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.


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.
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, demonstrating 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 australiianus group; species with a finger-like gonopod, to the bengalensis group; and species with a sucker-like female gonopod, to the brasilianus 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, 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 comprises 82 ingroup species represented by 103 terminal taxa (Table 1; Fig. S1).

### 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 troglobiotic characters: Charinus brescovitii Giupponi & Miranda, 2016; C. carajas Giupponi & Miranda, 2016; C. fagei Weygoldt, 1972; C. loko Miranda et al., 2021, C. longipes Weygoldt, 2006; C. madagascariensis Page, 1954; C. milloti Fage, 1939; C. orientalis Giupponi & Miranda, 2016; C. susuwa Miranda et al., 2021, C. troglolius 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.

<table>
<thead>
<tr>
<th></th>
<th>Total species</th>
<th>Species %</th>
<th>Morphospecies</th>
<th>Terminal taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outgroup</td>
<td>4/4/4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ingroup</td>
<td>92/82/30</td>
<td>71/64/23</td>
<td>4/4/4</td>
<td>113/103/48</td>
</tr>
<tr>
<td>Charinus</td>
<td>65/55/15</td>
<td>70/59/16</td>
<td>1/1/1</td>
<td>71/61/21</td>
</tr>
<tr>
<td>Weygoldtia</td>
<td>2/2/2</td>
<td>100/100/100</td>
<td>3/3/3</td>
<td></td>
</tr>
</tbody>
</table>

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 Sereno (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/cma/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)
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 MAFFFT 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-HPC 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-HPC 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 (Sjoberg, 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, Parageralinauranaufra (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 ± 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 ucln.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 africanaus 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 koepeki 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 caverniculus 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 abbatii (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 ‘singaporae clade’. In the ML tree, the brachydactylus clade (BS = 6%) included Sarax indochnenis 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 singaporae clade (BS = 28%) comprised three subclades in the ML tree: the first (BS = 11%) comprising Sarax dumi Miranda et al., 2021, Sarax lembeh Miranda et al., 2021 and two undescribed morphospecies from Lombok and Sumbawa; the second (BS = 35%) comprising Sarax gravelyi Miranda et al., 2021, Sarax singaporae 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. abbatii, 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. indochnensis, 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 brachyactylus clade in the analysis with ML, the rest of which, i.e. Sarax bilua Miranda et al., 2021, Sarax bispinosus (Nair, 1934), Sarax brachyactylus Simon, 1892, Sarax cochinensis (Gravely, 1915), Sarax huberi Seiter et al., 2015 and Sarax palau Miranda et al., 2021, grouped sister to all other species of the singaporae clade (PP = 0.64). Other differences from the analysis with ML concerned the position of S. rahmani, placed sister to S. gravedy in the analysis with BI (PP = 0.92), rather than sister to S. yayukae, as in the ML analysis, and the position of Sarax willeei (Gravely, 1915), unresolved in the singaporae 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 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).

**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.

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

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 potiguara Vasconcelos et al., 2013, placed sister to Charinus gertschi (PP = 0.50). The
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 australis, 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 Charinidae 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
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 Phrynoidae 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 cochinensis (Gravely, 1915), ♀ [AMNH (LP 13118)]. C, Weygoldtia davidovi (Fage, 1946), ♂ [AMNH (LP 11377)]. D, Sarax gravielyi 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), ♀ (HUI INVAMB 111). L, Sarax abbatei (Delle Cave, 1986), ♀ (MZUF 1896–167). M, Charinus belizensis Miranda et al., 2016, ♂ (HUI INVAMB 117). N, Charinus cubensis (Quintero, 1983), ♀ (USNM ENT 784407). O, Charinus montanus Weygoldt, 1972, ♂ (MRJ 9087). Scale bars: A, B, D–O, 0.2 mm; C, 0.5 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 & Kukalová-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.
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* (Fage 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

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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 cochinensis (Gravely, 1915), ♂ [AMNH (LP 13118)]. F, L, Sarax willeyi Gravely, 1915, ♂ (SMF 64589). 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:}

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 cochinensis* (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 Gondwanian origin for *Sarax* is the presence

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**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* Fuge, 1946, ♀ [AMNH (LP 11377)]. Scale bars: A, B, E, 0.5 mm; C, D, 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. newbritainensis Rahmadi & Kojima, 2010, S. sangkulirangensis Rahmadi et al., 2010, S. timorensis Miranda & Reboleira, 2019.
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. cochinensis*. Also ignoring biogeographical lines, *S. brachydactylus*
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, *Charinus elegans neocaledonicus* Charinus Dunn, 1949 and Neocaledonian *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

**NEW CALEDONIAN CHARINUS AS GONDWANAN RELICS**

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 (*Murienne 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, *Rhynochetos 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 (*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

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

*Charax sarawakensis* (Thorell, 1888) was the first species to be described in the genus (Thorell, 1888) and, for many years, all *Charax* 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 epigean 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.
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...
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

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* Miranda et al., 2021, ♂ [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.
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.

ACKNOWLEDGEMENTS

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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 Mkiv model. 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

```
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---0???00-001-??1000 -0--00-- --0-00--
0-0------ --------0-0000---1000-
```

PHYLOGENY AND BIOGEOGRAPHY OF CHARINIDAE

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**Ingroup**

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**Charinus carajas**
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APPENDIX 2


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, 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. 8G): (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 2; GEA 38; MEA 13]
22. Basal segment, number of cusps on distal tooth (Fig. 8G): (0) 1; (1) 2. [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 rows 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 fustula (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 pseudoarticules (Fig. 20): (0) absent (undivided); (1) present (divided). *

50. Tibia, number of pseudoarticules: (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 pseudoarticules: (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) longineal. | [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, row of setae at base of cleaning organ: (0) absent; (1) present. [DQ 10; PW 17; MEA 63]
88. Tarsus, number of setae proximal to cleaning organ: (0) 1; (1) > 1. *
89. Coxae, position in relation to carapace (Fig. 12): (0) exposed; (1) obscured below carapace. *
90. Coxae, shape of sclerite (Fig. 12): (0) forming ring; (1) separated into small sclerites. *
91. Coxae, relative positions of plaques (sclerites) (Fig. 12): (0) adjacent to each other; (1) separated from each other. [MEA 64]
92. Coxae, dorsal surface, sclerotized rounded or oval carina (Fig. 12): (0) absent; (1) present. [MEA 65]
93. 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. *
94. 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. *
95. Coxae, dorsal surface, stated on rounded protuberance (Fig. 12): (0) absent; (1) present. *
96. Coxae, dorsal surface, stated 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 (Fig. 11): (0) 1; (1) 2; (2) 3. |
112. Patella, dorsal surface, long setiferous tubercle or spine between spine 1 and distal margin (Fig. 11): (0) absent; (1) present. |
113. Tibia, number of dorsal spines: (0) 1; (1) 2; (2) 3; (3) > 3. | [DQ 12; MEA 77]
114. Tibia, marked division distal to all trichobothria (Fig. 24): (0) absent; (1) present. |
115. Tarsus, dorsal surface, spine dorsal to cleaning organ: (0) absent; (1) present. | [MEA 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]

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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 nbf: (0) absent; (1) present. | [PW 24 (part); MEA 90]
127. Distitibia, trichobothrium series scb: (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]
132. 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, empodial claw: (0) absent; (1) present. | [DQ 14; MEA 99]
137. Tarsomere, weakly sclerotized area of second tarsal segment (Fig. 14): (0) absent; (1) present. | [DQ 11; MEA 100]
138. Tarsomere, 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). *