WILEY

Cladistics

Cladistics 39 (2023) 479–532

doi: 10.1111/cla.12557

Advances in the reconstruction of the spider tree of life: A roadmap for spider systematics and comparative studies

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Received 8 January 2022; Revised 27 July 2023; Accepted 17 August 2023

Abstract

In the last decade and a half, advances in genetic sequencing technologies have revolutionized systematics, transforming the field from studying morphological characters or a few genetic markers, to genomic datasets in the phylogenomic era. A plethora of molecular phylogenetic studies on many taxonomic groups have come about, converging on, or refuting prevailing morphology or legacy-marker-based hypotheses about evolutionary affinities. Spider systematics has been no exception to this transformation and the inter-relationships of several groups have now been studied using genomic data. About 51 500 extant spider species have been described, all with a conservative body plan, but innumerable morphological and behavioural peculiarities. Inferring the spider tree of life using morphological data has been a challenging task. Molecular data have corroborated many hypotheses of higher-level relationships, but also resulted in new groups that refute previous hypotheses. In this review, we discuss recent advances in the reconstruction of the spider tree of life and highlight areas where additional effort is needed with potential solutions. We base this review on the most comprehensive spider phylogeny to date, representing 131 of the 132 spider families. To achieve this sampling, we combined six Sanger-based markers with newly generated and publicly available genome-scale datasets. We find that some inferred relationships between major lineages of spiders (such as Austrochiloidea, Palpimanoidea and Synspermiata) are robust across different classes of data. However, several new hypotheses have emerged with different classes of molecular data. We identify and discuss the robust and controversial hypotheses and compile this blueprint to design future studies targeting systematic revisions of these problematic groups. We offer an evolutionary framework to explore comparative questions such as evolution of venoms, silk, webs, morphological traits and reproductive strategies.

Introduction

In animal taxonomy, spiders are a unique group among all animals because their binomial naming by Clerck's (1757) *Svenska Spindlar* predates Linnaeus's (1758) 10th edition of *Systema Naturae*. Linnaeus's (1758) is established as the starting point of zoological nomenclature by the International Code of Zoological Nomenclature (ICZN). Spiders are a remarkably diverse lineage among arthropods. An apt example of their evolutionary success is that there are ≈51 500 described species (World Spider Catalog, 2023), but with an estimated two-fold number of species remaining undiscovered (Platnick, 1999; Agnarsson et al., 2013). This species richness is greatly asymmetrical compared to the species richness of its sister group, Pedipalpi, which contains <700 described species (Harvey, 2013; Ballesteros et al., 2021; Miranda et al., 2021, 2022). Spiders occupy all terrestrial and some aquatic habitats, and are distributed on all continents except Antarctica. The origin of spiders is estimated to be *c.* 400 Ma (Magalhaes et al., 2020; Kallal et al., 2021a), after which they have evolved a great diversity of shapes, sizes, behaviours, silk uses, web

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architectures, respiratory systems and venom compounds (Platnick, 2020).

Morphological and biological makeup

The synapomorphies of spiders include the production of silk from the associated spinning apparatus and the presence of venom glands opening through the cheliceral fang (Fig. 1). Spigots (and their silk) originated before the evolution of spinnerets (Shultz, 1987), a claim that is supported by the presence of spinneretless spigots in the order Uraraneida (Selden et al., 2008). However, the hypothesis that spinnerets are exclusive to Araneae was challenged by the discovery of *Chimerarachne yingi* Wang et al. (2018) (popularly known as "the spider with a tail") from Burmese amber (dated 99 Ma). This fossil bears spinnerets, male pedipalps presumably modified for sperm transfer (both characters being synapomorphies of spiders) and a uropygid-like telson, and is placed as a sister group to all spiders (Wang et al., 2018; Huang et al., 2018). In extant spiders, silk is used for many tasks critical to spider biology and survival, such as constructing foraging webs (e.g. the characteristic orb web), wrapping prey, dispersal via ballooning, bonding to substrates and producing egg sacs (Fig. 3). These myriad utilities of silks have been attained by the secretions of up to seven different types of glands that function individually or in combination (Kovoor, 1972, 1977). Some web-building spiders bear a short transverse field of spigots (homologous to the primitive anterior median spinnerets) called the cribellum that is used to secrete a distinctive type of silk (as in net-casting Deinopidae webs).

The cribellum is coupled with a row of curved setae on the metatarsus of the fourth leg called the calamistrum, which is used to process and lay the cribellate silk. Webs are constructed by many lineages to capture prey, yet many other spiders (some which have secondarily lost web-building, some which never had this behaviour) use alternative strategies such as ambushing or active hunting. A peculiar adaptation—adhesive setae on legs such as scopulae or claw tufts—are found in most of these wandering spiders (webless) and have evolved multiple times, although some web-building spiders also bear adhesive setae (Wolff et al., 2013). Recently, an encyclopaedic treatment of spider webs by William Eberhard revealed unparalleled diversity

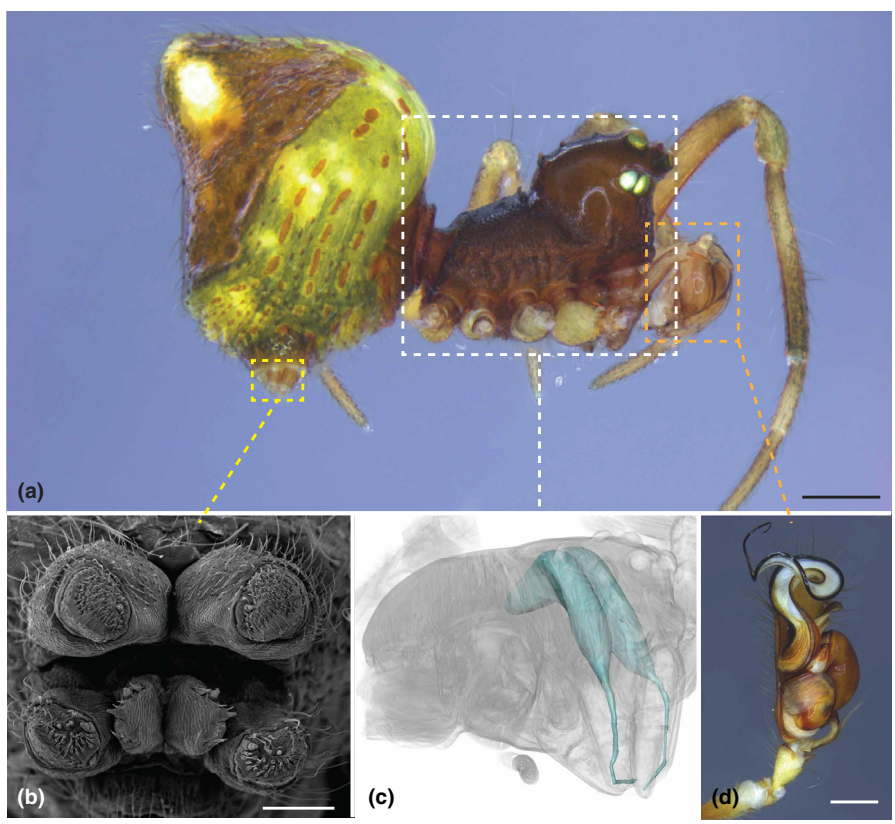

Fig. 1. A schematic figure showing characteristics of spiders. (a) Habitus of *Pecanapis* sp. GH2900 (Anapidae). (b) Silk-secreting spinnerets in *Tylorida striata* (Tetragnathidae). (c) MicroCT graph of the venom glands in *Latrodectus geometricus* (Theridiidae). (d) Male pedipalp of *Orsinome* sp. (Tetragnathidae). Scale. (a, d) 200 μm, (b) 50 μm.

of webs with intricate behaviours and functions (Eberhard, 2020), forming a framework for posing many new questions about evolutionary transitions.

Spiders are generalist predators with the exception of a small proportion of specialists with a reduced diet (such as preying exclusively on terrestrial isopods, ants, moths, dipterans or even other spiders) (Pekár and Toft, 2015). In web-building spiders, silk is used in combination with the chelicerae to inject venom through fangs, in order to capture and immobilize the prey, whereas many hunters only rely on their legs, pedipalps and chelicerae to grasp prey while injecting venom. A large variety of venom compositions have evolved within spiders, with >3000 compounds recorded so far (Kuhn-Nentwig et al., 2011; Lüddecke et al., 2022). In general, venomic complexity and venom gland sizes are larger in generalist spiders compared to their specialist counterparts (Pekár et al., 2018; Lüddecke et al., 2022).

In addition to these synapomorphies, another characteristic feature of spiders includes the occurrence of two types of respiratory systems—book lungs and tracheae, with most spiders having both of these types. It is hypothesized that the book lungs are the symplesiomorphic condition because they are found in the three orders of Tetrapulmonata and earliest-diverging clades of spiders, Mesothelae and Mygalomorphae and some early-diverging Araneomorphae, for example, Gradungulidae and Hypochilidae (<35 of *c.* 47, 500 species of araneomorph spiders) (Ramírez, 2000; Schmitz, 2013; Ramírez et al., 2021). They have two pairs of book lungs whereas most "modern" spiders (Araenomorphae) have either a combination of one pair of book lungs and tracheae [e.g. water spider *Argyroneta aquatica* (Clerck, 1757)] or exclusively only tracheae (for example, Symphytognathidae).

