0031.1994.tb00187.x.

Crane, P.R. and Lidgard, S., 1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. In: Major Evolutionary Radiations, pp. 377–407.

Currano, E.D., Wilf, P., Wing, S.L., Labandeira, C.C., Lovelock, E.C. and Royer, D.L., 2008. Sharply increased insect herbivory during the Paleocene–Eocene Thermal Maximum. Proc. Natl Acad. Sci. 105(6), 1960–1964. https://doi.org/10.1073/pnas.0708646105.

De Pinna, M.C., 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7(4), 367–394.

Dimitrov, D. and Hormiga, G., 2021. Spider diversification through space and time. Ann. Rev. Entomol. 66, 225–241.

Diniz, M.R., Paiva, A.L., Guerra-Duarte, C., Nishiyama, M.Y., Jr., Mudadu, M.A., Oliveira, U.D., Borges, M.H., Yates, J.R. and Junqueira-de-Azevedo, I.D.L., 2018. An overview of *Phoneutria nigriventer* spider venom using combined transcriptomic and proteomic approaches. PloS One 13(8), e0200628. https://doi.org/10.1371/journal.pone.0200628.

Dondale, C.D., 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). Actas X Congr. Aracnol. 1, 327–332.

Dornburg, A., Townsend, J.P., Friedman, M. and Near, T.J., 2014. Phylogenetic informativeness reconciles ray-finned fish molecular divergence times. BMC Evol. Biol. 14(1), 1–14.

Duperre, N., 2015. Description of a new genus and thirteen new species of Ctenidae (Araneae, Ctenidae) from the Chocó region of Ecuador. Zootaxa 4028(4), 451–484. https://doi.org/10.11646/zootaxa.4028.4.1.

Eberhard, W.G., 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution, 1067–1095.

Eberhard, W., 2020. Spider webs: Behavior, function, and evolution. The University of Chicago Press.

Estrada-Gomez, S., Vargas Munoz, L.J., Lanchero, P. and Segura Latorre, C., 2015. Partial characterization of venom from the Colombian spider *Phoneutria boliviensis* (Aranae: Ctenidae). Toxins 7(8), 2872–2887. https://doi.org/10.3390/toxins7082872.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. and Kluge, A.G., 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12(2), 99–124. https://doi.org/10.1006/clad.1996.0008.

Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G. and Hormiga, G., 2018. Phylogenomics, diversification dynamics, and comparative transcriptomics across the spider tree of life. Curr. Biol. 28(9), 1489–1497. https://doi.org/10.1016/j.cub.2018.03.064.

Foelix, R.F., 2011. Biology of Spiders, 3rd edition. Oxford University Press.

Folt, B. and Lapinski, W., 2017. New observations of frog and lizard predation by wandering and orb-weaver spiders in Costa Rica. Phyllomedusa J. Herpetol. 16(2), 269–277. https://www.revistas.usp.br/phyllo/article/view/141880.

Forest, F., 2009. Calibrating the tree of life: fossils, molecules and evolutionary timescales. Ann. Bot. 104(5), 789–794.

Gasnier, T.R., de Azevedo, C.S., Torres-Sanchez, M.P. and Höfer, H., 2002. Adult size of eight hunting spider species in central Amazonia: temporal variations and sexual dimorphisms. J. Arachnol. 30(1), 146–154. https://doi.org/10.1636/0161-8202(2002)030[0146:asoehs]2.0.co;2.

Gasnier, T.R. and Hofer, H., 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in central Amazonia. J. Arachnol. 29, 95–103.

Gasnier, T.R., Höfer, H., Torres-Sanchez, M.P. and Azevedo, C.S., 2009. História natural de algumas espécies de aranhas das famílias Ctenidae e Lycosidae na Reserva Ducke: bases para um modelo integrado de coexistência. In: Fonseca, C.R.V., Magalhães, C., Rafael, J.A. and Franklin, E. (Eds.), In a fauna de Artrópodes da Reserva Florestal Ducke: estado atual do conhecimento taxonômico e biológico. Instituto Nacional de Pesquisas da Amazônia—INPA, Manaus, pp. 223–230.

Gingerich, P.D., 2006. Environment and evolution through the Paleocene–Eocene thermal maximum. Trends Ecol. Evol. 21(5), 246–253. https://doi.org/10.1016/j.tree.2006.03.006.

Goloboff, P.A. and Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32(3), 221–238. https://doi.org/10.1111/cla.12160.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramıacute; rez, M.N.J. and Szumik, C.A., 2003. Improvements to resampling measures of group support. Cladistics 19(4), 324–332. https://doi.org/10.1111/j.1096-0031.2003.tb00376.x.

Goloboff, P.A., Farris, J.S. and Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24(5), 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x.

Gomez, M.V., Kalapothakis, E., Guatimosim, C. and Prado, M.A., 2002. Phoneutria nigriventer venom: a cocktail of toxins that affect ion channels. Cell. Mol. Neurobiol. 22(5), 579–588. https://doi.org/10.1023/A:1021836403433.

Grabherr, M.G., Haas, B.J., Yassour, M., Levin, J.Z., Thompson, D.A., Amit, I., Adiconis, X., Fan, L., Raychowdhury, R., Zeng, Q. and Chen, Z., 2011. Full-length transcriptome assembly from RNA-Seq data without a reference genome. Nat. Biotechnol. 29 (7), 644–652. https://doi.org/10.1038/nbt.1883.

Griswold, C.E., 1993. Investigations into the phylogeny of lycosid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithsonian Contribut. Zool. 539, 1–39. https://doi.org/10.5479/si.00810282.539.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. and Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. 59(3), 307–321. https://doi.org/10.1093/sysbio/syq010.

Hazzi, N.A., 2014. Natural history of *Phoneutria boliviensis* (Araneae: Ctenidae): habitats, reproductive behavior, postembryonic development and prey-wrapping. J. Arachnol. 42, 303–310. https://doi.org/10.1636/Hi13-05.1.

Hazzi, N.A., Petrosky, A., Karandikar, H., Henderson, D. and Jiménez-Conejo, N., 2020. Effect of forest succession and microenvironmental variables on the abundance of two wandering spider species (Araneae: Ctenidae) in a montane tropical forest. J. Arachnol. 48(2), 140–145. https://doi.org/10.1636/0161-8202-48.2.140.

Hazzi, N.A., Polotow, D., Brescovit, A.D., González-Obando, R. and Simó, M., 2018. Systematics and biogeography of Spinoctenus, a new genus of wandering spider from Colombia (Ctenidae). Invert. Syst. 32(1), 111–158. https://doi.org/10.1071/IS17022.

Hazzi, N.A. and Silva, D., 2012. A new species of *Caloctenus* (Araneae: Ctenidae) from Colombia. Zootaxa 3315(1), 65–68.

Hazzi, N.A., Valderrama-Ardila, C., Brescovit, A.D., Polotow, D. and Simo, M., 2013. New records and geographical distribution of ctenid spiders (Araneae: Ctenidae) in Colombia. Zootaxa 3709, 243–254.

Henrard, A. and Jocqué, R., 2017. Morphological and molecular evidence for new genera in the Afrotropical Cteninae (Araneae, Ctenidae) complex. Zool. J. Linnean Soc. 180(1), 82–154. https://doi.org/10.1111/zoj.12461.

Ho, S.Y., Tong, K.J., Foster, C.S., Ritchie, A.M., Lo, N. and Crisp, M.D., 2015. Biogeographic calibrations for the molecular clock. Biol. Lett. 11(9), 20150194. https://doi.org/10.1098/rsbl.2015.0194.

Homann, H., 1971. Die Augen der Araneae. Zeitschrift für Morphologie der Tiere 69, 201–272. https://doi.org/10.1007/bf00277623.

Hoorn, C., Wesselingh, F.P., Ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P. and Jaramillo, C., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330(6006), 927–931. https://doi.org/10.1126/science.1194585.

Hormiga, G., Scharff, N. and Coddington, J.A., 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). Syst. Biol. 49(3), 435–462.

Huber, K.C., Haider, T.S., Müller, M.W., Huber, B.A., Schweyen, R.J. and Barth, F.G., 1993. DNA sequence data indicates the polyphyly of the family Ctenidae (Araneae). J. Arachnol., 194–201.

Iturralde-Vinent, M.A. and MacPhee, R.D.E., 1996. Age and paleogeographical origin of Dominican amber. Science 273(5283), 1850–1852. https://doi.org/10.1126/science.273.5283.1850.

Jansa, S.A., Barker, F.K. and Heaney, L.R., 2006. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. Syst. Biol. 55(1), 73–88.

Jaramillo, C., 2019. 140 million years of tropical biome evolution. In: Gomez, J. and Pinilla-Chacon, A.O. (Eds.), The Geology of Colombia, Volume 2 Mesozoic, Vol. 2. Servicio Geológico Colombiano, Bogotá, pp. 1–28. https://doi.org/10.32685/pub.esp.36.2019.06.

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L. and Rodriguez, G., 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. Science 330(6006), 957–961. https://doi.org/10.1126/science.1193833.

Jocqué, R. and Alderweireldt, M., 2005. Lycosidae: the grassland spiders. Acta Zool. Bulgarica (Suppl 1), 125–130.

Jocqué, R. and Dippenaar-Schoeman, A.S., 2006. Spider Families of the World. Musée Royal de l'Afrique Central, Tervuren, Belgium.

Jocqué, R., Samu, F. and Bird, T., 2005. Density of spiders (Araneae: Ctenidae) in Ivory Coast rainforests. J. Zool. 266, 105–110. https://doi.org/10.1017/S0952836905006746.

Kallal, R.J. and Hormiga, G., 2018. Systematics, phylogeny and biogeography of the Australasian leaf-curling orb-weaving spiders (Araneae: Araneidae: Zygiellinae), with a comparative analysis of retreat evolution. Zool. J. Linnean Soc. 184(4), 1055–1141. https://doi.org/10.1093/zoolinnean/zly014.

Kallal, R.J., Kulkarni, S.S., Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G. and Hormiga, G., 2021. Converging on the orb: denser taxon sampling elucidates spider phylogeny and new analytical methods support repeated evolution of the orb web. Cladistics 37(3), 298–316. https://doi.org/10.1111/cla.12439.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A. and Jermiin, L.S., 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat. Methods 14(6), 587–589. https://doi.org/10.1038/nmeth.4285.

Kassambara, A., 2020. rstatix: pipe-friendly framework for basic statistical tests. R package version version 0.6.0.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C. and Thierer, T., 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12), 1647–1649.

Kulkarni, S., Kallal, R.J., Wood, H., Dimitrov, D., Giribet, G. and Hormiga, G., 2021. Interrogating genomic-scale data to resolve recalcitrant nodes in the spider tree of life. Mol. Biol. Evol. 38 (3), 891–903. https://doi.org/10.1093/molbev/msaa251.

Land, M.F., 1985. The morphology and optics of spider eyes. In: Neurobiology of Arachnids. Springer, Berlin, Heidelberg, pp. 53–78. https://doi.org/10.1007/978-3-642-70348-5_4.

Landis, M.J., 2017. Biogeographic dating of speciation times using paleogeographically informed processes. Syst. Biol. 66, 128–144. https://doi.org/10.1093/sysbio/syw040.

Lapinski, W. and Tschapka, M., 2013. Habitat use in an assemblage of Central American wandering spiders. J. Arachnol. 41(2), 151–159.

Lapinski, W. and Tschapka, M., 2014. Desiccation resistance reflects patterns of microhabitat choice in a Central American assemblage of wandering spiders. J. Exp. Biol. 217(15), 2789–2795.

Lapinski, W., Walther, P. and Tschapka, M., 2015. Morphology reflects microhabitat preferences in an assemblage of Neotropical wandering spiders. Zoomorphology 134(2), 219–236.

Leebens-Mack, J.H., Barker, M.S., Carpenter, E.J., Deyholos, M.K., Gitzendanner, M.A., Graham, S.W., Grosse, I., Li, Z., Melkonian, M., Mirarab, S., Porsch, M., Quint, M., Rensing, S.A., Soltis, D.E., Soltis, P.S., Stevenson, D.W., Ullrich, K.K., Wickett, N.J., DeGironimo, L., Edger, P.P., Jordon-Thaden, I.E., Joya, S., Liu, T., Melkonian, B., Miles, N.W., Pokorny, L., Quigley, C., Thomas, P., Villarreal, J.C., Augustin, M.M., Barrett, M.D., Baucom, R.S., Beerling, D.J., Benstein, R.M., Biffin, E., Brockington, S.F., Burge, D.O., Burris, J.N., Burris, K.P., Burtet-Sarramegna, V., Caicedo, A.L., Cannon, S.B., Çebi, Z., Chang, Y., Chater, C., Cheeseman, J.M., Chen, T., Clarke, N.D., Clayton, H., Covshoff, S., Crandall-Stotler, B.J., Cross, H., de Pamphilis, C.W., Der, J.P., Determann, R., Dickson,

R.C., Di Stilio, V.S., Ellis, S., Fast, E., Feja, N., Field, K.J., Filatov, D.A., Finnegan, P.M., Floyd, S.K., Fogliani, B., García, N., Gâteblé, G., Godden, G.T., Goh, F., Qi, Y., Greiner, S., Harkess, A., Heaney, J.M., Helliwell, K.E., Heyduk, K., Hibberd, J.M., Hodel, R.G.J., Hollingsworth, P.M., Johnson, M.T.J., Jost, R., Joyce, B., Kapralov, M.V., Kazamia, E., Kellogg, E.A., Koch, M.A., von Konrat, M., Könyves, K., Kutchan, T.M., Lam, V., Larsson, A., Leitch, A.R., Lentz, R., Li, F.W., Lowe, A.J., Ludwig, M., Manos, P.S., Mavrodiev, E., McCormick, M.K., McKain, M., McLellan, T., McNeal, J.R., Miller, R.E., Nelson, M.N., Peng, Y., Ralph, P., Real, D., Riggins, C.W., Ruhsam, M., Sage, R.F., Sakai, A.K., Scascitella, M., Schilling, E.E., Schlösser, E.M., Sederoff, H., Servick, S., Sessa, E.B., Shaw, A.J., Shaw, S.W., Sigel, E.M., Skema, C., Smith, A.G., Smithson, A., Stewart, C.N., Stinchcombe, J.R., Szövényi, P., Tate, J.A., Tiebel, H., Trapnell, D., Villegente, M., Wang, C.N., Weller, S.G., Wenzel, M., Weststrand, S., Westwood, J.H., Whigham, D.F., Wu, S., Wulff, A.S., Yang, Y., Zhu, D., Zhuang, C., Zuidof, J., Chase, M.W., Pires, J.C., Rothfels, C.J., Yu, J., Chen, C., Chen, L., Cheng, S., Li, J., Li, R., Li, X., Lu, H., Ou, Y., Sun, X., Tan, X., Tang, J., Tian, Z., Wang, F., Wang, J., Wei, X., Xu, X., Yan, Z., Yang, F., Zhong, X., Zhou, F., Zhu, Y., Zhang, Y., Ayyampalayam, S., Barkman, T.J., Nguyen, N., Matasci, N., Nelson, D.R., Sayyari, E., Wafula, E.K., Walls, R.L., Warnow, T., An, H., Arrigo, N., Baniaga, A.E., Galuska, S., Jorgensen, S.A., Kidder, T.I., Kong, H., Lu-Irving, P., Marx, H.E., Qi, X., Reardon, C.R., Sutherland, B.L., Tiley, G.P., Welles, S.R., Yu, R., Zhan, S., Gramzow, L., Theißen, G. and Wong, G.K.S., 2019. One thousand plant transcriptomes and the phylogenomics of green plants. Nature 574, 679–685. https://doi.org/10.1038/s41586-019-1693-2.

