

Phylogeny and biogeography of the pantropical whip spider family Charinidae (Arachnida: Amblypygi)

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The present contribution addresses the phylogeny and biogeography of the pantropical whip spider family Charinidae Quintero, 1986, the most species-rich in the arachnid order Amblypygi Thorell, 1883, based on morphology and multilocus DNA sequences, analysed simultaneously using parsimony, maximum likelihood and Bayesian inference. The morphological matrix comprises 138 characters, scored for four outgroup taxa and 103 ingroup terminals representing all genera and 64% of the species of Charinidae. The multilocus dataset comprises sequences from two nuclear and three mitochondrial gene loci for four outgroup taxa and 48 ingroup representing 30 (23%) taxa of Charinidae. Charinidae are monophyletic, with *Weygoldtia* Miranda *et al.*, 2018 sister to a monophyletic group comprising *Charinus* Simon, 1892 and *Sarax* Simon, 1892, neither of which are reciprocally monophyletic. Charinidae diverged from other amblypygid families in the Late Carboniferous, c. 318 Mya, on the supercontinent Pangaea. *Weygoldtia* diverged from the common ancestor of *Charinus* and *Sarax* during the Late Permian, c. 257 Mya, when changes in climate reduced tropical forests. The divergence of *Charinus* and *Sarax* coincides with the fragmentation of Pangaea, c. 216 Mya. *Sarax* colonized South-East Asia via Australia. The charinid fauna of New Caledonia originated before the Oligocene, when the island separated from Australia, c. 80 Mya.

ADDITIONAL KEYWORDS: phylogenetic systematics – morphological systematics – biogeography – molecular phylogeny – zoological nomenclature.

INTRODUCTION

Whip spiders, order Amblypygi Thorell, 1883, are exquisite arachnids with a dorsoventrally compressed body, robust, spinose pedipalps and a long whip-like first pair of antenniform legs (Weygoldt, 2000). All known species are nocturnal predators that vary in size from relatively small (c. 1 cm in total body length) to large (c. 5 cm). The order comprises five families of which the pantropical Charinidae Quintero, 1986, with 129 described species (Fig. 1), is the most speciose and has the broadest geographical distribution, inhabiting

the intertropical zone on all continents (Fig. 2; Miranda *et al.*, 2018a). A Gondwanan distribution pattern was previously suggested for Charinidae, according to which the early lineages diverged prior to the breakup of the supercontinent, during the Cretaceous (Weygoldt, 2000). However, neither the phylogeny of the family nor the processes of divergence and diversification that lead to its current disjunct distribution have ever been investigated.

The family Charinidae was first created as part of a revised classification of Pulvillata Quintero, 1986, a paraphyletic suborder of Amblypygi comprising eight genera with pulvilli (or arolia), soft, cushion-like lobes or pads between the claws of the telotarsi

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Figure 1. Selected Brazilian species of the whip spider genus *Charinus* Simon, 1892, habitus in life. A, *Charinus ricardoi* Giupponi & Miranda, 2016, Amazonas. B, *Charinus jibaossu* Vasconcelos, Giupponi & Ferreira, 2014, Minas Gerais. C, *Charinus vulgaris* Miranda & Giupponi, 2011, Rondônia. D, *Charinus potiguar* Vasconcelos et al., 2013, Rio Grande do Norte. E, *Charinus magalhaesi* Miranda et al., 2021, Amazonas. F, *Charinus cearensis* Miranda et al., 2021, Ceará. G, *Charinus eleonorae* Baptista & Giupponi, 2003, Minas Gerais. H, *Charinus asturius* Pinto-da-Rocha, Machado & Weygoldt, 2002, São Paulo. Photos by L. Sousa de Carvalho (A, F), R. Ferreira (B, D, G, H) and A.P.L. Giupponi (C, E).

with an adhesive function (Quintero, 1986; Weygoldt, 1996; Wolff *et al.*, 2015a, b). Quintero (1986) assigned *Catageus* Thorell, 1899, *Charinides* Gravely, 1911, *Charinus* Simon, 1892, *Phrynichosarax* Gravely, 1915, *Sarax* Simon, 1892 and *Tricharinus* Quintero, 1986 to Charinidae, and *Charon* Karsch, 1879 and *Stygophrynus* Kraepelin, 1895 to Charontidae Simon, 1892. Quintero's (1986) classification was based on a manual (pre-computer) phylogenetic analysis of 17 characters, polarized a priori as synapomorphic or plesiomorphic, and scored for supraspecific terminals representing genera, the monophyly of which was assumed (three of these genera were subsequently synonymized). Despite these limitations, most of Quintero's (1986) characters remain informative for phylogenetic analysis and classification to this day.

A subsequent phylogenetic analysis of all genera of Amblypygi by Weygoldt (1996), based on 29 morphological characters, upheld Charinidae and its component genera, but rejected the sister-group relationship with Charontidae. Whereas Charinidae remained within Euamblypygi Weygoldt, 1996 and sister to Neoamblypygi Weygoldt, 1996, Charontidae was placed sister to all other families, within Neoamblypygi. As with Quintero (1986), a manual cladistic analysis was presented by Weygoldt (1996), in which each character was polarized a priori and scored for supraspecific terminals representing genera, the monophyly of which was assumed. Weygoldt (1996) also tested the result using the parsimony program, Hennig86 (Farris, 1989). Despite its limitations, Weygoldt's (1996) phylogenetic hypothesis was influential and the characters were incorporated and built upon by subsequent authors investigating

the phylogeny and systematics of extant and fossil Amblypygi at various taxonomic levels (Prendini *et al.*, 2005; Garwood *et al.*, 2017; Miranda *et al.*, 2018b). Miranda *et al.* (2018b) further refined the characters previously used by Quintero (1986) and Weygoldt (1996), and added many new ones.

Whereas the monophyly and generic content of Charinidae have been tested over the course of several morphological phylogenetic analyses, its component genera have not received similar scrutiny. Previous authors initially separated the charinid genera according to the presence or absence of ventral sacs on the opisthosoma. Species with ventral sacs were placed in *Catageus*, *Phrynichosarax* or *Sarax*, whereas species without ventral sacs were placed in *Charinides*, *Charinus* or *Tricharinus*. Subsequently, the species of *Phrynichosarax* were transferred to *Sarax*, one species of *Sarax* was transferred to the recently described genus *Weygoldtia* Miranda *et al.*, 2018 and *Catageus*, demonstrated to be a senior synonym of *Stygophrynus*, was transferred to Charontidae (Harvey, 2003; Miranda *et al.*, 2018a). Consequently, only two genera, *Sarax* and *Weygoldtia*, presently accommodate species with ventral sacs in Charinidae.

Charinides, *Charinus* and *Tricharinus* were originally separated according to the number of articles on the basitibia of leg IV: species with three articles were accommodated in *Charinides*, species with four in *Charinus*, and species with two in *Tricharinus* (Gravely, 1911, 1915). Delle Cave (1986) considered this classification inconsistent. Weygoldt (2000) demonstrated that the number of articles decreases when the legs are regenerated. *Charinides* and *Tricharinus* were ultimately synonymized with

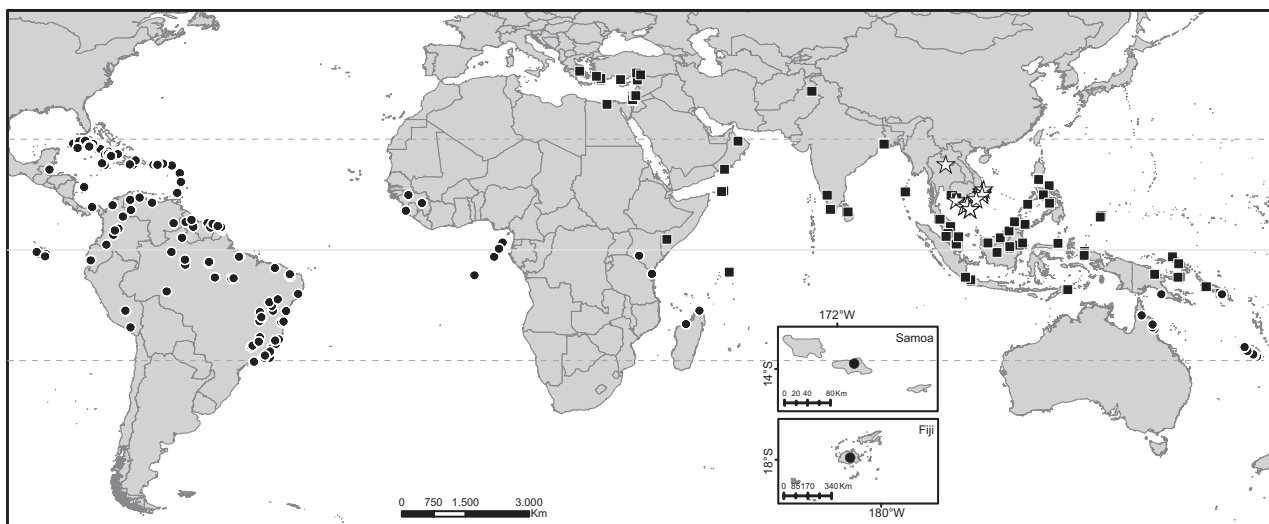


Figure 2. Distributions of the three whip spider genera of Charinidae Quintero, 1986: *Charinus* Simon, 1892 (circles); *Sarax* Simon, 1872 (squares); *Weygoldtia* Miranda *et al.*, 2018 (stars).

Charinus (Delle Cave, 1986; Weygoldt, 2000), regardless of the number of articles on basitibia IV.

In an attempt to better classify the species of *Charinus*, Weygoldt (2005) proposed three species groups based on the morphology of the female genitalia, a system followed until recently, although not tested phylogenetically. Species with a cushion-like surface on the gonopods were assigned to the *australianus* group; species with a finger-like gonopod, to the *bengalensis* group; and species with a sucker-like female gonopod, to the *brasiliensis* group.

Many new species of Charinidae have been described in recent years (e.g. Armas *et al.*, 2016; Giupponi & Miranda, 2016; Miranda *et al.*, 2016a, b, c, 2018a; Teruel, 2016; Vasconcelos & Ferreira, 2016, 2017; Vasconcelos *et al.*, 2016; Harms, 2018; Seiter *et al.*, 2018). These species are currently accommodated in three genera: *Weygoldtia* with two species restricted to Cambodia, Laos and Vietnam, *Sarax* Simon, 1872 with 36 species distributed from East Africa and the Arabian Peninsula to South-East Asia, and *Charinus* with 94 species widespread in the Americas, Africa and Oceania (Miranda *et al.*, 2021). However, the internal classification has remained uncertain, as neither the monophyly of the genera or species groups of *Charinus*, nor the phylogenetic relationships among them have ever been tested in a quantitative phylogenetic analysis. The timing and processes that resulted in the current distribution of taxa in the family have likewise never been investigated.

The present contribution addresses the phylogeny and biogeography of Charinidae for the first time, based on comprehensive datasets of morphological characters and multilocus DNA sequences, analysed simultaneously using Bayesian inference (BI), maximum likelihood (ML) and parsimony. A dated molecular phylogeny provides insight into the divergence and diversification of the family in the context of major geological and climatic events in Earth history. Weygoldt's (2006) hypothesis of a Gondwana origin of Charinidae is tested, and new evidence provided for the presence of relictual lineages of Charinidae in New Caledonia.

MATERIAL AND METHODS

TAXON SAMPLING

The matrix included four outgroup taxa, a schizomid, thelyphonid and exemplar species of two amblypygid genera representing Phrynidae Blanchard, 1852 and Phrynichidae Simon, 1872 (Table 1; Appendix 1; Supporting Information, Appendix S1). The taxonomy of Charinidae follows Miranda *et al.* (2021).

The ingroup comprised 92 (71%) species of Charinidae (in addition to four undescribed morphospecies), i.e. 65 (70%) species of *Charinus*, 25 (69%) species of *Sarax* and both species of *Weygoldtia*, and covered almost the entire geographical distribution of the family, including all continents on which charinids occur. Up to six conspecific terminals (individuals) represented each ingroup species, when available. Morphological data were replicated for conspecific terminals in order to minimize ambiguous optimizations due to missing entries (Grant *et al.*, 2006).

Ten ingroup taxa in the morphological matrix were ultimately omitted from the analyses due to the large number of missing entries caused by missing parts of specimens, the absence of one sex and/or an abundance of troglomorphic characters: *Charinus brescoviti* Giupponi & Miranda, 2016; *C. carajas* Giupponi & Miranda, 2016; *C. fagei* Weygoldt, 1972; *C. loko* Miranda *et al.*, 2021, *C. longipes* Weygoldt, 2006; *C. madagascariensis* Fage, 1954; *C. milloti* Fage, 1939; *C. orientalis* Giupponi & Miranda, 2016; *C. susuwa* Miranda *et al.*, 2021, *C. troglolobius* Baptista & Giupponi, 2002. The final morphological matrix comprises 82 ingroup species represented by 103 terminal taxa (Table 1).

A simultaneous analysis with the morphological matrix pruned to contain only the taxa represented by molecular and morphological data was also constructed and comprised the same outgroups and 30 ingroup taxa (15 species of *Charinus*, 13 species of *Sarax* and both species of *Weygoldtia*) represented by 48 terminal taxa (Table 1; Fig. S1).

Table 1. Counts and percentages of described species, undescribed morphospecies and terminal taxa per genus included in matrices used for simultaneous phylogenetic analysis of the whip spider family Charinidae Quintero, 1986. First count gives initial sample, second count after omitting ten ingroup taxa from the morphological matrix, and third count after pruning to contain only the taxa represented by molecular and morphological data

	Total species	Species %	Morphospecies	Terminal taxa
Outgroup	4/4/4			4/4/4
Ingroup	92/82/30	71/64/23	4/4/4	113/103/48
<i>Charinus</i>	65/55/15	70/59/16	1/1/1	71/61/21
<i>Sarax</i>	25/25/13	69/69/36	3/3/3	39/39/24
<i>Weygoldtia</i>	2/2/2	100/100/100		3/3/3

TISSUE SAMPLES AND MATERIAL EXAMINED

Field-collected specimens were preserved in 95% ethanol at ambient temperature and subsequently frozen at -20°C . Tissue samples used for DNA extraction are stored in the Ambrose Monell Collection for Molecular and Microbial Research at the American Museum of Natural History, New York (AMNH). Voucher specimens are deposited in the collections of the AMNH, the Coleção de História Natural da Universidade Federal do Piauí, Floriano, Brazil (CNHUFPI), the Hebrew University of Jerusalem, Israel (HUJ), the Museum of Comparative Zoology, Cambridge, USA (MCZ), the Museu Nacional, Rio de Janeiro, Brazil (MNRJ), and the Zoological Museum, University of Copenhagen, Denmark (ZMUC). Tissue samples, vouchers and material examined for scoring the morphological matrix are listed in the [Supporting Information, Appendix S1](#).

MORPHOLOGICAL DATA

A morphological data matrix comprising 138 characters ([Appendices 1 and 2](#); [Figs 7–14, 18–21](#)), scored for 92 ingroup taxa represented by 113 terminals (*Charinus* sp., a morphospecies from Grenada, is a juvenile and was not coded in the matrix) and four outgroup taxa, was prepared in MESQUITE v.3.2 (Maddison & [Maddison, 2017](#)) by direct examination of specimens. The matrix is deposited in Morphobank, project number 3538. Twenty-nine characters from [Weygoldt \(1996\)](#) were included unmodified or redefined when necessary. Characters from [Quintero \(1986\)](#) were also incorporated, as well as additions and modifications of characters published by [Garwood *et al.* \(2017\)](#) and [Miranda *et al.* \(2018b\)](#).

The logical character structure proposed by [Sereño \(2007\)](#) was followed in developing characters with care taken to observe logical and biological independence of characters ([Wilkinson, 1995](#)). No a priori assumptions were made concerning character transformation; 46 multistate characters were treated as unordered/non-additive ([Fitch, 1971](#)). Character-state reconstruction was performed on the preferred tree (below; [Figs 3 and 6](#)) using parsimony in MESQUITE.

Morphological terminology follows [Harvey & West \(1998\)](#), [Weygoldt \(2000\)](#) and [Giupponi & Kury \(2013\)](#). Most homology hypotheses for characters shared by Amblypygi and Uropygi Thorell, 1883 (the monophyletic group comprising Schizomida Petrunkevitch, 1945 and Thelyphonida Latreille, 1804) follow [Shultz \(2007\)](#). Due to the marked differences between the three orders, 80 characters were inapplicable to the schizomid, *Stenochrus sbordonii* (Brignoli, 1973) and 57 to the thelyphonid, *Mastigoproctus* aff. *giganteus*.

MICROSCOPY, IMAGING AND MAPPING

Morphological characters were observed and scored with a Leica M205AC stereomicroscope. Digital images were prepared with a BK plus Imaging System from Visionary Digital (Palmyra, PA, USA; <http://www.visionarydigital.com>) equipped with a Canon 7D digital camera at the ZMUC. Image stacks were combined using Zerene Stacker (Zerene Systems LLC; <http://zerenesystems.com/cms/stacker>) and processed in Photoshop CS6 (Adobe, San Jose, CA, USA) to adjust for colour, brightness and contrast. Plates were prepared with Adobe InDesign.

Specimens for scanning electron microscopy were dehydrated in a series of ethanol concentrations from 75% to 100% with 10% differences between consecutive concentrations for 20–30 min each and stored overnight in 100% ethanol. Specimens were subsequently cleaned ultrasonically for 30 s using a Branson 200 sonicator (Danbury, CT, USA). Parts to be mounted were then critical point dried using a Baltec CPD-030 critical point drier (Balzers, Liechtenstein) and attached to round-headed rivets using aluminium tape with conductive adhesive and coated with platinum-palladium in a JEOL JFC-2300HR high-resolution coater (Tokyo, Japan). Scanning electron micrographs were taken with JEOL JSM-6335F and JEOL JSM-6390LV scanning electron microscopes at the ZMUC and the Fundação Oswaldo Cruz, Rio de Janeiro, Brazil, respectively.

Distribution maps were created with ArcMap v.10.2 (ESRI, Redlands, CA, USA) using vector layers for countries obtained from Natural Earth <naturalearthdata.com>.

DNA ISOLATION, AMPLIFICATION AND SEQUENCING

Genomic DNA was isolated from leg muscle tissue dissected from specimens fixed in 95–100% ethanol, amplified and sequenced using standard protocols ([Nishiguchi *et al.*, 2002](#); [Prendini *et al.*, 2005](#)) at the AMNH Sackler Institute of Comparative Genomics. Primers used for the polymerase chain reaction (PCR) follow [Prendini *et al.* \(2005\)](#). The adjuvants bovine serum albumin, dimethyl sulphoxide and magnesium chloride were added when necessary to assist PCR amplifications.

Five phylogenetically informative gene loci were selected that evolve at different rates and would thus be expected to provide phylogenetic resolution at different, overlapping taxonomic levels ([Giribet *et al.*, 2001](#); [Prendini *et al.*, 2003, 2005](#)). Two loci from the nuclear genome were included primarily to resolve relationships among the outgroup taxa. The complete sequence of the small-subunit ribosomal RNA gene (18S rRNA, or 18S) and a variable fragment (D3 region)

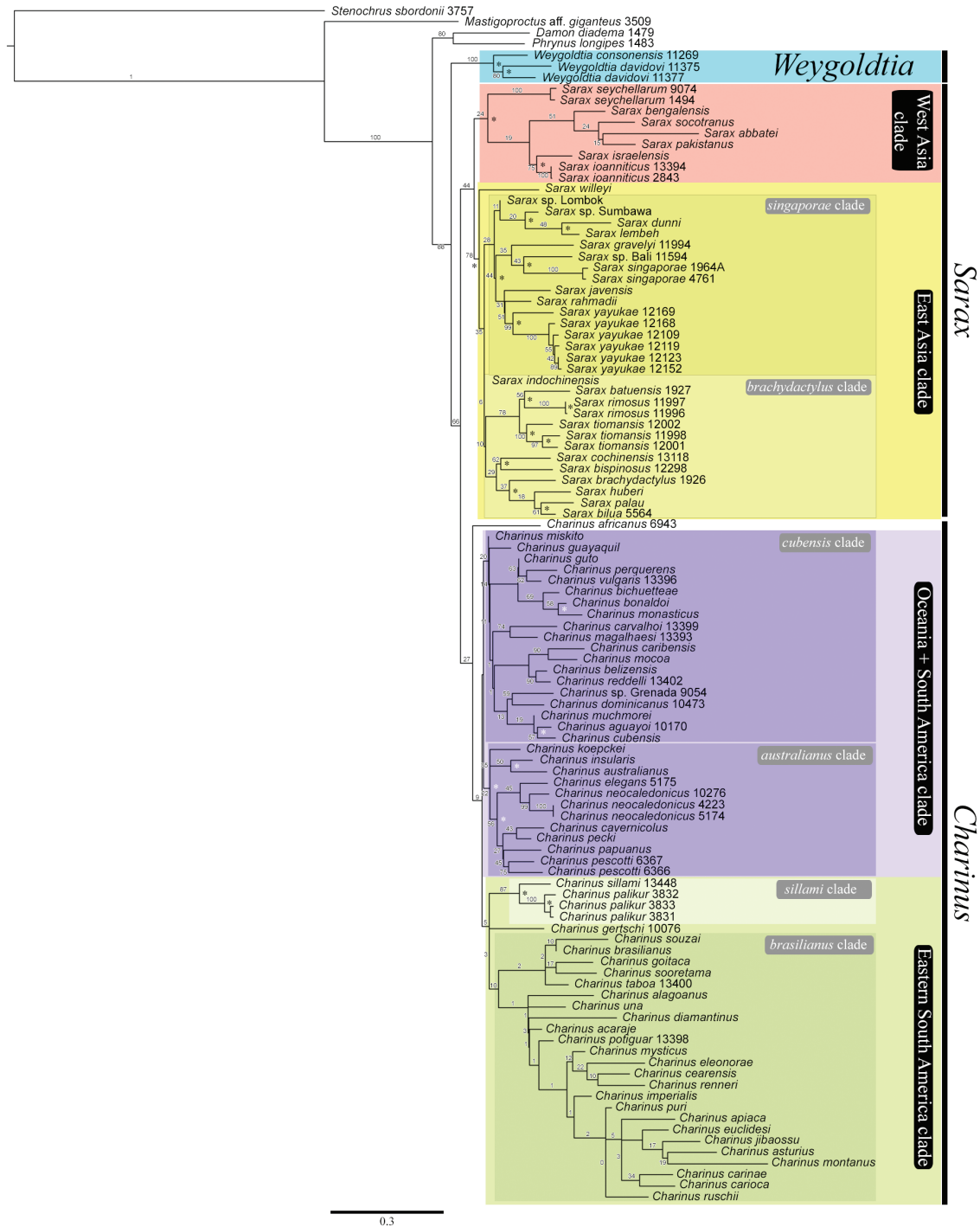


Figure 3. Phylogeny of the whip spider family Charinidae (Quintero, 1986: maximum likelihood tree of 138 morphological characters and DNA sequences from two nuclear and three mitochondrial gene loci. Support values (bootstrap) are indicated on the branches. Asterisks indicate nodes with 100% posterior probability support in an analysis with Bayesian Inference.

of the large-subunit ribosomal RNA gene (28S rRNA, or 28S) were amplified. Three loci were selected from the mitochondrial (mt) genome, to provide resolution

among the ingroup taxa. Fragments of the mt homologs of the nuclear small-subunit ribosomal RNA gene (12S rRNA, or 12S) and the nuclear large-subunit ribosomal

RNA gene (16S rRNA, or 16S), both of which also contain conserved regions, were chosen, together with a more conserved fragment of the cytochrome *c* oxidase subunit I (*COI*) protein-coding gene. These fragments have been used effectively in studies of arachnid phylogeny at higher and lower levels, e.g. [Giribet *et al.* \(2001\)](#), [Prendini *et al.* \(2003, 2005\)](#), [Gonzalez-Santillán & Prendini \(2015\)](#) and references therein.