The most common (and vital) acts in spider survival are thus the result of an integration of many behaviours, for example prey capture involves prey detection, hunting behaviours, venom composition amounting to toxicity, silk (such as web or prey capture) and energy demand (mitigated by respiration), in addition to other traits such as vision (except for eyeless spiders), and sensing movement and sound through vibration. All of these traits are highly diverse across Araneae and understanding their evolutionary history is essential to explore the influential factors on the evolutionary success of different spider lineages. To understand the evolutionary history of these characteristics, the prerequisite is a robust phylogenetic hypothesis.

In the last three decades there have been numerous phylogenetic studies of spiders using morphological data but it has been challenging, and in some cases impossible, to satisfactorily resolve many important nodes of the spider tree of life (e.g. Griswold et al., 2005; Ramírez, 2014). The sparse genomic resources (before the advent of parallel sequencing) have maintained ambiguity in phylogenetic relationships of several lineages and many earlier hypotheses have been refuted with high support by these more recent genomic studies. For example, Orbiculariae, which in the past grouped cribellate and ecribellate orb weavers (e.g. Coddington, 1990) has been shown not to be a natural group in multiple recent phylogenomic analyses (Bond et al., 2014; Fernández et al., 2014, 2018a; Garrison et al., 2016; Kallal et al., 2021a; Kulkarni et al., 2020, 2021), corroborating earlier hypotheses of nonmonophyly based on Sanger-sequencing datasets (e.g. Blackledge et al., 2009; Dimitrov et al., 2017).

Less than a decade after the Coddington and Levi (1991) review of spider systematics, Hausdorf (1999) published the first molecular phylogeny of spiders reconstructed using 900 characters (bp) of the 28S rRNA gene. Technological developments, its reach and cost effectiveness and the number of arachnologists using nucleotide sequence data have increased substantially helping to progress our understanding of spider biology and evolution. The rapid advancement of massive parallel sequencing technology and its cost effectiveness for genomic scale data generation (Christensen et al., 2015) rapidly increased the size of molecular datasets for spiders (Fig. 2). For example, some of the most recent phylogenies using genomic data were reconstructed using anchored hybrid enrichment data which included 33 taxa (19 of 114 families at the time) (Hamilton et al., 2016), transcriptomes which included 272 taxa (101 of 128 families at the time) (Kallal et al., 2021a), ultraconserved elements (UCEs) which included 248 taxa (88 of 120 families at the time) (Kulkarni et al., 2021), targeted 99 markers which included 303 taxa (105 of 132 families at the time) (Shao et al., 2023) and silkomes which included 1098 taxa (76 of 132 families at the time) (Arakawa et al. 2022). Wheeler et al. (2017) published a densely sampled phylogeny using six genetic markers acquired via Sanger sequencing, constrained using the transcriptomes-based phylogeny of Garrison et al. (2016), which included 932 taxa (115 of 116 families at the time). A few studies have used genome-scale data to reconstruct the evolutionary history of a specific group of spiders, such as Mygalomorphae (Hedin et al., 2019; Opatova et al., 2020); Leptonetidae (Ledford et al., 2021), Synspermiata (Ramírez et al., 2021), Austrochiloidea (Kulkarni and Hormiga, 2021), Palpimanoidea (Wood et al., 2018), Araneoidea (Fernández et al., 2018a; Kallal et al., 2020; Kulkarni et al., 2020, 2021) or Salticidae (Maddison et al., 2020). The hypotheses about relationships among different lineages of spiders have been converging to some degree, yet some recalcitrant nodes remain when reconstructed using different classes of data (Kulkarni et al., 2021). The need for better taxon sampling for addressing the

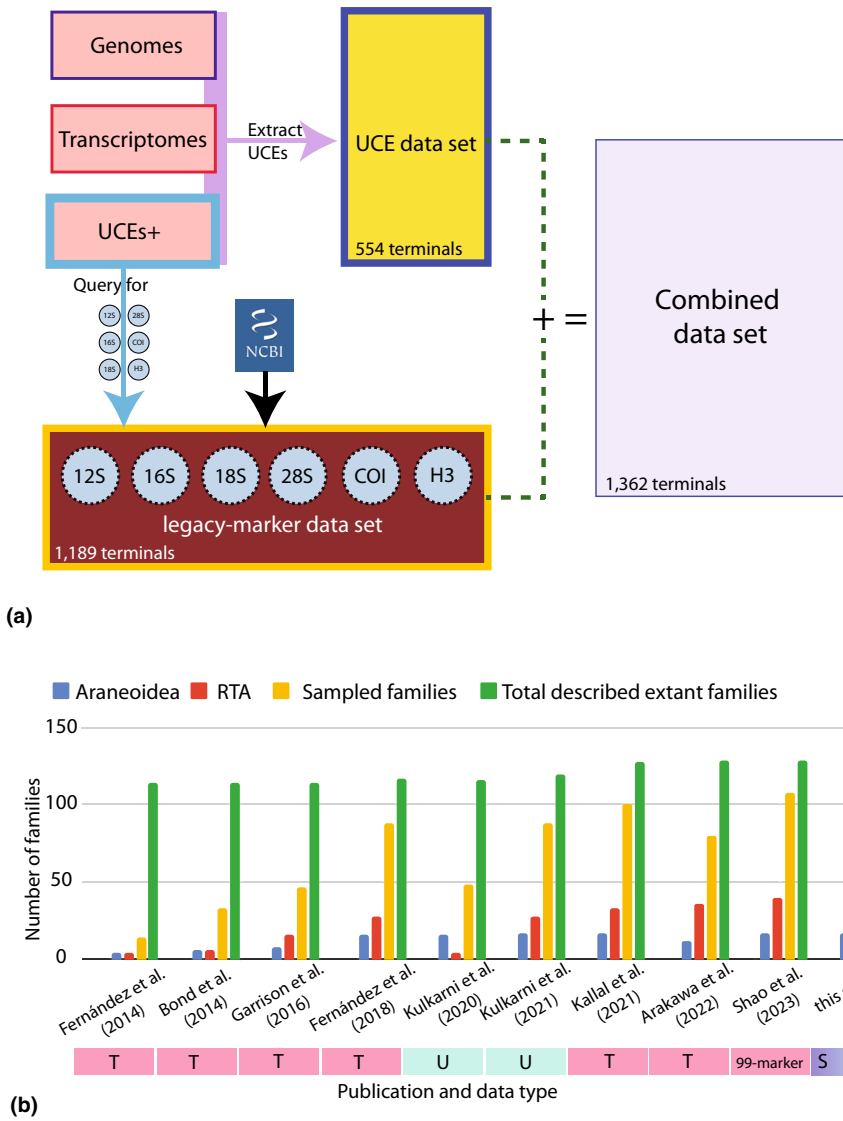

Fig. 2. (a) Schematic representation of data sampling and curation using target-enrichment and six legacy Sanger-sequenced markers. (b) Summary graph of progress in the sampling of Araneoidea, retrolateral tibial apophysis clade (RTA clade) and spider families in phylogenetic studies in comparison to the total number of described families. S, Sanger-sequencing based markers data; T, Transcriptomic data; U, Ultraconserved elements.

problem about recalcitrant nodes and resolution has been echoed in the literature (Dimitrov and Hormiga, 2020, and references therein).

In addition to morphology, Sanger-sequence-based markers, AHEs, transcriptomes and UCE datasets, hypotheses about the phylogenetic relationships of spiders have been tested using filtering of different genome-scale data classes such as ultraconserved regions within transcriptomes, coding regions within UCEs, combination of UCEs and transcriptomes and treating the coding regions as nucleotides and amino acids (Kulkarni et al., 2021). Most phylogenetic relationships have largely converged with well-supported branches, yet some relationships remain elusive. A prominent and largely explored example of recalcitrant nodes in the spider tree of life includes the relationships between the families of the superfamily Araneoidea (ecribellate orb weavers and their relatives). Orb-weaving families, both cribellate (i.e. Deinopidae and Uloboridae) and ecribellate (e.g. Araneidae, Tetragnathidae and some "symphytognathoids") were deemed to form a monophyletic group (Orbiculariae) based on morphological and behavioural characters (e.g., Coddington, 1990). While the monophyly of orb webs was appealing owing to its simplicity, some authors had suggested that the cribellate and ecribellate orb webs have evolved convergently (reviewed in Coddington, 1986a). Molecular data refuted the

monophyly of Orbiculariae (e.g. Hausdorf, 1999; Blackledge et al., 2009; Bond et al., 2014; Fernández et al., 2014; Wheeler et al., 2017; Dimitrov et al., 2017). This change in the phylogenetic relationships of orb weavers affected hypotheses about the evolution the iconic orb web, with several analyses using a diversity of methods of ancestral reconstruction hypothesizing multiple origins (e.g. Fernández et al., 2018a; Kallal et al., 2021a), whereas other analyses argued for a single origin (e.g. Coddington et al., 2019; Garrison et al., 2016).

Summing up, instability of phylogenetic relationships obscures our understanding about the evolutionary history of spiders. Here, we review recent advancements on interfamilial phylogenetic relationships across the spider tree of life. This study is designed to identify the recurring conflicting nodes with certain data classes. We discuss these relationships based on the analysis of the hitherto largest sample of spiders to date, using genome-scale data combined with a traditional Sanger-sequence dataset from the literature, representing 131 of the currently valid 132 spider families. We review some of the history and current understanding of family groupings and their biological characteristics in a phylogenetic context. We also provide potential future directions for spider phylogenetics and systematics such as evidence for potential taxonomic changes based on grouping by monophyly.