Lukoschek, V., Scott Keogh, J. and Avise, J.C., 2012. Evaluating fossil calibrations for dating phylogenies in light of rates of molecular evolution: a comparison of three approaches. Syst. Biol. 61(1), 22.

Maddison, W.P., and Maddison, D.R., 2010. Mesquite: a modular system for evolutionary analysis. Version 2.73. Available at: http://mesquiteproject.org (Accessed 10 January 2015).

Magalhaes, I.L., Azevedo, G.H., Michalik, P. and Ramírez, M.J., 2020. The fossil record of spiders revisited: implications for calibrating trees and evidence for a major faunal turnover since the Mesozoic. Biol. Rev. 95(1), 184–217. https://doi.org/10.1111/brv.12559.

Martins, R. and Bertani, R., 2007. The non-Amazonian species of the Brazilian wandering spiders of the genus Phoneutria Perty, 1833 (Araneae: Ctenidae), with the description of a new species. Zootaxa 1526(1526), 1–36.

Menin, M., de Jesus Rodrigues, D. and Salette de Azevedo, C., 2005. Predation on amphibians by spiders (Arachnida, Araneae) in the Neotropical region. Phyllomedusa 4, 39–47. https://doi.org/10.11606/issn.2316-9079.v4i1p39-47.

Mestre, L.A.M. and Gasnier, T.R., 2008. Populações de aranhas errantes do gênero *Ctenus* em fragmentos florestais na Amazônia Central. Acta Amazonica 38, 159–164. https://doi.org/10.1590/S0044-59672008000100018.

Miller, M.A., Pfeiffer, W. and Schwartz, T., 2011. The CIPRES science gateway: a community resource for phylogenetic analyses. In: Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery, pp. 1–8.

Minh, B.Q., Nguyen, M.A.T. and Von Haeseler, A., 2013. Ultrafast approximation for phylogenetic bootstrap. Mol. Biol. Evol. 30, 1188–1195. https://doi.org/10.1093/molbev/mst024.

Morehouse, N., 2020. Spider vision. Curr. Biol. 30(17), R975–R980. https://doi.org/10.1016/j.cub.2020.07.042.

Nabholz, B., Glémin, S. and Galtier, N., 2008. Strong variations of mitochondrial mutation rate across mammals—the longevity hypothesis. Mol. Biol. Evol. 25(1), 120–130.

Nguyen, L.T., Schmidt, H.A., Von Haeseler, A. and Minh, B.Q., 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. 32, 268–274. https://doi.org/10.1093/molbev/msu300.

Paradis, E., Claude, J. and Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20(2), 289–290. https://doi.org/10.1093/bioinformatics/btg412.

Paradis, E. and Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35(3), 526–528.

Peck, W.B., 1981. The Ctenidae of temperate zone North America. Bull. Am. Museum Nat. Hist. 170, 157–169.

Penney, D., 2001. Advances in the taxonomy of spiders in Miocene amber from the Dominican Republic (Arthropoda: Araneae). Palaeontology 44(5), 987–1009.

Penney, D., 2006. Fossil oonopid spiders in Cretaceous ambers from Canada and Myanmar. Palaeontology 49(1), 229–235. https://doi.org/10.1111/j.1475-4983.2005.00521.x.

Piacentini, L.N. and Ramírez, M.J., 2019. Hunting the wolf: a molecular phylogeny of the wolf spiders (Araneae, Lycosidae). Mol. Phylogenet. Evol. 136, 227–240. https://doi.org/10.1016/j.ympev.2019.04.004.

Polotow, D. and Brescovit, A.D., 2009a. Revision and cladistic analysis of *Isoctenus* and description of a new neotropical genus (Araneae, Ctenidae, Cteninae). Zool. J. Linnean Soc. 155, 583–614. https://doi.org/10.1111/j.1096-3642.2008.00452.x.

Polotow, D. and Brescovit, A.D., 2009b. Revision of the new wandering spider genus Ohvida and taxonomic remarks on Celaetycheus Simon, 1897 (Araneae: Ctenidae). Zootaxa 2115(1), 1–20.

Polotow, D. and Brescovit, A.D., 2011. Phylogenetic relationships of the neotropical spider genus *Itatiaya* (Araneae). Zool. Scripta 40 (2), 187–193. https://doi.org/10.1111/j.1463-6409.2010.00463.x.

Polotow, D. and Brescovit, A.D., 2013. New species of the Neotropical spider genus *Celaetycheus* Simon, 1897 (Araneae: Ctenidae). Zootaxa 3637, 139–157. https://doi.org/10.11646/zootaxa.3637.2.5.

Polotow, D. and Brescovit, A.D., 2014. Phylogenetic analysis of the tropical wolf spider subfamily Cteninae (Arachnida, Araneae, Ctenidae). Zool. J. Linnean Soc. 170(2), 333–361. https://doi.org/10.1111/zoj.12101.

Polotow, D. and Brescovit, A.D., 2018. Kiekie, a new Neotropical spider genus of Ctenidae (Cteninae, Araneae). Zootaxa 4531(3), 353–373.

Polotow, D., Carmichael, A. and Griswold, C.E., 2015. Total evidence analysis of the phylogenetic relationships of Lycosoidea spiders (Araneae, Entelegynae). Invertebr. Syst. 29(2), 124–163. https://doi.org/10.1071/IS14041.

Polotow, D. and Jocqué, R., 2015. Afroneutria, a new spider genus of Afrotropical Ctenidae (Arachnida, Araneae). Eur. J. Taxonomy 121.

R Core Team, 2021. R: A language and environment for statistical computing. In: R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. and Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. 67(5), 901–904. https://doi.org/10.1093/sysbio/syy032.

Ramírez, M.J., 2014. The morphology and phylogeny of dionychan spiders (Araneae: Araneomorphae). Bull. Am. Museum Nat. History 2014(390), 1–374. https://doi.org/10.1206/821.1.

Rego, F.N., Venticinque, E.M. and Brescovit, A.D., 2005. Densidades de aranhas errantes (Ctenidae e Sparassidae, Araneae) em uma floresta fragmentada. Biota Neotropica 5, 45–52. https://doi.org/10.1590/S1676-06032005000200004.

Rego, F.N.A.A., Venticinque, E.M. and Brescovit, A.D., 2005. Densidades de aranhas errantes (Ctenidae e Sparassidae, Araneae) em uma floresta fragmentada. Biota Neotropica.jjjjk https://doi.org/10.1590/s1676-06032005000200004.

Rego, F.N.A.A., Venticinque, E.M. and Brescovit, A.D., 2007. Effects of forest fragmentation on four *Ctenus* spider populations (Araneae: Ctenidae) in central Amazonia, Brazil. Stud Neotrop.

Fauna Environ. 42, 137–144. https://doi.org/10.1080/01650520600935082.
Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 2, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x.
Richter, C.J., 1970. Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa, Araneae, Lycosidae). Oecologia 5 (3), 200–214. https://doi.org/10.1007/BF00344884.
Saclier, N., François, C.M., Konecny-Dupré, L., Lartillot, N., Guéguen, L., Duret, L., Malard, F., Douady, C.J. and Lefébure, T., 2018. Life history traits impact the nuclear rate of substitution but not the mitochondrial rate in isopods. Mol. Biol. Evol. 35(12), 2900–2912.
Samu, F. and Szinetár, C., 2002. On the nature of agrobiont spiders. J. Arachnol. 30(2), 389–402. https://doi.org/10.1636/0161-8202(2002)030[0389:OTNOAS]2.0.CO;2.
Sierwald, P., 1993. Revision of the spider genus Paradossenus, with notes on the family Trechaleidae and the subfamily Rhoicininae (Araneae: Lycosoidea). Revue Arachnologique 10(3), 53–74.
Sierwald, P., 1997. Phylogenetic analysis of pisaurine nursery web spiders, with revisions of Tetragonophthalma and Perenethis (Araneae, Lycosoidea, Pisauridae). J. Arachnol., 361–407. https://doi.org/10.2307/3705602.
Silva, D., 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). Bull. Am. Mus. Nat. Hist. 274, 1–86.
Silva, D., 2004. Revision of the spider genus *Caloctenu*s Keyserling, 1877 (Araneae, Ctenidae). Rev. Peruana Biol. 11, 5–26.
Simó, M. and Brescovit, A.D., 2001. Revision and cladistic analysis of the Neotropical spider genus *Phoneutria* Perty, 1833 (Araneae, Ctenidae), with notes on related Cteninae. Bull. Br. Arachnol. Soc. 12, 67–82.
Smith, S.A., 2009. Taking into account phylogenetic and divergence-time uncertainty in a parametric biogeographical analysis of the northern hemisphere plant clade Caprifolieae. J. Biogeogr. 36, 2324–2337. https://doi.org/10.1111/j.1365-2699.2009.02160.x.
Torres-Sanchez, M.P. and Gasnier, T.R., 2010. Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* (Araneae: Ctenidae) in a Central Amazonian rainforest. J. Arachnol. 38, 433–440. https://doi.org/10.1636/p08-93.1.
Valenzuela-Rojas, J.C., González-Gómez, J.C., Van der Meijden, A., Cortés, J.N., Guevara, G., Franco, L.M., Pekár, S. and García, L.F., 2019. Prey and venom efficacy of male and female wandering spider, *Phoneutria boliviensis* (Araneae: Ctenidae). Toxins 11(11), 622. https://doi.org/10.3390/toxins11110622.
van Tuinen, M. and Torres, C.R., 2015. Potential for bias and low precision in molecular divergence time estimation of the Canopy of Life: an example from aquatic bird families. Front. Genet. 6, 203.
Víquez, C., 2020. Aracnofauna (Arachnida) de la Isla del Coco, Costa Rica, con la descripción de tres nuevas especies 68.
Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramírez, M.J., Sierwald, P., Almeida-Silva, L., Alvarez-Padilla, F., Arnedo, M.A., Benavides Silva, L.R., Benjamin, S.P., Bond, J.E., Grismado, C.J., Hasan, E., Hedin, M., Izquierdo, M.A., Labarque, F.M., Ledford, J., Lopardo, L., Maddison, W.P., Miller, J.A., Piacentini, L.N., Platnick, N.I., Polotow, D., Silva-Dávila, D., Scharff, N., Szűts, T., Ubick, D., Vink, C.J., Wood, H.M. and Zhang, J., 2017. The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. Cladistics 33, 574–616. https://doi.org/10.1111/cla.12182.
Woolley, C., Thomas, C.G., Blackshaw, R.P. and Goodacre, S.L., 2016. Aerial dispersal activity of spiders sampled from farmland in southern England. J. Arachnol. 44(3), 347–358. https://doi.org/10.1636/P15-56.1.
World Spider Catalog. (2022). World Spider Catalog. Version 23.5. Natural History Museum Bern, online at http://wsc.nmbe.ch, accessed on June 2, 2022.
Yang, Z., 1995. A space-time process model for the evolution of DNA sequences. Genetics 139(2), 993–1005. https://doi.org/10.1093/genetics/139.2.993.
Zhang, Y. and Li, S., 2013. Ancient lineage, young troglobites: recent colonization of caves by Nesticella spiders. BMC Evol. Biol. 13(1), 1–10. https://doi.org/10.1186/1471-2148-13-183.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Maximum likelihood phylogenetic tree with GTR+ FreeRate model for each partition depicting the main phylogenetic relationships. Support values on the left side are ultrafast bootstraps, and on the right side are Shimodaira–Hasegawa approximate likelihood-ratio test.

Figure S2. Maximum likelihood phylogenetic tree with GTR+ FreeRate for the best partition scheme obtained in Modelfinder. Support values on the left side are ultrafast bootstraps, and on the right side are Shimodaira–Hasegawa approximate likelihood-ratio test.

Figure S3. Maximum likelihood phylogenetic tree with GTR+ Gamma + Invariant site for the best partition scheme obtained in Modelfinder. Support values on the left side are ultrafast bootstraps, and on the right side are Shimodaira–Hasegawa approximate likelihood-ratio test.

Figure S4. Majority 50% consensus of 13 parsimony trees (8880 steps). Support values forgroups are Jackknife resampling expressed as GC "Group present/Contradicted" frequency differences.

Figure S5. Strict consensus of 13 parsimony trees (8880 steps). Support values for groups are Jackknife resampling expressed as GC "Group present/Contradicted" frequency differences.

Figure S6. Constrained likelihood tree estimated used for the estimation of the time-calibrated tree in Beast. Support values on the left side are ultrafast bootstraps, and on the right side are Shimodaira–Hasegawa approximate likelihood-ratio test.

Figure S7. Constrained likelihood tree estimated in IQTREE and time calibrated only using fossils in BEAST depicting the divergence times and phylogenetic relationships. Bars represent 95% highest posterior density interval.

Figure S8. Constrained likelihood tree estimated in IQTREE and time calibrated with fossils and biogeography events in BEAST depicting the divergence times

and phylogenetic relationships. Bars represent 95% highest posterior density interval.

Figure S9. Unordered parsimony ancestral state reconstruction of the eye pattern in the RTA families.

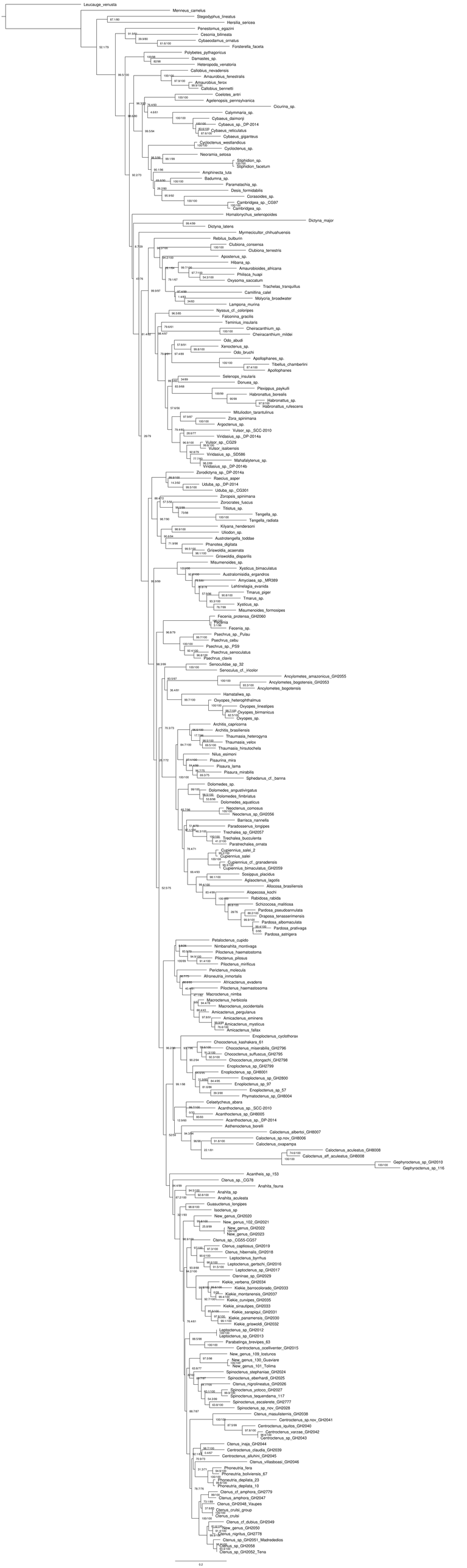
Figure S10. Box plots of the mean substitution rates estimated using only fossils, and fossil and biogeography events.