SEQUENCE ASSEMBLY AND ALIGNMENT

Sequences of the 52 terminals (34 taxa) were edited and assembled with SEQUENCHER v.5.0 (Gene Codes Corporation, Ann Arbor, MI, USA) and GENEIOUS v.9 (Biomatters Ltd., Auckland, New Zealand) and subsequently aligned with MAFFT v.7 ([Kuraku *et al.*, 2013](#)).

The ends of the alignments were trimmed to remove primers and marginal positions with poor coverage. The *COI* protein-coding gene was aligned using the L-INS-i method ([Katoh *et al.*, 2005](#)). However, ribosomal RNA genes contain variable regions and structural constraints that affect the distribution of insertions and deletions in stem regions ([Rix *et al.*, 2008](#)), so the rRNA secondary structure was also considered during alignment of the 18S, 28S, 12S and 16S rRNA gene loci, by using the Q-INS-i method ([Katoh & Toh, 2008](#)). After alignment, ambiguously aligned regions of the 12S and 16S rRNA loci were identified and removed with GBlocks ([Talavera & Castresana, 2007](#)).

A total of 250 sequences were generated for this study, with five sequences for *Damon diadema* (Simon, 1876) added from GenBank ([Supporting Information, Appendix S2](#)). Eight sequences were missing for the 16S locus and one each for the 18S and 28S loci. Seven 16S sequences, one 18S sequence and one *COI* sequence were incomplete.

After trimming ends and removing alignment-ambiguous regions, the remaining 241 sequences varied in length as follows: 18S, 1760–1764 basepairs (bp) (mean, mode: 1763); 28S, 503–524 bp (mean: 520; mode: 521); 12S, 196–201 bp (mean, mode: 201); 16S, 330–339 bp (mean: 338; mode: 339); *COI* 253–702 bp (mean: 693, mode: 702) ([Supporting Information, Appendix S2](#)). The concatenated, aligned dataset was 3535 bp, with 1889 bp variable and 729 parsimony informative. The nucleotide composition of the concatenated, aligned dataset was 26% A, 22% C, 25% G and 27% T.

DATA PARTITIONS AND MODELS OF EVOLUTION

The concatenated molecular dataset was partitioned into seven data blocks: three for each codon position of the protein-coding *COI* locus and four for the ribosomal loci. PartitionFinder v.2 ([Guindon *et al.*, 2010](#); [Lanfear *et al.*, 2016](#)) and PhyML ([Guindon *et al.*, 2010](#)) were

used to identify the best-fitting models of evolution for the respective partitions.

The performance of the data under different parameters was tested with the GREEDY algorithm in PartitionFinder to assess the influence of ambiguously aligned regions on the models and how partition schemes affected the results. Matrices before and after trimming alignment-ambiguous regions with GBlocks were analysed with linked and unlinked branch-length estimations. Three information criteria (Akaike Information Criterion, AIC; AIC with small-sample correction, AICc; Bayesian Information Criterion, BIC) were tested for each analysis, using RAxML-HP v.8 ([Stamatakis, 2014](#)) and MrBayes v.3.2.2 ([Ronquist *et al.*, 2012](#)). The log-likelihood, information criteria, tree topology and branch support were then evaluated to identify which combination of parameters generated the best partitioning and model of evolution for the data. The unlinked branch-length estimation using AICc for the GBlocks-trimmed matrix retrieved the best branch support hence the trees generated under these parameters were selected.

PHYLOGENETIC ANALYSIS

The matrix used for the simultaneous analysis in the maximum likelihood (ML), Bayesian inference (BI) and parsimony analyses comprised 86 ingroup (82 described species plus four morphospecies) and four outgroup taxa represented by 107 terminals (103 ingroup and four outgroup terminals) and 3673 characters (3535 bp and 138 morphological characters). Sixty-two species and two morphospecies were represented only by morphological data. Fourteen morphological characters (41, 42, 47, 48, 55, 56, 77, 78, 79, 89, 96, 99, 108, 110) were uninformative and deactivated in the analysis.

Maximum likelihood was performed with RAxML-HP v.8.2.0 ([Stamatakis, 2014](#)) on the USNM High-Performance Computer Cluster (Hydra). Branches were allowed independently selected gamma-shape parameters under a GTR model for the molecular data and a multistate model for the morphological characters (-m MULTIGAMMA -K MK), applied for each partition as selected by PartitionFinder ([Lewis, 2001](#); [Lanfear *et al.*, 2012](#)). Nodal support was assessed with the fast bootstrap algorithm (BS, 1000 replicates) ([Stamatakis *et al.*, 2008](#)). Long branch lengths resulting from missing data introduced by taxa with incomplete molecular data were fixed using the branch-length stealing algorithm (-f k). Best-scoring ML trees were inferred for each gene locus to assess potential incongruence between the individual gene trees.

Bayesian inference was performed using MrBayes v.3.2.2 with two simultaneous and independent runs, consisting of four Metropolis-coupled Markov chain

Monte Carlo simulations (MCMCs), one cold and three incrementally heated, running for 100 million generations. The following models were selected by PartitionFinder (Lanfear *et al.*, 2012) for each partition: GTR+I+G for the 12S, 16S, 18S, 28S and third-codon position of the *COI*; GTR+G for the first-codon position of the *COI*; SYM+I+G for the second-codon position of the *COI*; and the MkV model for the morphological characters. Trees were sampled every 1000 generations to calculate posterior probabilities (PP). In order to assess the convergence of runs, the split frequencies and effective sample size (ESS) of all the parameters were evaluated and the log-likelihood of the samples plotted against the number of generations in TRACER v.1.6 (Rambaut *et al.*, 2014). An ESS exceeding 200 was acknowledged as a good indicator of convergence. All trees sampled prior to reaching the log-likelihood plateau were discarded as burn-in and the remaining samples used to generate a 50% majority rule consensus tree.

Parsimony analyses were performed in TNT v.1.1 (Goloboff *et al.*, 2008), using new technology algorithms (Nixon, 1999). All characters were unordered and multistate characters treated as non-additive (Fitch, 1971). A batch file used in the TNT run is provided in Morphobank, project number 3538. Equal weighting (EW) and extended implied weighting (IW) with different values of the concavity constant, k (Goloboff, 2013), were applied to explore the sensitivity of the data. Extended implied weighting was used as it reduces the effect of missing data in the final calculations of character weights (Mirande, 2019).

Support for nodes was estimated for the EW tree using group frequencies under jackknifing with probability of alteration, $P = 0.33$. Support in the implied weighting was measured as the absolute (non-GC) frequency from symmetric resampling, a jack-knifing method that accounts for character weights and the GC frequency from symmetric resampling (Goloboff *et al.*, 2003). Groups with no support or contradictory support in the most-parsimonious tree received zero (absolute frequency) or negative (GC frequency) values.

Morphological characters were optimized in the maximum likelihood tree to assess character homoplasy. Statistics such as consistency indices (CIs), retention indices (RIs) and fit were calculated using TNT and charts prepared using the R packages *tidyverse* (Wickham, 2019), *hablar* (Sjöberg, 2020), *ggplot2* (Wickham, 2016) and *egg* (Auguie, 2019) (Fig. 5).

FOSSIL CALIBRATION AND DIVERGENCE DATING

Divergence times were estimated indirectly based on two node calibration points, one each for Amblypygi,

Weygoldtina anglica (Pocock, 1911) and the outgroup Thelyphonida, *Parageralinura naufraga* (Brauckmann & Koch, 1983), constraining the minimum age of the internal node.

Weygoldtina anglica, from the British Middle Coal Measures of Coseley, near Dudley, Staffordshire, UK (Late Carboniferous, Westphalian B or Duckmantian), is the oldest fossil reliably identified as a whip spider. Dunlop *et al.* (2007) redescribed *W. anglica* and considered it a member of the Amblypygi crown group due to its similarity to the putatively basal whip spider, *Paracharon* Hansen, 1921 and, subsequently, Dunlop (2018) placed it sister to Paracharontidae Weygoldt, 1996. U-Pb dating of zircons constrains the upper boundary of the Duckmantian to 313.78 Mya $\pm$ 0.08 Myr, hence a minimum age for *W. anglica* is 313.7 Myr (Wolfe *et al.*, 2016).

Parageralinura naufraga, from deposits of 'Ziegelei-Grube', Hagen-Vorhalle, near Ruhr, North Rhine-Westphalia, Germany (Late Carboniferous, Namurian B or Marsdenian), is the oldest known fossil of Tetrapulmonata and considered the plesion of extant Thelyphonidae Lucas, 1835 (Tetlie & Dunlop, 2008). The (Upper) Namurian–(Lower) Westphalian boundary lacks a precise isotopic date but an age of c. 319.9 Mya was estimated for the base of the Westphalian (top of the Namurian, only slightly younger than the Marsdenian) according to Milankovitch cycles of sedimentation, providing a minimum age for *P. naufraga* (Wolfe *et al.*, 2016). Geological names and dates follow Cohen *et al.* (2013; updated).

Two independent runs of 100 million generations, with trees sampled every 5000 generations, were performed in BEAST v.1.8.0 (Drummond *et al.*, 2012) on the CIPRES Science Gateway v.3.3 (<https://www.phylo.org>). Convergence was visualized in TRACER v.1.6 (Rambaut *et al.*, 2014), ensuring all ESS values were above 200. The dataset was partitioned by genes and the clock and site partitions unlinked. A randomly generated starting tree was used together with an uncorrelated lognormal relaxed clock with a birth–death tree prior. Most priors were set at default values but the ucl.d.mean was set to a gamma distribution with shape value 0.001 and scale 1000.0 (Heath, 2012; Dimitrov *et al.*, 2016). Post-burn in trees were combined using LogCombiner and maximum clade credibility trees created using TreeAnnotator, with additional annotation in FigTree v.1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree>) and Adobe Photoshop CS6.

Historical events that might have affected the evolution and diversification of Charinidae around the time of the median age estimates (with highest posterior probability) are hypothesized based on the literature. The highest posterior density (HPD) for each time age estimate is provided in parenthesis.

RESULTS

MAXIMUM LIKELIHOOD ANALYSIS

The ML tree recovered the monophyly of Charinidae (BS = 88%), with *Weygoldtia* (BS = 100%) placed sister to a clade comprising *Charinus* and *Sarax* (BS = 66%), neither of which was reciprocally monophyletic (Fig. 3). *Charinus africanus* Hansen, 1921 was placed sister to the rest of *Charinus* (BS = 27%), which formed two main clades, hereafter referred to as the 'Oceania + South America clade' (BS = 11%) and the 'eastern South America clade' (BS = 5%). The Oceania + South America clade, in turn, comprised two subclades: the first comprising 19 species from northern South America (mostly Amazonia) and the Caribbean (BS = 20%), hereafter referred to as the '*cubensis* clade', and the second comprising nine species from Oceania (Papua New Guinea, Australia and New Caledonia) or the Pacific coast of South America (BS = 22%), hereafter referred to as the '*australianus* clade'. Two species of the *cubensis* clade, *Charinus guayaquil* Miranda et al., 2021, and *Charinus miskito* Miranda et al., 2021, diverged prior to the rest, which also formed two subclades: the first comprising six species from the Brazilian Amazon (BP = 14%), including *Charinus monasticus* Miranda et al., 2021, probably a human introduction to a monastery in Rio de Janeiro, and the second comprising 11 species from the Amazon, the Caribbean and Central America (BS = 1%; Fig. 3). In the *australianus* clade, *Charinus koepcke* Weygoldt, 1972 from Peru was placed sister to a clade comprising *Charinus insularis* Banks, 1902 from the Galapagos Islands and *Charinus australianus* (L. Koch, 1867) (BS = 35%) from Samoa. This clade was in turn placed sister to a clade of six species, in which a clade comprising *Charinus elegans* Weygoldt, 2006 and *Charinus neocaledonicus* Kraepelin, 1895 (BP = 45%) was placed sister to a clade comprising *Charinus cavernicolus* Weygoldt, 2006, *Charinus papuanus* Weygoldt, 2006, *Charinus pecki* Weygoldt, 2006 and *Charinus pescotti* Dunn, 1949 (BP = 27%).

The eastern South America clade also comprised two subclades: the first, hereafter referred to as the '*sillami* clade' (BS = 87%), comprising two species from French Guiana, and the second, hereafter referred to as the '*brasilianus* clade' (BS = 3%), comprising 24 species from north-eastern Brazil, with *Charinus gertschi* Goodnight & Goodnight, 1946 sister to all the rest. The low branch support for the *brasilianus* clade may be due to the high amount of missing data (only two of the 24 terminals were represented by both morphological and molecular data).

Sarax was divided into two clades, hereafter referred to as the 'West Asia clade' (BS = 24%) and the 'East Asia clade' (BS = 78%). The West Asia clade comprised seven species previously assigned to

Charinus, which are transferred to *Sarax* (Miranda et al., 2021): *Sarax abbatei* (Delle Cave, 1986), *Sarax bengalensis* (Gravely, 1911), *Sarax ioanniticus* (Kritscher, 1959), *Sarax israelensis* (Miranda et al., 2016), *Sarax pakistanus* (Weygoldt, 2005), *Sarax seychellarum* (Kraepelin, 1898) and *Sarax socotranus* (Weygoldt et al., 2002). *Sarax seychellarum* was placed sister to two subclades: one comprising *S. ioanniticus* and *S. israelensis* (BS = 75%), the other comprising the four remaining species (BS = 19%). All of these species, except *S. seychellarum*, were previously part of the *bengalensis* species group, with finger-like female gonopods (Weygoldt, 2005; Miranda & Giupponi, 2011).

The East Asia Clade comprised *Sarax willeyi* Gravely, 1915, placed sister to two clades, hereafter referred to as the '*brachydactylus* clade' and the '*singaporeae* clade'. In the ML tree, the *brachydactylus* clade (BS = 6%) included *Sarax indochinensis* Miranda et al., 2021, placed sister to two subclades: the first comprising three species from the Malay Peninsula and adjacent Tioman Island (subclade 6; BS = 78%) and the second comprising six species from India, Sri Lanka, the Philippines, Palau and the Solomon Islands (subclade 7; BS = 29%).

The *singaporeae* clade (BS = 28%) comprised three subclades in the ML tree: the first (BS = 11%) comprising *Sarax dunni* Miranda et al., 2021, *Sarax lembeh* Miranda et al., 2021 and two undescribed morphospecies from Lombok and Sumbawa; the second (BS = 35%) comprising *Sarax gravellyi* Miranda et al., 2021, *Sarax singaporeae* Gravely, 1911 and an undescribed morphospecies from Bali; and the third (BS = 31%) comprising *Sarax javensis* (Gravely, 1915), *Sarax rahmadii* Miranda et al., 2021, and *Sarax yayukae* Rahmadi et al., 2010.

BAYESIAN INFERENCE

As in the analysis with ML, BI recovered the monophyly of Charinidae (PP = 0.96), with *Weygoldtia* (PP = 1) placed sister to a clade comprising *Charinus* and *Sarax* (PP = 0.96), neither of which was reciprocally monophyletic. *Charinus* was divided into two main clades: the Oceania + South America clade and the eastern South America clade. The taxonomic composition of these clades closely resembled the corresponding clades in the tree obtained with ML. The primary differences concerned the placement of *Charinus sooretama* Miranda et al., 2021, from eastern Brazil, sister to all other *Charinus* (PP = 0.57), and *Charinus guayaquil* sister to a clade comprising *C. africanus*, *S. abbatei*, *S. bengalensis*, *S. pakistanus* and *S. socotranus* (PP = 0.68), all of which were placed in the *cubensis* clade.

The topology obtained with BI also separated the species of *Sarax* into two clades (PP = 0.93): the

West Asia clade (PP = 0.95) and the East Asia clade (PP = 0.99). However, four of the seven species assigned to the West Asia clade in the ML analysis (*S. abbatei*, *S. bengalensis*, *S. pakistanus* and *S. socotranus*) were placed within the *cubensis* clade in the analysis with BI (PP = 0.68), leaving only *S. ioanniticus*, *S. israelensis* and *S. seychellarum* in the West Asia clade.

The East Asia clade was divided into two main clades: one comprising four species, *Sarax batuensis* Roewer, 1962, *S. indochinensis*, *S. rimosus* (Simon, 1901) and *S. tiomanensis* Miranda *et al.*, 2021 (PP = 0.54), the other comprising 16 species (PP = 0.59). The first of these clades included some species assigned to the *brachydactylus* clade in the analysis with ML, the rest of which, i.e. *Sarax bilua* Miranda *et al.*, 2021, *Sarax bispinosus* (Nair, 1934), *Sarax brachydactylus* Simon, 1892, *Sarax cochinchensis* (Gravely, 1915), *Sarax huberi* Seiter *et al.*, 2015 and *Sarax palau* Miranda *et al.*, 2021, grouped sister to all other species of the *singaporeae* clade (PP = 0.64). Other differences from the analysis with ML concerned the position of *S. rahmadii*, placed sister to *S. gravelyi* in the analysis with BI (PP = 0.92), rather than sister to *S. yayukae*, as in the ML analysis, and the position of *Sarax willeyi* (Gravely, 1915), unresolved in the *singaporeae* clade in the analysis with BI (PP = 0.59), unlike the analysis with ML, in which it grouped sister to all other East Asian species of *Sarax*.

PARSIMONY ANALYSIS

Parsimony analysis with equal weighting recovered 871 trees of 6945 steps, resulting in extensive polytomies, with low support, in the strict consensus (Fig. S2). In contrast, only two trees were obtained in all analyses with implied weighting and *k* values varying from six to 90. The CIs and RIs of the trees obtained with implied weighting are predictably higher than those of the trees obtained with equal weighting. Whereas the trees obtained with *k* values greater than 40 are identical in length (6946 steps) and topology, those obtained with lower *k* values differ topologically and are less parsimonious (Table 2).

Charinidae and *Weygoldtia* were monophyletic, whereas *Charinus* and *Sarax* were paraphyletic, in all parsimony analyses (Figs S2–S7; trees with branch support available in Morphobank, project number 3538). *Weygoldtia davidovi* was paraphyletic with low support (GC = 21) in the analyses with *k* = 6–30 but monophyletic with low support (GC = 28) in the analyses with *k* = 40–90. *Sarax abbatei*, *S. bengalensis*, *S. pakistanus* and *S. socotranus* were placed sister to a clade of *Charinus* in the implied weighting analyses with *k* = 6–30 (GC = 43, GF = 15) and nested within a clade of *Sarax* in the implied weighting analyses with *k* = 40–90 (GC = 13). *Sarax seychellarum* was placed

Table 2. Length (steps), Fit, consistency index (CI) and retention index (RI), of most parsimonious trees (MPTs) obtained with equal weighting (EW) and implied weighting (IW) using incremental values of the concavity constant, *k*, in simultaneous phylogenetic analysis of the whip spider family Charinidae Quintero, 1986

Weighting	Length	Fit	CI	RI	MPTs
EW	6945	553.57	0.163	0.167	871
IW <i>k</i> = 6	6979	438.79	0.257	0.532	2
IW <i>k</i> = 10	6972	439.09	0.258	0.532	2
IW <i>k</i> = 20	6963	439.51	0.258	0.533	2
IW <i>k</i> = 30	6955	440.05	0.258	0.534	2
IW <i>k</i> = 40	6946	440.84	0.259	0.535	2
IW <i>k</i> = 50	6946	440.84	0.259	0.535	2
IW <i>k</i> = 60	6946	440.84	0.259	0.535	2
IW <i>k</i> = 70	6946	440.84	0.259	0.535	2
IW <i>k</i> = 80	6946	440.84	0.259	0.535	2
IW <i>k</i> = 90	6946	440.84	0.259	0.535	2
IW <i>k</i> = 100	6946	440.84	0.259	0.535	2

sister to a clade comprising species of *Charinus* and *Sarax* in all parsimony analyses.