Materials and methods

Taxon sampling

The ultra-conserved sequences for this study were obtained from the following sources: (1) published UCE studies: Starrett et al. (2017), Wood et al. (2018), Hedin et al. (2019), Kulkarni et al. (2020), Maddison et al. (2020), Ramírez et al. (2021), Azevedo et al. (2022); (2) transcriptome-based studies: Sharma et al. (2014), Zhao et al. (2014), Fernández et al. (2014, 2018a), Rix et al. (2017), Kallal et al. (2018), Shao and Li (2018), Kallal et al. (2021a); (3) publicly available spider genomes on Sequence Read Archive (SRA): *Latrodectus hesperus* (Theridiidae; i5K Consortium, 2013 Consortium, 2013), *Loxosceles reclusa* (Sicariidae; i5K Consortium, 2013), *Trichonephila clavipes* (Araneidae; Babb et al., 2017), *Parasteatoda tepidariorum* (Theridiidae; Schwager et al., 2017) and *Stegodyphus mimosarum* (Eresidae; Sanggaard et al., 2014); and (4) our sequencing efforts.

We analysed 554 terminals of UCE data, representing 125 of 132 (94.6% sampling) spider families (World Spider Catalog, 2023). The phylogenetic trees were rooted at the node containing the Xiphosura representatives, *Tachypleus tridentatus* and *Limulus polyphemus*. In addition, we combined the UCE data, with the Sanger-based six-marker dataset Wheeler et al. (2017), Piacentini and Ramírez (2019), additional publicly available sequences and bycatch from UCE assemblies with our UCE dataset to result in a 1362-taxon dataset belonging to 131 families (99% familial representation). The details of concatenation are provided in Table S2.

The specimens sequenced for this study come from our own fieldwork or from the collections of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; the Museum of Comparative Zoology (MCZ), Harvard University, Boston, Massachusetts; and the California Academy of Sciences (CAS), San Francisco, California.

For the specimens we sequenced, three to four legs were used for DNA extractions from 58 spider specimens using the DNeasy™ Tissue Kit (Qiagen Inc., Valencia, CA, USA). The homogenate was incubated at 55 °C overnight and then purified following the manufacturer's protocol. The DNA extractions were quantified using high sensitivity Qubit fluorometry (Life Technologies, Inc./Thermo Fisher Scientific, Waltham, MA, USA) and quality checked using gel electrophoresis on a 1.5% agarose gel.

Library preparation, enrichment and sequencing

Libraries were prepared and enriched following protocols in Faircloth et al. (2015), but following the modifications detailed below. Depending on prior degradation and quality of the DNA, between 7 and 100 ng of DNA were sheared between 0 and 60 s (amp = 25%, pulse = 10–10 s, to a target size of *c*. 250–600 bp) by sonication (Q800R; Qsonica LLC, Newtown, CT, USA).

Sheared DNA was dried completely and rehydrated to the required input volume (13 μL) and used as input for DNA library preparation (Hyper Prep Library kit; Kapa Biosystems, Inc., Wilmington, MA, USA). After ligation of universal stubs (Faircloth and Glenn, 2012), a 0.8× SPRI bead clean was done (Kapa Pure Beads; Kapa Biosystems, Inc.) on a Wafergen Apollo liquid handler (Wafergen Biosystems, Fremont, CA, USA), resulting in 30 μL of post-ligation library. For adapter ligation, we used TruSeq adapters (Faircloth and Glenn, 2012). PCR conditions were as follows: 15 μL post-ligation library, 25 μL HiFi HotStart polymerase (Kapa Biosystems), 2.5 μL each of Illumina TruSeq- style i5 and i7 primers, and 5 μL double-distilled water (ddH_2O). We used the following thermal protocol (Kapa Biosystems): 98 °C for 45 s; 13 cycles of 98 °C for 15 s, 65 °C for 30 s and 72 °C for 60 s; and final extension at 72 °C for 5 m. PCR cleanup was done with a 0.8 × SPRI bead clean (Kapa Pure Beads) on a Wafergen Apollo (TaKaRa Bio Inc., Tokyo, Japan) with a final library volume of 20 μL. Following clean-up, libraries were divided into enrichment pools containing eight libraries combined at equimolar ratios with final concentrations of 137–184 ng/μL.

All pools were enriched with the Spider2Kv1 probes (Kulkarni et al., 2020) following the myBaits protocol 4.01 (Daicel Arbor Biosciences, Ann Arbor, MI, USA). Hybridization reactions were incubated for 24 h at 65 °C, subsequently all pools were bound to streptavidin beads (MyOne C1; Life Technologies, Inc.), and washed. We combined 15 μL of streptavidin bead-bound, washed, enriched library with 25 μL HiFi HotStart Taq (Kapa Biosystems, Inc.), 5 μL of Illumina TruSeq primer mix (5 μM forward and reverse primers) and 5 μL of ddH2O. Post-enrichment PCR used the following thermal profile: 98 °C for 45 s; 18 cycles of 98 °C for 15 s, 60 °C for 30 s and 72 °C for 60 s; and a final extension of 72 °C for 5 m. We purified the resulting reactions using 1× bead clean using Kapa Pure Beads and resuspended the enriched pools to total 22 μL.

We then quantified pools using qPCR library quantification (Kapa Biosystems, Inc.) with two serial dilutions of each pool (1:100 000, 1:1 000 000), assuming an average library fragment length of 600 bp. Based on the size-adjusted concentrations estimated by qPCR, we combined all pools at an equimolar concentration of 30 nM, and size selected for 250–600 bp with a BluePippin (SageScience, Beverly, MA, USA). We sequenced the pooled libraries in a single lane of a paired-end run on an Illumina HiSeq 2500 (2 × 150 bp rapid run) at the University of Utah Huntsman Cancer Institute.

Recovering UCEs from transcriptomes and genomes

We followed the assembly, sanitation and reading frame detection pipeline as in Fernández et al. (2018a) for assembling the transcriptomes. Additionally, we ran the Perl script for Rcorrector (Song and Florea, 2015) for error correction and downstream efficiency before assembly. The FASTA files of transcriptomes resulting from CD-HIT-EST were converted to 2-bit format using faToTwoBit (Kent, 2002). Then, in the PHYLUCE environment (publicly available at https://phyluce.readthedocs.io/en/latest/tutorial-three.html), we created a temporary relational database to summarize probe to assembly match using: *phyluce_probe_run_multiple_lastzs_sqlite* function on the 2-bit files. The ultraconserved loci were recovered by the *phyluce_probe_slice_sequence_from_genomes* command. The resulting FASTA files were treated as contigs and used to match the reads to the Spider2Kv1 probes.

The GC content can influence the phylogenetic relationships reconstructed using genome-scale data (Benjamini and Speed 2012). To explore this, we computed GC content in each taxon in the concatenated UCE dataset using BBMap (https://github.com/BioInfoTools/BBMap). We also computed missing data to map their distribution and compare if they corresponded to the inconsistent nodes. GC and content and missing data was mapped on the phylogeny using the phytools package v.0.7–70 in R Studio v.1.3.1093. We reanalyzed our UCE dataset with subsequent exclusion of taxa with high missing data and taxa with stable placement across analyses were kept and others were omitted from the analysis.

Concatenation of our UCE and legacy marker datasets

The Sanger-based dataset of Wheeler et al. (2017) included the following Sanger-sequenced loci: mitochondrial markers—12S ribosomal RNA (12S), 16S ribosomal RNA (16S) and cytochrome c oxidase subunit 1 (COI); and nuclear markers—protein-coding histone H3 (H3), and small and large subunits of ribosomal RNA genes (18S and 28S, respectively). Conspecific taxa with UCE and Sanger-sequenced data were concatenated. A phylogeny resulting from this dataset rendered some unusual results in our preliminary analyses, such as polyphyly of Salticidae, Malkaridae, Thomisidae and Lycosidae, which has been extensively studied and is always recovered as monophyletic. Therefore, we increased the taxon sampling for these families based on publicly available sequences, from studies such as Piacentini and Ramírez (2019), and through bycatch of sequences from the UCE assemblies. To extract bycatch, we generated a Blast database of the UCE assembly using Blast+ v.2.9.0, queried against the longest congeneric legacy marker sequence with an evalue of 1e-100 and extracted all the sequence matches of Blastn. Each match was visualized against the original assembly (before fishing out UCEs) using Geneious v.R10 and the most complete sequence was binned to concatenate with the UCE sequence. We also concatenated congeneric taxa to maximize the data completeness (see Table S2). Our goal to perform this exercise was to maximize the taxon representation and minimize the missing data class. For a more stringent tree search space within the marronoids and Dionycha clade to test if some of the polyphyletic families are rendered monophyletic, we compiled two datasets including these taxa and a few outgroups extracted from the 25% occupancy UCE dataset.

Phylogenomic analyses

UCE dataset: The assembly for *de novo* generated sequences was done using SPAdes v.3.14 and, alignment (using Mafft), trimming (using GBlocks) and concatenation of data were done using the PHYLUCE pipeline (publicly available at https://phyluce.readthedocs.io/en/latest/). We applied gene occupancies of 10%, 25% and 40% on the UCE dataset. We screened for orthologous and duplicate loci with the minimum identity, and coverage of 65 and 65 matches. Phylogenetic analyses were performed on the unpartitioned nucleotide data using IQ-Tree (Nguyen et al., 2015) v.2. Model selection was allowed for each unpartitioned dataset using the TEST function (Kalyaanamoorthy et al., 2017, Hoang et al., 2018). Nodal support was estimated via 1000 ultrafast bootstrap replicates (Hoang et al., 2018) with 15 000 iterations. To reduce the risk of overestimating branch support with ultrafast bootstrap resulting from model violations, we appended the command *-bnni*. With this command, the ultrafast bootstrap optimizes each bootstrap tree using a hill-climbing nearest neighbour interchange (NNI) search based on the corresponding bootstrap alignment (Hoang et al., 2018).