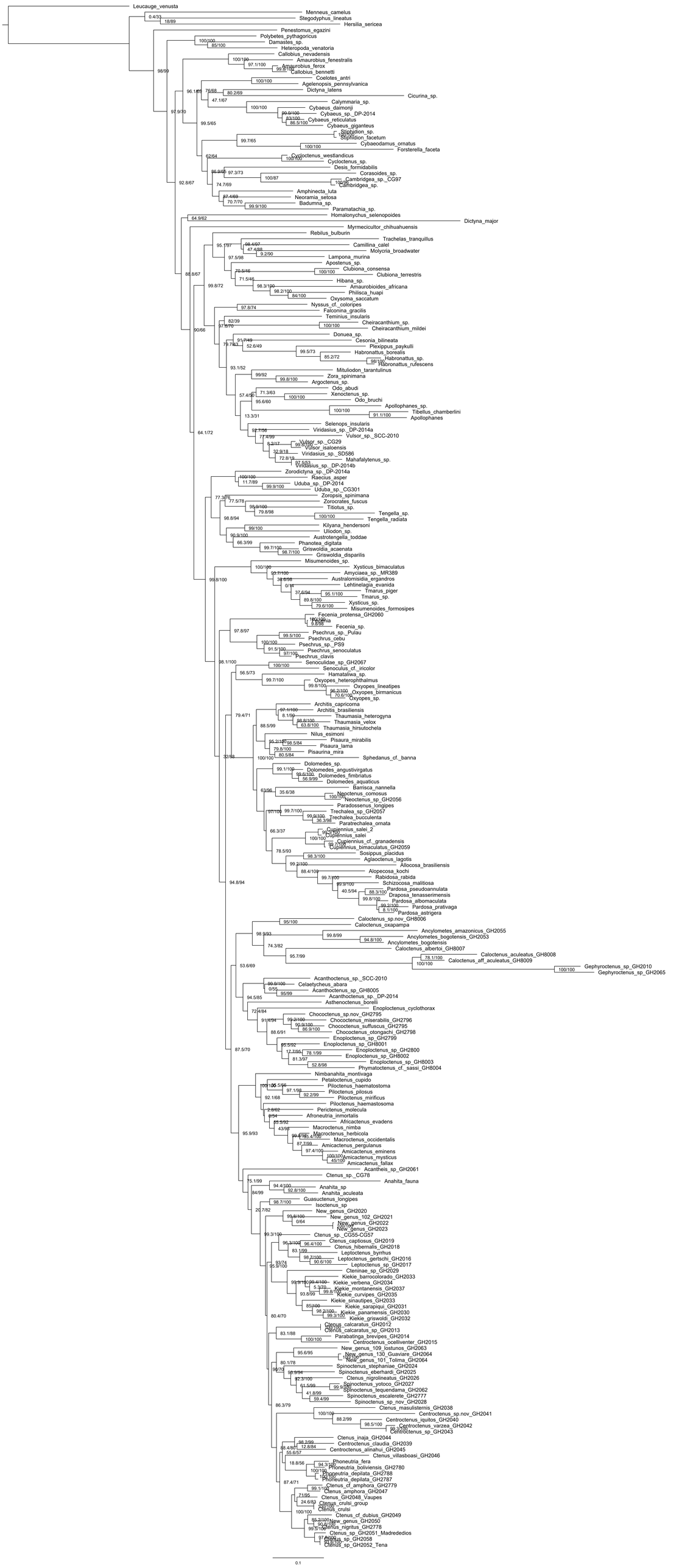
Table S1. Substitution rates estimated with only fossils as calibration points in BEAST2. Lower and upper bounds of the 95% HPD are indicated by parentheses.

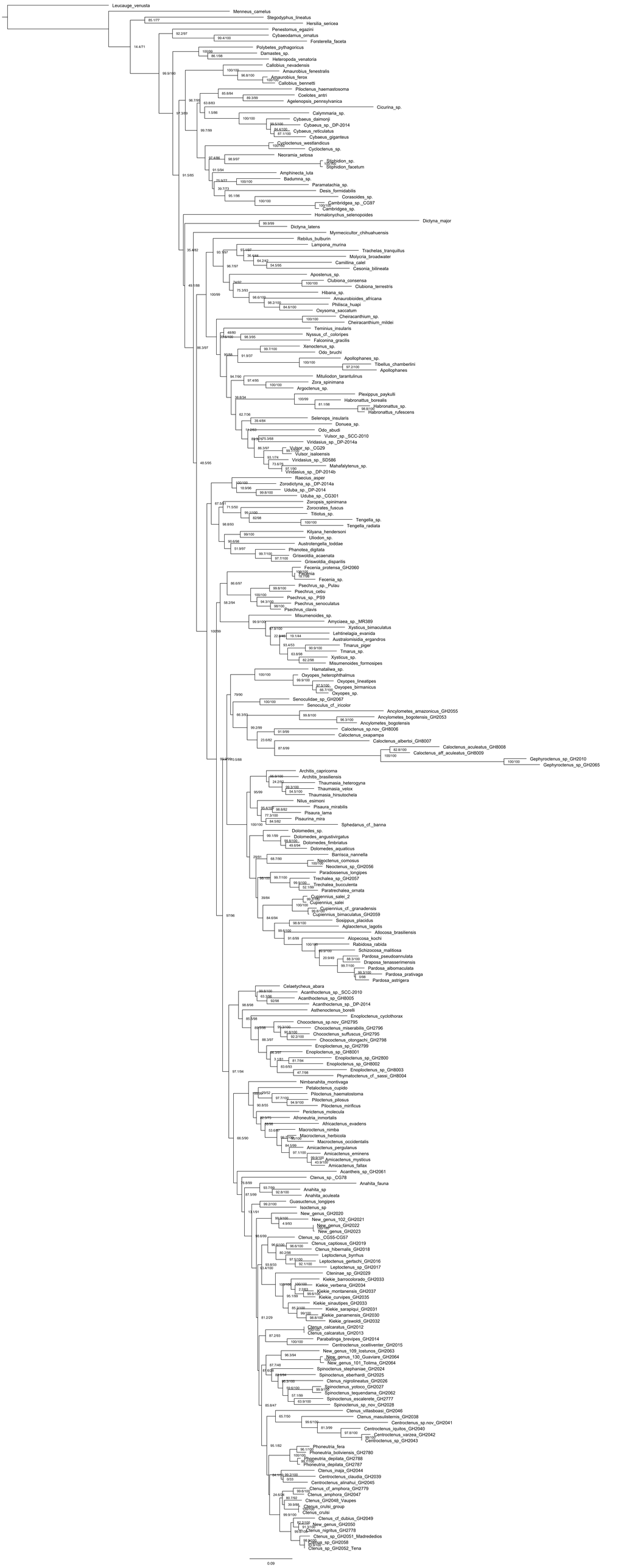
Table S2. Substitution rates estimated with fossils and biogeography events as calibration points in BEAST2. Lower and upper bound of the 95% HPD are indicated by parentheses.

Table S3. DNA taxon sampling with GenBank accession numbers. Accession numbers in bold are new sequences generated by this study