PREFERRED TREE

Branch support values for the trees recovered with ML, BI and parsimony were mostly low due to the absence of molecular data for over half the terminal taxa in the analysis. However, the tree obtained with ML was better resolved and received greater nodal support (Fig. 3) than the trees obtained with BI and parsimony (Figs S2–S8) and its topology was more congruent with the individual gene trees (Figs S9–S13). Additionally, the CIs and RIs of the morphological characters were generally greater in the ML tree than in the trees obtained with parsimony and BI (see Fig. 5 and Morphobank Project 3538). The ML tree is, therefore, presented as the preferred tree, on which the results and discussion are based.

DIVERGENCE TIME ESTIMATION

The phylogeny obtained by the divergence dating analysis (Fig. 4) was largely congruent with the preferred phylogeny obtained by the simultaneous analysis with ML (Fig. 3). The tree topology differed primarily in relationships among the species of *Charinus*, notably *C. africanus*, placed sister to *Charinus vulgaris* Miranda & Giupponi, 2011 (PP = 0.50), and *Charinus potiguars* Vasconcelos *et al.*, 2013, placed sister to *Charinus gertschi* (PP = 0.50). The

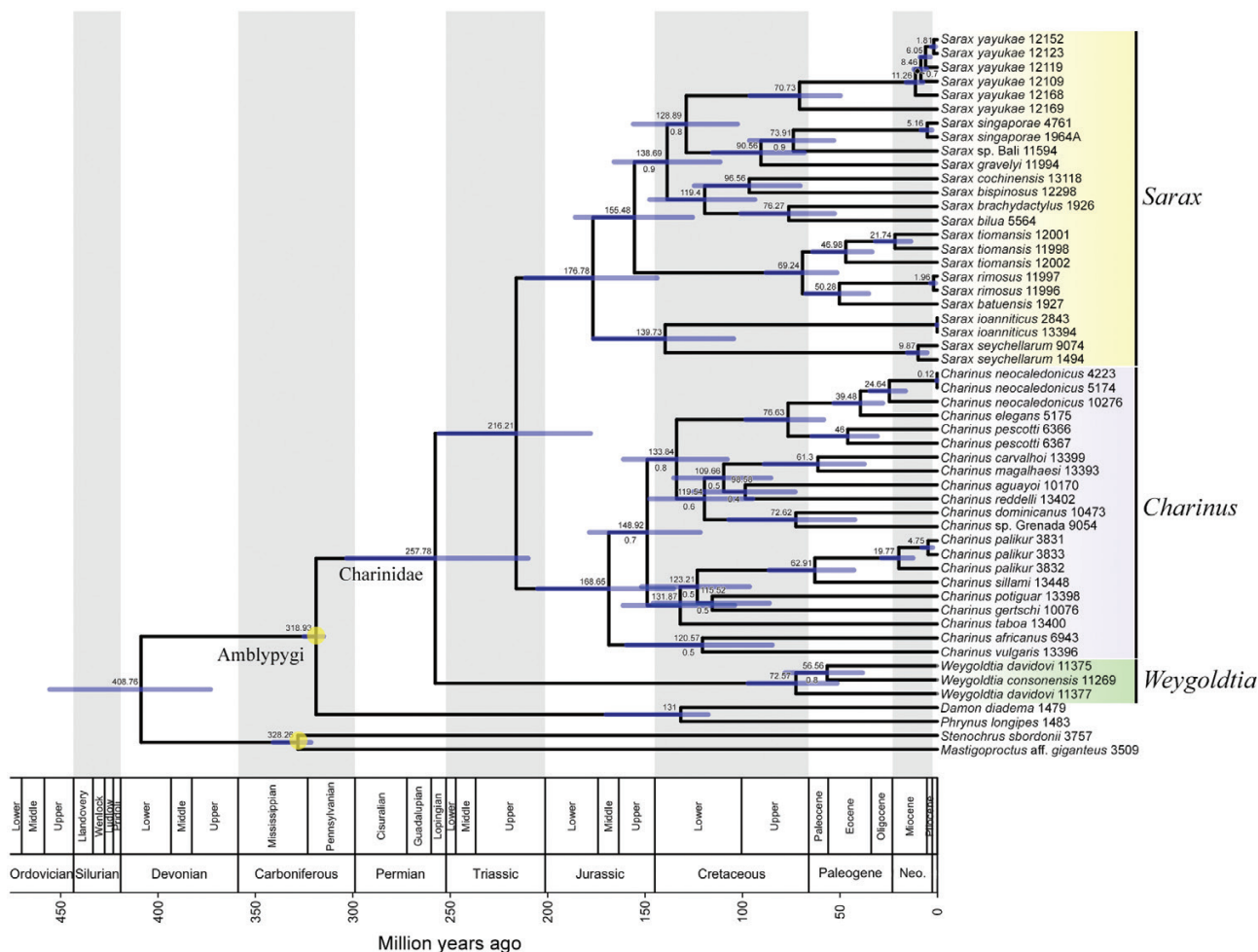


Figure 4. Phylogeny of the whip spider family Charinidae (Quintero, 1986; maximum clade credibility tree obtained by analysis with BEAST. Calibration points for Uropygi and Amblypygi indicated with yellow circles at nodes. Median dates and posterior probabilities indicated above and below branches, respectively. Support values (PP) less than 1 indicated below branches. Neo: Neogene.

highest branch support values (PP = 1) were obtained for Charinidae, *Charinus*, *Sarax* and *Weygoldtia*.

The age estimate for the most recent common ancestor of extant Charinidae is 318.9 Mya (95% HPD interval: 315–325 Mya). The age estimate for the divergence between *Weygoldtia* and the clade comprising *Charinus* and *Sarax* is 257.8 Mya (95% HPD interval: 210–303 Mya) and for the divergence between *Charinus* and *Sarax*, 216.2 Mya (95% HPD interval: 178.0–255.8 Mya).

DISCUSSION

HOMOPLASY AND RELATIONSHIPS

The morphology of whip spiders is rather homogeneous (Weygoldt, 1998, 1999a; Miranda *et al.*, 2016a, 2018a, b). Diagnostic and phylogenetic characters

in the order are based on qualitative and meristic differences, resulting in a limited number of phylogenetically informative characters. A well-resolved topology may be obtained when a small taxon sample is used to reconstruct a morphological phylogeny within Amblypygi (Garwood *et al.*, 2017; Miranda *et al.*, 2018b). However, when the ingroup is densely sampled, and all variation within character states is accounted for, as in the present study, homoplasy negatively affects the resolution and support of clades. In the discussion that follows, some morphological synapomorphies and diagnostic characters historically used to define taxonomic groups of Charinidae are discussed, based on the simultaneous phylogenetic analysis of the morphological and molecular data with ML (Fig. 3). Diagnostic characters and details of the variation

within the genera and species of Charinidae are provided elsewhere (Miranda *et al.*, 2021).

Among the different character systems (carapace, cheliceral basal segment, cheliceral claw, eyes, genital operculum, male gonopod, female gonopod, basitibia IV, tarsomere IV, opisthosoma, pedipalp coxae, pedipalp femur, pedipalp patella, pedipalp tarsus, pedipalp tibia, pedipalp trochanter, sternum, tarsi I and tibia I), the best CI and RI (mean/median) were obtained for characters of the carapace (CI = 0.78/0.90, RI = 0.93/0.95), pedipalp trochanter (CI = 0.75/0.75, RI = 0.75/0.75), tibia I (CI = 0.75/0.75, RI = 0.75/0.75) and pedipalp tibia (CI = 0.73/1, RI = 0.9/1) (Fig. 5). The best fit (mean/median) were obtained for the characters of the pedipalp trochanter (Fit = 1.5/1.5), tibia I (Fit = 1.5/1.5), opisthosoma (Fit = 2/2), carapace (Fit = 2/2.67), eyes (Fit = 2.5/3.17) and tarsomere IV (Fit = 1/3.6) (Fig. 5).

One seta posterior to the lateral ocular triad (character 13; CI = 0.50, RI = 0.97, Fit = 2; Figs 6A, 7N), a plesiomorphic state occurring in most Amblypygi analysed, is absent in the East Asian clade of *Sarax*, for which setae adjacent to the lateral eyes (character 14; CI = 1, RI = 1, Fit = 1) are synapomorphic (Figs 6B, 7B). A curved carina on the carapace (character 9; CI = 0.20, RI = 0.91, Fit = 5), diagnostic for most species of *Sarax*, as noted by Kraepelin (1899), is also homoplastic, occurring in *Weygoldtia* and some species of *Charinus* (Fig. 7). A straight carina, anterior to the lateral eyes (character 11; CI = 1, RI = 1, Fit = 1), is synapomorphic for *Weygoldtia* (Fig. 7C).

A long, projecting tooth on the retrolateral surface of the chelicera, adjacent to the bifid tooth (character 19; CI = 0.07, RI = 0.63, Fit = 14), widespread among Amblypygi, is variable within Charinidae; it is long in a few *Charinus* species but short in *W. davidovi* and some species of *Sarax* (character 20; CI = 1, RI = 1, Fit = 1; Fig. 8J). The number of teeth on the cheliceral fang is extremely variable among Charinidae (character 31; CI = 0.17, RI = 0.59, Fit = 29; Fig. 8C; Vasconcelos *et al.*, 2013). Although four or five teeth is the ancestral state, Charinidae possess three to 13.

The relative size of the cusps of the bifid tooth (character 23; Fig. 8G), a diagnostic character among Caribbean and Central American *Charinus* (Miranda *et al.*, 2016b), was not synapomorphic for any groups within the genus (CI = 0.29, RI = 0.44, Fit = 7). The ventral sac cover (character 35; Fig. 9) is known to be homoplastic in Amblypygi, occurring in *Charon* (Charontidae; Weygoldt, 1996), *Sarax* and, although reduced to a small exposed border, *Weygoldtia* (CI = 0.50, RI = 0.97, Fit = 2).

The primary diagnostic character for *Sarax* is the finger-like female gonopod (character 43; CI = 0.33, RI = 0.93, Fit = 6; Figs 6C, 10C), which occurs in all species of the genus and supported the transfer of eight species from *Charinus* to *Sarax* (below). One exception

is *S. seychellarum*, considered not to possess a gonopod (Weygoldt, 1999b), an autapomorphy for this species. A variation of the finger-like gonopod morphology is also present, i.e. the plunger-like gonopod, characterized by a stalk similar to the finger-like gonopod, but with a small terminal invagination and the apex sometimes broader than the base. *Charinus africanus*, the only species outside *Sarax* with a modified finger-like gonopod bearing small claws at the apex (see fig. 3 of Weygoldt, 2008), is nevertheless highly supported as a member of *Charinus* (Figs 3 and 5).

Whereas the number of articles on the tarsus of leg I (character 52; CI = 0.46, RI = 0.77, Fit = 13) varies among the species of Charinidae, the number of articles on the tibia of leg I (character 50; CI = 0.50, RI = 0.50, Fit = 2) is conserved, with 21–25 observed in most species of the family, except *Charinus montanus* Weygoldt, 1972, with 26–45.

A ventromedial apophysis anteriorly directed on the pedipalp trochanter (character 60; CI = 1, RI = 1, Fit = 1; Fig. 11A) is synapomorphic for Charinidae (Weygoldt, 1996). The number of spines on the pedipalp femur and patella is not synapomorphic, but two ventral spines on the patella is the ancestral state of *Charinus*, and three spines the ancestral state of *Sarax* (character 72; CI = 0.17, RI = 0.69, Fit = 23).

A row of setae at the base of the cleaning organ (pedipalp tarsus; character 88; CI = 1, RI = 1, Fit = 1) was considered synapomorphic for Charontidae by Weygoldt (1996). The charontid genera, *Charon* and *Catageus*, each possess a row of more than four setae near the proximal border of the cleaning organ. However, one or two setae also occur in the charinid genus, *Weygoldtia*. Therefore, the diagnostic character state for Charontidae is a row on more than two setae, rather than a row of setae.

A carina with a semicircular configuration, on the dorsal surface of the pedipalp coxae (character 93; CI = 1, RI = 1, Fit = 1; Fig. 12), was synapomorphic for Charinidae, as first noted by Delle Cave (1986). This carina is also present in Charontidae, in which it has a triangular configuration. The anterior border of the carina often bears three prominent setae (character 94, state 1; CI = 0.20, RI = 0.59, Fit = 25). Whereas these setae are markedly separated in *Charinus* (Fig. 12), the two largest setae on the anterior border are adjacent to one another in *Sarax* (character 95, state 1; CI = 0.25, RI = 0.92, Fit = 4), a synapomorphy for the genus.

The number of articles on the basitibia of leg IV (character 121; CI = 0.20, RI = 0.66, Fit = 15), once used to diagnose the genera *Charinides* and *Tricharinus*, presently in synonymy with *Charinus*, was demonstrated to be homoplastic. Most species of *Charinus* possess three articles and several species of *Sarax* possess four, but no state is exclusive to a

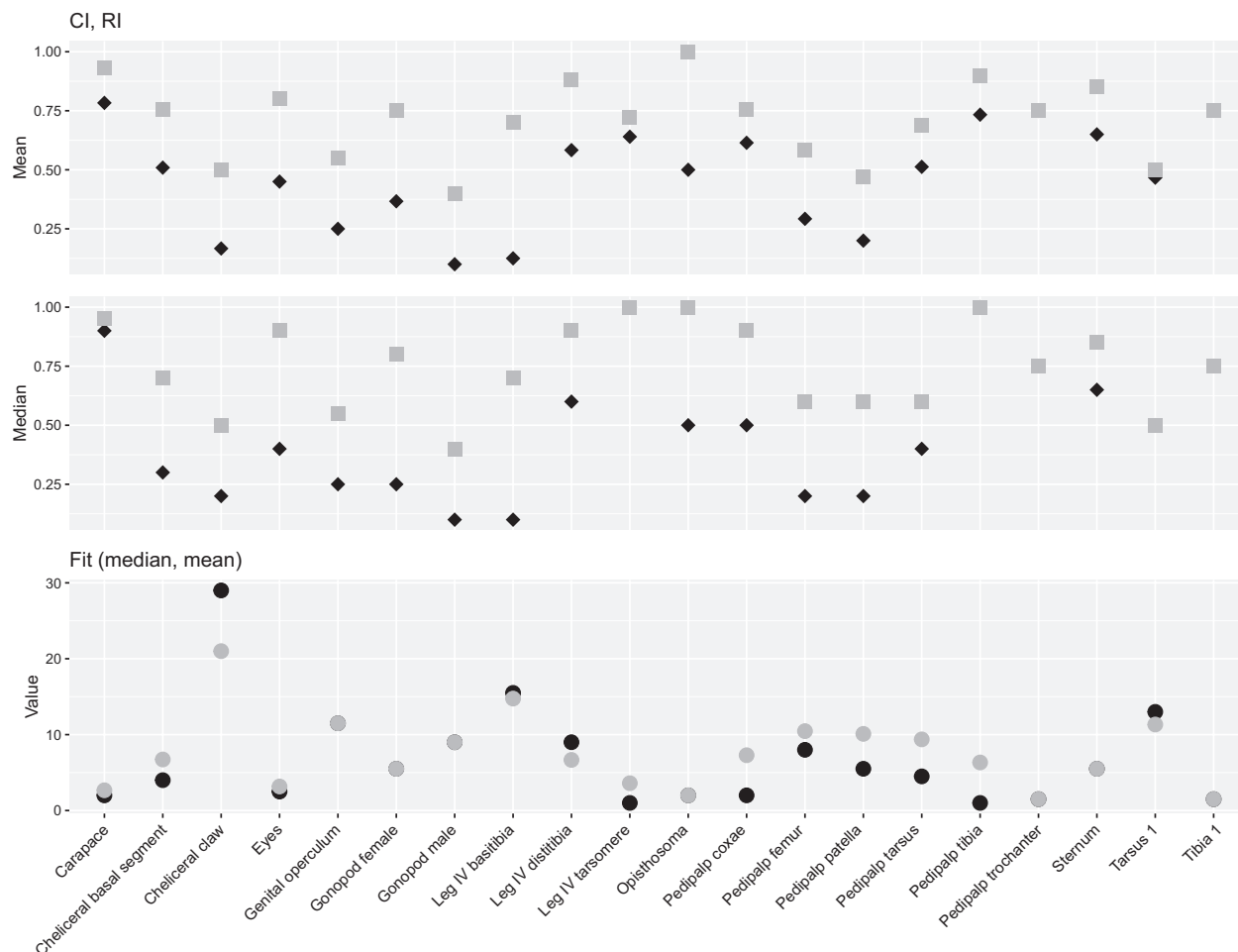


Figure 5. Mean and median homoplasy statistics, i.e. consistency index (CI, black diamond), retention index (RI, grey square) and Fit (mean, dark grey circles; median, black circles), for parsimony-informative morphological characters, arranged by character system (Appendix 2), on optimal phylogeny of the whip spider family Charinidae Quintero, 1986 (Fig. 3).

particular genus. A marked division of the distitibia of leg IV, distal to the triad of trichobothria (character 133; CI = 1, RI = 1, Fit = 1; Fig. 13), occurs in all Charinidae but also in Charontidae.

Charinus, *Sarax* and *Weygoldtia* exhibit equal numbers of trichobothria in the frontal and caudal series of leg VI [characters 130 (CI = 0.56, RI = 0.88, Fit = 9) and 131 (CI = 0.60, RI = 0.88, Fit = 10)], usually five, but sometimes six in *Charinus* and *Sarax* compared with six or nine in *Weygoldtia*. A pulvillus occurs in Paracharontidae, Charinidae and Charontidae (character 135; CI = 1, RI = 1, Fit = 1; Fig. 14), as noted by Quintero (1986) and Weygoldt (1996).

BIOGEOGRAPHY AND ORIGIN OF CHARINIDAE

According to the reconstruction presented here, the most recent common ancestor of Charinidae and Phrynoidea lived 318.9 Mya (95% HPD interval:

315–325 Mya), during the Late Carboniferous (Lower Pennsylvanian; Fig. 4), five million years older than the oldest known fossil of Amblypygi (Wolfe *et al.*, 2016; Dunlop, 2018). During the Late Carboniferous, Pangaea was intact and present-day Europe and North America (Euamerica) were situated over the equator and covered by humid rainforest (Fig. 4) (Sahney *et al.*, 2010). Based on what is known about the habitat of extant whip spiders in tropical rainforests, it may be assumed that the habitats of Palaeozoic species were similar to those of living species, which would explain the presence of Amblypygi fossils in the Coal Measures of Coseley, Staffordshire (UK), Mazon Creek, Illinois (USA) and Nova Scotia (Canada), all of which were tropical during the Palaeozoic. The oldest fossils of Uropygi, the sister-group of Amblypygi, also occur in eastern North America and Europe, which is hypothesized to be the ancestral area of the group (Clouse *et al.*, 2017).

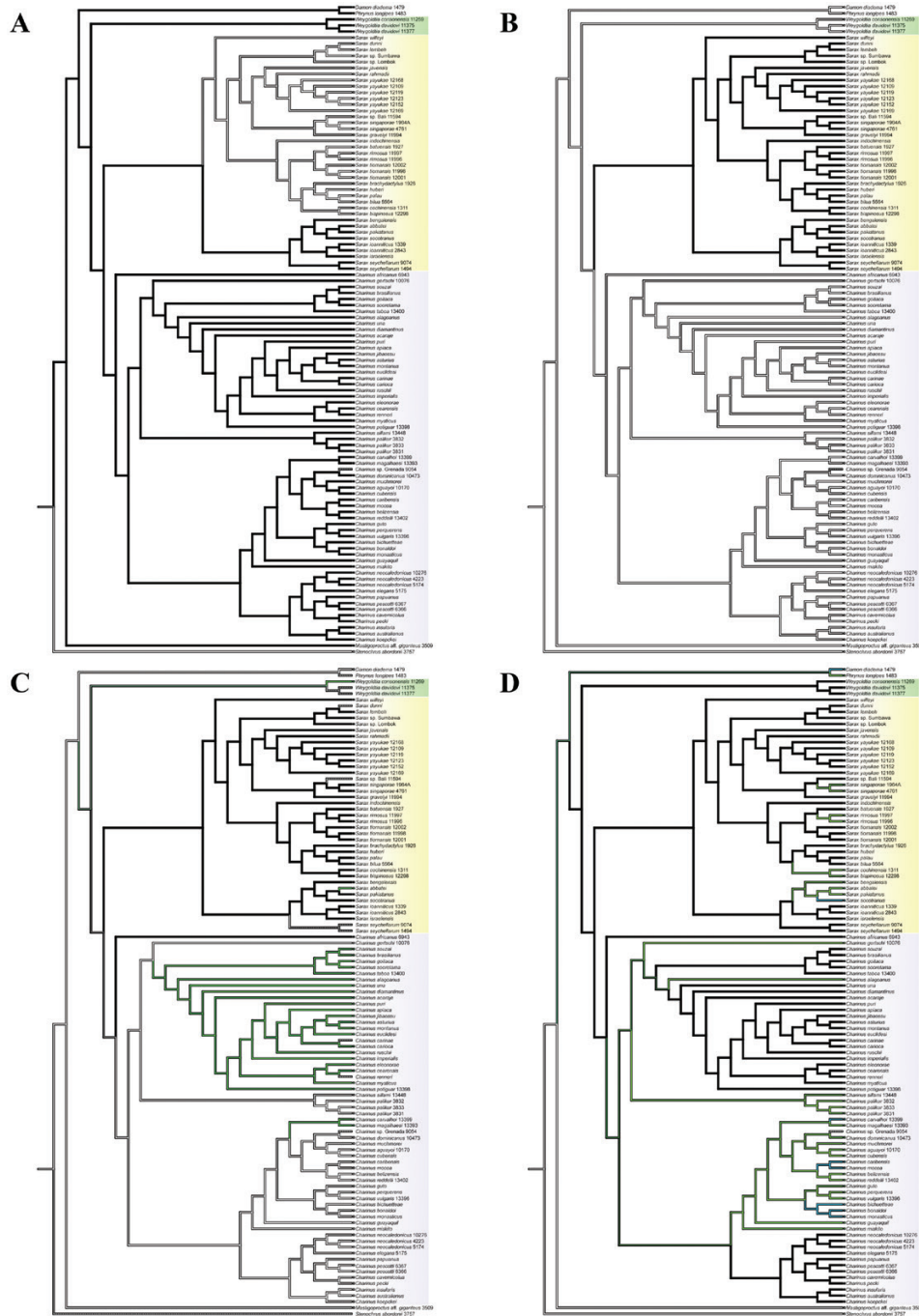


Figure 6. Ancestral state reconstruction of selected morphological characters on the phylogeny of the whip spider family Charinidae [Quintero, 1986](#). A, character 13; presence of setae posterior to lateral ocular triad; dark lines, present; grey lines, absent. B, character 14, presence of setae lateral to ocular triad; dark lines, present; grey lines, absent. C, character 43; shape of female gonopod; white lines, cushion-like; green lines, sucker-like; black lines, finger-like (includes plunger-like gonopods). D, character 121, number of articles on basitibia IV; white, 1; blue, 2; green, 3; black, 4. *Charinus* Simon, 1892 represented in blue, *Sarax* Simon, 1892 in yellow, and *Weygoldtia* [Miranda et al., 2018](#) in green.