Six-marker Sanger-sequencing dataset: COI and H3 markers were aligned using MACSE (Ranwez et al., 2011) with the invertebrate mitochondrial code followed for COI. The remaining markers (12S, 16S, 18S and 28S) were aligned using Mafft v.7 (Katoh and Standley 2013). Trimming was performed on all alignments using trimAL (Capella-Gutiérrez et al., 2009) with *-gappyout* setting. See Table S2 for a complete list of taxa and concatenation of UCE and six-marker dataset used in the study. We compared the relationships reconstructed using parsimony and maximum-likelihood method for a subset dataset including Araneoidea. We conducted parsimony searches using TNT (Goloboff and Catalano, 2016) applying the tree-building method of Simmons and Goloboff (2014) with 1000 bootstrap replicates.

Results and discussion

Our UCE dataset included 554 taxa representing ten nonspider arachnids including two Xiphosura (*Tachypleus tridentatus* and *Limulus polyphemus*), which were used to root the phylogeny. This dataset included 125 of the currently known 132 (94.6%) spider families (World Spider Catalog, 2023). Our Combined dataset (UCEs+legacy marker datasets) included 1362 taxa with 131 families (99%) of which 381 taxa were represented by both data classes (Table S2). Model testing using the Bayesian information criterion (BIC) in IQ-Tree selected the GTR + I + F + G4 model for the Combined dataset and all matrix occupancies (10%, 25% and 40%) UCE datasets. Statistics of captured UCE loci are listed in Table S1. The phylogenetic relationships were overall similar across except that at 1% and 10% occupancies where Araneidae was sister group to a clade including Synotaxidae plus Physoglenidae and Nesticidae, whereas Araneidae was sister to Synotaxidae at 25% occupancy. Within the miniature orb-weaving spiders clade (symphytognathoids), Theridiosomatidae formed a sister group to Mysmenidae at 1% and 10% occupancy, whereas Theridiosomatidae was sister group to the Anterior tracheal system (ANTS) clade that includes the remaining symphytognathoid families. Although GC-content was high in some taxa (Fig. S1), omitting them from the analyses did not alter the resulting phylogenetic relationships. Missing data were calculated for the UCE dataset, which was high for several taxa, particularly those that

were sequenced using Arachnid probe set of Starrett et al. (2017) but matched using the Spider2Kv1 probe set of Kulkarni et al. (2020) (Fig. S2).

All major clades that were obtained in the most recent transcriptomes-based study (Kallal et al., 2021a) and UCEs-based study (Kulkarni et al., 2021) were recovered in this study with both UCE and Combined datasets. These lineages include, for example, Araneae, Mesothelae, Opisthothelae, Mygalomorphae, Avicularioidea, Atypoidea, Araneomorphae, Hypochilidae+Filistatidae, Synspermiata, Austrochiloidea, Palpimanoidea, Nicodamoidea, Retrolateral tibial apophysis (RTA) clade, and Araneoidea. A general structure of relationships between these major lineages are shown in Fig. 3 and their family-level relationships are shown in Fig. 4.

Araneae

Platnick & Gertsch (1976) constructed the first cladogram about higher level grouping in spiders. They rejected the groupings by cheliceral orientation (Orthognatha and Labidognatha) and established two suborders Mesothelae and Opisthothelae and two infraorders within Opisthothelae—Mygalomorphae and Araneomorphae—which continue to be used to this day. In this section, we provide a review of the family-level relationships obtained from our UCE and Combined datasets and a comparison with prevailing hypotheses compiled from the literature. We use the term "Combined phylogeny" to indicate the phylogenetic tree resulting from the combination of the UCE-derived dataset and the Wheeler et al. (2017) six Sanger-based markers (Figs 5–20).

Mesothelae

This group is an ancient lineage which includes spiders that retain many primitive characters, such as an externally segmented abdomen, four pairs of multisegmented spinnerets, two pairs of book lungs and chelicerae organized at an angle (between paraxial and diaxial). In addition, their spinnerets are situated near the middle of the abdomen and abdominal segments 12–18 are present. The extant mesotheles are classified in two families, Liphistiidae and Heptathelidae, with one and seven genera, respectively, and *c*. 150 species known mainly from China, Japan and South-east Asia (Xu et al., 2021; Li, 2022; World Spider Catalog, 2023; see also Breitling 2022). The oldest mesothele fossils are from the late Carboniferous period (Magalhaes et al., 2020). They construct trapdoor burrows (similar to some mygalomorphs) with radiating trip lines for prey capture (Bristowe, 1976). The similarity of observable morphological characters in the spider fossils, phylogenetic placement and age (in dated phylogenies) in extant mesotheles indicate that these spiders retain a plesiomorphic state for many characters. Haupt (2003) reconstructed a morphology-based cladogram of relationships between the Mesothelae spiders. Morphological synapomorphies of Mesothelae include presence of abdominal tergites; invaginations at posteromedian corners of coxae IV; trichobothrial base on the dorsal surface of distal leg segments dome-shaped with two flattened plates; flattened spurs distally on the prolateral and retrolateral sides of tibiae I–III; oval, unsclerotized areas situated proximally on the sides of metatarsi I–III (Platnick & Gertsch, 1976; Platnick & Goloboff, 1985; Haupt, 2003). The phylogenetic placement of these spiders is robust with all previous molecular data (Xu et al., 2015; Bond et al., 2014; Fernández et al., 2014, 2018a; Wheeler et al., 2017; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a), and also with our phylogenetic results (Figs 3–5) with strong support [100% ultrafast bootstrap (UB in remaining text)] which is sister group to the Opisthothelae clade.

Opisthothelae

In Opisthothelae the spinnerets are located close to the caudal end of the abdomen such that the 12–18 segments are inconspicuous (beyond 5th opisthosomal segments). This group consists of two major clades, Mygalomorphae and Araneomorphae. Mygalomorph spiders have paraxial chelicerae and exhibit the plesiomorphic condition of two pairs of book lungs. Araneomorphae mostly have diaxial (opposing) chelicerae. However, all Opisthothelae lack the anterior median spinnerets, although its homologue—the cribellum, a plate-like field with numerous spigots—is present in many araneomorph spiders (see Araneomorphae section).

Our phylogenetic results (Figs 3 and 4) recover a monophyletic Opisthothelae consisting of two subclades Mygalomorphae and Araneomorphae with strong support (100% UB). These results corroborate other genome-scale molecular studies supporting the monophyly of these two well-established groups (Bond et al., 2014; Fernández et al., 2014, 2018a; Wheeler et al., 2017; Starrett et al., 2017; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a).

Mygalomorphae

Many mygalomorphs are large-sized spiders with two pairs of book lungs and paraxial fangs. Most species have both posterior median and lateral spinnerets, however, *Iberesia* (Nemesiidae), from Europe, has only posterior lateral spinnerets (Decae & Cardoso, 2006). A majority of these spiders construct silk-lined burrows mainly on the ground with some variations such