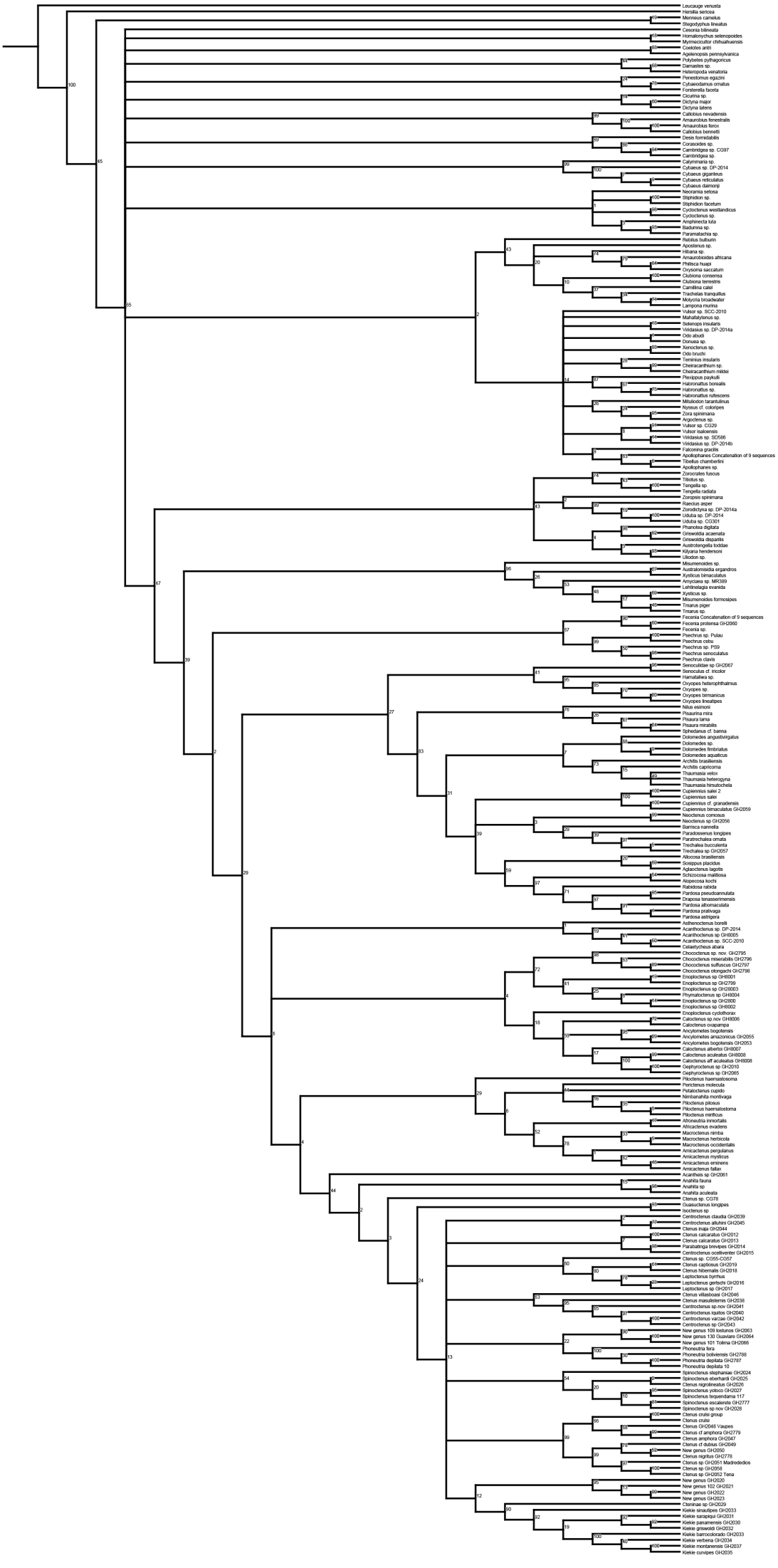
Table S4. Primers used in this study

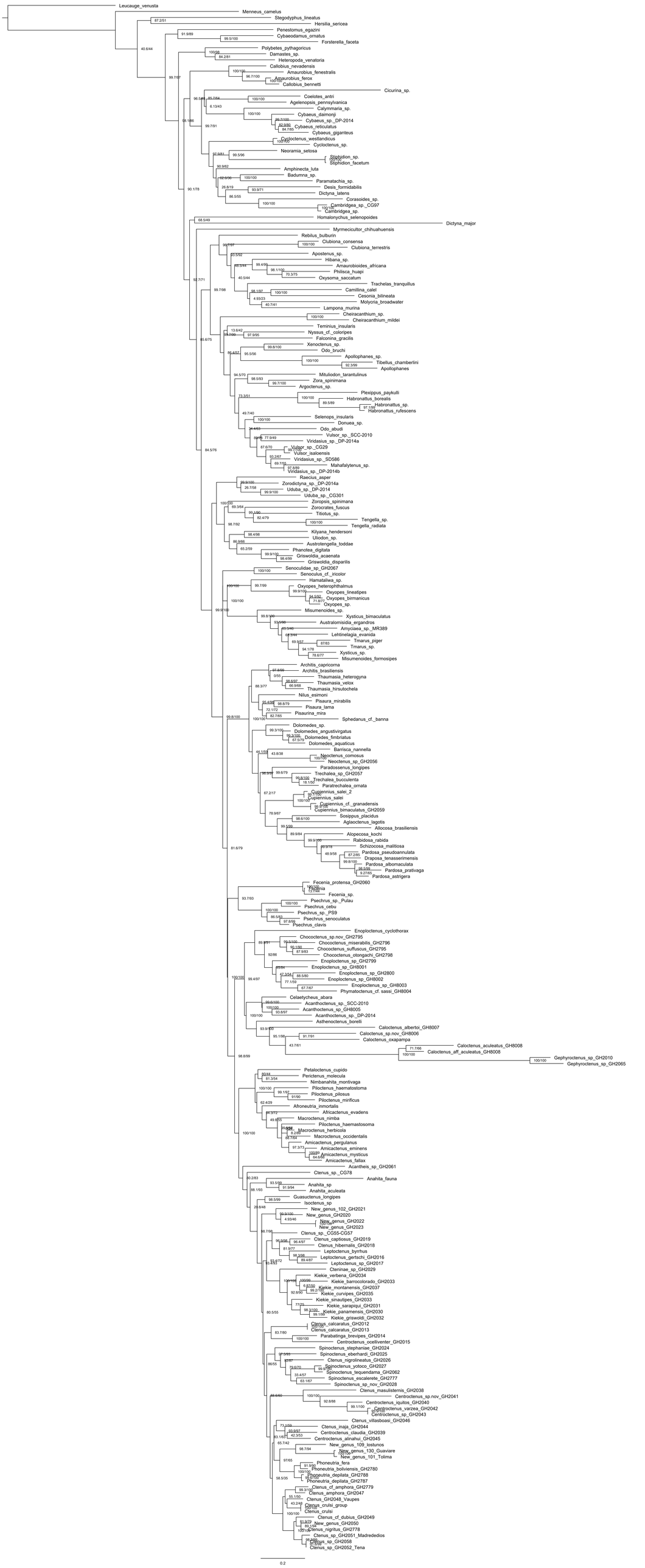

Leucauge_venusta
Menneus_camelus
Stegodyphus_lineatus
Hersilia_sericea
Penestomus_egazini
Cesonia_bilineata
Cybaeodamus_ornatus
Forsterella_faceta
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Calobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Calobius_bennetti
Coelotes_antri
Agelenopsis_pennsylvanica
Cicurina_sp.
Calymmaria_sp.
Cybaeus_dalmonji
Cybaeus_sp._DP-2014
Cybaeus_reticulatus
Cybaeus_gigianteus
Cyclocterus_westlandicus
Cyclocterus_sp.
Neoramia_setosa
Stiphidion_sp.
Stiphidion_facetum
Amphinecta_luta
Badumna_sp.
Paramatachia_sp.
Desis_formidabilis
Corasoides_sp.
Cambridgea_sp._CG97
Cambridgea_sp.
Homalonychus_selenopoides
Dictyna_major
Dictyna_latens
Myrmecicultor_chihuahuensis
Rebilus_bulburin
Clubiona_consensa
Clubiona_terrestris
Apostenus_sp.
Hibana_sp.
Amaurobioides_africana
Philisca_huapi
Owsyona_saccatum
Trachelas_tranquillus
Camillina_calel
Molycria_broadwater
Lampona_murina
Nyssus_cf._coloripes
Falconina_gracilis
Teminius_insularis
Cheiracanthium_sp.
Cheiracanthium_mildei
Odo_abudi
Xenoctenus_sp.
Odo_bruchi
Apollophanes_sp.
Tibellus_chamberlini
Apollophanes
Selenops_insularis
Doruea_sp.
Plexippus_paykulli
Habronattus_borealis
Habronattus_sp.
Habronattus_rufescens
Mituliodon_tarantulinus
Zora_spinimana
Argoctenus_sp.
Vulsor_sp._SCC-2010
Viridasius_sp._DP-2014a
Vultsor_sp._CG29
Vultsor_isaloensis
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Zorodictyna_sp._DP-2014a
Raecius_aspera
Uduba_sp._DP-2014
Uduba_sp._CG301
Zoropsis_spinimana
Zoroceates_fuscus
Titiotus_sp.
Tengella_sp.
Tengella_radiata
Kilyana_hendersoni
Uliodon_sp.
Austrotengella_toddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Misumenoides_sp.
Xysticus_bimaculatus
Australomisidia_ergandros
Amyciaea_sp._MR389
Lehtinelagia_evanida
Tmarus_piger
Tmarus_sp.
Xysticus_sp.
Misumenoides_formosipes
Fecenia_protensa_GH2060
Fecenia_sp.
Psechrus_sp._Pulau
Psechrus_cebu
Psechrus_sp._PS9
Psechrus_senoculatus
Psechrus_clavis
Senoculidae_sp._32
Senoculus_cf._ircolor
Ancylometes_amazonicus_GH2055
Ancylometes_bogotensis_GH2053
Ancylometes_bogotensis
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Architis_capricornia
Architis_brasiliensis
Thaumasia_heterogyna
Thaumasia_velox
Thaumasia_hirsutochela
Nilus_esimoni
Pisaurina_mira
Pisaura_lama
Pisaura_mirabilis
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_fimbriatus
Dolomedes_aquaticus
Nepctenus_comosus
Neoctenus_sp._GH2056
Barrisca_nannella
Paradossenus_longipes
Trechalea_sp._GH2057
Trechalea_bucculenta
Paratrechalea_ornata
Cupiennius_salei_2
Cupiennius_salei
Cupiennius_cf._granadensis
Cupiennius_bimaculatus_GH2059
Sosippus_placidus
Aglaoctenus_lagotis
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_mallitiosa
Pardosa_pseudoannulata
Draposa_tenasserimensis
Pardosa_albomaculata
Pardosa_prativaga
Pardosa_astrigera
Petaloctenus_cupido
Nimbanahita_montivaga
Pilocterus_haematostoma
Pilocterus_pilosus
Pilocterus_minificus
Pericterus_molecula
Afroneutria_inmortalis
Africactenus_evadens
Pilocterus_haemastosoma
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_perguianus
Amicactenus_eminens
Amicactenus_mysticus
Amicactenus_fallax
Enoplectenus_cyclothorax
Chococtenus_kashakara_61
Chococtenus_miserabilis_GH2796
Chococtenus_suffusicus_GH2795
Chococtenus_otongachi_GH2798
Enoplectenus_sp._GH2799
Enoplectenus_sp._GH801
Enoplectenus_sp_GH2800
Enoplectenus_sp._97
Enoplectenus_sp._57
Phymatoctenus_sp._GH8004
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp._GH8005
Acanthoctenus_sp._DP-2014
Asthenoctenus_borelli
Calloctenus_albertoi_GH8007
Calloctenus_sp.nov._GH8006
Calloctenus_oxapampa
Calloctenus_aculeatus_GH8008
Calloctenus_aff_aculeatus_GH8008
Gephyroctenus_sp._GH2010
Gephyroctenus_sp._116
Acantheis_sp._153
Ctenus_sp._CG78
Anahita_fauna
Anahita_sp
Anahita_aculeata
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2020
New_genus_102_GH2021
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_captiosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp._GH2017
Cteninae_sp_GH2029
Kiekie_verbena_GH2034
Kiekie_barrocolorado_GH2033
Kiekie_montanensis_GH2037
Kiekie_curvipes_GH2035
Kiekie_sinuatipes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_panamensis_GH2030
Kiekie_griswoldi_GH2032
Leptoctenus_sp._GH2012
Leptoctenus_sp._GH2013
Parabatinga_brevipes_63
Centroctenus_ocelliventer_GH2015
New_genus_109_Isaiunos
New_genus_130_Guaviare
New_genus_101_Tolima
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_yotoco_GH2027
Spinoctenus_fequendarria_117
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Ctenus_masuliasterria_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_varzae_GH2042
Centroctenus_sp._GH2043
Ctenus_inaja_GH2044
Centroctenus_claudia_GH2039
Centroctenus_alluhini_GH2045
Ctenus_villasboasi_GH2046
Phoneutria_fera
Phoneutria_bolivensis_67
Phoneutria_depilata_23
Phoneutria_depilata_10
Ctenus_cf_amphora_GH2779
Ctenus_amphora_GH2047
Ctenus_GH2048_Vaupes
Ctenus_cruisi_group
Ctenus_cruisi
Ctenus_cf_dubius_GH2049
New_genus_GH2050
Ctenus_nigritus_GH2778
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2058
Ctenus_sp_GH2052_Tena
0.2

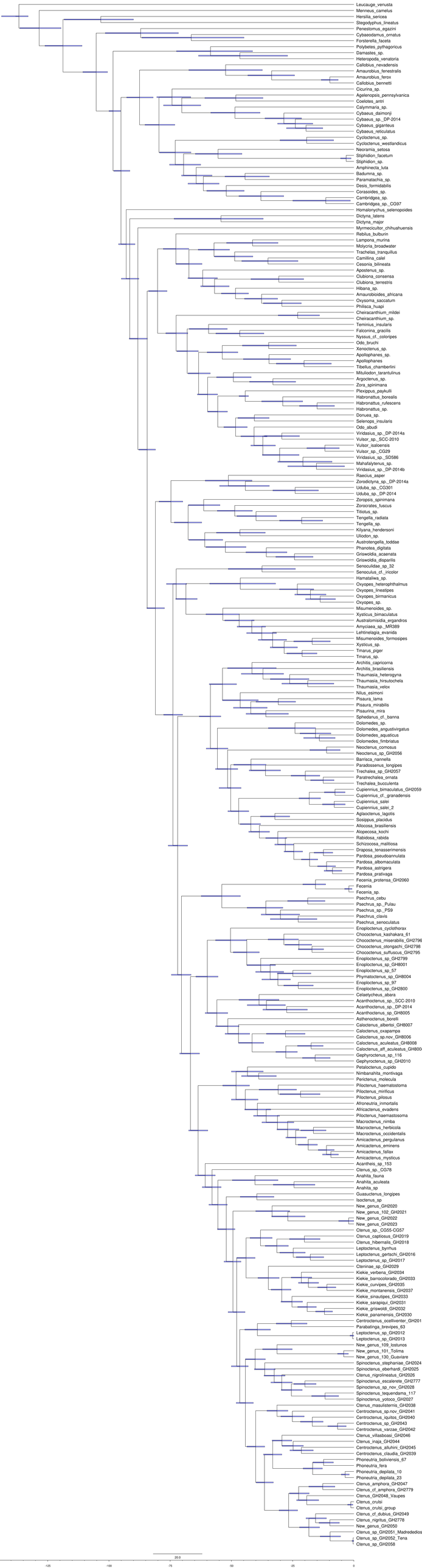

Leucauge_venusta
Menneus_camelus
Stegodyphus_lineatus
Hersilia_sericea
Penestomus_egazini
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Callobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Callobius_bennetti
Coelotes_antri
Agelenopsis_pennsylvanica
Dictyna_latens
Cicurina_sp.
Calymmaria_sp.
Cybaeus_daimonji
Cybaeus_sp._DP-2014
Cybaeus_reticulatus
Cybaeus_giganteus
Stiphidion_sp.
Stiphidion_facetum
Cybaeodamus_ornatus
Forsterella_faceta
Cyclosa_sp.
Cyclosa_sp.
Cyclosa_westlandicus
Desis_formidabilis
Corasoides_sp.
Cambridgea_sp._CG97
Cambridgea_sp.
Amphinecta_luta
Neoramia_setosa
Badumna_sp.
Paramatachia_sp.
Homalonychus_selenopoides
Dictyna_major
Myrmecicultor_chihuahuensis
Rebilus_bulburin
Trachelas_tranquillus
Camillina_calel
Molycria_broadwater
Lampona_murina
Apostenus_sp.
Clubiona_consensa
Clubiona_terrestris
Hibana_sp.
Amaurobioides_africana
Philisca_huapi
Oxysoma_saccatum
Nyssus_cf._coloripes
Falconina_gracilis
Teminius_insularis
Cheiracanthium_sp.
Cheiracanthium_mildei
Donuea_sp.
Cesonia_bilineata
Plexippus_paykulli
Habronattus_borealis
Habronattus_sp.
Habronattus_rufescens
Mituliodon_tarantulinus
Zora_spinimana
Argoctenus_sp.
Odo_abudi
Xenoctenus_sp.
Odo_bruchi
Apollophanes_sp.
Tibellus_chamberlini
Apollophanes
Selenops_insularis
Viridasius_sp._DP-2014a
Vulsor_sp._SCC-2010
Vulsor_sp._CG29
Vulsor_isaloensis
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Zorodictyna_sp._DP-2014a
Raecius_asper
Uduba_sp._DP-2014
Uduba_sp._CG301
Zoropsis_spinimana
Zorocrates_fuscus
Titiotus_sp.
Tengella_sp.
Tengella_radiata
Kilyana_hendersoni
Uliodon_sp.
Austrotengella_toddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Misumenoides_sp.
Xysticus_bimaculatus
Amyciaea_sp._MR389
Australomisidia_ergandros
Lehtinelagia_evanida
Tmarus_piger
Tmarus_sp.
Xysticus_sp.
Misumenoides_formosipes
Fecenia_protensa_GH2060
Fecenia_sp.
Psechrus_sp._Pulau
Psechrus_cebu
Psechrus_sp._PS9
Psechrus_senoculatus
Psechrus_clavis
Senoculidae_sp_GH2067
Senoculus_cf._iricolor
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Architis_capricorna
Architis_brasiliensis
Thaumasia_heterogyna
Thaumasia_velox
Thaumasia_hirsutochela
Nilus_esimoni
Pisaura_mirabilis
Pisaura_lama
Pisaurina_mira
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_fimbriatus
Dolomedes_aquaticus
Barrisca_nannella
Neoctenus_comosus
Neoctenus_sp_GH2056
Paradossenus_longipes
Trochalea_sp_GH2057
Trochalea_bucculenta
Paratrechalea_ornata
Cupiennius_salei_2
Cupiennius_salei
Cupiennius_cf._granadensis
Cupiennius_bimaculatus_GH2059
Sosippus_placidus
Aglaoctenus_lagotis
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_malitiosa
Pardosa_pseudoannulata
Draposa_tenasserimensis
Pardosa_albomaculata
Pardosa_prativaga
Pardosa_astrigera
Caloctenus_sp.nov_GH8006
Caloctenus_oxapampa
Ancylometes_amazonicus_GH2055
Ancylometes_bogotensis_GH2053
Ancylometes_bogotensis
Caloctenus_albertoi_GH8007
Caloctenus_aculeatus_GH8008
Caloctenus_aff_aculeatus_GH8009
Gephyroctenus_sp_GH2010
Gephyroctenus_sp_GH2065
Acanthoctenus_sp._SCC-2010
Celaetycheus_abara
Acanthoctenus_sp_GH8005
Acanthoctenus_sp._DP-2014
Asthenoctenus_borelli
Enoploctenus_cyclothorax
Chococtenus_sp.nov_GH2795
Chococtenus_miserabilis_GH2796
Chococtenus_suffuscus_GH2795
Chococtenus_otongachi_GH2798
Enoploctenus_sp_GH2799
Enoploctenus_sp_GH8001
Enoploctenus_sp_GH2800
Enoploctenus_sp_GH8002
Enoploctenus_sp_GH8003
Phymatoctenus_cf._sassi_GH8004
Nimbanahita_montivaga
Petaloctenus_cupido
Piloctenus_haematostoma
Piloctenus_pilosus
Piloctenus_mirificus
Piloctenus_haemastosoma
Perictenus_molecula
Afroneutria_inmortalis
Africactenus_evadens
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_pergulanus
Amicactenus_eminens
Amicactenus_mysticus
Amicactenus_fallax
Acantheis_sp_GH2061
Ctenus_sp._CG78
Anahita_fauna
Anahita_sp
Anahita_aculeata
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2020
New_genus_102_GH2021
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_captiosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp_GH2017
Cteninae_sp_GH2029
Kiekie_barrocolorado_GH2033
Kiekie_verbena_GH2034
Kiekie_montanensis_GH2037
Kiekie_curvipes_GH2035
Kiekie_sinautipes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_panamensis_GH2030
Kiekie_griswoldi_GH2032
Ctenus_calcaratus_GH2012
Ctenus_calcaratus_sp_GH2013
Parabatinga_brevipes_GH2014
Centroctenus_ocelliventer_GH2015
New_genus_109_lostunos_GH2063
New_genus_130_Guaviare_GH2064
New_genus_101_Tolima_GH2064
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_yotoco_GH2027
Spinoctenus_tequendama_GH2062
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Ctenus_masulisternis_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_varzea_GH2042
Centroctenus_sp_GH2043
Ctenus_inaja_GH2044
Centroctenus_claudia_GH2039
Centroctenus_alinahui_GH2045
Ctenus_villasboasi_GH2046
Phoneutria_fera
Phoneutria_boliviensis_GH2780
Phoneutria_depilata_GH2788
Phoneutria_depilata_GH2787
Ctenus_cf_amphora_GH2779
Ctenus_amphora_GH2047
Ctenus_GH2048_Vaupes
Ctenus_crulsi_group
Ctenus_crulsi
Ctenus_cf_dubius_GH2049
New_genus_GH2050
Ctenus_nigritus_GH2778
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2058
Ctenus_sp_GH2052_Tena
0.4/33
18/89
98/99
100/100
85/100
100/100
97.1/100
99.8/100
100/100
75/68
80.2/69
47.1/67
97.9/70
100/100
99.9/100
83/100
86.5/100
96.1/69
99.5/65
99.7/65
100/100
62/64
100/100
96.9/95
97.3/73
100/87
74.7/69
100/100
92.8/67
97.1/89
70.7/70
99.9/100
64.9/62
88.8/67
95.1/97
98.4/97
47.4/88
9.2/90
97.5/98
70.5/46
100/100
71.5/46
99.8/72
98.3/100
98.2/100
84/100
97.8/74
82/39
97.6/70
100/100
90/66
91.7/49
79.7/43
52.6/49
99.5/73
85.2/72
98/100
93.1/52
99/92
99.8/100
57.4/50
71.3/63
100/100
95.6/60
100/100
91.1/100
13.3/31
64.1/72
97.7/56
77.4/99
99.9/100
8.2/17
32.9/18
72.8/19
97.5/93
77.3/76
100/100
11.7/89
99.9/100
77.5/78
95.9/100
79.8/98
100/100
98.8/94
99/100
90.9/100
66.3/99
99.7/100
98.7/100
99.8/100
100/100
93.7/100
36.8/98
0/14
37.6/94
95.1/100
89.8/100
79.6/100
97.8/97
99.5/100
100/100
91.5/100
97/100
98.1/100
100/100
56.5/73
99.7/100
99.8/100
96.3/100
70.6/100
79.4/71
97.1/100
8.1/99
98.8/100
63.8/100
88.5/99
95.2/100
98.5/84
79.8/100
80.5/84
32/68
100/100
99.1/100
99.6/100
56.9/99
62/96
35.6/38
100/100
97/100
99.7/100
99.9/100
36.3/98
66.3/37
97.2/100
100/100
78.5/93
98.3/100
99.2/100
88.4/100
99.7/100
94.8/94
89.9/100
40.5/94
88.3/100
99.8/100
99.2/100
8.1/100
95/100
98.9/93
99.8/99
94.8/100
74.3/82
95.7/99
78.1/100
100/100
53.6/69
100/100
99.9/100
0/55
95/99
94.5/85
72/84
91/94
99.2/100
90.9/100
86.9/100
88.6/91
65.5/92
12.7/95
78.1/99
81.3/97
52.8/98
100/100
95.5/96
97.1/98
92.2/99
92.1/68
2.8/62
8/54
65.5/92
43/98
99.4/95
87.7/99
97.4/100
100/100
45/100
95.9/93
87.5/70
75.1/99
94.4/100
92.8/100
84/99
98.7/100
20.7/82
95.8/100
0/64
100/100
99.3/100
96.3/100
96.4/100
83.1/99
98.7/100
90.6/100
83/74
85.9/100
99.9/100
99.4/100
5.3/20
99.8/
93.8/99
85/100
98.2/100
99.9/100
80.4/70
83.1/88
100/100
95.6/95
100/100
80.1/78
96/70
98.9/94
97.3/100
61.5/99
99.9/99
41.8/99
59.4/99
86.3/79
100/100
88.2/99
98.5/100
99.4/100
98.2/99
12.8/84
68.4/87
55.6/57
18.8/56
94.3/100
100/100
100/100
87.4/71
99.1/
71/95
24.6/63
100/100
85.2/100
90.8/100
99.5/100
97.6/100
0.1