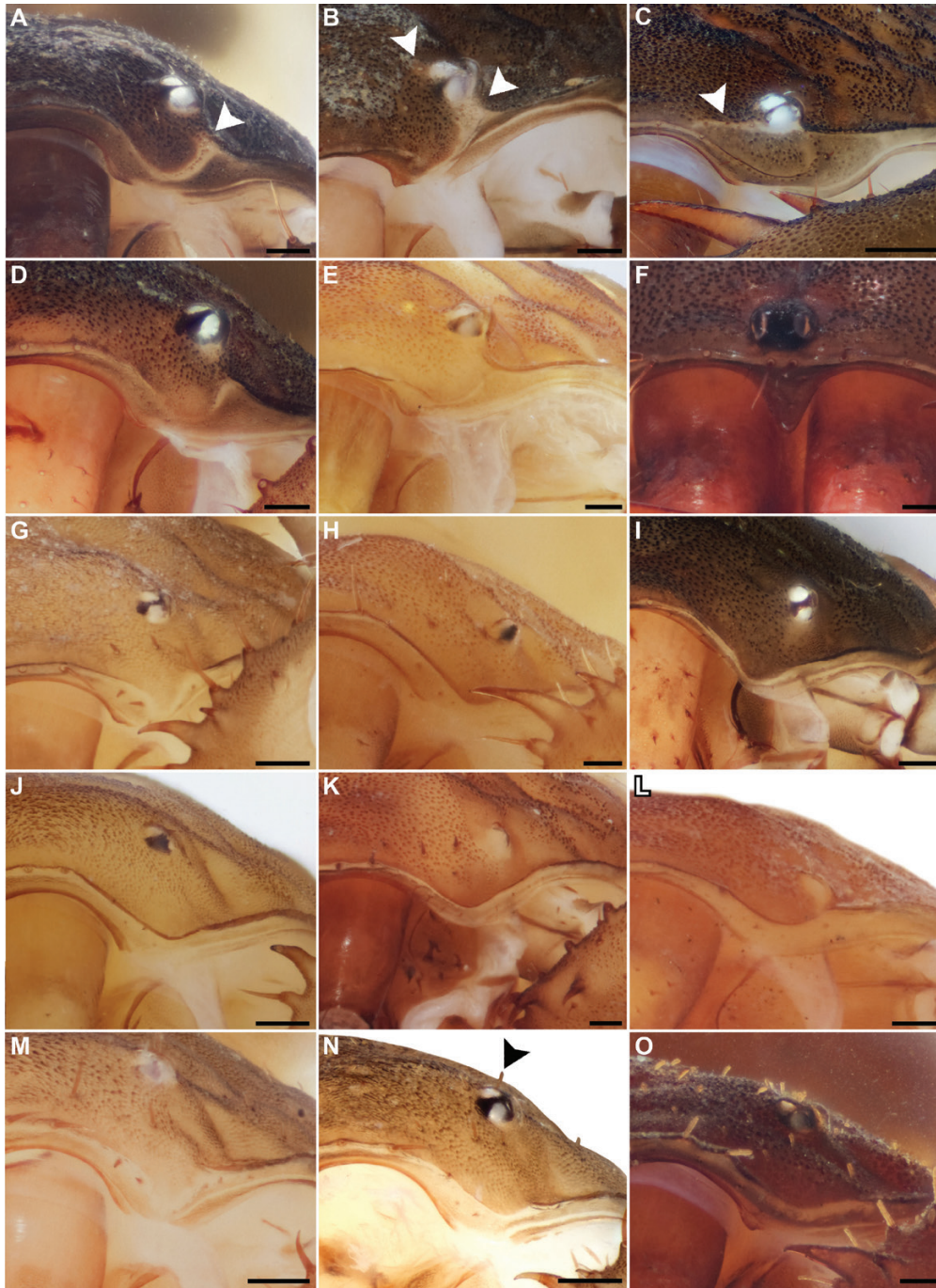


Figure 7. Whip spiders of the family Charinidae [Quintero, 1986](#), carapace, sinistral margin, retrolateral view, illustrating curved or straight carina between lateral eyes and lateral carapace margin (arrows in A, B, C; characters 9–12), and setae posterior or adjacent to lateral ocular triad (arrows in B, N; characters 13, 14). A, *Sarax brachydactylus* Simon, 1892, ♂ (AMNH [LP 1926]). B, *Sarax cochiniensis* (Gravely, 1915), ♀ [AMNH (LP 13118)]. C, *Weygoldtia davidovi* (Fage, 1946), ♂ [AMNH (LP 11377)]. D, *Sarax graveli* [Miranda et al., 2021](#), ♀ [AMNH (LP 11995)]. E, *Sarax willeyi* Gravely, 1915, ♀ (SMF 64589). F, *Sarax yayukae* [Rahmadi et al., 2010](#), ♂ [AMNH (LP 12109)]. G, *Charinus dominicanus* Armas & González Perez, 2001, ♂ (AMNH). H, *Sarax ioanniticus* ([Kritscher, 1959](#)), ♀ (NHMW 19137). I, *Sarax seychellarum* ([Kraepelin, 1898](#)), ♀ [AMNH (LP 9075)]. J, *Sarax pakistanus* ([Weygoldt, 2005](#)), ♂ (MHNG). K, *Sarax israelensis* ([Miranda et al., 2016](#)), ♀ (HUJ INVAMB 111). L, *Sarax abbatei* ([Delle Cave, 1986](#)), ♀ (MZUF 1896–167). M, *Charinus belizensis* [Miranda et al., 2016](#), ♂ (HUJ INVAMB 117). N, *Charinus cubensis* ([Quintero, 1983](#)), ♀ (USNM ENT 784407). O, *Charinus montanus* [Weygoldt, 1972](#), ♀ (MNRJ 9087). Scale bars: A, B, D–O, 0.2 mm; C, 0.5mm.

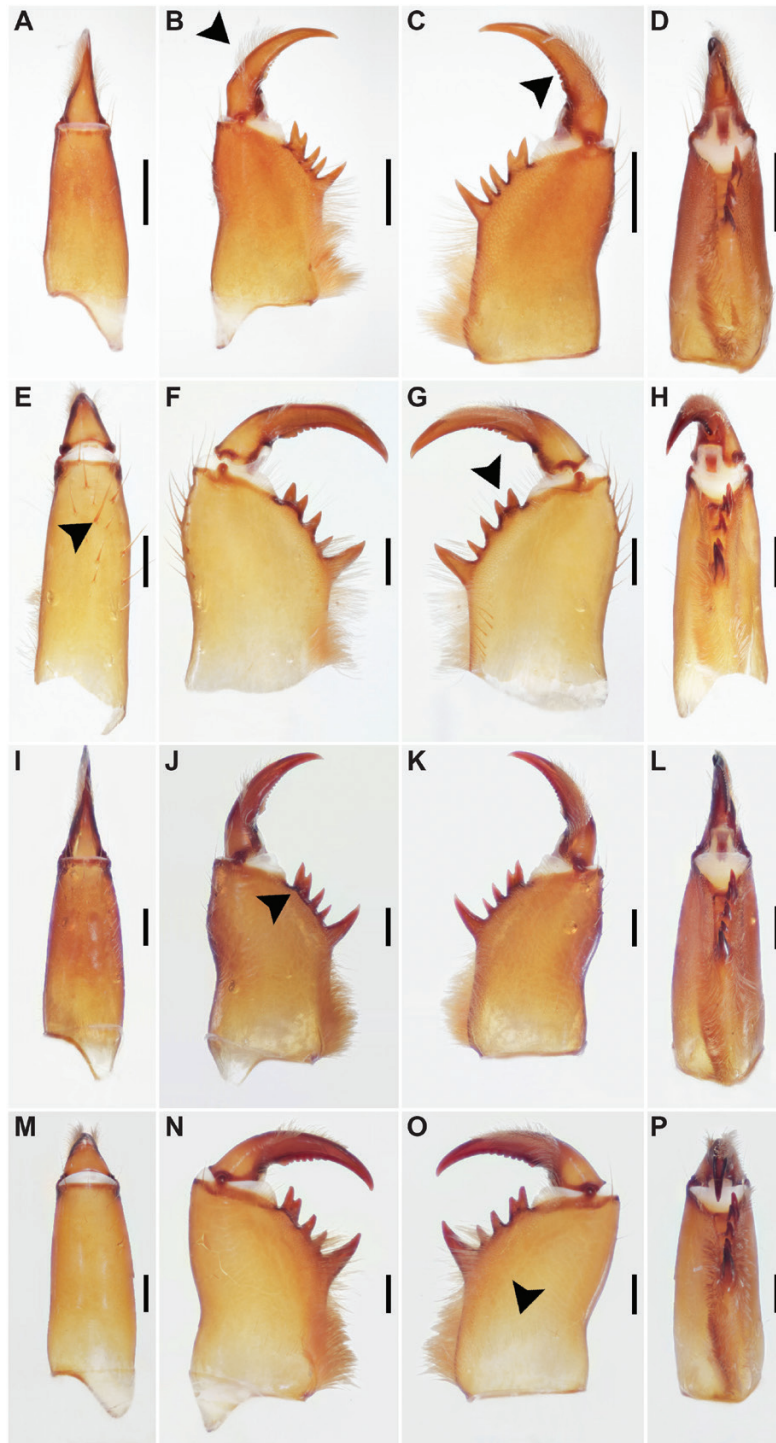


Figure 8. Whip spiders of the family Charinidae [Quintero, 1986](#), chelicerae, dorsal, retrolateral, prolateral and ventral views, illustrating dentition and setation (characters 17–34; arrow in B, characters 32 and 33; arrow in C character 31; arrow in E, characters 27–30; arrow in G, characters 22–24; arrow in J, characters 18, 19; arrow in O characters 25–26). A–D, *Charinus montanus* [Weygoldt, 1972](#), ♀ (MNRJ 9087). E–H, *Charinus troglobius* Baptista & Giupponi, 2002, ♂ (MNRJ 9069). I–L, *Charinus mysticus* Giupponi & Kury, 2002, ♀ (MNRJ 9022). M–P, *Charinus diamantinus* [Miranda et al., 2021](#), ♂ (MNRJ 9189). Scale bars: 0.5 mm.

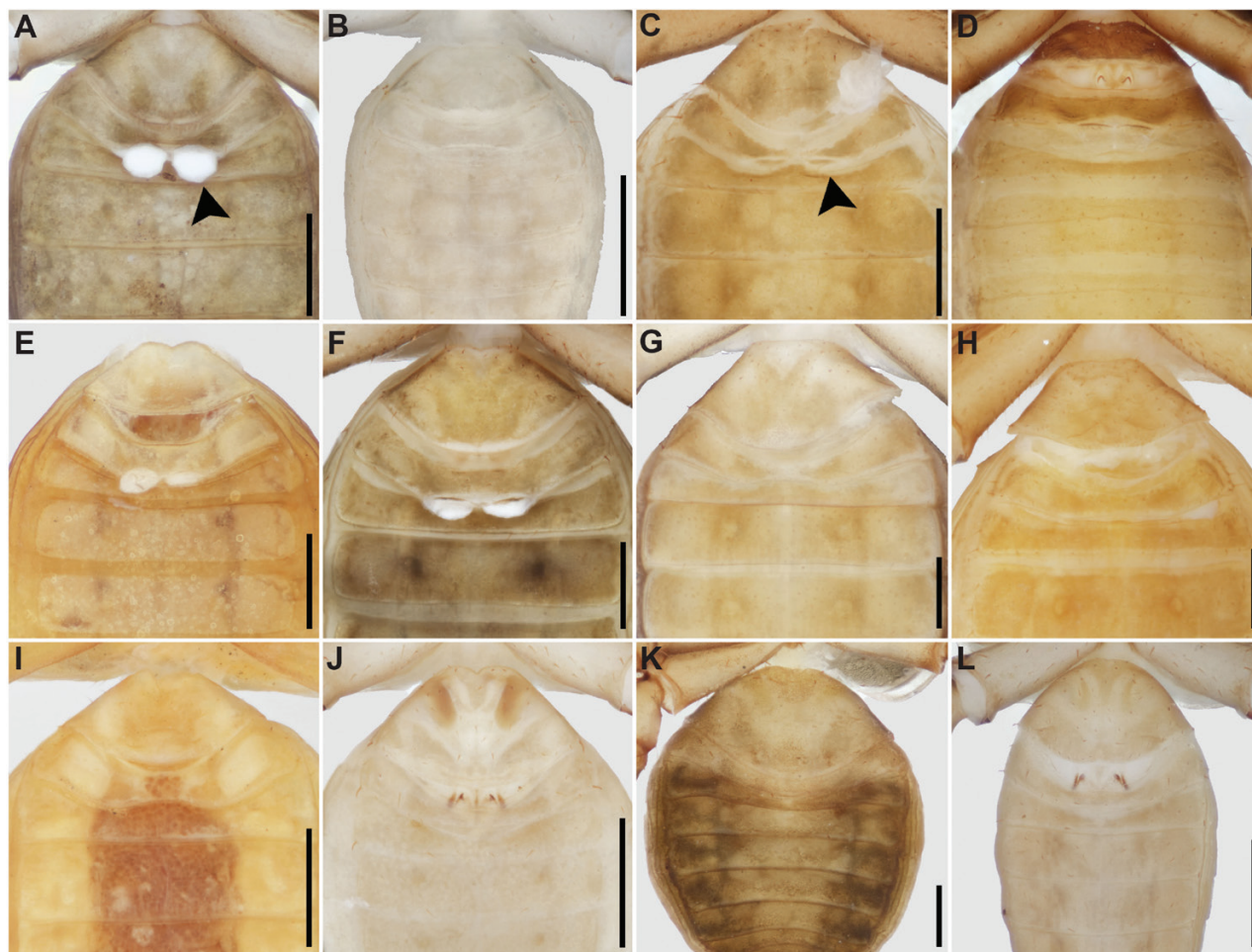


Figure 9. Whip spiders of the family Charinidae [Quintero, 1986](#), opisthosoma, ventral view illustrating ventral sac and ventral sac cover (arrows in A, C; character 35). A, *Sarax gravelyi* [Miranda et al., 2021](#), ♀ [AMNH (LP 11995)]. B, *Sarax bispinosus* (Nair, 1934), ♂ [AMNH (LP 12298)]. C, *Sarax brachydactylus* Simon, 1892, ♂ [AMNH (LP 1926)]. D, *Sarax* sp. from Bali, ♂ [AMNH (LP 11594)]. E, *Sarax willeyi* Gravely, 1915, ♀ (SMF 64589). F, *Sarax yayukae* [Rahmadi et al., 2010](#), ♂ [AMNH (LP 12119)]. G, *Weygoldtia davidovi* Fage, 1946, ♂ [AMNH (LP 11377)]. H, *Charinus ruschii* Miranda et al., 2016, ♀ (MNRJ 9235). I, *Sarax abbatei* ([Delle Cave, 1986](#)), ♀ (MZUF 1896–167). J, *Charinus dominicanus* Armas & González Perez, 2001, ♂ (AMNH). K, *Charinus palikur* [Miranda et al., 2021](#), ♂ [AMNH (LP 3831)]. L, *Charinus belizensis* Miranda, Giupponi & Wizen, 2016, ♂ (HUI INVAMB 117). Scale bars: 1 mm.

The Late Carboniferous was marked by major changes in climate, with temperature shifts and atmospheric carbon dioxide fluctuations that led to aridification and a reduction and fragmentation of forest coverage in the tropics ([DiMichele et al., 2009, 2010](#); [Sahney et al., 2010](#); [Hedge et al., 2019](#)). Divergence between the Charinidae and other families of Amblypygi may have occurred in those fragmented forests ([Fig. 4](#)). Speciation associated with environmental change is among the limited evidence of climatic regionalization during the Palaeozoic. At this time, arthropods were highly diverse: arachnids, insects and myriapods formed sophisticated interconnected communities and a high abundance of rainforest leaf-litter arthropods

comprised elaborate food chains ([Shear & Kukalova-Peck, 1990](#); [Falcon-Lang et al., 2006](#); [Labandeira, 2006](#)). Whip spiders were almost certainly part of the dynamic leaf-litter environment during the Palaeozoic.

Another 60 Myr passed before the ancestor of all living genera of Charinidae diverged into two lineages, *Weygoldtia* and the common ancestor of *Charinus* and *Sarax*. By the late Permian ([Fig. 4](#)), around 257.8 Mya (95% HPD interval: 210–303 Mya), terrestrial organismal diversity was rich with complex amphibian and reptile faunas, and numerous plant taxa providing new habitats ([Benton, 2003](#)). Some floras were endemic, indicating geographical differentiation associated with climatic zonation

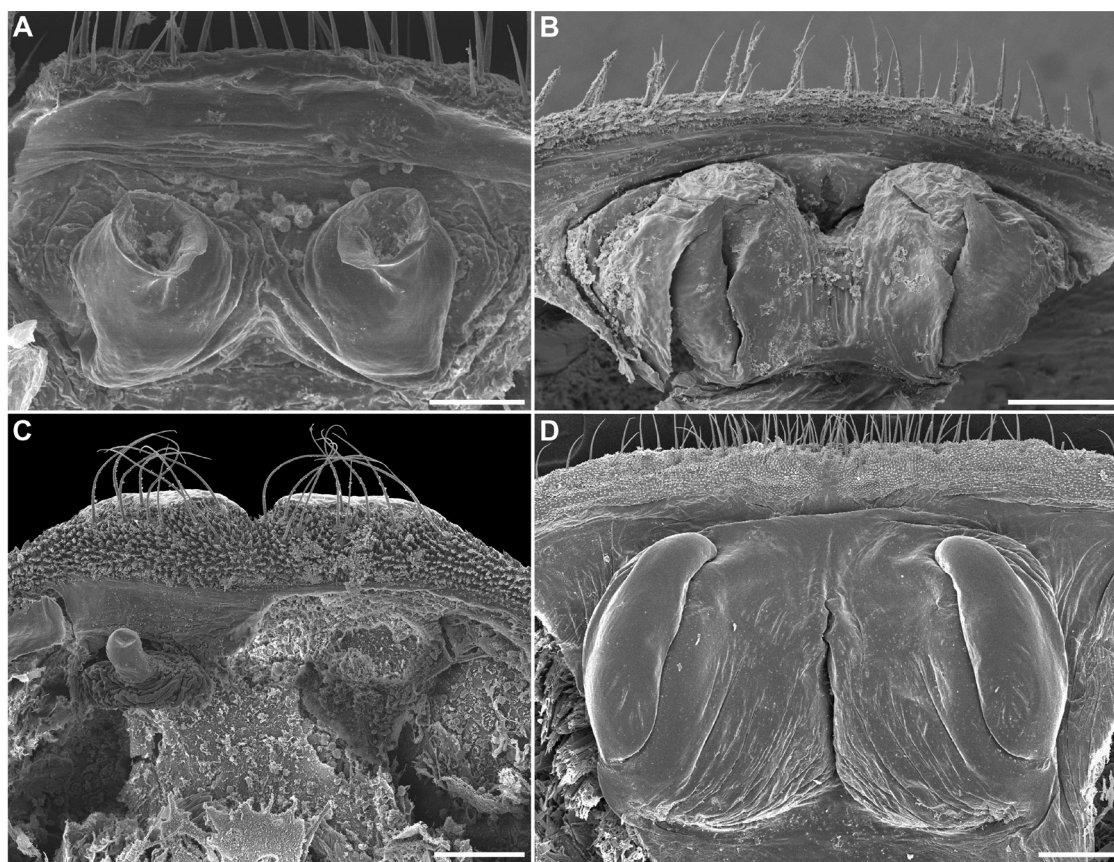


Figure 10. Whip spiders of the families Charinidae Quintero, 1986 and Phrynidae Blanchard, 1852, ♀ gonopod, dorsal view illustrating diverse shapes (characters 37–43). A, *Charinus ruschii* Miranda *et al.*, 2016, ♀ (MNRJ 9237). B, *Charinus belizensis* Miranda *et al.*, 2016, ♀ (HUI INVAMB 118). C, *Sarax tiomanensis* Miranda *et al.*, 2021, ♀ [AMNH (LP 11998)] D, *Heterophrynus vesanicus* Mello-Leitão, 1931, ♀ (MNRJ 09026). Scale bars: A–C, 100 µm; D, 300 µm.