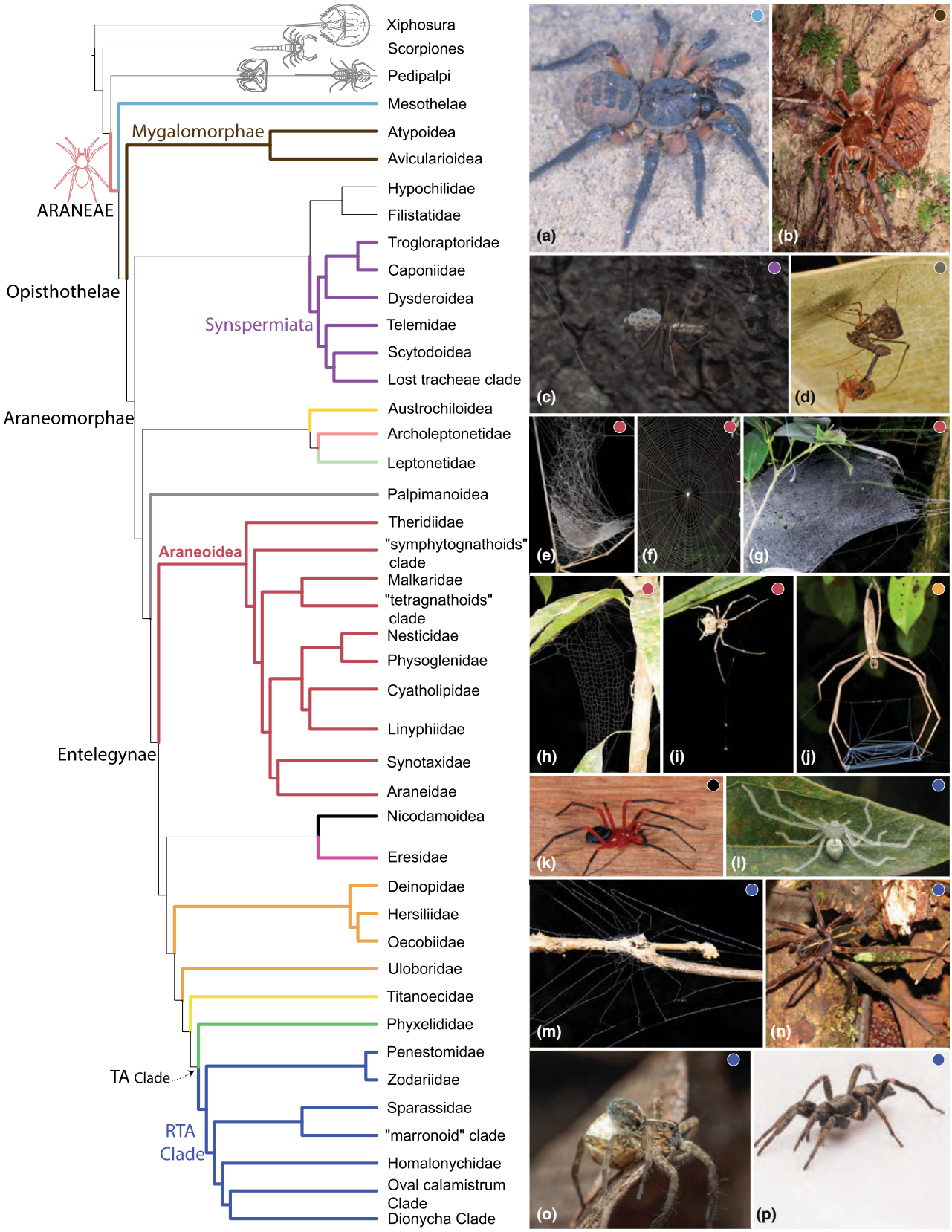
Xiphosura
Scorpiones
Pedipalpi
Mesothelae
Mygalomorphae
Atypoidea
Avicularioidea
ARANEAE
Hypochilidae
Filistatidae
Opisthothelae
Trogloraptoridae
Caponiidae
Dysderoidea
Synspermiata
Telemidae
Scytodoidea
Lost tracheae clade
Araneomorphae
Austrochiloidea
Archoleptonetidae
Leptonetidae
Palpimanoidea
Theridiidae
Araneoidea
"symphytognathoids" clade
Malkaridae
"tetragnathoids" clade
Nesticidae
Physoglenidae
Cyatholipidae
Linyphiidae
Entelegynae
Synotaxidae
Araneidae
Nicodamoidea
Eresidae
Deinopidae
Hersiliidae
Oecobiidae
Uloboridae
Titanoecidae
Phyxelididae
Penestomidae
TA Clade
Zodariidae
Sparassidae
RTA Clade
"marronoid" clade
Homalonychidae
Oval calamistrum Clade
Dionycha Clade
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)

Fig. 3. Maximum-likelihood phylogeny reconstructed using the 25% occupancy dataset of the ultraconserved elements (UCEs) with higher-level groups highlighted. Branch colours correspond to the circles in the top right of the photographs. (a) *Liphistius* sp. (Liphistiidae), (b) *Theraphosa* sp. (Theraphosidae), (c) Pholcidae sp., (d) *Eriauchenius workmani* (Archaeidae), (e) typical web of Linyphiidae, (f) orb web of *Ocrepeira darlingtoni* (Araneidae), (g) typical aerial sheet web of *Forstera* (Cyatholipidae), (h) modular vertical web of *Synotaxus* sp. (Synotaxidae), (i) *Exechocentrus lancearius* (Araneidae), (j) *Deinopis* sp. (Deinopidae) with its cribellate orb web, (k) Nicodamidae sp., (l) Sparassidae, (m) cribellate web of *Paramatachia* sp. (Desidae), (n) *Centroctenus alinahui* (Ctenidae), (o) Lycosidae sp., (p) *Poecilochroa* sp. (Gnaphosidae). Photo credits: (c, l, o, p) Atul Vartak; (n) Nicolas Hazzi; remaining photos, Gustavo Hormiga.

as the open burrow of *Acanthoscurria* (Theraphosidae), tubular silk-lined burrows with trapdoor of *Actinopus* (Actinopodidae), burrow with collar door of *Antrodiaetus* (Antrodiaetidae), purse web of *Atypus* (Atypidae) and the trap-door found on tree trunks aboveground (Migidae) (Opatova et al., 2021, Wilson et al. 2023). There are >3000 mygalomorph described species classified in *c*. 30 families (Opatova et al., 2020; World Spider Catalog 2023). Raven (1985) reviewed the systematics, provided the first family-level cladistic hypothesis for this lineage and suggested that that loss of the anterior median spinnerets, the reduction of the anterior lateral spinnerets and the reduction of the number of sclerites in the male palp are synapomorphies of the group.

Recent advances using modern sequencing methods have resulted in radical changes to Mygalomorphae systematics. Several molecular phylogenies have recovered this group as monophyletic consisting of two subclades Avicularioidea and Atypoidea (Hedin and Bond, 2006; Bond et al., 2012, 2014; Garrison et al., 2016; Wheeler et al., 2017; Hedin et al., 2018, 2019; Starrett et al., 2017; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a; Opatova et al., 2020) including our phylogenetic results (Figs 3–5) with strong support (100% UB). The most recent phylogenetic hypothesis was proposed by Opatova et al. (2020) based on a densely sampled phylogeny of mygalomorphs using anchored hybrid enrichment (AHE) data.

Our UCE-based phylogeny included representatives of 23 mygalomorph families including four Atypoidea (nine terminals) and 19 Avicularioidea families (40 terminals) (Fig. 4). In our analysis, the phylogenetic relationships within Atypoidea are similar to those of the UCE-based phylogeny of Hedin et al. (2019) (the AHE-based phylogeny of Opatova et al., 2021, included only two atypoid families). The avicularioid family Euagridae was paraphyletic with one group representing *Allothele*, *Australothele* and *Cethegus* as a sister group to a clade of avicularioid families (including Ischnothelidae, Hexathelidae and *Euagrus*) whereas the other group representing the type genus *Euagrus* as a sister group to Ischnothelidae (Fig. 4). The AHE analysis of Opatova et al. (2021) recovered Ischnothelidae as a sister group to all remaining avicularioid families, and Euagridae including *Cethegus* and *Euagrus* was monophyletic with 100% UB. Aside from this conflicting hypothesis, the familial relationships between our UCE phylogeny and that of Opatova et al. (2020) are mostly congruent. The combination of Wheeler et al.'s (2017) six-marker dataset with our UCE dataset elevated the taxon sampling of Avicularioidea to 82 terminals (24 families). However, in the resulting phylogeny of this Combined dataset, Euagridae, Hexathelidae, Ischnothelidae, Bemmeridae, Cyrtaucheniidae, Halonoproctidae, Barycheliidae, Actinopodidae, Nemesiidae and Idiopidae were not monophyletic (Fig. 5). In our Combined phylogeny, the taxon sampling differed from that of Opatova et al. (2020) owing to multiple reasons. Only 40 of 82 avicularioid terminals were represented by both UCE and Sanger six-marker datasets (Fig. 5) and thus it is possible that the missing data may have influenced the phylogenetic inference. Incongruent phylogenetic results also could be attributed to the difference in the nature of two data classes, the AHE sequences of Opatova et al. (2020) and our UCE + Sanger dataset. Differences in the taxon sampling between the studies also may have caused disparities: for example, Nemesiidae polyphyly is caused by two *Calisoga* terminals (Nemesiidae) representing UCE + Sanger datasets being sister to Anamidae yet two other nemesiids from Wheeler et al.'s (2017) dataset form a sister group to *Fufius* (Cyrtaucheniidae). Owing to this limitation, we do not propose any taxonomic changes.

Araneomorphae

These so-called "modern or true spiders" represent the most speciose lineage of extant spiders with >100 families, and *c*. 47 500 species (World Spider Catalog, 2023). Synapomorphies of Araneomorphae (Platnick & Gertsch, 1976) include the presence of a cribellum, piriform silk glands (Coddington, 1989), diaxial (opposing) chelicerae, by having expanded palpal coxae, forming the endites that bear a distal-lateral serrula (Ramírez, 2014), and the presence of a single pair of coxal glands (mesotheles and mygalomorphs have two pairs; Millot, 1949). Additional support for the monophyly of this suborder is provided by the presence of cleistospermia (which refers to the transfer of individually encapsulated sperm cells) and the type of cytoplasmic inclusions during spermiogenesis (in the form of clusters of glycogen surrounded by membranes after the coiling process; Michalik & Ramírez, 2014,