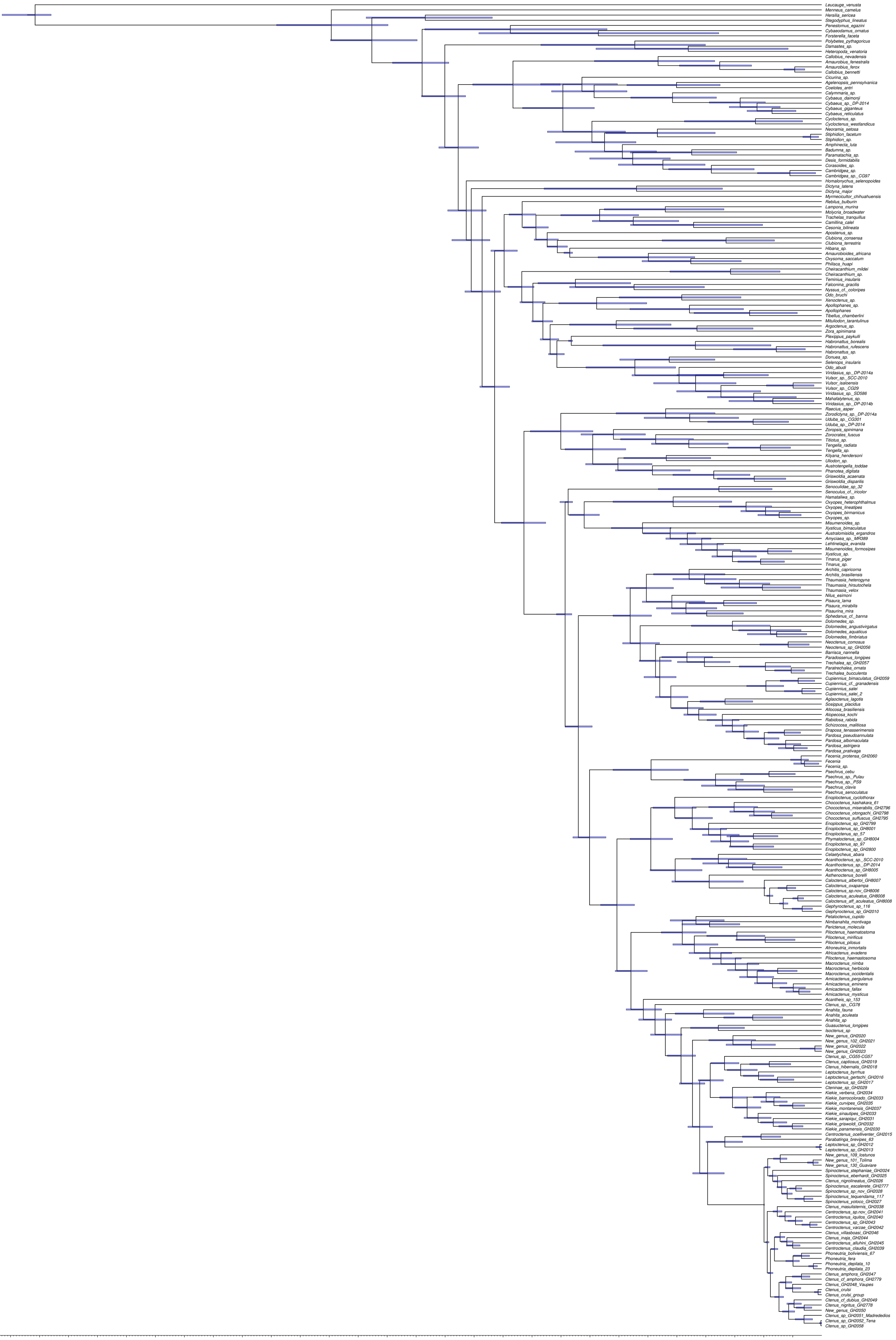

Leucauge_venusta
Menneus_camelus
Stegodyphus_lineatus
Hersilia_sericea
Penestomus_egazini
Cybaeodamus_ornatus
Forsterella_faceta
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Callobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Callobius_bennetti
Piloctenus_haemastosoma
Coelotes_antri
Agelenopsis_pennsylvanica
Cicurina_sp.
Calymmaria_sp.
Cybaeus_daimonji
Cybaeus_sp._DP-2014
Cybaeus_reticulatus
Cybaeus_giganteus
Cyclocteninae_westlandicus
Cyclocteninae_sp.
Neoramia_setosa
Stiphidion_sp.
Stiphidion_facetum
Amphinecta_luta
Badumna_sp.
Paramatachia_sp.
Desis_formidabilis
Corasoides_sp.
Cambridgea_sp._CG97
Cambridgea_sp.
Homalonychus_selenopoides
Dictyna_major
Dictyna_latens
Myrmecicultor_chihuahuensis
Rebilus_bulburin
Lampona_murina
Trachelas_tranquillus
Molycria_broadwater
Camillina_calel
Cesonia_bilineata
Apostenus_sp.
Clubiona_consensa
Clubiona_terrestris
Hibana_sp.
Amaurobioides_africana
Phlisica_huapi
Oxysoma_saccatum
Cheiracanthium_sp.
Cheiracanthium_mildei
Teminius_insularis
Nyssus_cf._coloripes
Falconina_gracilis
Xenoctenus_sp.
Odo_bruchi
Apollophanes_sp.
Tibellus_chamberlini
Apollophanes
Mituliodon_tarantulinus
Zora_spinimana
Argoctenus_sp.
Plexippus_paykulli
Habronattus_borealis
Habronattus_sp.
Habronattus_rufescens
Selenops_insularis
Donuea_sp.
Odo_abudi
Vulsor_sp._SCC-2010
Viridasius_sp._DP-2014a
Vulsor_sp._CG29
Vulsor_isaloensis
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Raecius_asper
Zoroditcyna_sp._DP-2014a
Uduba_sp._DP-2014
Uduba_sp._CG301
Zoropsis_spinimana
Zorocrates_fuscus
Titiotus_sp.
Tengella_sp.
Tengella_radiata
Kilyana_hendersoni
Uliodon_sp.
Austrotengella_boddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Fecenia_protensa_GH2060
Fecenia_sp.
Psechrus_sp._Pulau
Psechrus_cebu
Psechrus_sp._PS9
Psechrus_senoculatus
Psechrus_clavis
Misumenoides_sp.
Amyciaea_sp._MR389
Xysticus_bimaculatus
Lehtinelagia_evanida
Australomisidia_ergandros
Tmarus_piger
Tmarus_sp.
Xysticus_sp.
Misumenoides_formosipes
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Senoculidae_sp_GH2067
Senoculus_cf._ircolor
Ancylometes_amazonicus_GH2055
Ancylometes_bogotensis_GH2053
Ancylometes_bogotensis
Caloctenus_sp.nov_GH8006
Caloctenus_oxapampa
Caloctenus_albertoi_GH8007
Calocteninae_aculeatus_GH8008
Caloctenus_aff_aculeatus_GH8009
Gephyroctenus_sp_GH2010
Gephyroctenus_sp_GH2065
Architis_capricorna
Architis_brasiliensis
Thaumasia_heterogyna
Thaumasia_velox
Thaumasia_hirsutochela
Nilus_esimoni
Pisaura_mirabilis
Pisaura_lama
Pisaurina_mira
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_fimbriatus
Dolomedes_aquaticus
Barrisca_nannella
Neoctenus_comosus
Neoctenus_sp._GH2056
Paradossenus_longipes
Trechalea_sp_GH2057
Trechalea_bucculenta
Paratrechalea_ornata
Cupiennius_salei_2
Cupiennius_salei
Cupiennius_cf._granadensis
Cupiennius_bimaculatus_GH2059
Sosippus_placidus
Aglaoctenus_lagotis
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_malitiosa
Pardosa_pseudoannulata
Drapoa_tenasserimensis
Pardosa_albomaculata
Pardosa_prativaga
Pardosa_astrigera
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp_GH8005
Acanthoctenus_sp._DP-2014
Asthenoctenus_borelli
Enoploctenus_cyclothorax
Chococtenus_sp.nov_GH2795
Chococtenus_miserabilis_GH2796
Chococtenus_suffluscus_GH2795
Chococtenus_otongachi_GH2798
Enoploctenus_sp_GH2799
Enoploctenus_sp_GH8001
Enoploctenus_sp_GH2800
Enoploctenus_sp_GH8002
Enoploctenus_sp_GH8003
Phymatoctenus_cf._sassi_GH8004
Nimbanahita_montivaga
Petalocteninae_cupido
Piloctenus_haematostoma
Piloctenus_pilosus
Piloctenus_mirificus
Pericteninae_molecula
Afroneutria_inmortalis
Africactenus_evadens
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_pergulanus
Amicactenus_eminens
Amicactenus_mysticus
Amicactenus_fallax
Acantheis_sp_GH2061
Ctenus_sp._CG78
Anahita_fauna
Anahita_sp
Anahita_aculeata
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2020
New_genus_102_GH2021
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_capitosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp._GH2017
Cteninae_sp_GH2029
Kiekie_barrocolorado_GH2033
Kiekie_verbena_GH2034
Kiekie_montanensis_GH2037
Kiekie_curvipes_GH2035
Kiekie_sinaulpes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_panamensis_GH2030
Kiekie_griswoldi_GH2032
Ctenus_calcaratus_GH2012
Ctenus_calcaratus_GH2013
Parabatinga_brevipes_GH2014
Centroctenus_ocelliventer_GH2015
New_genus_109_lostunos_GH2063
New_genus_130_Guaviare_GH2064
New_genus_101_Tolima_GH2064
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_yoboco_GH2027
Spinoctenus_tequendama_GH2062
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Ctenus_villasboasi_GH2046
Ctenus_masulisternis_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_varzea_GH2042
Centroctenus_sp_GH2043
Phoneutria_fera
Phoneutria_boliviensis_GH2780
Phoneutria_depilata_GH2788
Phoneutria_depilata_GH2787
Ctenus_inaja_GH2044
Centroctenus_claudia_GH2039
Centroctenus_alinahui_GH2045
Ctenus_cf_amphora_GH2779
Ctenus_amphora_GH2047
Ctenus_GH2048_Vaupes
Ctenus_crulsi_group
Ctenus_crulsi
Ctenus_cf_dubius_GH2049
New_genus_GH2050
Ctenus_nigritus_GH2778
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2058
Ctenus_sp_GH2052_Tena
0.09