(Benton & Twitchett, 2002). However, by the end of the Permian, mass extinctions caused more than 90% of the organisms to vanish (Benton & Twitchett, 2002). The split between *Weygoldtia* and its sister-group occurred during that time, around the Guadalupian and Permian extinctions (Raup & Sepkoski, 1982; Jin *et al.*, 1994; Stanley & Yang, 1994). Both events had severe effects on marine and terrestrial life, purging 58% of all marine invertebrate genera during the Guadalupian extinction (Knoll *et al.*, 1996) and 70% of the remainder during the Permian extinction (Benton & Twitchett, 2002; Clapham *et al.*, 2009).

According to the reconstruction presented here, *Charinus* and *Sarax* diverged around 216 Mya (95% HPD interval: 178.0–255.8 Mya; Fig. 4). This was a time of recovery from the Permian extinctions, reappearance of new vegetation cover and, consequently, the availability of new niches for terrestrial arthropods (Grauvogel-Stamm & Ash, 2005). Pangaea had moved northwards, northern South America and central Africa were situated across the equator, large parts

of North America were still tropical and whip spiders could presumably occupy much of the Americas and Africa. The divergence between *Charinus* and *Sarax* probably resulted from vicariance events following continental drift.

EARLY EVOLUTION OF THE CHARINID GENERA

Weygoldtia diverged from its closest relatives early in the evolution of Charinidae (257.8 Mya; Fig. 4), but the separation of its two species, *Weygoldtia consonensis* Miranda *et al.*, 2021 and *W. davidovi* (Page 1946) occurred much later, around 72.6 Mya (95% HPD interval: 51.4–97.1 Mya; Campanian, Late Cretaceous). Today, *W. davidovi* occurs in southern Vietnam, whereas *W. consonensis* is endemic to the Con Dao Islands in the South China Sea, c. 90 km south of the mainland. The time of emergence of the Con Dao Islands is unknown, but the archipelago is situated on the broad, shallow continental shelf of the South China Sea, strongly influenced by the East

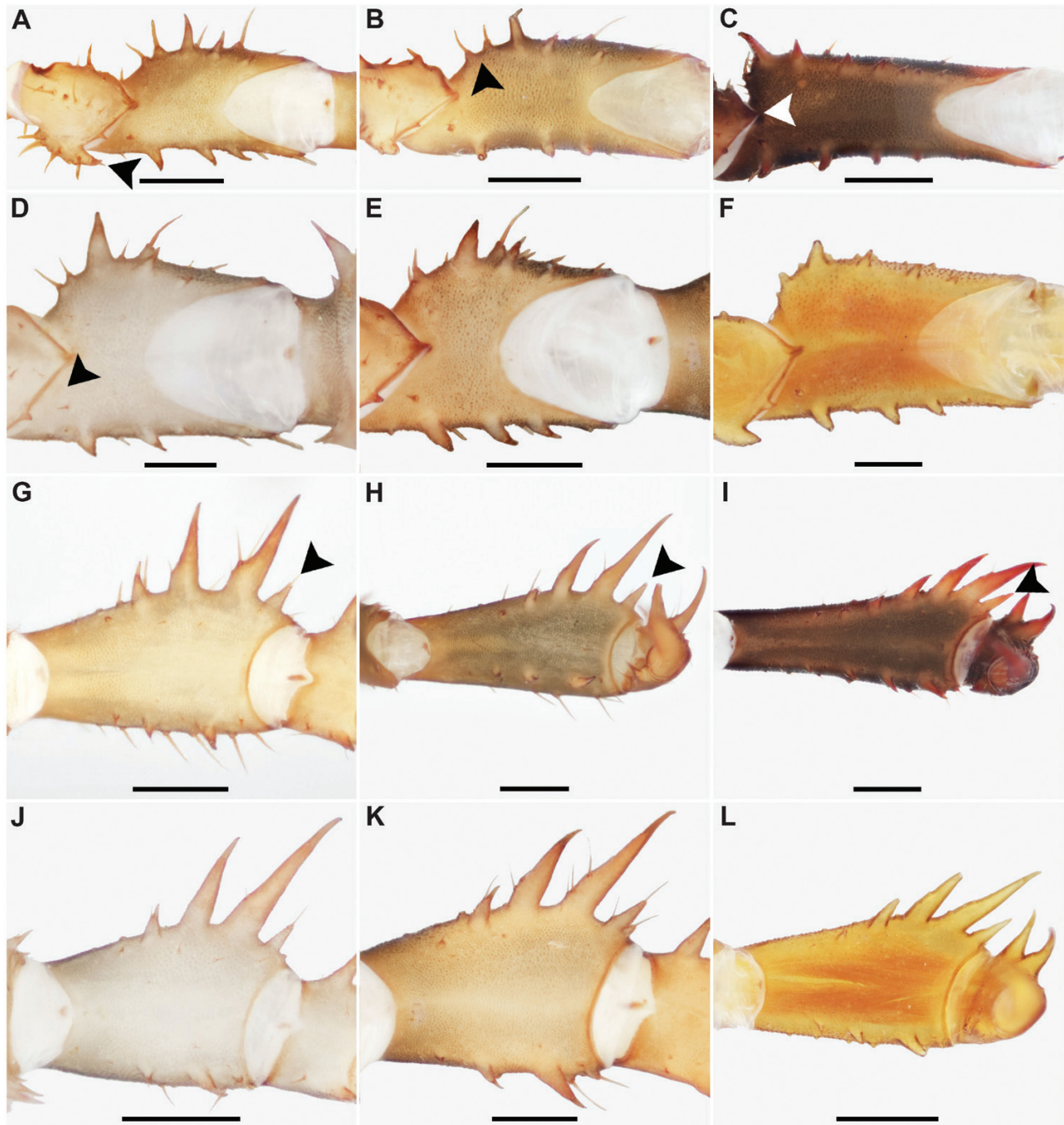


Figure 11. Whip spiders of the family Charinidae [Quintero, 1986](#), pedipalp trochanter, femur and patella, prolateral view illustrating dorsal articulation (hinge) between trochanter and femur (arrow in C; character 56), trochanter with anteriorly directed ventromedian apophysis; arrow-shaped apophysis (arrow in A; character 58), spine or conspicuous setiferous tubercle adjacent to proximal margin or parallel to spine 1 on pedipalp femur (arrow in D; characters 62–64) and projection between spine 1 and distal margin of patella (arrow in G–I; characters 107–112). A, G, *Charinus sillami* Réveillon & Maquart, 2015, ♀ [AMNH (LP 13448)]. B, H, *Charinus palikur* [Miranda et al., 2021](#), ♂ [AMNH (LP 3831)]. C, I, *Charinus gertschi* Goodnight & Goodnight, 1946, ♂ [AMNH (LP 10076)]. D, J, *Sarax bispinosus* (Nair, 1934), ♂ [AMNH (LP 12298)]. E, K, *Sarax cochiniensis* (Gravely, 1915), ♀ [AMNH (LP 13118)]. F, L, *Sarax willeyi* Gravely, 1915, ♀ (SMF 64589). Scale bars: 0.5 mm.



Figure 12. Whip spiders of the family Charinidae [Quintero, 1986](#), pedipalp coxae, dorsal view illustrating semicircular carina (characters 91–97); setae indicated with white dots. A, *Charinus ruschii* [Miranda et al., 2016](#), ♀ (MNRJ 9237). B, *Charinus montanus* [Weygoldt, 1972](#), ♂ (MNRJ 9242). C, *Charinus australianus* (L. Koch, 1867), ♂ (SMF). D, *Charinus koepcke* [Weygoldt, 1972](#), ♀ (SMF 25762). E, *Charinus cavernicolus* [Weygoldt, 2006](#), ♀ (MNHN AM 2). F, *Charinus elegans* [Weygoldt, 2006](#), ♀ (MNHN AM 4). G, *Charinus longipes* [Weygoldt, 2006](#), ♀ (MNHN AM 5). H, *Charinus fagei* [Weygoldt, 1972](#), ♀ (MNHN). I, K, *Sarax indochinensis* [Miranda et al., 2021](#), ♀ (MNHN AM 15). J, *Sarax pakistanus* [Weygoldt, 2005](#), ♂ (SMF 40168). L, *Sarax batuensis* (Roewer, 1962), ♂ (SMF 13906). M, *Sarax rimosus* (Simon, 1901), ♀ (SMF 35614). N, *Sarax willeyi* (Gravely, 1915), ♀ (SMF 64592). O, *Sarax gravelyi* [Miranda et al., 2021](#), ♀ (SMF 62287). P, *Sarax cochinchensis* (Gravely, 1915), ♀ (SMF 64592). Scale bars: 0.5 mm.

Asian monsoon, as well as discharges from the Mekong River ([Dang et al., 2004](#)), suggesting some, if not all, the biota of the archipelago may have dispersed from the South-East Asian mainland.

Among the species of *Sarax*, the most recent common ancestor of the East Asia clade and the clade comprising *S. ioanniticus* and *S. seychellarum*, separated into two distinct lineages around 177 Mya (95% HPD interval:

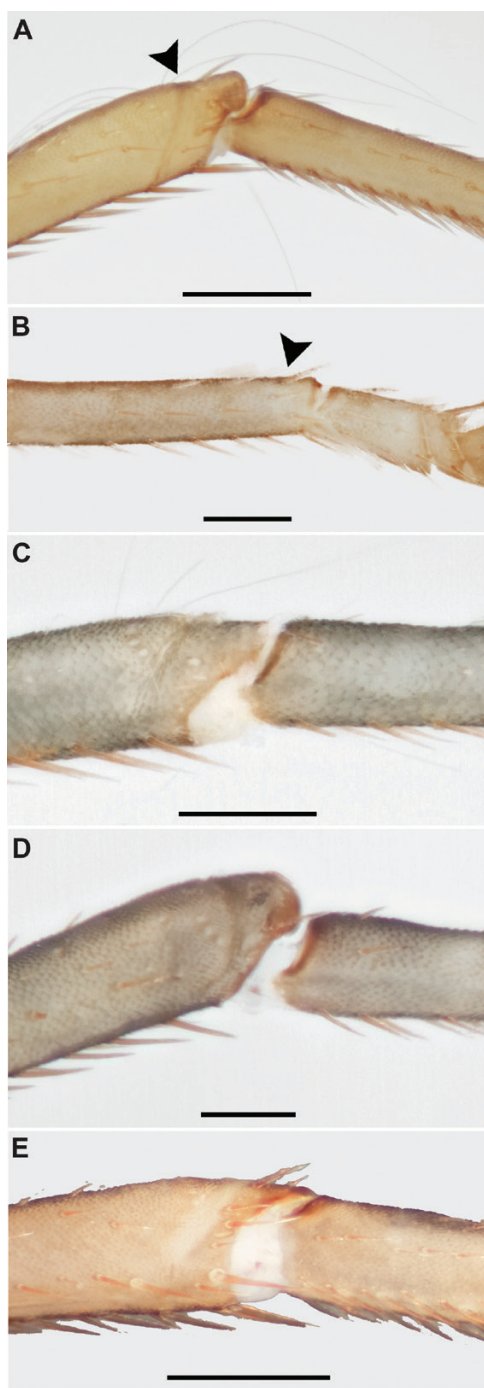


Figure 13. Whip spiders of the family Charinidae [Quintero, 1986](#), leg IV distitibia, lateral view illustrating marked division distal to trichobothria (arrows in A, B; character 131, 137). A, *Charinus insularis* Banks, 1902, ♀ (KBIN). B, *Charinus palikur* [Miranda et al., 2021](#), ♂ [AMNH (LP 3831)]. C, *Sarax bispinosus* (Gravely, 1915), ♂ [AMNH (LP 12298)]. D, *Weygoldtia davidovi* Fage, 1946, ♀ [AMNH (LP 11377)]. Scale bars: A, B, E, 0.5 mm; C, D, 0.3 mm.

143.9–211.4 Mya; Toarcian, Early Jurassic). During the Early Jurassic, Pangaea began to fragment, with the landmass comprising the precursors of South America and Africa (West Gondwana) separating from the landmass comprising the precursors of Antarctica, Australia, India, Madagascar and Seychelles (East Gondwana) ([Ali & Aitchison, 2008](#)). The divergence between the East Asia clade and the clade comprising *S. ioanniticus* and *S. seychellarum* followed the separation of those supercontinents. Species of the East Asia clade currently occur in South-East Asia and part of Oceania and Melanesia, whereas the clade comprising *S. ioanniticus* and *S. seychellarum*, including the species transferred from *Charinus* to *Sarax*, occur in the eastern Mediterranean, East Africa, the Arabian Peninsula, the Seychelles and Pakistan ([Miranda et al., 2021](#)).

The species in the clade comprising *S. ioanniticus* and *S. seychellarum* drifted with Africa and the Arabian Peninsula during the Cretaceous before attaining their current distributions. During Late Miocene (c. 10 Mya), the Afro-Arabian plate reached the Eurasian plate and the *Sarax* species dispersed from the Arabian Peninsula to mainland Asia, eventually attaining their current distribution ([Zhang et al., 2014](#)). The presently arid climate of the Middle East and the Arabian Peninsula restricts living species of *Sarax* almost exclusively to caves, e.g. *Sarax dhofarensis* ([Weygoldt et al., 2002](#)), *Sarax israelensis* ([Miranda et al., 2016](#)), and *Sarax stygochthobius* ([Weygoldt & Van Damme, 2004](#)).

The ancestor of the species in the East Asia clade probably reached South-East Asia and Melanesia by rafting from Australia, as no Indonesian islands existed at that time ([Hall, 2012](#)), or by rafting on landmasses detached from Gondwana, such as the Western Burma Block ([Poinar, 2018](#)). This hypothesis is supported by evidence that the peak of *Sarax* diversification occurred during the Cretaceous, a prolific time for life on Earth ([Shear & Kukalova-Peck, 1990](#)).

The timing of divergence between the clades comprising *Sarax brachydactylus* Simon, 1872 and *Sarax bilua* [Miranda et al., 2021](#), from the Philippines and the Solomon Islands, respectively, and the clade comprising *Sarax cochinchensis* (Gravely, 1915) and *Sarax bispinosus* (Nair, 1934), from India and Sri Lanka, respectively, occurred during the Lower Cretaceous, before India reached Asia. The presence of this clade in South Asia can only be explained by dispersal after the Indian continent reached Asia during the Eocene (c. 40 Mya) ([Ali & Aitchison, 2008](#)), a pattern demonstrated by some other terrestrial invertebrates (e.g. [Köhler & Glaubrecht \(2007\)](#)). Further evidence of an early Gondwanan origin for *Sarax* is the presence

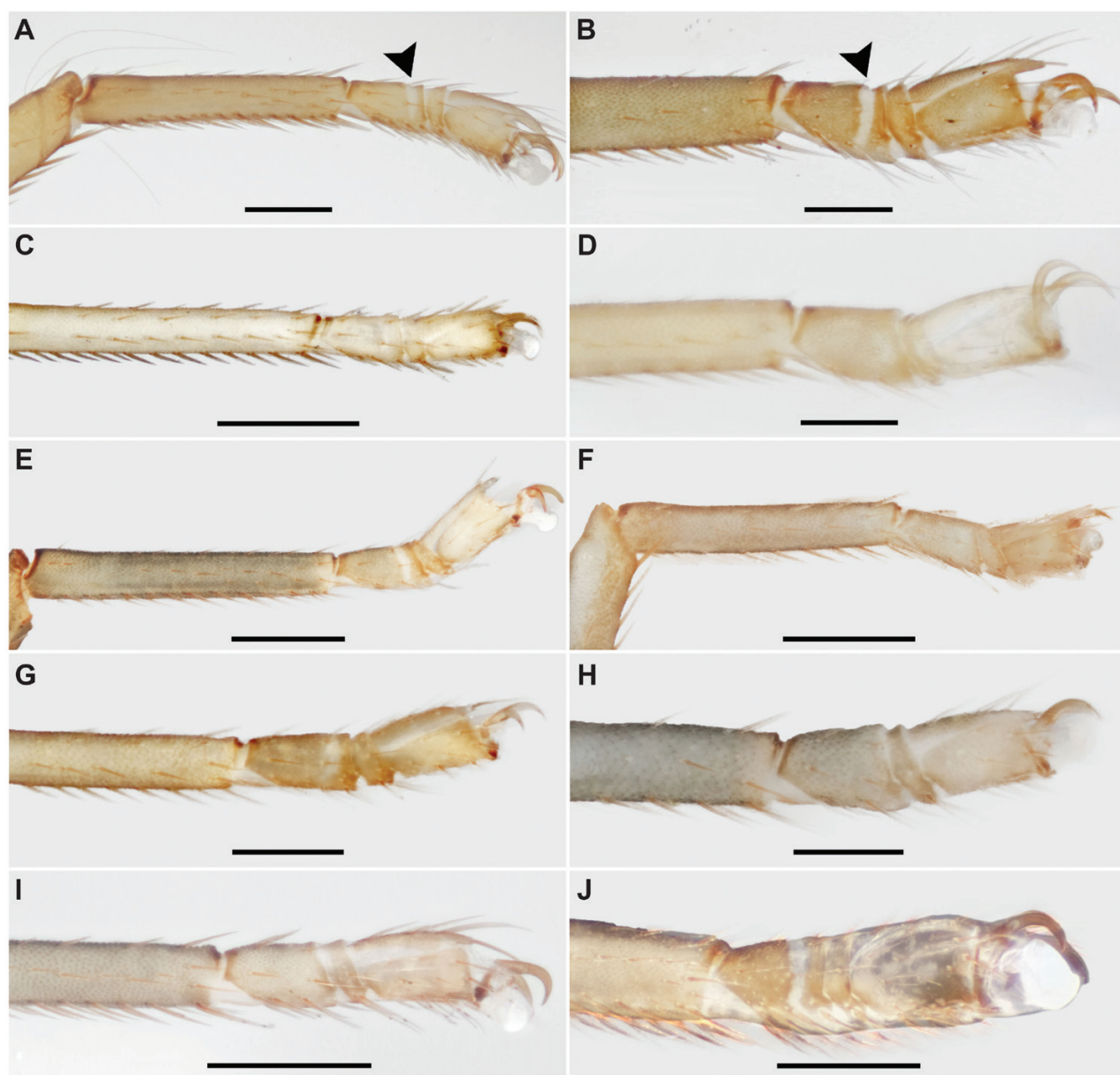


Figure 14. Whip spiders of the family Charinidae [Quintero, 1986](#), leg IV second tarsal segment, lateral view illustrating presence and extent of weakly sclerotized area (arrows in A, B; characters 135, 136). A, *Charinus insularis* Banks, 1902, ♀ (KBIN). B, *Charinus pescotti* Dunn, 1949, ♂ [AMNH (LP 6367)]. C, *Charinus belizensis* Miranda *et al.*, 2016, ♂ (HUJ INV AMB 117). D, *Sarax pakistanus* ([Weygoldt, 2005](#)), ♂ (MHNG). E, *Sarax seychellarum* ([Kraepelin, 1898](#)), ♀ [AMNH (LP 9075)]. F, *Charinus palikur* [Miranda *et al.*, 2021](#), ♂ (AMNH LP 3831). G, *Charinus sillami* Réveillon & Maquart, 2015, ♀ [AMNH (LP 13448)]. H, *Sarax bispinosus* (Nair, 1934), ♂ [AMNH (LP 12298)]. I, *Sarax cochinchensis* Gravely, 1915, ♀ [AMNH (LP 13118)]. J, *Weygoldtia davidovi* (Fage, 1946), ♂ [AMNH (LP 11377)]. Scale bars: A, B, C, E, F, I, J, 0.5 mm; D, 0.25 mm; G, 0.4 mm; H, 0.3 mm.

of the genus on the Sahul Shelf, the continental shelf uniting the Australian continent and New Guinea, which is of Gondwanan origin ([Atkins *et al.*, 2001](#)). The early divergence between *Sarax willeyi* Gravely, 1915, from New Guinea, and all other species of the East Asia clade, adds additional evidence for the hypothesis

that species of *Sarax* dispersed northwards from Gondwanaland.