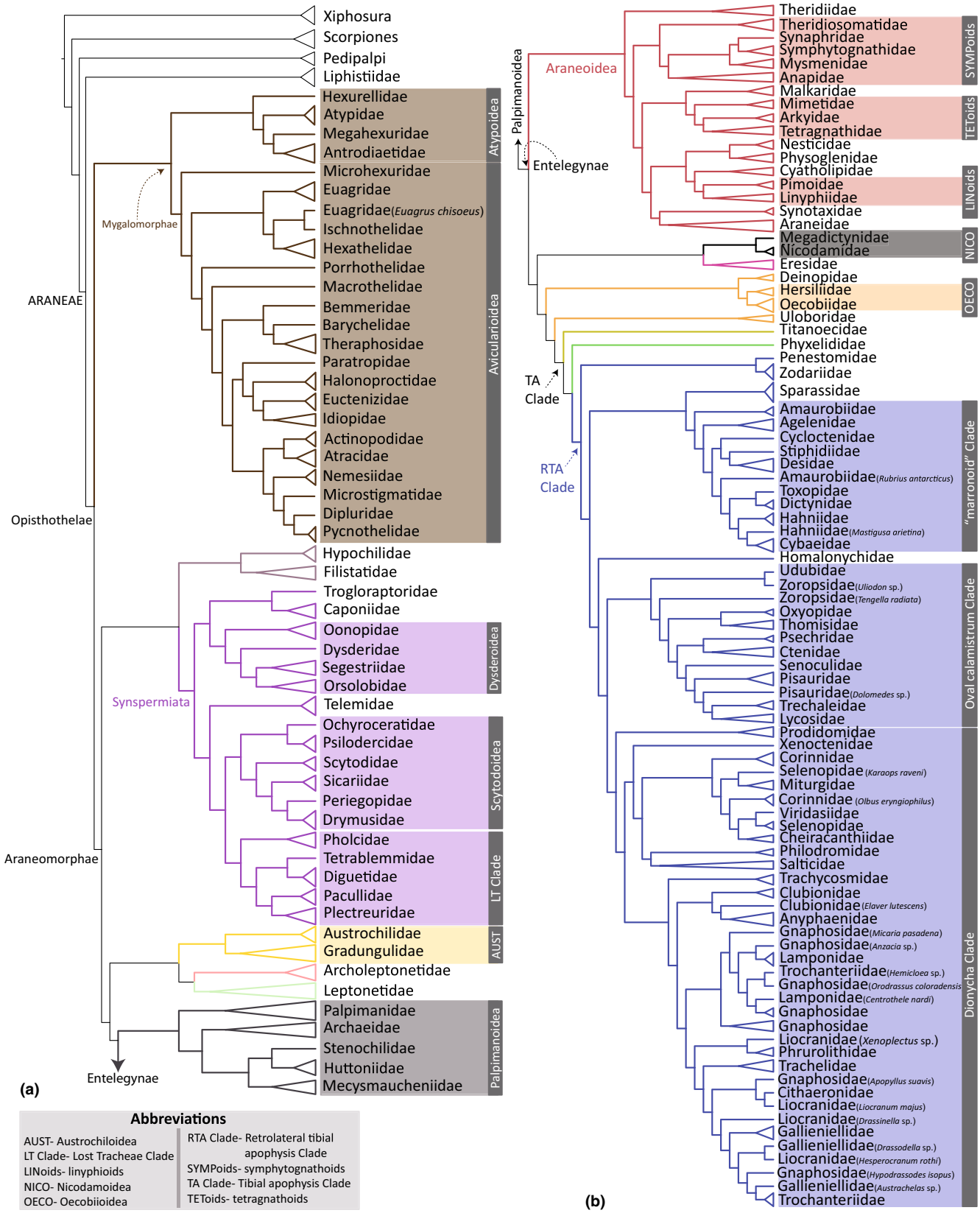

Fig. 4. Maximum-likelihood phylogeny of the family-level relationships of spiders reconstructed using the 25% occupancy dataset of the ultra-conserved elements (UCEs).

and references therein). The posterior PLS of araneomorphs have one or two segments, whereas mesotheles have multisegmented PLS and mygalomorphs have three or four segments (Platnick & Gertsch, 1976). The cribellum is a short plate-like field that is considered to be homologous to the anterior median spinnerets and occurs intermittently throughout the Araneomorphae. The cribellum sits anterior to the three pairs of spinnerets and accommodates thousands of spigots that secrete long-lasting sticky silk (called "cribellate silk") which is woven using a functionally co-dependent calamistrum, which is a specialized comb of setae on the fourth metatarsus. The presence of a cribellum was first used by Bertkau (1882) for classification of higher groups of spiders into Cribellata and Ecribellata.

Petrunkevitch (1923) postulated that the ecribellate families are derived from cribellate spiders. In several araneomorph groups the cribellum is reduced to a nonfunctional colulus or lost altogether. Piriform silk glands, another synapomorphy of araneomorphs, secrete glue that anchors ampullate silk lines to a substrate or to stick them to each other. This glue is released through spigots (called "piriform spigots") which are adjacent to the major ampullate spigots on the anterior lateral spinnerets (Coddington 1989).

Araneomorphae is a well-established clade, robustly supported in all morphological and molecular phylogenies (Platnick & Gertsch, 1976; Coddington & Levi, 1991; Hausdorf 1999, Bond et al., 2014, Fernández et al., 2014, 2018a, Wheeler et al., 2017, Starrett et al., 2017; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a).

Hypochilidae and Filistatidae

Hypochilidae is a small family of 33 cribellate species which includes the two genera *Hypochilus* and *Ectatosticta* which are known exclusively from the United States and China, respectively (World Spider Catalog, 2023). *Hypochilus* spiders construct a mesh web resembling a lampshade attached to a rock overhang and the spider rests in the middle of the web (called "lampshade web"; Forster et al., 1987). *Ectatosticta* spiders construct sheet webs among rocks or tree trunks (Lin & Li, 2020). Marx (1888) who described the first hypochilid, *Hypochilus thorelli* Marx, 1888, remarked that this spider "is so anomalous that it appears like the representative of a prototype, in which characters were united in one individual which are now distributed into widely differing genera". It is one of the relictual groups of "modern" (Araneomorphae) spiders that retain the primitive arrangement of two pairs of book lungs and venom glands restricted to the chelicerae (Gertsch, 1958) and that lack paracribellar spigots from posterior median spinnerets (Forster et al., 1987).

The transcriptomic analysis of Bond et al. (2014) recovered Filistatidae as the sister group to Hypochilidae, an affinity grouping based on morphology first suggested by Petrunkevitch (1923). Filistatidae is a large family with 18 genera and 189 species distributed globally (World Spider Catalog, 2023). They are reclusive, mostly cribellate spiders, with most species found in subtropical arid and semiarid regions of the world (Magalhaes & Ramírez 2019). The synapomorphies of this family are a narrow metatarsus stopper (narrow socket associated to the lyriform organ) in second legs of males, an anterior row of specialized setae in the anterior lateral spinnerets, an anteriorly pronounced clypeus and a tongue-like labrum with lateral extensions (Magalhaes & Ramírez 2017). Adult members of this family possess an anterior book lung system and a posterior tracheal system. However, remnants of the primitive posterior pair of book lungs are seen in their spiderlings (Ramírez 2014, Ramírez et al., 2021). In our study, these early diverging lineages of araneomorph spiders form a clade which is a sister group to Synspermiata (Fig. 6c). All high-throughput molecular data and Sanger-sequenced markers support this placement of the Hypochilidae + Filistatidae clade (Bond et al., 2014, Garrison et al., 2016, Wheeler et al., 2017, Fernández et al., 2018a; Kulkarni et al., 2020, 2021, Kallal et al., 2021a).

Synspermiata

The name of this group was coined by Michalik & Ramírez (2014), it includes ecribellate haplogyne spiders which have multiple spermatids fused into one synsperm (Alberti & Weinmann, 1985; Burger et al., 2010). In general, spiders with a haplogyne condition have relatively simple male genitalia with fused sclerites and female genitalia with a single duct for both copulation and fertilization (Platnick et al., 1991), but some haplogyne spiders have complex palps (e.g. liphistiids). Several studies have shown that the internal genitalia of some haplogyne spiders also are very complex, departing from the traditional definition of the haplogyne female genitalia of Wiehle (1967) (e.g. Burger et al., 2003, and references therein). At least in some Synspermiata, males insert both palps simultaneously when mating, which is a unique behaviour in this group (Burger et al., 2010). Some synspermiate members of the Pholcidae, Tetrablemmidae, Oonopidae, Ochyroceratidae and Trogloraptoridae are known to have evolved entelegyne condition independently (Michalik et al., 2019). Synspermiata includes three monophyletic groups, Dysderoidea, Scytodoidea and the Lost Tracheae clade, in addition to the families Caponiidae, Telemidae and Trogloraptoridae. The Dysderoidea families are grouped by having a unique respiratory system of