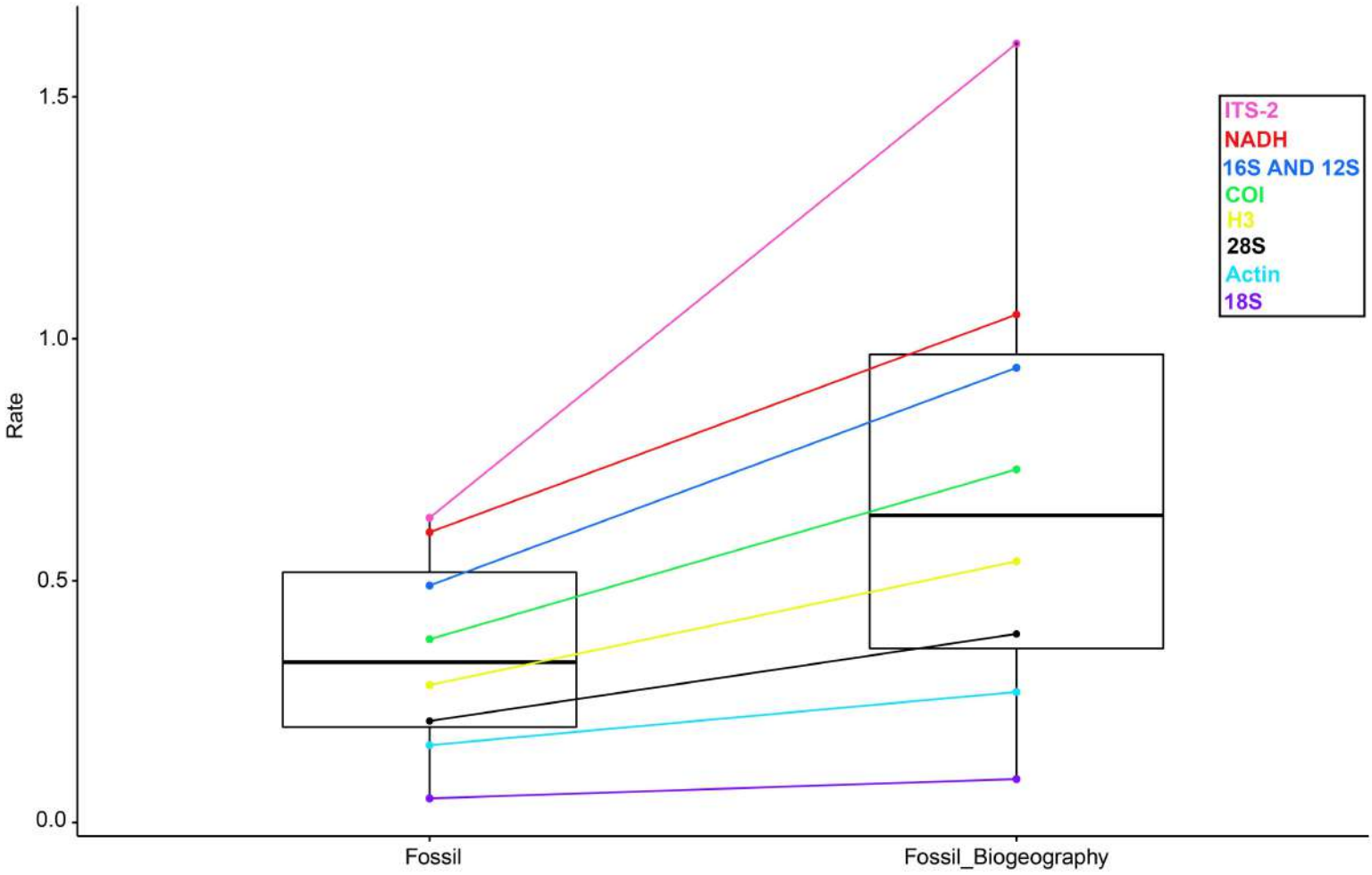

Leucauge venusta
Hersilia sericea
Menneus camelus
Stegodyphus lineatus
Penestomus egazini
Cybaeodamus ornatus
Forsterella faceta
Amphinecta luta
Badumna sp.
Paramatachia sp.
Neoramia setosa
Stiphidion sp.
Stiphidion facetum
Cyclactenus westandicus
Cyclactenus sp.
Coelotes antri
Agelenopsis pennsylvanica
Desis formidabilis
Corasoides sp.
Cambridgea sp. CG97
Cambridgea sp.
Cicurina sp.
Dictyna major
Dictyna latens
Calymmaria sp.
Cybaeus giganteus
Cybaeus sp. DP-2014
Cybaeus reticulatus
Cybaeus daimonji
Polybetes pythagoricus
Cesonia bilineata
Damastes sp.
Heteropoda venatoria
Callobius nevadensis
Amaurobius fenestralis
Amaurobius ferox
Callobius bennetti
Falconina gracilis
Homalonychus selenopoides
Myrmecicultor chihuahuensis
Hebilus bulburin
Apostenus sp.
Hibana sp.
Amaurobioides africana
Phillisca huapi
Oxyopoma saccatum
Clubiona consensa
Clubiona terrestris
Trachelas tranquillus
Camillina calel
Molycria broadwater
Lampona murina
Teminius insularis
Cheiracanthium sp.
Cheiracanthium mildei
Tibellus chamberlini
Apollophanes
Apollophanes sp.
Plexippus paykulli
Habronattus borealis
Habronattus sp.
Habronattus rufescens
Mituliodon tarantulinus
Nyssus cf. coloripes
Zora spinimana
Argoctenus sp.
Odo abudi
Selenops insularis
Xenoctenus sp.
Odo bruchi
Donuea sp.
Mahafalytenus sp.
Viridasius sp. SD586
Vulsor sp. CG29
Vulsor isaloensis
Vulsor sp. SCC-2010
Viridasius sp. DP-2014a
Viridasius sp. DP-2014b
Zonpasis spinimana
Zorodictyna sp. DP-2014a
Raecius asper
Uduba sp. DP-2014
Uduba sp. CG301
Austrotengella toddae
Phanotea digitata
Griswoldia acaenata
Griswoldia disparilis
Kilyana hendersoni
Uliodon sp.
Zorocrates fuscus
Titiotus sp.
Tengella sp.
Tengella radiata
Fecenia
Fecenia protensa GH2060
Fecenia sp.
Psechrus sp. Pulau
Psechrus cebu
Psechrus sp. PS9
Psechrus senoculatus
Psechrus clavis
Misumenoides sp.
Australomisidia ergandros
Xysticus bimaculatus
Amyciaea sp. MR389
Tmarus piger
Tmarus sp.
Lehtinelagia evanida
Xysticus sp.
Misumenoides formosipes
Senoculidae sp. GH2067
Senoculus cf. tricolor
Hamataliwa sp.
Oxyopes heterophthalmus
Oxyopes sp.
Oxyopes birmanicus
Oxyopes lineatipes
Nilus esimoni
Pisaurina mira
Pisaura lama
Pisaura mirabilis
Sphedanus cf. banna
Dolomedes angustivirgatus
Dolomedes sp.
Dolomedes fimbriatus
Dolomedes aquaticus
Architis capricorna
Architis brasiliensis
Thaumasia hirsutochela
Thaumasia velox
Thaumasia heterogyna
Cupiennius salei 2
Cupiennius salei
Cupiennius cf. granadensis
Cupiennius bimaculatus GH2059
Neoctenus comosus
Neoctenus sp GH2056
Barrisca nannella
Paradossenus longipes
Paratrechalea ornata
Trechalea bucculenta
Trechalea sp GH2057
Sosippus placidus
Aglaoctenus lagotis
Allocosa brasiliensis
Schizocosa malitiosa
Alopecosa kochi
Rabidosa rabida
Pardosa pseudoannulata
Draposa tenasserimensis
Pardosa prativaga
Pardosa astrigera
Pardosa albomaculata
Asthenoctenus borelli
Acanthoctenus sp. SCC-2010
Celaetycheus abara
Acanthoctenus cf. spinipes GH8005
Acanthoctenus sp. DP-2014
Chococtenus sp. nov GH2795
Chococtenus miserabilis GH2796
Chococtenus sufflucus GH2795
Chococtenus otongschi GH2798
Enoploctenus sp GH8001
Enoploctenus sp GH2799
Enoploctenus sp GH2800
Enoploctenus sp GH8002
Enoploctenus sp GH8003
Phymatoctenus sp GH8004
Enoploctenus cyclothorax
Calloctenus sp.nov GH8006
Calloctenus oxapampa
Ancylometes bogotensis
Ancylometes amazonicus GH2055
Ancylometes bogotensis GH2053
Calloctenus albertoi GH8007
Calloctenus aculeatus GH8008
Calloctenus aff aculeatus GH8008
Gephyroctenus sp GH2010
Gephyroctenus sp GH2065
Petalocteninae cupido
Pericteninae molecula
Nimbanahita montivaga
Pilocteninae pilosus
Pilocteninae haematostoma
Pilocteninae mirificus
Afroneutria inmortalis
Africactenus evadens
Amicactenus mysticus
Amicactenus eminens
Amicactenus fallax
Amicactenus pergulanus
Macroctenus nimba
Pilocteninae haemaetosoma
Macroctenus herbicola
Macroctenus occidentalis
Acantheis sp GH2061
Anahita sp
Anahita aculeata
Ctenus sp. CG78
Anahita fauna
Guasuctenus longipes
Isoctenus sp
Ctenus sp. CG55-CG57
Ctenus captivosus GH2019
Ctenus hibernalis GH2018
Leptoctenus gertschi GH2016
Leptoctenus byrrhus
Leptoctenus sp GH2017
New genus GH2020
New genus 102 GH2021
New genus GH2022
New genus GH2023
Cteninae sp GH2029
Kiekie barrocolorado GH2033
Kiekie verbena GH2034
Kiekie montanensis GH2037
Kiekie curvipes GH2035
Kiekie sinautipes GH2033
Kiekie sarapiqui GH2031
Kiekie panamensis GH2030
Kiekie griswoldi GH2032
Leptoctenus sp GH2012
Leptoctenus sp GH2013
Parabatinga brevipes GH2014
Centroctenus ocelliventer GH2015
Centroctenus claudia GH2039
Spinoctenus eberhardi GH2025
Spinoctenus stephaniae GH2024
Spinoctenus yotoco GH2027
Spinoctenus tequendama GH2062
Ctenus nigrolineatus GH2026
Spinoctenus escalerete GH2777
Spinoctenus sp nov GH2028
Ctenus crulsi group
Ctenus crulsi
Ctenus GH2048 Vaupes
Ctenus cf amphora GH2779
Ctenus amphora GH2047
Ctenus cf dubius GH2049
Ctenus sp. GH2050
Ctenus nigritus GH2778
Ctenus sp GH2051 Madrededios
Ctenus sp GH2058
Ctenus sp GH2052 Tena
Ctenus villasboasi GH2046
Ctenus masulisternis GH2038
Centroctenus sp.nov GH2041
Centroctenus iquitos GH2040
Centroctenus varzea GH2042
Centroctenus sp GH2043
Centroctenus aluhini GH2045
Ctenus inaja GH2044
New genus lostunos GH2063
New genus Guaviare GH2064
New genus Tolima GH2066
Phoneutria fera
Phoneutria bolivisensis GH2780
Phoneutria depilata GH2788
Phoneutria depilata GH2787