How *Sarax* came to occupy the islands of the Indo-Pacific is difficult to answer with the current dataset due to a shortage of records from those islands and samples for molecular divergence dating. The

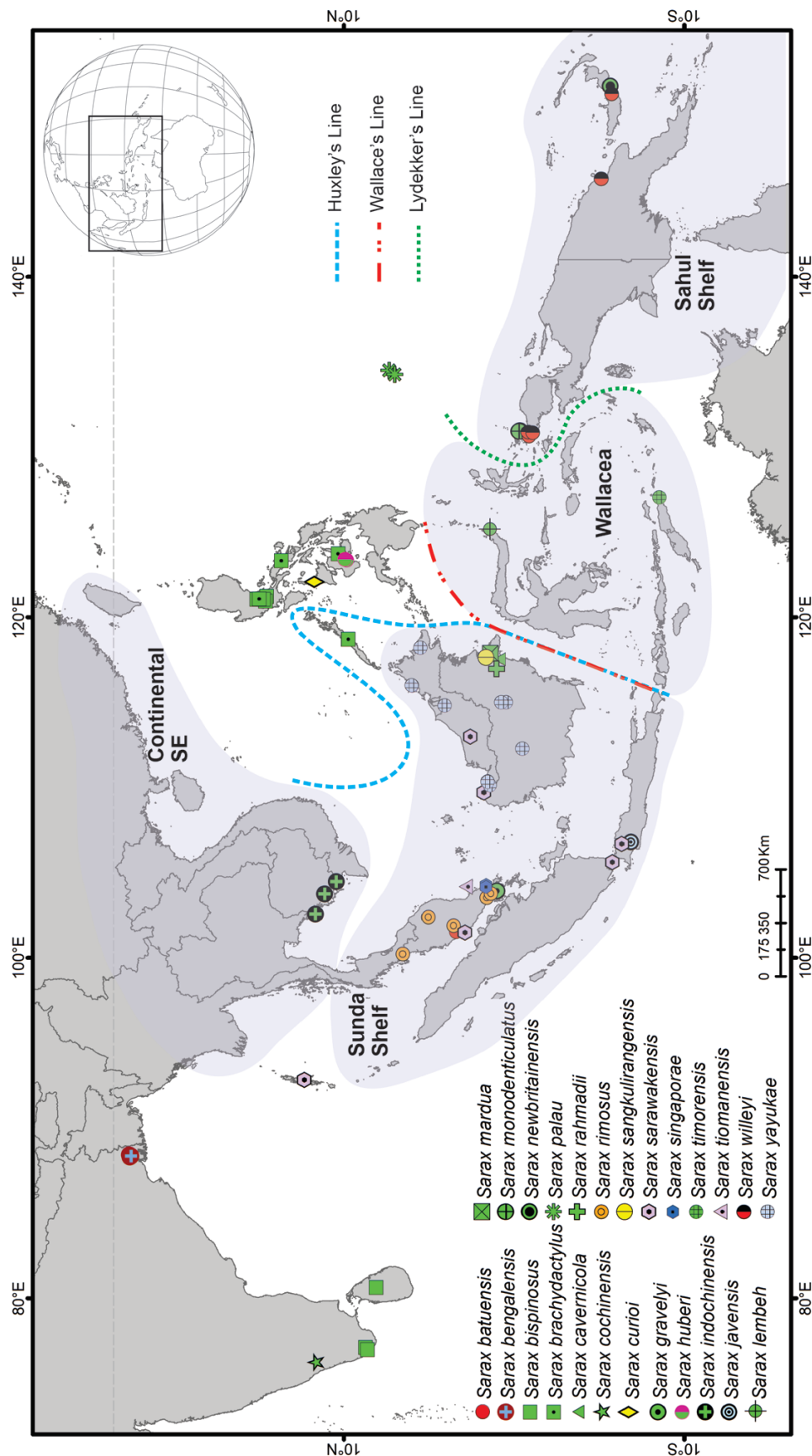


Figure 15. Contemporary islands and biogeographical divisions of the Indo-Pacific Archipelago, modified from [Lohman *et al.* \(2011\)](#), illustrating distributions of *Sarax* Simon, 1872 whip spiders in the region. Map includes all species known from the region, including those excluded from the study due to absence of samples for analysis, such as *S. cavernicola* [Rahmadi *et al.*, 2010](#), *S. curioi* [Giupponi & Miranda, 2012](#), *S. mardua* [Rahmadi *et al.*, 2010](#), *S. monodenticulatus* [Rahmadi & Kojima, 2010](#), *S. newbritannensis* [Rahmadi & Kojima, 2010](#), *S. sangkulirangensis* [Rahmadi *et al.*, 2010](#), *S. timorensis* [Miranda & Reboleira, 2019](#).

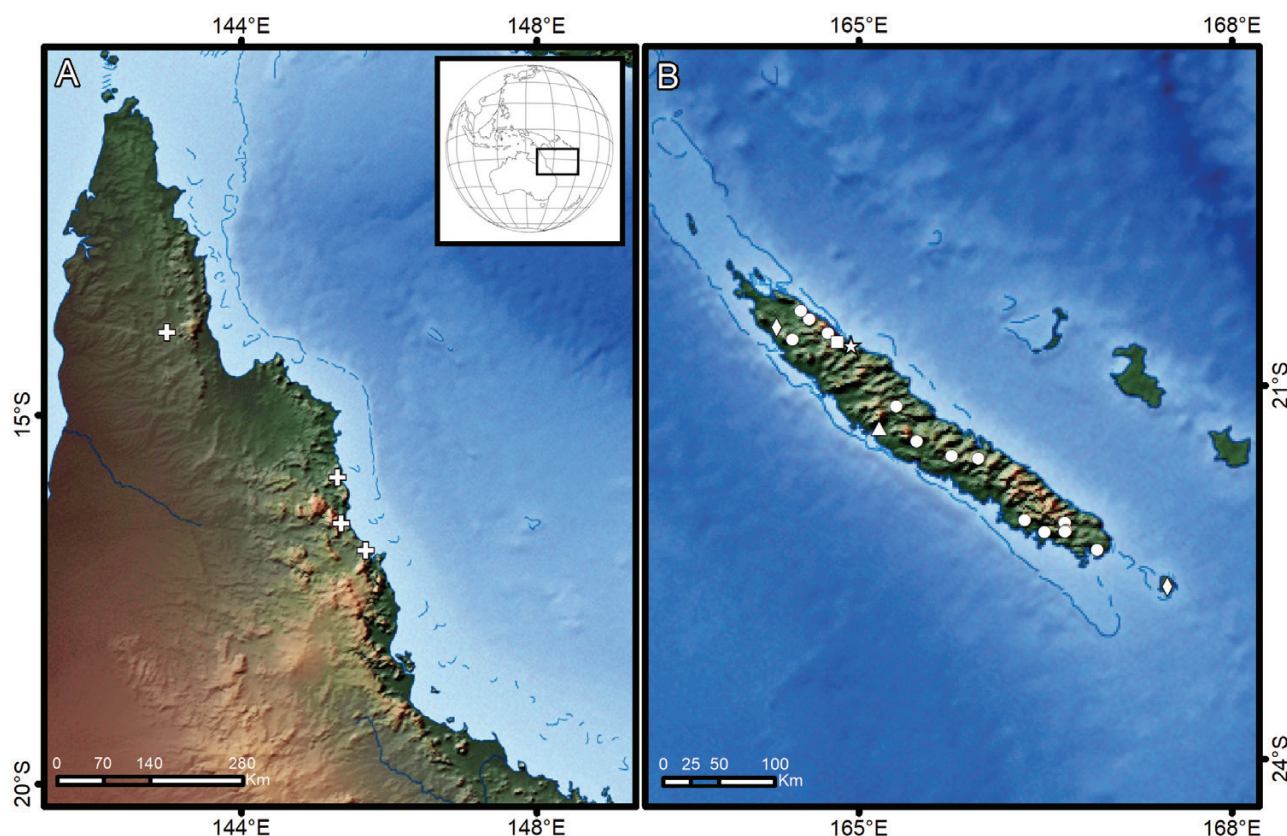


Figure 16. Distributions of the Australian (A) and New Caledonian (B) species of *Charinus* Simon, 1892 whip spiders: *Charinus cavernicolus* Weygoldt, 2006 (diamond); *Charinus elegans* L. Koch, 1867 (triangle); *Charinus longipes* Weygoldt, 2006 (star); *Charinus neocaledonicus* Simon in Kraepelin, 1895 (circles); *Charinus pecki* Weygoldt, 2006 (square); *Charinus pescotti* Dunn, 1949 (cross).

Indonesian Archipelago, for example, comprises more than 20 000 islands and is among the most geographically complex tropical regions on Earth (Lohman *et al.*, 2011; Tänzler *et al.*, 2014). The archipelago has undergone many geological changes over the past million years (Lohman *et al.*, 2011) and the changes that resulted in its present configuration occurred over the last 60 Mya, a time frame younger than most branches on the *Sarax* tree. However, one interpretation is offered for the current distribution of the species in the next section.

DISTRIBUTION AND BIOGEOGRAPHY OF ASIAN CHARINIDAE

The study of faunal changes in South-East Asia dates to the earliest zoogeographical investigations by Müller (1846), Sclater (1858) and Wallace (1860, 1869). Several zoogeographical 'lines' have been proposed to demarcate the limits between faunas with Laurasian and Gondwanan origins in South-East Asia (Simpson, 1977; Atkins *et al.*, 2001), but the most widely accepted

are Wallace's Line, Huxley's Line and Lydekker's Line (Fig. 13) (Lohman *et al.*, 2011). Wallace's Line (Huxley, 1868) separates Asia and a transitional zone between Asia and Australia (Wallace, 1860). Species occurring to the west of the line are usually more closely related to Asiatic species, whereas species to the east are a mix of Asian and Australasian species (Tänzler *et al.*, 2014).

In accordance with Wallace's Line, two clades of *Sarax* occur on the Sunda shelf: the *brachydactylus* clade, comprising species on the Malay Peninsula, which is sister to *S. indochinensis* from Continental South-East Asia; and the *singaporae* clade, comprising species mostly present on the Sunda shelf and sister to a clade comprising species found in Wallacea (Fig. 15). Another pattern is illustrated by the *Sarax* species from Bali, which is most closely related to the species from Borneo and Malaysia, again in accordance with Wallace's Line. On the other hand, the two species occurring west of Wallace's Line, *S. bilua* and *S. brachydactylus*, are more closely related to the South Asian taxa, *S. bispinosus* and *S. cochinchensis*. Also ignoring biogeographical lines, *S. brachydactylus*

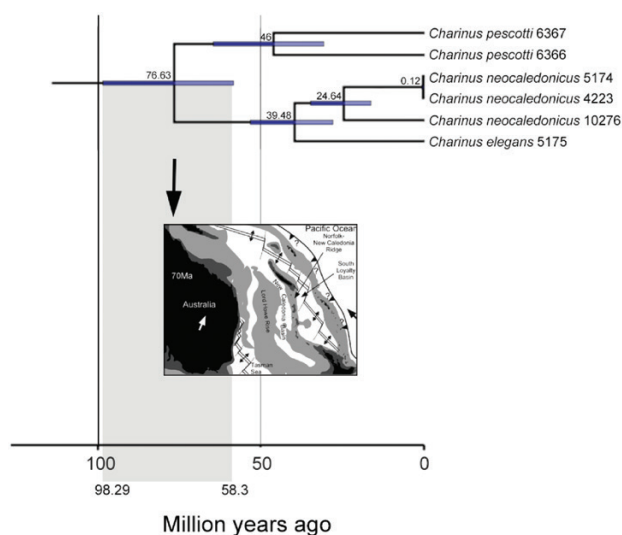


Figure 17. Phylogeny of the whip spider genus *Charinus* Simon, 1892: excerpt of tree obtained by analysis with BEAST, showing divergence between clades of Australian *Charinus pescotti* Dunn, 1949 and Neocaledonian *Charinus neocaledonicus* Kraepelin, 1895 and *Charinus elegans* Weygoldt, 2006. Paleomap of part of Oceania at 70 Mya, modified from Crawford *et al.* (2003).

occurs on either side of Huxley's Line, on Palawan as well as on the main islands of the Philippines.

Sarax sarawakensis (Thorell, 1888) was the first species to be described in the genus (Thorell, 1888) and, for many years, all *Sarax* species from South-East Asia were assigned to it (Fage, 1929; Weygoldt, 1994). As currently defined, *S. sarawakensis* is restricted to the Sunda Shelf, extending from the Andaman Islands to Java. Its wide distribution may be explained by dispersal, as it is an epigaeic species (Rahmadi *et al.*, 2010), but might also be an artefact of the poor understanding of its taxonomy. For example, records of *S. sarawakensis* from the Andaman Islands, Peninsular Malaysia and Java (Rahmadi *et al.*, 2010), may prove to be different species upon closer examination.

Despite occurring in New Guinea, species of *Charinus* have not been recorded from the Indonesian Archipelago (Fig 2). *Charinus* has only been recorded on the Sahul Shelf and there are no records west of Wallace's Line. This does not appear to be a sampling artefact, as the amblypygid fauna of South-East Asia is fairly well known. The absence of *Charinus* from the Indonesian Archipelago suggests they never got there.

Diversification events linked to divergence dates among the basal clades of *Charinus* are difficult to estimate due to the limited data available for the genus in the present study (c. 13% of the described species diversity). Therefore, the remaining discussion

focuses on the *Charinus* of New Caledonia, a clade with comprehensive taxonomic and geographical sampling.

NEW CALEDONIAN *CHARINUS* AS GONDWANAN RELICTS

New Caledonia is a tropical island in the south-western Pacific with a remarkably diverse and largely endemic fauna and flora (Grandcolas *et al.*, 2008). Despite being connected to the western part of Australia until 80 Mya as part of an old Gondwana tectonic plate, much of the biota of the island is thought to be the product of recent diversification after colonization during the Pliocene–Pleistocene (Muriénne *et al.*, 2005). Stratigraphical and fossil evidence strongly support the hypothesis that New Caledonia was completely submerged during the Palaeocene–Eocene, suggesting the biota on this island is the result of recolonization after the island re-emerged during the Oligocene, consistent with studies of molecular dating (Grandcolas *et al.*, 2008).

However, exceptions to this hypothesis exist (Giribet & Baker, 2019). For example, Mathews & Donoghue (1999) placed *Amborella trichopoda* Baill. (Amborellaceae), an angiosperm endemic to New Caledonia, as the sister-group of all flowering plants, a position supported to this day (Drew *et al.*, 2014; APG, 2016). The near-flightless kagu bird, *Rhynchotus jubatus* Verreaux & DesMurs, 1860, is also endemic to New Caledonia, with its closest relatives occurring in New Zealand and South America (Cracraft, 2001). Boyer *et al.* (2007) discovered a lineage of endemic harvestmen, Troglosironidae Shear, 1993, in New Caledonia with sister-lineages in South America and West Africa. The most parsimonious explanation for the presence of these endemic taxa in New Caledonia would appear to be as Gondwanan relicts (Giribet & Baker, 2019). However, Grandcolas *et al.* (2008) argue that the absence of sister-taxa on nearby landmasses, such as Australia or New Zealand, requires the assumption of many extinction events, while not providing much biogeographical and temporal information.

Whip spiders of the genus *Charinus* provide a unique model system for understanding the biogeographical history of New Caledonia. Five species are endemic to the island: *Charinus neocaledonicus* Simon in Kraepelin, 1895 is widespread and can be considered a regional endemic, whereas the other four, *Charinus cavernicolus* Weygoldt, 2006, *Charinus elegans* L. Koch, 1867, *Charinus longipes* Weygoldt, 2006 and *Charinus pecki* Weygoldt, 2006, are local endemics restricted to caves (Fig. 16) (Weygoldt, 2006).

In the phylogeny presented here, *Charinus pescotti* Dunn, 1949, from Queensland, Australia, groups with *Charinus papuanus* Weygoldt, 2006, from Papua New Guinea. This clade is in turn placed sister to

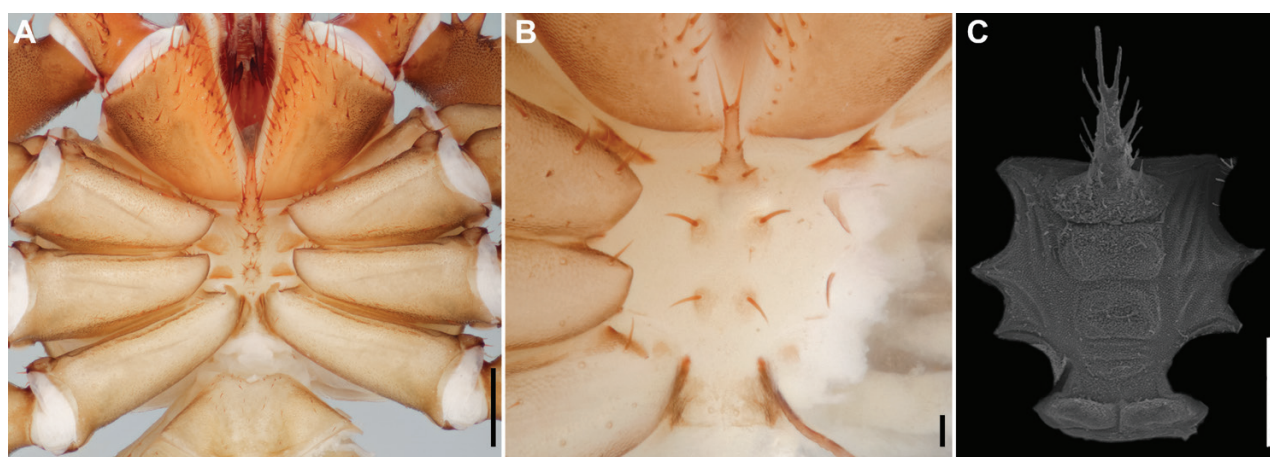


Figure 18. Whip spiders of the family Charinidae (Quintero, 1986, sternum, ventral view (characters 15, 16) A. *Sarax tiomanensis* Miranda *et al.*, 2021, ♂ (AMCC [LP 12001]), B. *Charinus cubensis* (Quintero, 1983), ♀ (USNM 784407), C. *Charinus montanus* Weygoldt, 1972, ♀ (MNRJ 9087). Scale bars: 1 mm.

C. cavernicolus and *C. pecki*, both from New Caledonia. All four species are placed sister to another clade, comprising *C. elegans* and *C. neocaledonicus*.

Only three species of this clade, *C. elegans*, *C. neocaledonicus* and *C. pescotti*, are included in the molecular dating analysis (Fig. 17). The suggested divergence date between the Australian and New Caledonian clades is *c.* 76 Mya, slightly more recent than the separation of the two landmasses (Fig. 17). The recent divergence date could be attributed to the conservative approach used in the analysis for the oldest calibration point for Amblypygi, which shares several similarities with extant taxa, implying that the Amblypygi stem lineage is probably older. The time interval estimated by the BEAST analysis is between 98.3 and 58.3 Mya (Fig. 17), hence the only possible explanation for the presence of *Charinus* in New Caledonia is that these taxa are Gondwanan relicts. The divergence date for two of the species endemic to New Caledonia, i.e. *C. elegans* and *C. neocaledonicus*, is estimated at *c.* 37 Mya (95% HPD interval: 27.9–53.0 Mya), during the Oligocene, the period in which New Caledonia re-emerged (Cluzel *et al.*, 2001, 2012).

The absence of *Charinus* or any other Amblypygi from New Zealand might be attributed to extinction, after the temperate climate of that island became unsuitable for continued survival. The only charinid known to occur south of the Tropic of Capricorn is *Charinus asturius* Pinto-da-Rocha *et al.*, 2002, occurring at 23°44'S 45°19'W, in the Brazilian Atlantic rainforest, a region with a stable, tropical climate, different from New Zealand. Another possibility is that *Charinus* species never occurred in New Zealand, which has a unique terrestrial invertebrate fauna composed of relictual temperate taxa (Giribet & Boyer, 2010).

Charinus australianus, another Melanesian species, was not included in the dated analysis but was placed sister to *C. insularis* from the Galapagos Islands. Most of the taxa occurring on the Galapagos Islands, a young oceanic and volcanic archipelago, are closely related to the taxa of Central and South America (Parent *et al.*, 2008). This unexpected relationship could be an artefact of the lack of knowledge about whip spiders in that part of South America or additional evidence for an eastward trans-Pacific dispersal event involving a terrestrial invertebrate, as observed in the landsnail genus *Tornatellides* Pilsbry, 1910 and the spider genus *Desis* Walckenaer, 1837 (Carlquist, 1965; Grehan, 2001). Such a dispersal event might have happened if an ancestral population of *Charinus* was carried from Melanesia to the Pacific Coast of South America by the eastward flowing Pacific Equatorial Countercurrent, but such events are rare (Dennis & Gunn, 1971).

WHY ARE THERE SO FEW SPECIES OF AMBLYPYGI?

Despite the recent increase in described species, Amblypygi remains a low-diversity arachnid order (Harvey, 2003). The small number of living and fossil species suggests Amblypygi was never diverse. The close resemblance between the oldest fossil taxon, *Weygoldtina anglica*, and the living *Paracharon caecus* Hansen, 1921, implies a conservative groundplan (Weygoldt, 1999c). Unlike their close relatives, the spiders, for which the evolution of silk facilitated diversification into new habitats and adaptation to a broader range of prey (Fernández *et al.*, 2018), few novelties appeared in the evolution of whip spiders. Whip spiders appear to have always occupied the same niche as ambush predators on rock surfaces and tree trunks, among the leaf litter or

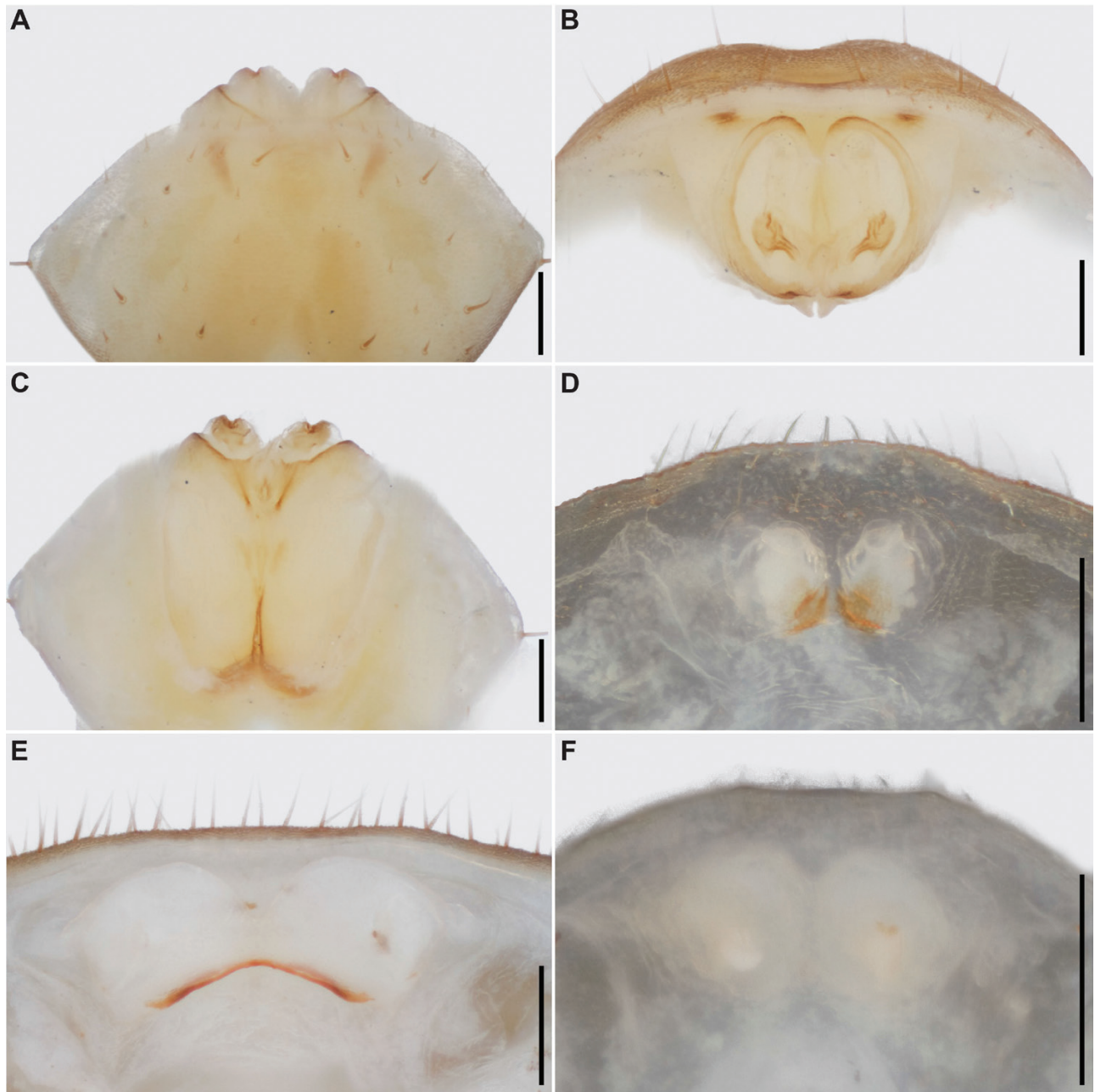


Figure 19. Whip spiders of the family Charinidae [Quintero, 1986](#), male and female gonopods, ventral view (characters 36–46). A–C, *Sarax pakistanus* ([Weygoldt, 2005](#)), ♂ (MHNG). D, *Charinus brasiliensis* [Weygoldt, 1972](#), ♀ (MNRJ 9232). E, *Charinus gertschi* Goodnight & Goodnight, 1946, ♀ (AMNH [LP 10076]). F, *Charinus cubensis* ([Quintero, 1983](#)), ♀ (USNM ENT 784407). Scale bars: 0.25 mm.

inside caves, not exploring three-dimensional habitats in the vegetation, like web-building spiders, for example. Even extant whip spiders inhabiting vastly different habitats, such as the Amazon rainforest (*Charinus*) and the Namib Desert (*Xerophrynus* [Weygoldt, 1996](#)), share most characters besides differences in their physiological tolerance for temperature and humidity.