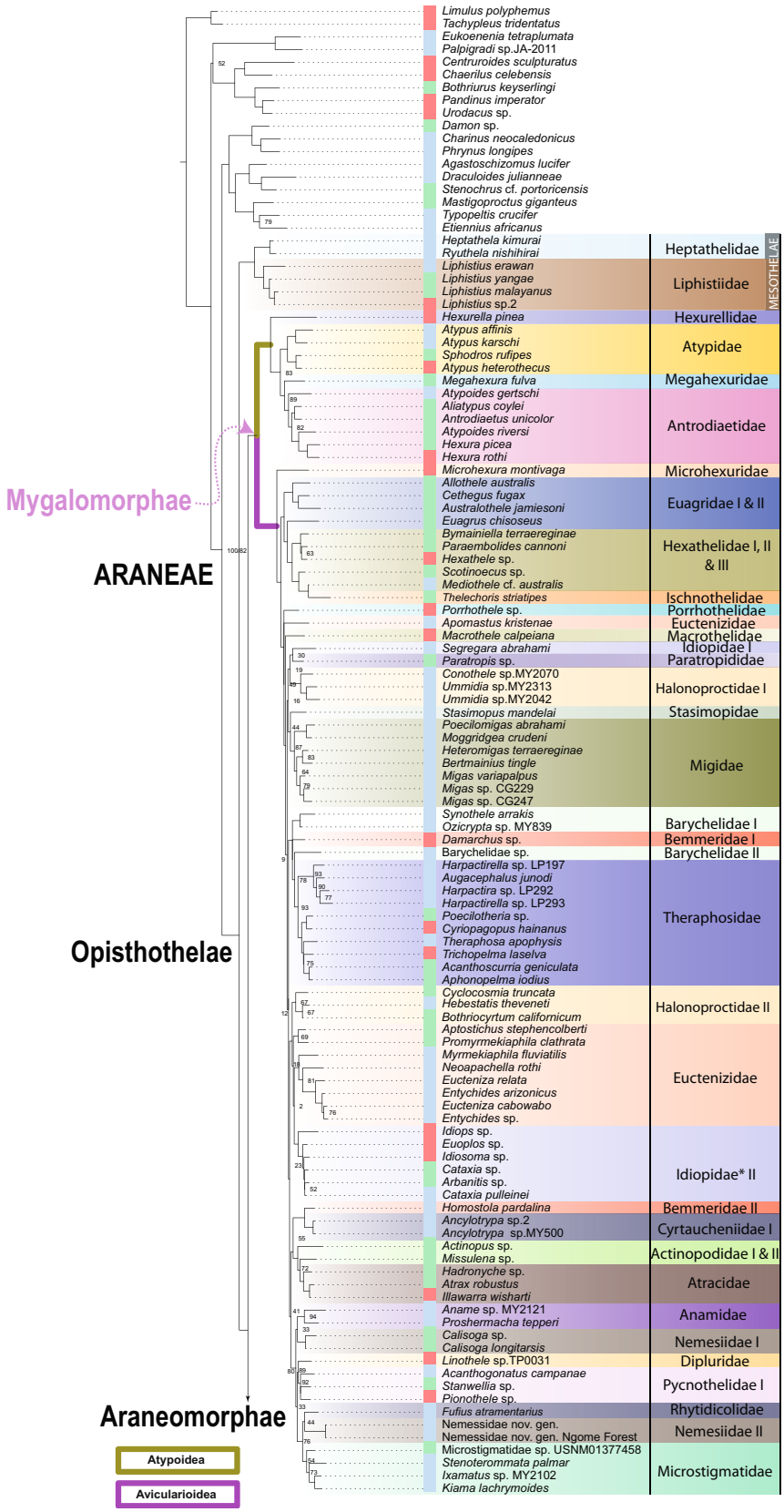
Limulus polyphemus
Tachypleus tridentatus
Eukoenenia tetraplumata
Palpigradi sp.JA-2011
Centruroides sculpturatus
Chaerilus celebensis
Bothriurus keyserlingi
Pandinus imperator
Urodacus sp.
Damon sp.
Charinus neocaledonicus
Phrynus longipes
Agastoschizomus lucifer
Draculoides julianneae
Stenochrus cf. portoricensis
Mastigoproctus giganteus
Typopeltis crucifer
Etiennius africanus
Heptathela kimurai
Ryuthela nishihirai
Heptathelidae
Liphistius erawan
Liphistius yangae
Liphistius malayanus
Liphistius sp.2
Liphistiidae
MESOTHELAE
Hexurella pinea
Hexurellidae
Atypus affinis
Atypus karschi
Sphodros rufipes
Atypus heterothecus
Atypidae
Megahexura fulva
Megahexuridae
Atypoides gertschi
Aliatypus coylei
Antrodiaetus unicolor
Atypoides riversi
Hexura picea
Hexura rothi
Antrodiaetidae
Microhexura montivaga
Microhexuridae
Mygalomorphae
Allothele australis
Cethegus fugax
Australothele jamiesoni
Euagrus chisoseus
Euagridae I & II
Bymainiella terraereginae
Paraembolides cannoni
Hexathele sp.
Scotinoecus sp.
Mediothele cf. australis
Hexathelidae I, II & III
ARANEAE
Thelechoris striatipes
Ischnothelidae
Porrhothele sp.
Porrhothelidae
Apomastus kristenae
Euctenizidae
Macrothele calpeiana
Macrothelidae
Segregara abrahami
Idiopidae I
Paratropis sp.
Paratropididae
Conothele sp.MY2070
Ummidia sp.MY2313
Ummidia sp.MY2042
Halonoproctidae I
Stasimopus mandelai
Stasimopidae
Poecilomigas abrahami
Moggridgea crudeni
Heteromigas terraereginae
Bertmainius tingle
Migas variapalpus
Migas sp. CG229
Migas sp. CG247
Migidae
Synothele arrakis
Ozicrypta sp. MY839
Barychelidae I
Damarchus sp.
Bemmeridae I
Barychelidae sp.
Barychelidae II
Opisthothelae
Harpactirella sp. LP197
Augacephalus junodi
Harpactira sp. LP292
Harpactirella sp. LP293
Poecilotheria sp.
Cyriopagopus hainanus
Theraphosa apophysis
Trichopelma laselva
Acanthoscurria geniculata
Aphonopelma iodius
Theraphosidae
Cyclocosmia truncata
Hebestatis theveneti
Bothriocyrtum californicum
Halonoproctidae II
Aptostichus stephencolberti
Promyrmekiaphila clathrata
Myrmekiaphila fluviatilis
Neoapachella rothi
Eucteniza relata
Entychides arizonicus
Eucteniza cabowabo
Entychides sp.
Euctenizidae
Idiops sp.
Euoplos sp.
Idiosoma sp.
Cataxia sp.
Arbanitis sp.
Cataxia pulleinei
Idiopidae* II
Homostola pardalina
Bemmeridae II
Ancylotrypa sp.2
Ancylotrypa sp.MY500
Cyrtaucheniidae I
Actinopus sp.
Missulena sp.
Actinopodidae I & II
Hadronyche sp.
Atrax robustus
Illawarra wisharti
Atracidae
Araneomorphae
Aname sp. MY2121
Proshermacha tepperi
Anamidae
Calisoga sp.
Calisoga longitarsis
Nemesiidae I
Linothele sp.TP0031
Dipluridae
Acanthogonatus campanae
Stanwellia sp.
Pionothele sp.
Pycnothelidae I
Fufius atramentarius
Rhytidicolidae
Nemessidae nov. gen.
Nemessidae nov. gen. Ngome Forest
Nemesiidae II
Microstigmatidae sp. USNM01377458
Stenoterommata palmar
Ixamatus sp. MY2102
Kiama lachrymoides
Microstigmatidae
Atypoidea
Avicularioidea

Fig. 5. Phylogenetic relationships of Mesothelae and Mygalomorphae lineages derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

tracheae placed immediately behind the book lungs and an additional posterior sperm receptacle (diverticulum) and muscle-operated valves, which allow for control of the stored sperm by the female (Burger, 2013). Caponiids have advanced tracheal spiracles (book lungs are absent) and eye reductions and are relatively larger than other spiders with only tracheal systems (Platnick, 1994; Ramírez, 2000). Trogloraptoridae is an unusual family of a single cave-dwelling species—*Trogloraptor marchingtoni* Griswold, Audisio & Ledford, 2012—with characteristic striking raptorial claws, known from caves and their surroundings in the western United States (Griswold et al., 2012a). Telemidae spiders have a global distribution, with 16 genera classified in 106 species (World Spider Catalog, 2023). They produce large stacks of sperm cells (called rouleaux or spermatophores) which correspond with the dimensions of the female reproductive tract (Wang et al., 2012; Michalik & Ramírez, 2014). A study on *Telema tenella* Simon, 1882 showed that these spiders can live for up to 12 years in captivity (and produce about four egg cases each containing 3–4 eggs annually; Juberthie 1985), a lifespan that is much longer than many araneomorph spiders. The Lost Tracheae clade includes the spider families Diguetidae, Pacullidae, Pholcidae, Plectreuridae and Tetrablemmidae. As the name suggests, these spiders have secondarily lost the posterior respiratory system (Ramírez 2000). Pholcidae is the most speciose family of the Lost Tracheae clade, with 1896 species classified in 97 genera distributed globally, the remaining families of this clade are relatively less speciose.

All molecular data, such as the six Sanger-sequenced markers, transcriptomes and UCEs, have supported the monophyly of Synspermiata and its sister group relationship with the Hypochilidae plus Filistatidae clade (Wheeler et al., 2017; Garrison et al., 2016; Fernández et al., 2018a; Michalik et al., 2019; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a).

In our Combined phylogeny, the Dysderoidea clade (Oonopidae, Segestriidae, Orsolobidae and Dysderidae) was the sister group to Caponiidae. Trogloraptoridae and Telemidae formed a clade which was sister group Scytodoidea and the Lost Tracheae clade (Fig. 6a). In the transcriptomic analysis of Kallal et al. (2021a) and the UCE analysis of Ramírez et al. (2021) and this study, Trogloraptoridae formed a sister group to Caponiidae whereas Telemidae was a sister group to a large clade including Scytodoidea and the Lost Tracheae clade (Fig. 4). The sister group to Dysderidae in our Combined phylogeny was Orsolobidae (99% UB), similar to the results of Wheeler et al. (2017) and Ramírez et al. (2021), whereas the UCE dataset placed dysderids as a sister group to Segestriidae + Orsolobidae (Figs 4 and 6a). However, within the Dysderoidea clade, Oonopidae was a sister group to remaining families in our study (Fig. 6a), whereas Segestriidae was a sister group to the remaining dysderoids in Wheeler et al. (2017). A further study exploring the effect of data classes (such as exons, introns, UCEs) and taxon sampling on the interrelationships of Synspermiata may be useful in deriving a robust phylogeny of these spiders.