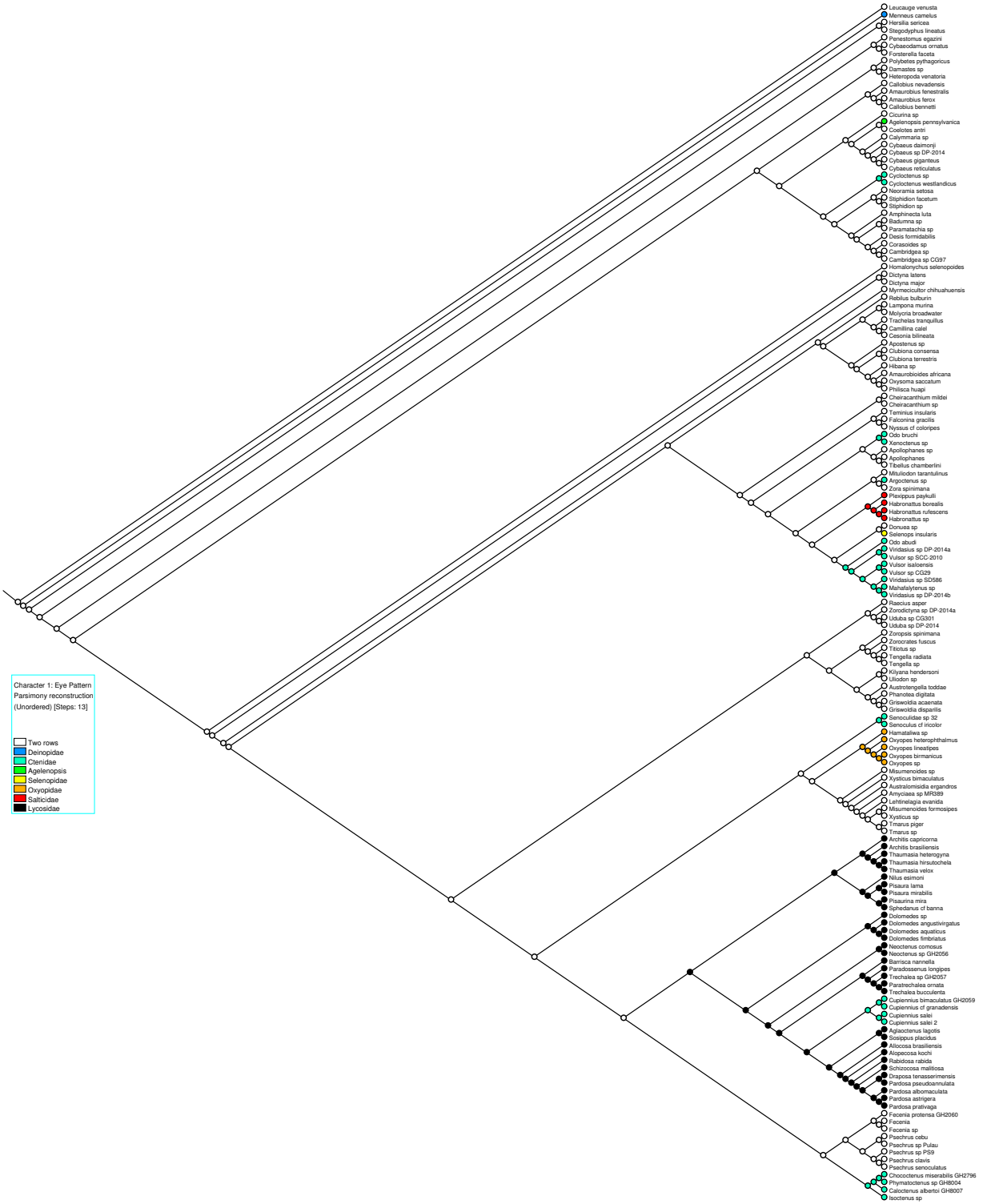

Leucauge venusta
Hasarius adansoni
Menneus camelus
Stegodyphus lineatus
Cesonia bilineata
Homalonychus selenopoides
Myrmecicultor chihuahuaensis
Coelotes antri
Agelenopsis pennsylvanica
Polybetes pythagonicus
Damastes sp.
Heliompoda venatoria
Penestomus egazinii
Cytaeodamus ornatus
Fronterrella faceta
Cicurina sp.
Dictyna major
Dictyna latens
Callobius nevadensis
Amaurobius fenestralis
Amaurobius ferox
Callobius bennetti
Desis formidabilis
Corasoides sp.
Cambridgea sp. CG97
Cambridgea sp.
Calymmaria sp.
Cytaeus sp. DP-2014
Cytaeus gigantieus
Cytaeus reticulatus
Cytaeus daimonji
Neoramia setosa
Stiphidion sp.
Stiphidion facetum
Cyclocteinus westlandicus
Cyclocteinus sp.
Amphinecta lutia
Badumna sp.
Paramaclachia sp.
Rabilus bulburin
Apoticnus sp.
Hibana sp.
Amaurobioides africana
Philisca huapi
Oxysoma saccatum
Clubiona consensa
Clubiona terrestris
Camillina calel
Trachelas tranquillus
Molycria broadwater
Lampona murina
Vulsor sp. SCC-2010
Mahafalylsinus sp.
Selenops insularis
Viridasius sp. DP-2014a
Odo abadi
Doruea sp.
Xenoctenus sp.
Odo bruchi
Teminius insularis
Cheiracanthium sp.
Cheiracanthium mildei
Pisaippus paykulli
Habronattus borealis
Habronattus sp.
Habronattus rufescens
Mituliodon tarantulinus
Nyssus cf. coloripes
Zora spinimana
Argoctenus sp.
Vulsor sp. CG29
Vulsor isalkensis
Viridasius sp. SD586
Viridasius sp. DP-2014b
Falconina gracilis
Apollophanes Concatenation of 9 sequences
Tibellus chamberlini
Apollophanes sp.
Zoroctenus fuscus
Tibitus sp.
Tengella sp.
Tengella radiata
Zoropsis spinimana
Raecius aspet
Zorodictyna sp. DP-2014a
Uduba sp. DP-2014
Uduba sp. CG301
Phanotea digitata
Griswoldia acanrata
Griswoldia disparitis
Austrotengella toddae
Kilyana hendersoni
Ulliodon sp.
Misumenoides sp.
Australomisidia ergandros
Xysticus bimaculatus
Amyciaea sp. MR389
Lehtinelagia evanida
Xysticus sp.
Misumenoides formosipes
Tmarus piger
Tmarus sp.
Fecenia Concatenation of 9 sequences
Fecenia protensa GH2060
Fecenia sp.
Psechrus sp. Pulau
Psechrus cebu
Psechrus sp. PS9
Psechrus senoculatus
Psechrus clavis
Senoculidae sp GH2067
Senoculus cf. inicolor
Hamataliwa sp.
Oxyopes heterophthalmus
Oxyopes sp.
Oxyopes birmanicus
Oxyopes lineatipes
Nilus esimoni
Pisaurina mira
Pisaura lama
Pisaura mirabilis
Sphedanus cf. lianna
Dolomedes angustivirgatus
Dolomedes sp.
Dolomedes fimbriatus
Dolomedes aquaticus
Archilis brasiliensis
Archilis capricorna
Thaumasia velox
Thaumasia heterogyna
Thaumasia hirsutochela
Cupiennius salei 2
Cupiennius salei
Cupiennius cf. granadensis
Cupiennius bimaculatus GH2059
Neoctenus comosus
Neoctenus sp GH2056
Barrisca nannella
Paradossenus longipes
Parathrechalea ornata
Trechalea bucculenta
Trechalea sp GH2057
Allocosa brasiliensis
Sosippus placidus
Aglaoctenus lagotis
Schizocosa malitiosa
Aleipecosa kochi
Rabidosa rabida
Pardosa pseudoannulata
Draposa tenasserimensis
Pardosa albomaculata
Pardosa prativaga
Pardosa astrigera
Asthenoctenus borelli
Acanthoctenus sp. DP-2014
Acanthoctenus sp GH8005
Acanthoctenus sp. SCC-2010
Celaetycheus abara
Chococtenus sp. nov. GH2795
Chococtenus mineralbills GH2796
Chococtenus suffuscus GH2797
Chococtenus olongachi GH2798
Enoploctenus sp GH8001
Enoploctenus sp GH2799
Enoploctenus sp GH28003
Phymatoctenus sp GH8004
Enoploctenus sp GH2800
Enoploctenus sp GH8002
Enoploctenus cyclothorax
Calloctenus sp.nov GH8006
Calloctenus oxapampa
Ancylometes bogotensis
Ancylometes amazonicus GH2055
Ancylometes bogotensis GH2053
Calloctenus alberisi GH8007
Calloctenus aculeatus GH8008
Calloctenus aff aculeatus GH8008
Gephyroctenus sp GH2010
Gephyroctenus sp GH2065
Phoctenus haematostoma
Pericternus molecula
Petaloctenus cupido
Nimbanahita montivaga
Phoctenus pilosus
Phoctenus haematostoma
Phoctenus mirificus
Afronextia immortalis
Africactenus evaziens
Macroctenus nimba
Macroctenus herbicola
Macroctenus occidentalis
Amicactenus pergulanus
Amicactenus mysticus
Amicactenus eminens
Amicactenus fallax
Acantheis sp GH2061
Anahita fauna
Anahita sp
Anahita aculeata
Ctenus sp. CG78
Guasuctenus longipes
Isoctenus sp.
Centroctenus claudia GH2039
Centroctenus alluhini GH2045
Ctenus inaja GH2044
Ctenus calcaratus GH2012
Ctenus calcaratus GH2013
Parabatinga brevipes GH2014
Centroctenus ocellilventer GH2015
Ctenus sp. CG55-CG57
Ctenus captiosus GH2019
Ctenus hibernalis GH2018
Leptoctenus byrrhus
Leptoctenus gertschi GH2016
Leptoctenus sp GH2017
Ctenus villasboasi GH2046
Ctenus masulistemis GH2038
Centroctenus sp.nov GH2041
Centroctenus iquitos GH2040
Centroctenus varzae GH2042
Centroctenus sp GH2043
New genus 109 Iostunos GH2063
New genus 130 Guaviare GH2064
New genus 101 Tolima GH2066
Phoneutria fera
Phoneutria bolivinesis GH2788
Phoneutria depilata GH2787
Phoneutria depilata 10
Spinoctenus stephaniae GH2024
Spinoctenus eberhardi GH2025
Ctenus nigrolineatus GH2026
Spinoctenus yotoco GH2027
Spinoctenus tequendama 117
Spinoctenus escalerete GH2777
Spinoctenus sp nov GH2028
Ctenus crulsi group
Ctenus crulsi
Ctenus GH2048 Vaupes
Ctenus cf amphora GH2779
Ctenus amphora GH2047
Ctenus cf dubius GH2049
New genus GH2050
Ctenus nigritus GH2778
Ctenus sp GH2051 Madrededios
Ctenus sp GH2058
Ctenus sp GH2052 Tona
New genus GH2020
New genus 102 GH2021
New genus GH2022
New genus GH2023
Cteninae sp GH2029
Kiekie sinaulipes GH2033
Kiekie sarapiqui GH2031
Kiekie panamensis GH2030
Kiekie griswoldi GH2032
Kiekie barrocolorado GH2033
Kiekie verbena GH2034
Kiekie montanensis GH2037
Kiekie curvipes GH2035


Leucauge_venusta
Menneus_camelus
Stegodyphus_lineatus
Hersilia_sericea
Penestomus_egazini
Cybaeodamus_ornatus
Forsterella_faceta
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Callobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Callobius_bennetti
Cicurina_sp.
Coelotes_antri
Agelenopsis_pennsylvanica
Calymmaria_sp.
Cybaeus_daimonji
Cybaeus_sp._DP-2014
Cybaeus_reticulatus
Cybaeus_giganteus
Cycloctenus_westlandicus
Cycloctenus_sp.
Neoramia_setosa
Stiphidion_sp.
Stiphidion_facetum
Amphinecta_luta
Badumna_sp.
Paramatachia_sp.
Desis_formidabilis
Dictyna_latens
Corasoides_sp.
Cambridgea_sp._CG97
Cambridgea_sp.
Homalonychus_selenopoides
Dictyna_major
Myrmeciultor_chihuahuensis
Rebilus_bulburin
Clubiona_consensa
Clubiona_terrestris
Apostenus_sp.
Hibana_sp.
Amaurobioides_africana
Phalisca_huapi
Oxysoma_saccatum
Trachelas_tranquillus
Camillina_calel
Cesonia_bilineata
Molycria_broadwater
Lampona_murina
Cheiracanthium_sp.
Cheiracanthium_mildei
Teminius_insularis
Nyssus_cf._coloripes
Falconina_gracilis
Xenoctenus_sp.
Odo_bruchi
Apollophanes_sp.
Tibellus_chamberlini
Apollophanes
Mituliodon_tarantulinus
Zora_spinimana
Argoctenus_sp.
Plexippus_paykulli
Habronattus_borealis
Habronattus_sp.
Habronattus_rufescens
Selenops_insularis
Donuea_sp.
Odo_abudi
Vulsor_sp._SCC-2010
Viridasius_sp._DP-2014a
Vulsor_sp._CG29
Vulsor_isaloensis
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Raecius_asper
Zorodictyna_sp._DP-2014a
Uduba_sp._DP-2014
Uduba_sp._CG301
Zoropsis_spinimana
Zorocrates_fuscus
Titiotus_sp.
Tengella_sp.
Tengella_radiata
Kilyana_hendersoni
Uliodon_sp.
Austrotengella_toddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Senoculidae_sp_GH2067
Senoculus_cf._iricolor
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Misumenoides_sp.
Xysticus_bimaculatus
Australomisidia_ergandros
Amyciaea_sp._MR389
Lehtinelagia_evanida
Tmarus_piger
Tmarus_sp.
Xysticus_sp.
Misumenoides_formosipes
Archilis_capricorna
Archilis_brasiliensis
Thaumasia_heterogyna
Thaumasia_velox
Thaumasia_hirsutochela
Nilus_esimoni
Pisaura_mirabilis
Pisaura_lama
Pisaurina_mira
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_fimbriatus
Dolomedes_aquaticus
Barrisca_nannella
Neoctenus_comosus
Neoctenus_sp_GH2056
Paradossenus_longipes
Trechalea_sp_GH2057
Trechalea_bucculenta
Paratrechalea_ornata
Cupiennius_salei_2
Cupiennius_salei
Cupiennius_cf._granadensis
Cupiennius_bimaculatus_GH2059
Sosippus_placidus
Aglaoctenus_lagotis
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_malitiosa
Pardosa_pseudoannulata
Draposa_tenasserimensis
Pardosa_albomaculata
Pardosa_prativaga
Pardosa_astrigera
Fecenia_protensa_GH2060
Fecenia_sp.
Psechrus_sp._Pulau
Psechrus_cebu
Psechrus_sp._PS9
Psechrus_senoculatus
Psechrus_clavis
Enoploctenus_cyclothorax
Chococtenus_sp.nov_GH2795
Chococtenus_miserabilis_GH2796
Chococtenus_suffuscus_GH2795
Chococtenus_otongachi_GH2798
Enoploctenus_sp_GH2799
Enoploctenus_sp_GH8001
Enoploctenus_sp_GH2800
Enoploctenus_sp_GH8002
Enoploctenus_sp_GH8003
Phymatoctenus_cf._sassi_GH8004
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp_GH8005
Acanthoctenus_sp._DP-2014
Asthenoctenus_borelli
Caloctenus_albertoi_GH8007
Caloctenus_sp.nov_GH8006
Caloctenus_oxapampa
Caloctenus_aculeatus_GH8008
Caloctenus_aff_aculeatus_GH8008
Gephyroctenus_sp_GH2010
Gephyroctenus_sp_GH2065
Petaloctenus_cupido
Pericticnus_molecula
Nimbanahita_montivaga
Piloctenus_haematostoma
Piloctenus_pilosus
Piloctenus_mirificus
Afroneutria_inmortalis
Africactenus_evadens
Macroctenus_nimba
Piloctenus_haemastosoma
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_pergulanus
Amicactenus_eminens
Amicactenus_mysticus
Amicactenus_fallax
Acantheis_sp._GH2061
Ctenus_sp._CG78
Anahita_fauna
Anahita_sp
Anahita_aculeata
Guasuctenus_longipes
Isoctenus_sp
New_genus_102_GH2021
New_genus_GH2020
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_captiosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp_GH2017
Cteninae_sp_GH2029
Kiekie_verbena_GH2034
Kiekie_barrocolorado_GH2033
Kiekie_montanensis_GH2037
Kiekie_curvipes_GH2035
Kiekie_sinautipes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_panamensis_GH2030
Kiekie_griswoldi_GH2032
Ctenus_calcaratus_GH2012
Ctenus_calcaratus_GH2013
Parabatinga_brevipes_GH2014
Centroctenus_ocelliventer_GH2015
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_yotoco_GH2027
Spinoctenus_tequendama_GH2062
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Ctenus_masulistemis_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_varzea_GH2042
Centroctenus_sp_GH2043
Ctenus_villasboasi_GH2046
Ctenus_inaja_GH2044
Centroctenus_claudia_GH2039
Centroctenus_alinahui_GH2045
New_genus_109_lostunos
New_genus_130_Guaviare
New_genus_101_Tolima
Phoneutria_fera
Phoneutria_boliviensis_GH2780
Phoneutria_depilata_GH2788
Phoneutria_depilata_GH2787
Ctenus_cf_amphora_GH2779
Ctenus_amphora_GH2047
Ctenus_GH2048_Vaupes
Ctenus_crulsi_group
Ctenus_crulsi
Ctenus_cf_dubius_GH2049
New_genus_GH2050
Ctenus_nigritus_GH2778
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2058
Ctenus_sp_GH2052_Tena
0.2


Leucauge_venusta
Menneus_camelus
Hersilia_sericea
Steppdyphus_lineatus
Penestomus_egazini
Cybaeodamus_ornatus
Forsterella_faceta
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Callobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Callobius_bennetti
Cicurina_sp.
Agelenopsis_pennsylvanica
Coelotes_antri
Calymmaria_sp.
Cybaeus_daimonji
Cybaeus_sp._DP-2014
Cybaeus_giganteus
Cybaeus_reticulatus
Cyclosternus_sp.
Cyclosternus_westlandicus
Neoramia_setosa
Sliphidion_facetum
Sliphidion_sp.
Amphinecta_luta
Badumna_sp.
Paramatachia_sp.
Desis_formidabilis
Corasoides_sp.
Cambridgea_sp.
Cambridgea_sp._CG97
Homalonychus_selenopoides
Dictyna_latens
Dictyna_major
Myrmecicultor_chihuahuensis
Rebilus_bulburin
Lampona_murina
Molycria_broadwater
Trachelas_tranquillus
Camillina_calel
Cesonia_bilineata
Apostenus_sp.
Clubiona_consensa
Clubiona_terrestris
Hibana_sp.
Amaurobioides_africana
Oxysoma_saccatum
Phillsca_huapi
Cheiracanthium_mildei
Cheiracanthium_sp.
Teminius_insularis
Falconina_gracilis
Nyssus_cf._coloripes
Odo_bruchi
Xenoctenus_sp.
Apollophanes_sp.
Apollophanes
Tibellus_chamberlini
Mituliodon_tarantulinus
Argoctenus_sp.
Zora_spinimana
Pleroppus_paykulli
Habronattus_borealis
Habronattus_rufescens
Habronattus_sp.
Donuea_sp.
Selenops_insularis
Odo_abudi
Viridasius_sp._DP-2014a
Vulsor_sp._SCC-2010
Vulsor_isaloensis
Vulsor_sp._CG29
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Raecius_jasper
Zoroictyna_sp._DP-2014a
Uduba_sp._CG301
Uduba_sp._DP-2014
Zoropsis_spinimana
Zorocrates_fuscus
Tiliotus_sp.
Tengella_radiata
Tengella_sp.
Kilyana_hendersonii
Ulliodon_sp.
Austrotengella_toddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Senoculidae_sp_32
Senoculus_cf._iricolor
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Misumenoides_sp.
Xysticus_bimaculatus
Australomisidia_ergandros
Amyclaea_sp._MR389
Lehtinelagia_evanida
Misumenoides_formosipes
Xysticus_sp.
Tmarus_piger
Tmarus_sp.
Architis_capricorna
Architis_brasiliensis
Thaumasia_heterogyna
Thaumasia_hirsutochela
Thaumasia_velox
Nilus_esimoni
Pisaura_lama
Pisaura_mirabilis
Pisaurina_mira
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_aquaticus
Dolomedes_fimbriatus
Neoctenus_comosus
Neoctenus_sp_GH2056
Barrisca_nannella
Paradossenus_longipes
Trechalea_sp_GH2057
Paratrechalea_ornata
Trechalea_bucculenta
Cupiennius_bimaculatus_GH2059
Cupiennius_cf._granadensis
Cupiennius_salei
Cupiennius_salei_2
Aglaoctenus_lagotis
Sosippus_placidus
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_malitiosa
Drapoa_tenasserimensis
Pardosa_pseudoannulata
Pardosa_albomaculata
Pardosa_astrigera
Pardosa_prativaga
Fecenia_protensa_GH2060
Fecenia
Fecenia_sp.
Psechrus_cebu
Psechrus_sp._Pulau
Psechrus_sp._PS9
Psechrus_clavis
Psechrus_senoculatus
Enoplocteneus_cyclothorax
Chococtenus_kashakara_61
Chococtenus_miserabilis_GH2796
Chococtenus_otongachi_GH2798
Chococtenus_suffuscus_GH2795
Enoplocteneus_sp_GH2799
Enoplocteneus_sp_GH8001
Enoplocteneus_sp_57
Phymatoctenus_sp_GH8004
Enoplocteneus_sp_97
Enoplocteneus_sp_GH2800
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp._DP-2014
Acanthoctenus_sp_GH8005
Asthenoctenus_borelli
Caloctenus_albertoi_GH8007
Calocteneus_oxapampa
Calocteneus_sp.nov_GH8006
Calocteneus_aculeatus_GH8008
Calocteneus_aff_aculeatus_GH800
Gephyroctenus_sp_116
Gephyroctenus_sp_GH2010
Petaloctenus_cupido
Nimbanahita_montivaga
Pericteneus_molecula
Pilocteneus_haematostoma
Pilocteneus_mirificus
Pilocteneus_pilosus
Afroneutria_immortalis
Africacteneus_evadens
Pilocteneus_haematostosoma
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicacteneus_pergulanus
Amicacteneus_eminens
Amicacteneus_fallax
Amicacteneus_mysticus
Acantheis_sp_153
Ctenus_sp._CG78
Anahita_fauna
Anahita_aculeata
Anahita_sp
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2020
New_genus_102_GH2021
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_captiosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp_GH2017
Cteninae_sp_GH2029
Kiekie_verbena_GH2034
Kiekie_barrocolorado_GH2033
Kiekie_curvipes_GH2035
Kiekie_montanensis_GH2037
Kiekie_sinautipes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_griswoldi_GH2032
Kiekie_panamensis_GH2030
Centroctenus_ocelliventer_GH201
Parabatinga_brevipes_63
Leptoctenus_sp_GH2012
Leptoctenus_sp_GH2013
New_genus_109_lostunos
New_genus_101_Tolima
New_genus_130_Guaviare
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Spinoctenus_tequendama_117
Spinoctenus_yotoco_GH2027
Ctenus_masulistemis_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_sp_GH2043
Centroctenus_varzae_GH2042
Ctenus_villasboasi_GH2046
Ctenus_inaja_GH2044
Centroctenus_alluhini_GH2045
Centroctenus_claudia_GH2039
Phoneutria_boliviensis_67
Phoneutria_fera
Phoneutria_depilata_10
Phoneutria_depilata_23
Ctenus_amphora_GH2047
Ctenus_cf_amphora_GH2779
Ctenus_GH2048_Vaupes
Ctenus_crulsi
Ctenus_crulsi_group
Ctenus_cf_dubius_GH2049
Ctenus_nigritus_GH2778
New_genus_GH2050
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2052_Tena
Ctenus_sp_GH2058
20.0
-125
-100
-75
-50
-25
0