Stabilizing selection, when slightly deleterious, and advantageous mutations (i.e. neutral variations) reach fixation at a similar rate by the process of genetic drift ([Kimura, 1981](#)), has been suggested to explain the low diversity of Amblypygi ([Weygoldt, 2000](#)). Amblypygi appear to have developed the required physiological and morphological adaptations early in

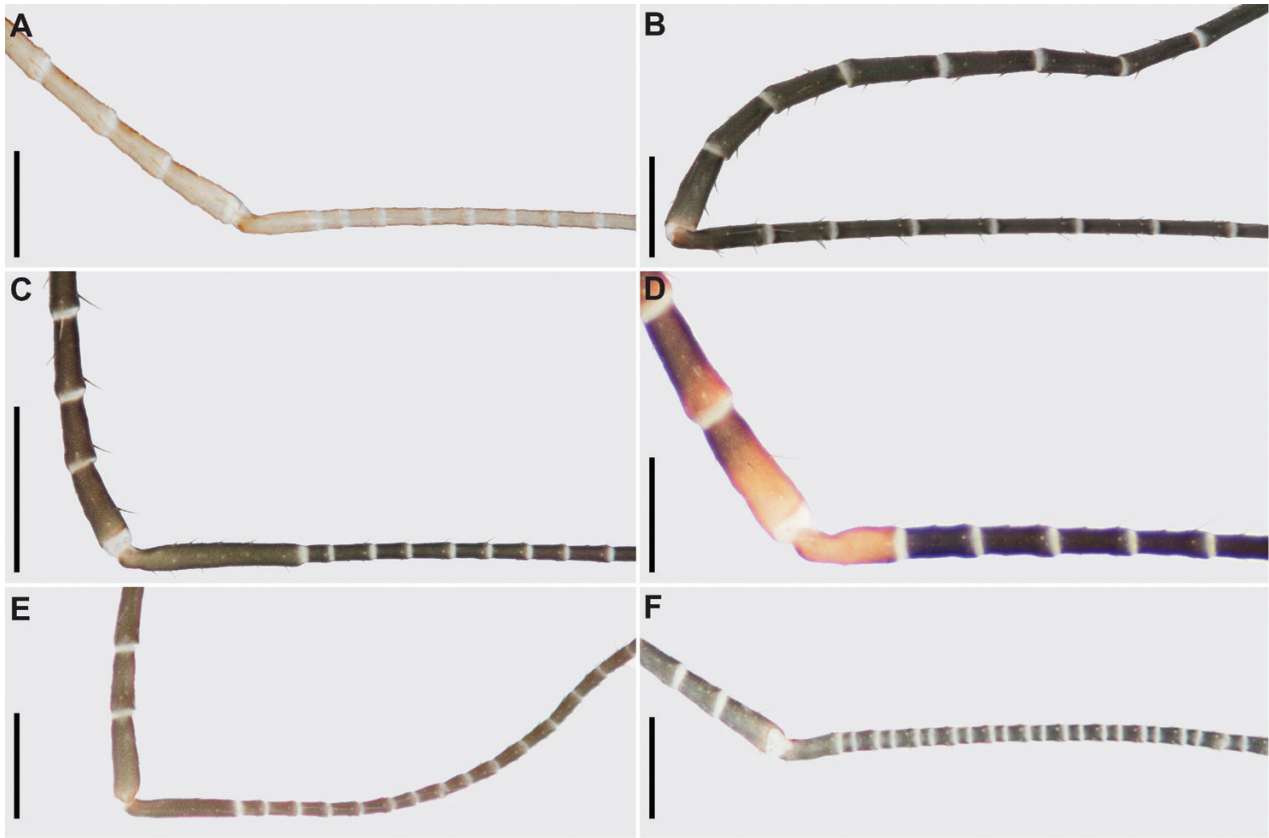


Figure 20. Whip spiders of the family Charinidae Quintero, 1986, tarsus I, lateral view illustrating size of first (proximal) article (character 53); note regenerated leg in (F), where total number of articles is augmented compared to 'normal' leg. A, *Charinus belizensis* Miranda *et al.*, 2016, ♂ (HUI INVAMB 117). B, *Sarax seychellarum* (Kraepelin, 1898), ♀ [AMNH (LP 9075)]. C, *Charinus pescotti* Dunn, 194 [AMNH (LP 10076)]. E, *Charinus palikur* Miranda *et al.*, 2021, ♂ [AMNH (LP 3831)]. F, *Sarax bispinosus* (Nair, 1934), ♂ [AMNH (LP 12298)]. Scale bars: 0.5 mm.

their evolution and, despite past changes in global climate, managed to surpass major extinction events by finding stable habitats in refugia such as forest remnants and caves, thereby avoiding the selection pressures that would have induced evolutionary novelty.

The relatively long generation times of whip spiders may perhaps also explain why most families of Amblypygi are not diverse. Among Charontidae, Phrynichidae and Phrynidae, embryonic development takes about three months and time to sexually maturity about one to two years (Weygoldt, 2000). The family Charinidae includes smaller species with faster generation times and some parthenogenetic species produce eggs even as small juveniles (Armas, 2000; Weygoldt, 2007; Seiter & Wolff, 2014). Perhaps because of their faster generation times, Charinidae is the most speciose family in the order.

CONCLUSIONS

The phylogenetic analysis of Charinidae presented here provides the first estimate of relationships among the genera and species of the family, divergence dates for its major clades, and a framework for its classification, on the basis of which nine species possessing a finger-like female gonopod, formerly assigned to *Charinus*, are transferred to *Sarax* (Miranda *et al.*, 2021). Multilocus DNA sequence data and morphology greatly assisted the phylogenetic reconstruction. The efficacy of the molecular data suggests that the collection of more tissue samples, both for Sanger-dideoxy DNA sequencing and phylogenomics, should be prioritized in future.

Most currently known species of Amblypygi were described based on characters of the somatic and genitalic morphology. As in many other taxa, research based on DNA sequence data has revealed cryptic

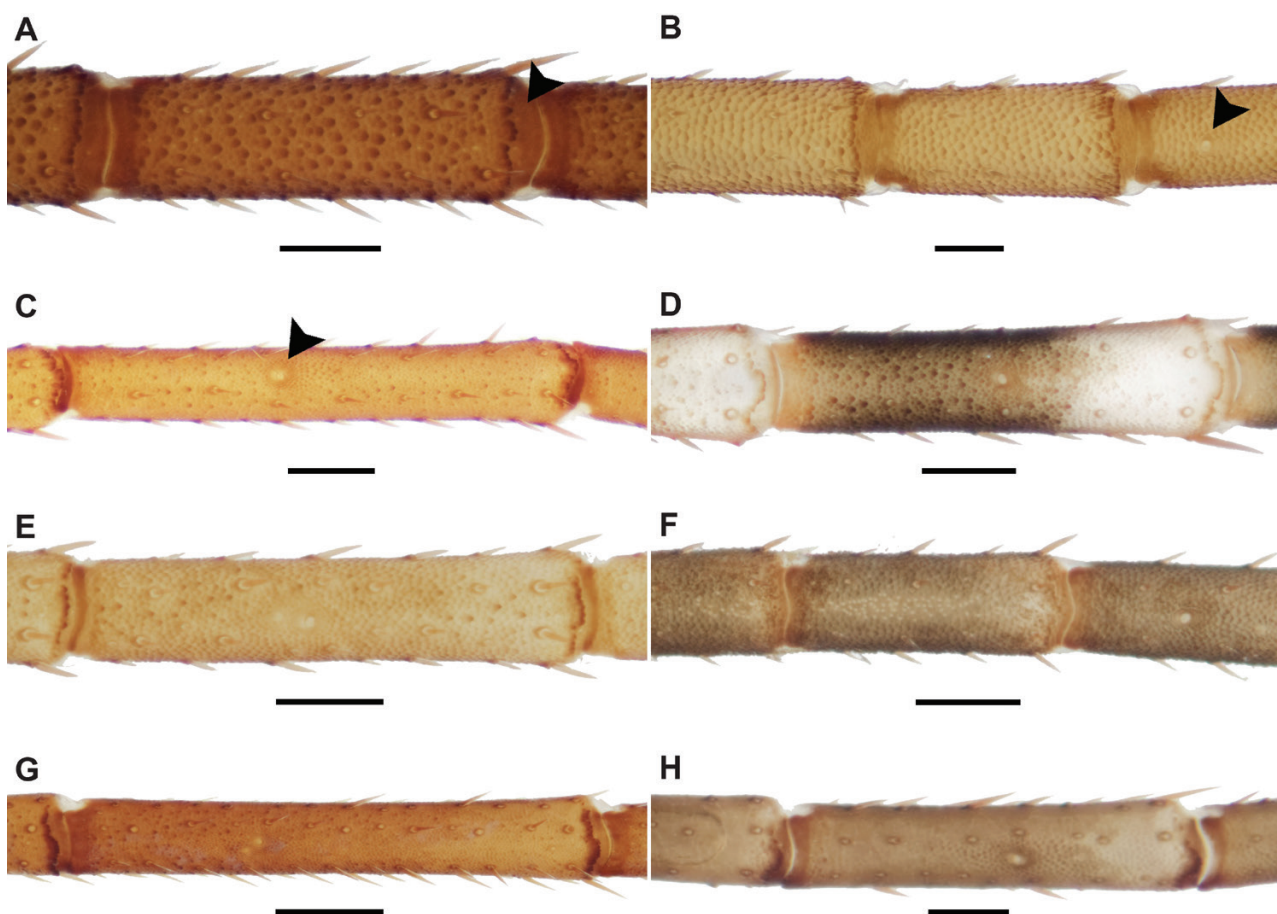


Figure 21. Whip spiders of the family Charinidae Quintero, 1986, leg IV basitibia, dorsal view illustrating strongly sclerotized denticulate border, projecting (or not) from distal apex (arrow in A; characters 121–124), and position of trichobothria *bt* on distal article (arrows in B, C; character 120). A, *Charinus insularis* Banks, 1902, ♀ (KBIN). B, *Sarax pakistanus* (Weygoldt, 2005), ♂ (MHNG). C, *Charinus carioca* Miranda et al., 2021, ♀ (MNRJ 9201). D, *Charinus gertschi* Goodnight & Goodnight, 1946, ♂ [AMNH (LP 10076)]. E, *Charinus souzai* Miranda et al., 2021, ♀ (MNRJ 9090). F, *Charinus pescotti* Dunn, 1949, ♂ [AMNH (LP 6367)]. G, *Charinus goitaca* Miranda et al., 2021, ♂ (MNRJ 9224). H, *Sarax yayukae* Rahmadi et al., 2010, ♂ [AMNH (LP 12109)]. Scale bars: A, D, E, F, H, 0.25 mm; B, 0.3 mm; C, G, 0.5 mm.

diversity (Prendini et al., 2005; Esposito et al., 2015). Whip spider species, with broad distributions and variation in pedipalp spine number and female genitalia shape, such as *Charon grayi* (Gervais, 1842) (Charontidae), *Damon variegatus* C. L. Koch, 1850, *Phrynichus orientalis* Weygoldt, 1998 (Phrynichidae), *Heterophrynus longicornis* (Butler, 1873) (Phrynidae) and *Sarax yayukae* (Charinidae), may comprise more species than presently recognized (Prendini et al., 2005; Rahmadi et al., 2010; Miranda et al., 2018b; Miranda & Zamani, 2018). Continued research into the molecular systematics of Amblypygi will likely provide a more accurate assessment of the ordinal diversity.

Nevertheless, there remains room for the development of morphological characters that, in combination with molecular data, may help to resolve clades while

providing diagnostic characters at higher and lower levels in the taxonomic hierarchy. The morphological characters revised and newly generated in the present study, together with new microstructural data from the integument (Wolff et al., 2015b, 2016, 2017), provide phylogenetically informative data that should be further explored. Scanning electron microscopy has scarcely been applied in studies of Amblypygi morphology, hence a substantial amount of new phylogenetic data can be expected from this technique.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of material examined.

Appendix S2. List of GenBank accession codes.

Appendix S3. Supplemental figures.

Figure S1. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Matrix pruned to include only taxa with both molecular and morphological data. Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S2. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and equal weighting.

Figure S3. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and implied weighting with $k = 6$.

Figure S4. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and implied weighting with $k = 10$.

Figure S5. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and implied weighting with $k = 20$.

Figure S6. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and implied weighting with $k = 30$.

Figure S7. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with parsimony and implied weighting with $k = 40-90$.

Figure S8. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with Bayesian inference. Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S9. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Tree based on morphological characters analysed with Mkv model. Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S10. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Gene tree of fragments 12S and 16S (partition 1). Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S11. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Gene tree of 18S, 28S and *COI* third-codon position (partition 2). Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S12. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Gene tree of *COI* first-codon position (partition 3). Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

Figure S13. Phylogeny of the whip spider family Charinidae [Quintero, 1986](#) reconstructed with maximum likelihood. Gene tree of *COI* second-codon position (partition 4). Green, *Weygoldtia* [Miranda et al., 2018](#); yellow, *Sarax* Simon 1892; blue, *Charinus* Simon 1892.

APPENDIX 1

Morphological matrix of four outgroup taxa and 92 ingroup taxa (plus three morphospecies of *Sarax*) used for phylogenetic analysis of the whip spider family Charinidae [Quintero, 1986](#). Numbers following some taxon names refer to samples in Ambrose Monell Cryocollection at the American Museum of Natural History, from which DNA sequences were generated. Character states scored numerically from 0 to 7, polymorphic states indicated within [], inapplicable states are denoted with -, and unknown/missing

entries with question marks. Character descriptions provided in Appendix 2. Material examined provided in Supplementary material (Appendix S1).

OUTGROUP

STENOCHRUS SBORDONII 3757

10--0--00- 0-00000--- 50--10010-?0--0000--
 ---0????0- 001-??1000 --0---00-- ----- --0-00---0
 0-0----- -----0 0-000----- ---1000-

MASTIGOPROCTUS AFF. *GIGANTEUS* 3509

110411010- 0010000--- 00--0-040- 0130002010
 --00???0- 000-??1001 0710--000-?0-----0 100-10---1
 0-0----- 10001-0--- -----1 0-000----- --1000-

DAMON *DIADEMA* 1479

011411110- 0010121110 0100111410 21[12]1002010
 --0010??12 17022?0101 0611120151 14111-0310
 00100110-1110---1-04011500-----110---111100111106
 7100010-

PHRYNUS *LONGIPES* 1483

011411110- 0010101111 0110111211 21[12]00020??
 1?-1011112 070?2?0001 0110--0050 0211111013
 -010011--11105-----23010401122--2-0---112100100105
 61000110

INGROUP

CHARINUS *ACARAJE*

010111110 0?10101100 1100100311 3130002000
 --11????11 0402??0001 1101110030 020000---0
 11110120-0 111200-01- 30002110-- 0011111110
 3011100102 21101010

CHARINUS *AFRICANUS* 6943

010111110- 0010101100 1100100210 3120004001
 0-21000011 0402??0001 1101000020 010000---0
 11110110-0 111201001- 20002110-- 0011112110
 3111100101 11101010

CHARINUS *AGUAYOI* 10170

010110110- 0010111100 1100100210 2110002000
 --0011??11 0312??0001 1101010020 010-00---0
 11100110-0 111200-01- 20002110-- 0011112310
 2000100101 11101010

CHARINUS *ALAGOANUS*

010111110 0010101100 1100110210 3120002000
 --11????11 0412??0001 1101110020?20000---0
 11100110-0 111201[01]02- 20003010-- 0011111210
 2011100110 01101011

CHARINUS *APIACA*

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 11100110-0 111[23]01[35]02- 40015010-- 0011110010
 3011100102 21101011

CHARINUS *ASTURIUS*

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 11100110-0 111400-01- 40004010-- 0011110010
 3010100102 21101010

CHARINUS *AUSTRALIANUS*

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 11100110-0 111201101- 30014010-- 0011111210
 3000100101 11101010

CHARINUS *BELIZENSIS*

010100110- 0010101100 1120100210 2130002001
 0-0111??11 0422??0001 1101010020 010-00---0
 11100120-0 111201101- 20002010-- 0011112310
 2000100101 11101010

CHARINUS *BICHUETTEAE*

0101001100 0010101100 1100100210 30-0002000
 --0011??11 0302??0001 1101010020 010-00---0
 111001[12]0-0 111301101- 10002010-- 0011112310
 1000100111 11101010

CHARINUS *BONALDOI*

010100110- 0010101100 1100100210 20-0000000
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 11110120-0 111301401- 20002010-- 0011112310
 1000100111 11101010

CHARINUS *BRASILIANUS*

010111110- 0010101100 1101100210 3100002000
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 0011111[01]10 3011100101 11101010

CHARINUS *BRESCOVITI*

010111110- 0010101100 1100100210 2110002001
 0-00????11 030??0001 1101110030?10-00---0
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CHARINUS *CARAJAS*

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CHARINUS CARIBENSIS

010100010- 0010111100 1120100210 2110000000
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CHARINUS CARINAE

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CHARINUS CARIOCA

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CHARINUS CARVALHOI 13399

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CHARINUS CAVERNICOLUS

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CHARINUS CEARENSIS

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CHARINUS CUBENSIS

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CHARINUS DIAMANTINUS

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CHARINUS DOMINICANUS 13399

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 2000100111 11101010

CHARINUS ELEGANS 5175

010111110- 0010131100 1100100311 3110002000
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 11130110-0 111201002- 20002110-- 0011112310
 3100100111 11101010

CHARINUS ELEONORAE

0103101110 0010101100 1101100311 5110002000
 --1011??11 0402??0001 1101110021 12111-0200
 11110110-0 111301201- 30002010-- 0011111010
 3011100102 21101010

CHARINUS EUCLIDESI

010111110- 0010101100 1101100311 4100002000
 --1000??11 0402??0001 1101110041 130000---0
 11100110-0 111301002- 40004010-- 0011121010
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CHARINUS FAGEI

010111110- 0010101100 1100100311 41000?????
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CHARINUS GERTSCHI 10076

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 2111100101 11101010

CHARINUS GOITACA

010111110- 0010101100 11011[01]0210
 [45]1[012]0002000 --1111??11 0402??0001
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 40005010-- 001112[01][01]10 3011100102 21101010

CHARINUS GUAYAQUIL

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CHARINUS GUTO

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 0-00????11 0302??0001 1101000020?10-00---0
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 2000100111 11101010

CHARINUS MAGALHAESI 13393

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CHARINUS IMPERIALIS

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CHARINUS MILLOTI

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 3211100011 11101010

CHARINUS INSULARIS

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 3010100101 11101010

CHARINUS MISKITO

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CHARINUS JIBAOSSU

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CHARINUS MOCOA

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CHARINUS KOEPCKEI

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CHARINUS MONASTICUS

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CHARINUS LOKO

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CHARINUS MONTANUS

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CHARINUS LONGIPES

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CHARINUS MUCHMOREI

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CHARINUS MADAGASCARIENSIS

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CHARINUS MYSTICUS

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 3011100102 21101010

CHARINUS NEOCALEDONICUS 4223 5174 10276

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CHARINUS ORIENTALIS

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CHARINUS PALIKUR 3831–3833

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CHARINUS PAPUANUS

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CHARINUS PECKI

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CHARINUS PERQUERENS

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CHARINUS PESCOTTI 6366 6367

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CHARINUS POTIGUAR 13398

010111110 0010101100 1101110311 5100002000
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 3011100102 21101010

CHARINUS PURI

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 11110110-0 111301102- 40014010-- 0011111010
 3011100102 21101010

CHARINUS REDDELLI 13402

010100110- 0010101100 1120100210 2130002001
 0-0111??11 0402??0001 1101010020 010-00---0
 11100120-0 111201101- 30002110-- 0011112310
 2010100101 11101010

CHARINUS RENNERI

0101101110 0010101100 1100100310 410000?00?
 ????11??11 0402??0001 1101100121 120000---0
 11110110-0 111200-01- 30003010-- 0011111110
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CHARINUS RUSCHII

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CHARINUS SILLAMI 13448

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CHARINUS SOORETAMA

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CHARINUS SOUZAI

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CHARINUS SUSUWA

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APPENDIX 2

Morphological characters and character states used in phylogenetic analysis of the whip spider family Charinidae [Quintero, 1986](#). Characters corresponding to previous matrices of [Quintero \(1986\)](#), [Weygoldt & Hoffmann \(1995\)](#), [Weygoldt \(1996\)](#), [Shultz \(2007\)](#), [Garwood *et al.* \(2017\)](#) and [Miranda *et al.* \(2018b\)](#) denoted, respectively, by abbreviations DQ, W&H, PW, JS, GEA and MEA, followed by the corresponding number. New characters indicated with asterisks.