Leucauge_venusta
Menneus_camelus
Hersilia_sericea
Stegodyphus_lineatus
Penestomus_egazini
Cybaeodamus_ornatus
Forsterella_faceta
Polybetes_pythagoricus
Damastes_sp.
Heteropoda_venatoria
Callobius_nevadensis
Amaurobius_fenestralis
Amaurobius_ferox
Callobius_bennetti
Cicurina_sp.
Agelenopsis_pennsylvanica
Coelotes_antri
Calymmaria_sp.
Cybaeus_daimonji
Cybaeus_sp._DP-2014
Cybaeus_giganteus
Cybaeus_reticulatus
Cyclоctenus_sp.
Cyclоctenus_westlandicus
Neoramia_setosa
Stiphidion_facetum
Stiphidion_sp.
Amphinecta_luta
Badumna_sp.
Paramatachia_sp.
Desis_formidabilis
Corasoides_sp.
Cambridgea_sp.
Cambridgea_sp._CG97
Homalonychus_selenopoides
Dictyna_latens
Dictyna_major
Myrmecicultor_chihuahuensis
Rebilus_bulburin
Lampona_murina
Molycria_broadwater
Trachelas_tranquillus
Camillina_calel
Cesonia_bilineata
Apostenus_sp.
Clubiona_consensa
Clubiona_terrestris
Hibana_sp.
Amaurobioides_africana
Oxysoma_saccatum
Philisca_huapi
Cheiracanthium_mildei
Cheiracanthium_sp.
Teminius_insularis
Falconina_gracilis
Nyssus_cf._coloripes
Odo_bruchi
Xenoctenus_sp.
Apollophanes_sp.
Apollophanes
Tibellus_chamberlini
Mituliodon_tarantulinus
Argoctenus_sp.
Zora_spinimana
Plexippus_paykulli
Habronattus_borealis
Habronattus_rufescens
Habronattus_sp.
Donuea_sp.
Selenops_insularis
Odo_abudi
Viridasius_sp._DP-2014a
Vulsor_sp._SCC-2010
Vulsor_isaloensis
Vulsor_sp._CG29
Viridasius_sp._SD586
Mahafalytenus_sp.
Viridasius_sp._DP-2014b
Raecius_asper
Zorodictyna_sp._DP-2014a
Uduba_sp._CG301
Uduba_sp._DP-2014
Zoropsis_spinimana
Zorocrates_fuscus
Titiotus_sp.
Tengella_radiata
Tengella_sp.
Kilyana_hendersoni
Uliodon_sp.
Austrotengella_toddae
Phanotea_digitata
Griswoldia_acaenata
Griswoldia_disparilis
Senoculidae_sp_32
Senoculus_cf._iricolor
Hamataliwa_sp.
Oxyopes_heterophthalmus
Oxyopes_lineatipes
Oxyopes_birmanicus
Oxyopes_sp.
Misumenoides_sp.
Xysticus_bimaculatus
Australomisidia_ergandros
Amyciaea_sp._MR389
Lehtinelagia_evanida
Misumenoides_formosipes
Xysticus_sp.
Tmarus_piger
Tmarus_sp.
Architis_capricorna
Architis_brasiliensis
Thaumasia_heterogyna
Thaumasia_hirsutochela
Thaumasia_velox
Nilus_esimoni
Pisaura_lama
Pisaura_mirabilis
Pisaurina_mira
Sphedanus_cf._banna
Dolomedes_sp.
Dolomedes_angustivirgatus
Dolomedes_aquaticus
Dolomedes_fimbriatus
Neoctenus_comosus
Neoctenus_sp_GH2056
Barrisca_nannella
Paradossenus_longipes
Trechalea_sp_GH2057
Paratrechalea_ornata
Trechalea_bucculenta
Cupiennius_bimaculatus_GH2059
Cupiennius_cf._granadensis
Cupiennius_salei
Cupiennius_salei_2
Aglaoctenus_lagotis
Sosippus_placidus
Allocosa_brasiliensis
Alopecosa_kochi
Rabidosa_rabida
Schizocosa_malitiosa
Draposa_tenasserimensis
Pardosa_pseudoannulata
Pardosa_albomaculata
Pardosa_astrigera
Pardosa_prativaga
Fecenia_protensa_GH2060
Fecenia
Fecenia_sp.
Psechrus_cebu
Psechrus_sp._Pulau
Psechrus_sp._PS9
Psechrus_clavis
Psechrus_senoculatus
Enoploctenus_cyclothorax
Chococtenus_kashakara_61
Chococtenus_miserabilis_GH2796
Chococtenus_otongachi_GH2798
Chococtenus_suffuscus_GH2795
Enoploctenus_sp_GH2799
Enoploctenus_sp_GH8001
Enoploctenus_sp_57
Phymatoctenus_sp_GH8004
Enoploctenus_sp_97
Enoploctenus_sp_GH2800
Celaetycheus_abara
Acanthoctenus_sp._SCC-2010
Acanthoctenus_sp._DP-2014
Acanthoctenus_sp_GH8005
Asthenoctenus_borelli
Caloctenus_albertoi_GH8007
Caloctenus_oxapampa
Caloctenus_sp.nov_GH8006
Caloctenus_aculeatus_GH8008
Caloctenus_aff_aculeatus_GH8008
Gephyroctenus_sp_116
Gephyroctenus_sp_GH2010
Petaloctenus_cupido
Nimbanahita_montivaga
Pericteneus_molecula
Piloctenus_haematostoma
Piloctenus_mirificus
Piloctenus_pilosus
Afroneutria_inmortalis
Africactenus_evadens
Piloctenus_haemastosoma
Macroctenus_nimba
Macroctenus_herbicola
Macroctenus_occidentalis
Amicactenus_pergulanus
Amicactenus_eminens
Amicactenus_fallax
Amicactenus_mysticus
Acantheis_sp_153
Ctenus_sp._CG78
Anahita_fauna
Anahita_aculeata
Anahita_sp
Guasuctenus_longipes
Isoctenus_sp
New_genus_GH2020
New_genus_102_GH2021
New_genus_GH2022
New_genus_GH2023
Ctenus_sp._CG55-CG57
Ctenus_captiosus_GH2019
Ctenus_hibernalis_GH2018
Leptoctenus_byrrhus
Leptoctenus_gertschi_GH2016
Leptoctenus_sp_GH2017
Cteninae_sp_GH2029
Kiekie_verbena_GH2034
Kiekie_barrocolorado_GH2033
Kiekie_curvipes_GH2035
Kiekie_montanensis_GH2037
Kiekie_sinautipes_GH2033
Kiekie_sarapiqui_GH2031
Kiekie_griswoldi_GH2032
Kiekie_panamensis_GH2030
Centroctenus_ocelliventer_GH2015
Parabatinga_brevipes_63
Leptoctenus_sp_GH2012
Leptoctenus_sp_GH2013
New_genus_109_lostunos
New_genus_101_Tolima
New_genus_130_Guaviare
Spinoctenus_stephaniae_GH2024
Spinoctenus_eberhardi_GH2025
Ctenus_nigrolineatus_GH2026
Spinoctenus_escalerete_GH2777
Spinoctenus_sp_nov_GH2028
Spinoctenus_tequendama_117
Spinoctenus_yotoco_GH2027
Ctenus_masulisternis_GH2038
Centroctenus_sp.nov_GH2041
Centroctenus_iquitos_GH2040
Centroctenus_sp_GH2043
Centroctenus_varzae_GH2042
Ctenus_villasboasi_GH2046
Ctenus_inaja_GH2044
Centroctenus_alluhini_GH2045
Centroctenus_claudia_GH2039
Phoneutria_boliviensis_67
Phoneutria_fera
Phoneutria_depilata_10
Phoneutria_depilata_23
Ctenus_amphora_GH2047
Ctenus_cf_amphora_GH2779
Ctenus_GH2048_Vaupes
Ctenus_crulsi
Ctenus_crulsi_group
Ctenus_cf_dubius_GH2049
Ctenus_nigritus_GH2778
New_genus_GH2050
Ctenus_sp_GH2051_Madrededios
Ctenus_sp_GH2052_Tena
Ctenus_sp_GH2058
-140
-135
-130
-125
-120
-115
-110
-105
-100
-95
-90
-85
-80
-75
-70
-65
-60
-55
-50
-45
-40
-35
-30
-25
-20
-15
-10
-5


Rate
1.5
1.0
0.5
0.0
Fossil
Fossil_Biogeography
ITS-2
NADH
16S AND 12S
COI
H3
28S
Actin
18S


Character 1: Eye Pattern
Parsimony reconstruction
(Unordered) [Steps: 13]
Two rows
Deinopidae
Ctenidae
Agelenopsis
Selenopidae
Oxyopidae
Salticidae
Lycosidae
Leucauge venusta
Menneus camelus
Hersilia sericea
Stegodyphus lineatus
Penestomus egazini
Cybaeodamus ornatus
Forsterella faceta
Polybetes pythagoricus
Damastes sp
Heteropoda venatoria
Callobius nevadensis
Amaurobius fenestralis
Amaurobius ferox
Callobius bennetti
Cicurina sp
Agelenopsis pennsylvanica
Coelotes antri
Calymmaria sp
Cybaeus daimonji
Cybaeus sp DP-2014
Cybaeus giganteus
Cybaeus reticulatus
Cyclocteinus sp
Cyclocteinus westlandicus
Neoramia setosa
Stiphidion facetum
Stiphidion sp
Amphinecta luta
Badumna sp
Paramatachia sp
Desis formidabilis
Corascides sp
Cambridgea sp
Cambridgea sp CG97
Hematonychus selenopoides
Dictyna latens
Dictyna major
Myrmecicultor chihuahuensis
Rebilus bulburin
Lampona murina
Molycria broadwater
Trachelas tranquillus
Camillina calel
Cesonia bilineata
Apostenus sp
Clubiona consensa
Clubiona terrestris
Hibana sp
Amaurobioides africana
Oxysoma saccatum
Phillisca huapi
Cheiracanthium mildei
Cheiracanthium sp
Teminius insularis
Falconina gracilis
Nyssus cf coloripes
Odo bruchi
Xenocteinus sp
Apollophanes sp
Apollophanes
Tibellus chamberlini
Mituliodon tarantulinus
Argoctenus sp
Zora spinimana
Plexippus paykulli
Habronattus borealis
Habronattus rufescens
Habronattus sp
Donuea sp
Selenops insularis
Odo abudi
Viridasius sp DP-2014a
Vulsor sp SCC-2010
Vulsor isaloensis
Vulsor sp CG29
Viridasius sp SD586
Mahafalytenus sp
Viridasius sp DP-2014b
Raecius asper
Zorodictyna sp DP-2014a
Uduba sp CG301
Uduba sp DP-2014
Zoropsis spinimana
Zorocrates fuscus
Titiotus sp
Tengella radiata
Tengella sp
Kilyana hendersoni
Ulliodon sp
Austrotengella toddae
Phanotea digitata
Griswoldia acaenata
Griswoldia disparilis
Senoculidae sp 32
Senoculus cf inicolor
Hamataliwa sp
Oxyopes heterophthalmus
Oxyopes lineatipes
Oxyopes birmanicus
Oxyopes sp
Misumenoides sp
Xysticus bimaculatus
Australomisidia ergandros
Amyciaea sp MR389
Lehtinelagia evanida
Misumenoides formosipes
Xysticus sp
Tmarus piger
Tmarus sp
Archilis capricorna
Archilis brasiliensis
Thaumasia heterogyna
Thaumasia hirsutochela
Thaumasia velox
Nilus esimoni
Pisaura lama
Pisaura mirabilis
Pisaurina mira
Sphedanus cf banna
Dolomedes sp
Dolomedes angustivirgatus
Dolomedes aquaticus
Dolomedes fimbriatus
Neoctenus comosus
Neoctenus sp GH2056
Barrisca nannella
Paradossenus longipes
Trechalea sp GH2057
Paratrechalea ornata
Trechalea bucculenta
Cupiennius bimaculatus GH2059
Cupiennius cf granadensis
Cupiennius salei
Cupiennius salei 2
Aglaoctenus lagotis
Sosippus placidus
Allocosa brasiliensis
Alopecosa kochi
Rabidosa rabida
Schizocosa mallitiosa
Draposa tenasserimensis
Pardosa pseudoannulata
Pardosa albomaculata
Pardosa astrigera
Pardosa prativaga
Fecenia protensa GH2060
Fecenia
Fecenia sp
Psechrus cebu
Psechrus sp Pulau
Psechrus sp PS9
Psechrus clavis
Psechrus senoculatus
Chococtenus miserabilis GH2796
Phymatoctenus sp GH8004
Calocteinus albertoi GH8007
Isoctenus sp