CARAPACE

1. Tegument division: (0) absent; (1) present. | [JS 2]
2. Anterior margin, setae: (0) absent; (1) present. *
3. Anterior margin, position of setal sockets: (0) carapace; (1) spines. | [MEA 1]
4. Anterior margin, number of setae or spines/setae: (0) 4; (1) 6; (2) 8; (3) 10; (4) > 10. | [MEA 2]
5. Median eyes: (0) absent; (1) present. | [PW 29 (part)]
6. Median ocular tubercle: (0) absent; (1) present. | [PW 29 (part)]
7. Median ocular tubercle, pair of setae on/close to tubercle, or in corresponding position if tubercle absent: (0) absent; (1) present. | [MEA 5]
8. Lateral eyes: (0) absent; (1) present. *
9. Curved carina between lateral eyes and carapace lateral margin ([Fig. 7 A, B, D, E](#)): (0) absent; (1) present. | [MEA 6].
10. Distance from carina to lateral eyes ([Fig. 7](#)): (0) > four times one eye diameter; (1) ≤ twice one eye diameter; (2) smaller than one eye diameter, carina adjacent to lateral eyes. *
11. Straight carina anterior to lateral eyes, projecting from lateral ocular triad ([Fig. 7C](#)): (0) absent; (1) present. *
12. Distance from lateral eyes to carapace lateral margin if carina absent ([Fig. 7](#)): (0) ≤ twice one eye diameter; (1) > twice one eye diameter. *

13. Setae posterior to lateral ocular triad ([Fig. 7N](#)): (0) absent; (1) present. | [MEA 7]
14. Setae adjacent to lateral ocular triad: (0) absent; (1) present. *

STERNUM

15. Tritosternum development: (0) short; (1) long, projecting anteriorly. | [MEA 8]
16. Number of medial and posterior sternum sclerites ([Fig. 18](#)): (0) one narrow sclerite only; (1) pair of narrow sclerites; (2) one flat, broad plaque; (3) two flat, broad plaques. | [MEA 9]

CHELICERAE

17. Basal segment, number of rows of teeth: (0) one; (1) two. *
18. Basal segment, tooth adjacent to bifid tooth (tooth 1) ([Fig. 8J](#)): (0) absent; (1) present. | [MEA 10]
19. Basal segment, size of tooth adjacent to bifid tooth ([Fig. 8J](#)): (0) small (sclerotized bump); (1) large (marked projection). | [MEA 11]
20. Basal segment, additional tooth adjacent to second tooth (tooth 2): (0) absent; (1) present. | [MEA 12]
21. Basal segment, number of teeth in prolateral row ([Fig. 8C, G, K, O](#)): (0) 3; (1) 4; (2) 5; (3) 6; (4) 7; (5) 8. | [DQ 2; PW 1; GEA 38; MEA 13]
22. Basal segment, number of cusps on distal tooth ([Fig. 8G](#)): (0) 1; (1) 2; (2) 3. | [PW 2; GEA 39; MEA 14]
23. Basal segment, relative size of cusps on bifid tooth ([Fig. 8G](#)): (0) distal (dorsal) larger than proximal; (1) proximal (ventral) larger than distal; (2) subequal. | [PW 3; MEA 15]
24. Basal segment, shape of distal (dorsal) cusp of bifid tooth ([Fig. 8G](#)): (0) straight; (1) with curved apex and concavity on retrolateral surface. *
25. Basal segment, prolateral surface, clavate or long, fine setae ([Fig. 8O](#)): (0) absent; (1) present. *
26. Basal segment, prolateral surface, number of rows of clavate or long, fine setae (additional row/s from base to apex) ([Fig. 8O](#)): (0) one; (1) > two. | [MEA 16]
27. Basal segment, dorsal setae, setiferous tubercle ([Fig. 8E](#)): (0) not projecting; (1) projecting. | [MEA 17]
28. Basal segment, number of dorsal setae ([Fig. 8E](#)): (0) 1; (1) 2; (2) 5–10; (3) 11–20; (4) > 20. | [MEA 18]
29. Basal segment, anterior retrolateral margin, setae ([Fig. 8E](#)): (0) absent; (1) present. | [MEA 19]
30. Basal segment, anterior retrolateral margin, number of setae ([Fig. 8E](#)): (0) 1; (1) 2. | [MEA 20]

31. Cheliceral claw, number of teeth (Fig. 8C): (0) 1; (1) 3; (2) 4 or 5; (3) 6 or 7; (4) 8 or 9; (5) 10–13. | [MEA 21].
32. Cheliceral claw, retrolateral surface, row of setae (Fig. 8B): (0) absent; (1) present. | [MEA 22]
33. Cheliceral claw, retrolateral surface, position of row of setae (Fig. 8B): (0) extending from base to dorsal side of fang (almost reaching row of setae on prolateral surface); (1) restricted to base of fang; (2) restricted to dorsal surface of fang; (3) extending from base to middle of fang. *
34. Cheliceral claw, dorsal surface, rows of setae between prolateral and retrolateral rows (Fig. 8): (0) absent; (1) present. *

OPISTHOSOMA AND GENITALIA

35. Opisthosoma, ventral sac cover (Fig. 9): (0) absent; (1) present. | [DQ 15; PW 26; GEA 124; MEA 23].
36. Genital operculum (♀), distal margin, shape and color of surface (Fig. 9): (0) flat, same color as rest of operculum; (1) with two medial convexities, paler, whitish ventrally. *
37. Genital operculum (♀), curvature of distal margin (Figs. 9, 10, 19): (0) concave; (1) straight; (2) convex; (3) with broad projection; (4) with small projection. | [MEA 24]
38. Gonopod (♀) (dorsal view), size of posterior border (Fig. 10): (0) short (thin layer; gonopods usually close to border); (1) long (longer than or equal to length of base of gonopod/gonopods far from border) | [PW 25 (part)]
39. Gonopod (♀), shape (Fig. 10): (0) circular or oval (1) rectangular (wider than long). | [PW 25 (part); MEA 25]
40. Gonopod (♀), claw-like projection (Fig. 10): (0) absent (1) present. | [DQ 4; PW 25 (part); MEA 26]
41. Gonopod (♀), tegument of claw-like projection (Fig. 10): (0) soft (1) sclerotized. | [W&H 8; PW 25 (part); MEA 27]
42. Gonopod (♀), tegument of claw-like projection, extent of sclerotization (Fig. 10): (0) restricted to apex; (1) extending from base to apex. | [PW 25 (part); MEA 28]
43. Gonopod (♀), shape of medial surface (Fig. 10): (0) cushion-like; (1) sucker-like; (2) finger-like (includes plunger-like gonopods). | [PW 25 (part); MEA 29]
44. Gonopod (♀), basal sclerotization: (0) absent (unsclerotized) (1) present (sclerotized). | [MEA 30]
45. Gonopod (♂), sclerotizations at distal margin of fistula (Fig. 19): (0) absent (unsclerotized) (1) present (sclerotized). | [MEA 31]
46. Gonopod (♂), sclerotizations at base of LoL1 (Fig. 19): (0) absent (unsclerotized) (1) present (sclerotized). | [MEA 32]

47. Spermatophore, position of sperm sac: (0) superficial (1) obscured. | [PW 27]
48. Spermatophore, shape: (0) simple; (1) complex sculpturing (with bars and levers). | [PW 27]

LEG I

49. Tibia, divided into pseudoarticles (Fig. 20): (0) absent (undivided); (1) present (divided). *
50. Tibia, number of pseudoarticles: (0) 16; (1) 21–25; (2) 26–45; (3) > 43. | [PW 18; MEA 33]
51. Tarsus, leaf-like setae on articles: (0) absent; (1) present. | [PW 20; MEA 34]
52. Tarsus, number of pseudoarticles: (0) 6–8; (1) 23; (2) 26–28; (3) 33–39; (4) 41–43; (5) 44–47; (6) 51–59; (7) 60–79; (8) 90–110. | [MEA 35]
53. Tarsus, size of first (proximal) article (Fig. 20): (0) subequal to others; (1) equal to sum of two articles; (2) equal to sum of three articles; (3) equal to sum of four articles. *
54. Tarsus, number of articles with slit sense organ (article has small elongation at distal margin): (0) 11–13; (1) 17; (2) 18; (3) 20; (4) 21; (5) 22; (6) 25. | [PW 19; MEA 36]
55. Tarsus, shape of rod sensilla: (0) rounded; (1) elliptical; (2) longilineal. | [MEA 37]
56. Tarsus, position of setae on rod sensilla: (0) on surface; (1) depressed into tegument. *

PEDIPALP

57. Coxae fused ventrally, forming posterior wall of pre-oral chamber: (0) absent (free); (1) present (fused). | [JS 30]
58. Dorsal articulation (hinge) of trochanter and femur, position: (0) anterior surface of femur; (1) dorsal surface of femur. | [PW 6; MEA 38]
59. Trochanter, posteriorly directed clavate apophysis: (0) absent; (1) present. | [PW 4, 5 (part)]
60. Trochanter, ventral surface, anteriorly directed ventromedial apophysis (Fig. 11): (0) absent; (1) present. | [PW 4, 5 (part)]
61. Trochanter, ventral surface, shape of anteriorly directed ventromedial apophysis (Fig. 11): (0) spine; (1) seta (broad projection with acute apex). | [PW 4 (part); GEA 65 (part); MEA 39]
62. Trochanter, ventral surface, number of spines (excluding anteriorly directed ventromedial apophysis, if spine-like) (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6; (6) 7; (7) > 7. | [MEA 40]
63. Trochanter, dorsal surface, spines: (0) absent; (1) present. | [MEA 41]
64. Femur, ventral surface, spine or conspicuous setiferous tubercle proximal to spine 1 (Fig. 11): (0) absent; (1) present. | [MEA 42]

65. Femur, ventral surface, shape of projection proximal to spine 1 (Fig. 11): (0) setiferous tubercle; (1) spine. | [MEA 43]
66. Femur, ventral surface, position of spine/tubercle proximal to spine 1 (Fig. 11): (0) parallel to spine 1, prolateral; (1) adjacent to spine 1, in same row; (2) ventral to spine 1. | [MEA 44]
67. Femur, ventral surface, small spine close to articulation of femur and trochanter (Fig. 11): (0) absent; (1) present. *
68. Femur, ventral surface, spine parallel to spine 1 (in addition to aforementioned spine) (Fig. 11): (0) absent; (1) present. | [MEA 45]
69. Femur, ventral surface, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6. | [MEA 46]
70. Femur, ventral surface (♀), small spine between spines 1 and 2 (dorsal to main row) (Fig. 11): (0) absent; (1) present. | [MEA 47]
71. Femur, ventral surface (♂), small spine between spines 2 and 3 (dorsal to main row) (Fig. 11): (0) absent; (1) present. | [MEA 48]
72. Patella, ventral surface, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5. | [MEA 49]
73. Patella, ventral surface, small spine between spines 1 and 2 (Fig. 11): (0) absent; (1) present. | [MEA 50]
74. Patella, ventral surface, small spine between spines 2 and 3 (Fig. 11): (0) absent; (1) present. *
75. Patella, ventral surface, shape of projection between spine 1 and distal margin (Fig. 11): (0) setiferous tubercle; (1) spine. | [MEA 52]
76. Patella, ventral surface, size of setiferous tubercle between spine 1 and distal margin (Fig. 11): (0) short, equal to other setiferous tubercle; (1) long, one-third the length of spine 1; (2) very long, half the length of spine 1. *
77. Patella, ventral surface, number of spines between spine 1 and distal margin (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4. | [MEA 53]
78. Patella, ventral surface, size of apical or largest (if more than one) spine between spine 1 and distal margin (Fig. 11): (0) short, one-third the length of spine 1; (1) long, half the length of spine 1; (2) very long, two-thirds the length of spine 1; (3) longer than spine 1. | [MEA 54]
79. Patella, ventral surface, shape of apical or largest (if more than one) spine between spine 1 and distal margin (Fig. 11): (0) straight; (1) curved, anteriorly directed. | [MEA 55]
80. Tibia, ventral surface, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4. | [MEA 56]
81. Tibia, ventral surface, position of spine (if only one): (0) near proximal margin of basitarsus; (1) near distal margin of basitarsus; (2) medial. | [MEA 57]
82. Tibia, ventral surface, setiferous tubercle with long setae between spine 1 and distal margin of segment: (0) absent; (1) present. | [MEA 58]
83. Tibia, ventral surface, row of long, thin setae near distal margin: (0) absent; (1) present. | [MEA 59]
84. Tibia, ventral surface, number of setae in row near distal margin: (0) 1 or 2; (1) 3 or 4; (2) 5; (3) > 5. | [MEA 60]
85. Tarsus, ventral surface, spine: (0) absent; (1) present. | [DQ 16; PW 15, 16 (part); MEA 61]
86. Tarsus, ventral surface, cleaning organ: (0) absent; (1) present. | [JS 40]
87. Tarsus, ventral surface, number of setae in ventral row of cleaning organ: (0) 18–24; (1) 25–34; (2) 35–40. | [MEA 62]
88. Tarsus, row of setae at base of cleaning organ: (0) absent; (1) present. | [DQ 10; PW 17; MEA 63]
89. Tarsus, number of setae proximal to cleaning organ: (0) 1; (1) > 1. *
90. Coxae, position in relation to carapace (Fig. 12): (0) exposed; (1) obscured below carapace. *
91. Coxae, shape of sclerite (Fig. 12): (0) forming ring; (1) separated into small sclerites. *
92. Coxae, relative positions of plaques (sclerites) (Fig. 12): (0) adjacent to each other; (1) separated from each other. | [MEA 64]
93. Coxae, dorsal surface, sclerotized rounded or oval carina (Fig. 12): (0) absent; (1) present. | [MEA 65]
94. Coxae, dorsal surface, number of setae on anterior margin of rounded protuberance (Fig. 12): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6. *
95. Coxae, dorsal surface, relative positions of two proximal large setae/tubercles on anterior margin of rounded protuberance (Fig. 12): (0) separated from each other; (1) adjacent to each other. *
96. Coxae, dorsal surface, setae on rounded protuberance (Fig. 12): (0) absent; (1) present. *
97. Coxae, dorsal surface, number of setae on rounded protuberance (Fig. 12): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6; (6) 7. *
98. Femur, dorsal surface, shape of proximal series of spines/tubercles (Fig. 11): (0) setiferous tubercle; (1) spines. | [MEA 66]
99. Femur, dorsal surface, number of setiferous tubercles proximal to spine 1, situated in same row as primary series of spines (Fig. 11): (0) 1; (1) 2; (2) 3. *
100. Femur, dorsal, proximal series, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4. | [MEA 67]
101. Femur, dorsal surface, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6. | [MEA 68]
102. Femur, dorsal surface, small spine adjacent to spine 1 (Fig. 11): (0) absent; (1) present. *
103. Femur, dorsal surface (♀), small spine between spines 1 and 2 (Fig. 11): (0) absent; (1) present. | [MEA 69]

104. Femur, dorsal surface (♀), small spine between spines 2 and 3 (Fig. 11): (0) absent; (1) present. | [MEA 70]
105. Patella, dorsal surface, number of spines (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6. | [GEA 71 (part); MEA 71]
106. Patella, dorsal surface, long setiferous tubercle proximal to spine 3 (Fig. 11): (0) absent; (1) present. *
107. Patella, dorsal surface, long setiferous tubercle or spine between spine 1 and distal margin (Fig. 11): (0) absence; (1) presence. | [MEA 76]
108. Patella, dorsal surface, shape of projections between spine 1 and distal margin (Fig. 11): (0) setiferous tubercle; (1) spine. *
109. Patella, dorsal surface, number of spines between spine 1 and distal margin (Fig. 11): (0) 1; (1) 2; (2) 3; (3) 4; (4) 5. *
110. Patella, dorsal surface, length of proximal spine between spine 1 and distal margin (Fig. 11): (0) one-third the length of spine 1; (1) half the length of spine 1; (2) two-thirds the length of spine 1. *
111. Patella, dorsal surface, number of long setiferous tubercles between spine 1 and distal margin (refers only to setiferous tubercles that are broad basally and become acuminate apically; excludes tubercles of similar width from base to apex) (Fig. 11): (0) 1; (1) 2; (2) 3. *
112. Patella, dorsal surface, long setiferous tubercle between spine 1 and distal margin, size of proximal tubercle (Fig. 11): (0) one-third the length of spine 1; (1) half the length of spine 1; (2) two-thirds the length of spine 1. *
113. Tibia, number of dorsal spines: (0) 1; (1) 2; (2) 3; (3) > 3. | [DQ 12; MEA 77]
114. Tibia, relative size of dorsal spines (when two spines present): (0) proximal spine larger than distal; (1) distal spine larger than proximal. | [DQ 17; MEA 78]
115. Tarsus, dorsal surface, spine dorsal to cleaning organ: (0) absent; (1) present. | [GEA 76; MEA 79]
116. Tarsus, dorsal surface, number of spines: (0) 1; (1) 2; (2) 3; (3) > 3. | [PW 15, 16 (part); MEA 80]
117. Tarsus, dorsal surface, length of distal spine (or of single spine if only one present): (0) short (slightly longer than setiferous tubercle); (1) medium (one-third the length of distitarsus); (2) long (approximately half the length of distitarsus). | [MEA 81]
118. Tarsus, dorsal surface, relative size of two spines (or two distal spines, if more than two present): (0) proximal spine subequal to distal; (1) proximal spine two-thirds the length of distal; (2) proximal spine half the length of distal; (3) proximal spine one-third the length of distal. | [MEA 82]
119. Tarsus, dorsal surface, dorsal row of setae on cleaning organ: (0) absent; (1) present. | [MEA 83]
120. Tarsus and claw, fusion: (0) separate; (1) fused. | [DQ 11; PW 14; MEA 84]
- LEG IV
121. Basitibia, number of articles: (0) 1; (1) 2; (2) 3; (3) 4. | [DQ 14; PW 23; MEA 85]
122. Basitibia, position of trichobothrium *bt* (Fig. 21): (0) proximal third; (1) medial third; (2) distal third. | [MEA 86]
123. Basitibia, markedly sclerotized denticulate border at distal apex of article (Fig. 21): (0) absent; (1) present. | [MEA 87]
124. Basitibia, markedly sclerotized denticulate border projection medially (Fig. 21): (0) absent; (1) present. | [MEA 88]
125. Distitibia, trichobothria *bc*: (0) absent; (1) present. | [MEA 89]
126. Distitibia, trichobothrium *nbfc*: (0) absent; (1) present. | [PW 24 (part); MEA 90]
127. Distitibia, trichobothrium series *sbc*: (0) absent; (1) present. | [PW 24 (part); MEA 91]
128. Distitibia, relative positions of two most proximal trichobothria of *sf* and *sc*: (0) far apart (> 0.2 mm); (1) close to each other (0.05–0.1 mm, ratio of distance to length of distitibia between 0.01 and 0.09); (2) parallel or subparallel to each other (< 0.025 mm). | [MEA 92]
129. Distitibia, position of proximal trichobothria of *sf* and *sc*: (0) similar distance to the other trichobothria in the series; (1) distinctly displaced from series. | [MEA 93]
130. Distitibia, number of trichobothria on *sf*: (0) 4; (1) 5; (2) 6; (3) 7; (4) 8; (5) 9; (6) 10–12; (7) 20 (8) 26. | [MEA 94]
131. Distitibia, number of trichobothria on *sc*: (0) 3; (1) 5; (2) 6; (3) 7; (4) 8; (5) 9; (6) 10 or 11; (7) 12; (8) 13; (9) 19–21. | [MEA 95]
133. Distitibia, trichobothrium *tm* (tip of triad): (0) absent; (1) present. | MEA 96.
133. Distitibia, marked division distal to all trichobothria (Fig. 13): (0) absent; (1) present. | MEA 97.
134. Tarsomere, empodial claw: (0) absent; (1) present. *
135. Tarsomere, pulvillus: (0) absent; (1) present. | [DQ 1; MEA 98]
136. Tarsomere, oblique slit: (0) absent; (1) present. | [PW 21; MEA 99]
137. Tarsomere, weakly sclerotized area of second tarsal segment (Fig. 14): (0) absent; (1) present. | [MEA 100]
138. Tarsomere, extent of weakly sclerotized area of second tarsal segment (Fig. 14): (0) reaching ventrolateral setal row (1); not reaching ventrolateral setal row; (2) surpassing ventrolateral setal row (divides the article). *