Austrochiloidea

Austrochiloid spiders form an ancient lineage in the evolution of araneomorph spiders (Platnick 1977; Forster et al., 1987; Wheeler et al., 2017; Fernández et al., 2018a; Kallal et al., 2021a; Kulkarni et al., 2021; Ramírez et al., 2021). This group is composed of two families, Austrochilidae and Gradungulidae, that are distributed in the Southern Hemisphere. The early divergence of these spiders, supported by their phylogenetic placement within Araneomorphae, is suggested by the retention of the plesiomorphic configuration of two pairs of book lungs in some members such as *Hickmania* (Gradungulidae, formerly placed in Austrochilidae) (Zapfe, 1955; Platnick, 1977; Forster et al., 1987; Ramírez et al., 2021; Kulkarni & Hormiga, 2021).

Many austrochiloids are cribellate, but some species, such as those in *Gradungula* or *Tarlina*, are cursorial species and have lost the cribellum.

Austrochilidae includes nine species classified in two genera (*Austrochilus* and *Thaida*) which are distributed in the Andean forests of central and southern Chile and adjoining regions of Argentina. These spiders have one pair of book lungs and a posterior tracheal respiratory system (Zapfe, 1955; Platnick, 1977; Forster et al., 1987). Gradungulidae includes 17 species classified in eight genera restricted to continental Australia and New Zealand. They have retained the plesiomorphic character of two book lung pairs (Zapfe, 1955).

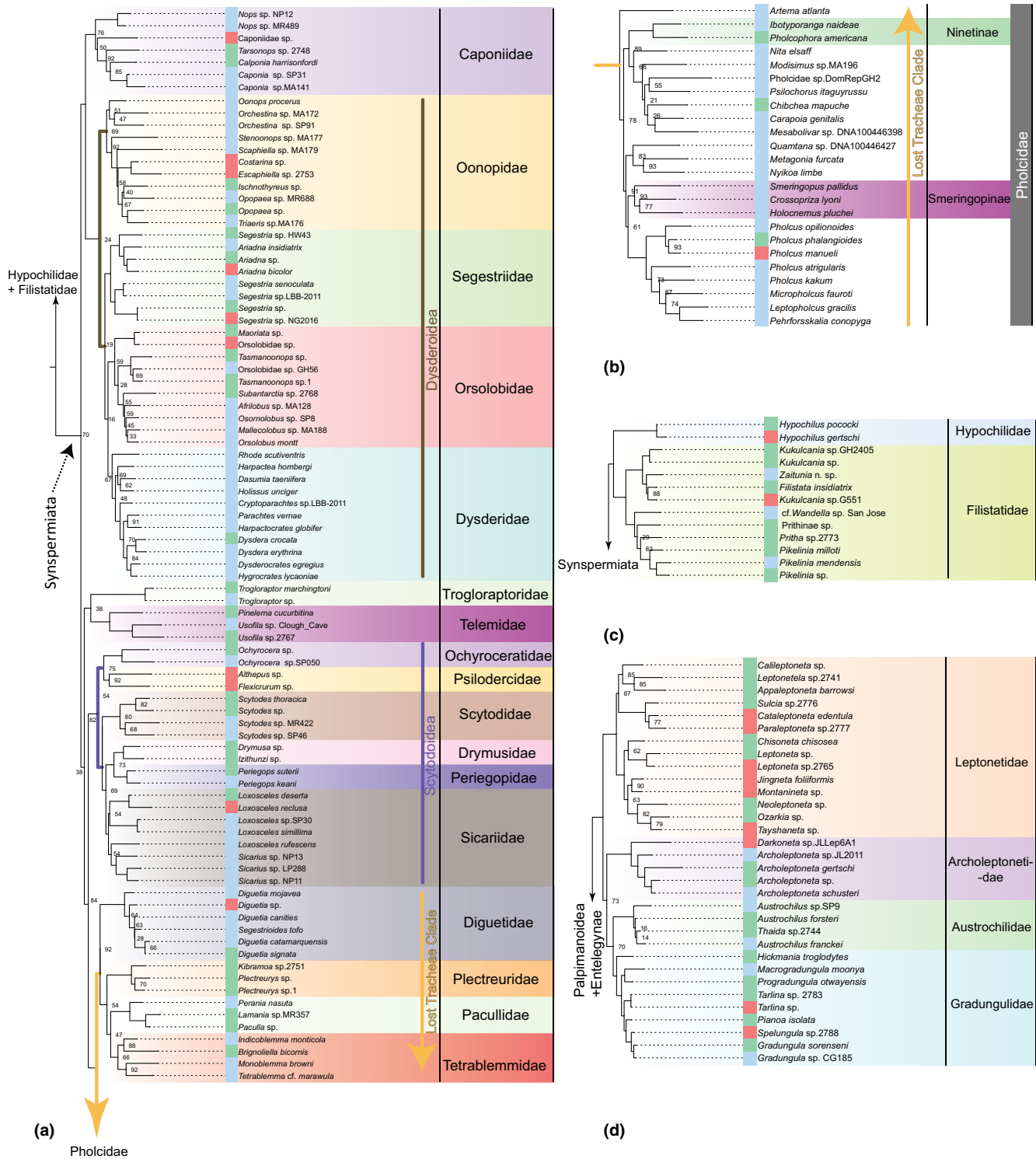

Fig. 6. Phylogenetic relationships of Synspermiata, Hypochilidae, Filistatidae, Austrochilioidea, Leptonetidae and Archoleptonetidae lineages derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Ultrafast bootstrap values are indicated at nodes, except when they were >95%.

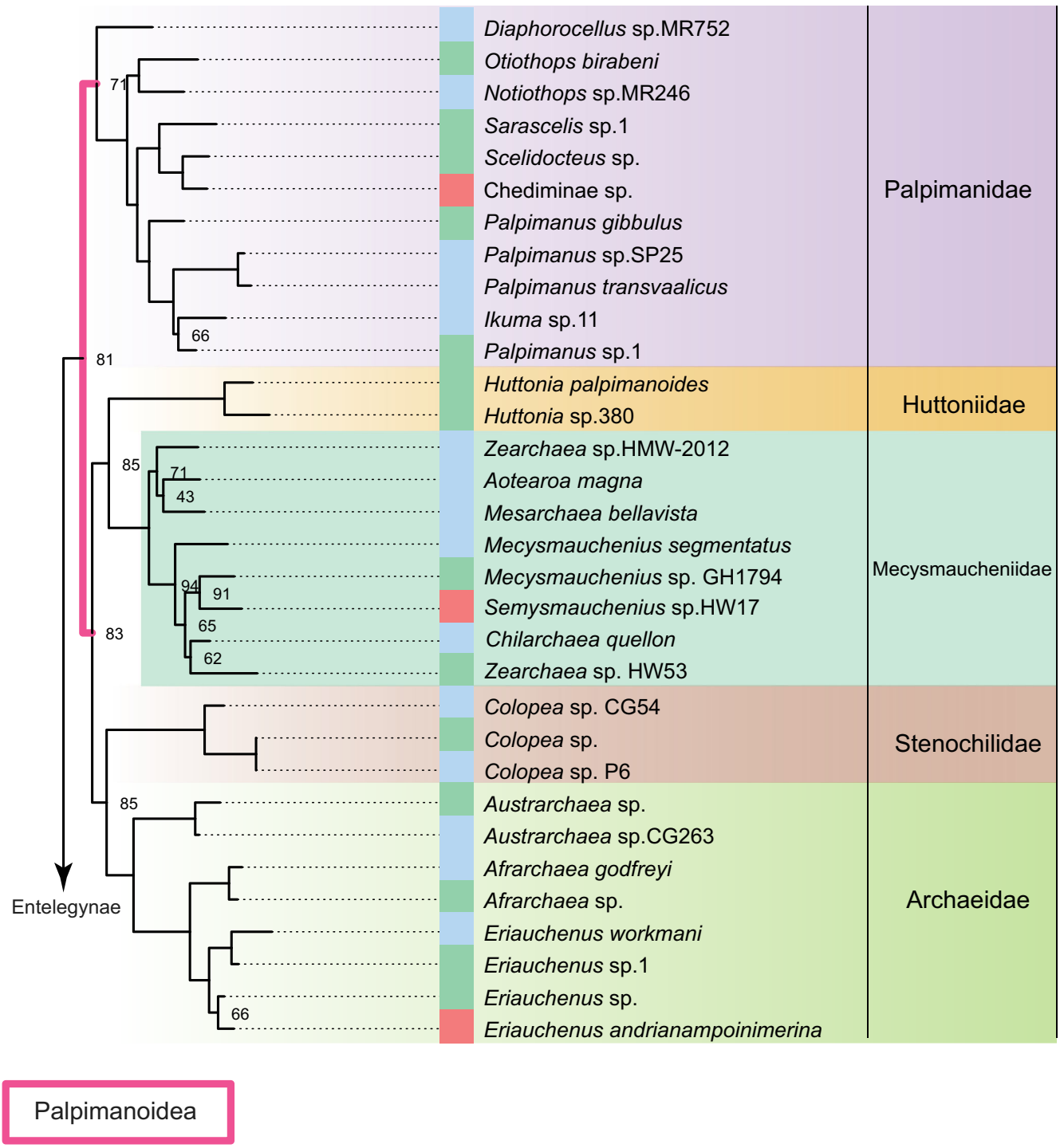

Fig. 7. Phylogenetic relationships of Palpimanoidea families derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

Our Combined dataset obtained a monophyletic Austrochilidae which was a sister group to Gradungulidae. This Austrochiloidea clade was a sister group to Archoleptonetidae (Fig. 6d). All genome-scale datasets support the monophyly of Austrochiloidea (Fernández et al., 2018a; Kulkarni et al., 2020, 2021; Ramírez et al., 2021; Kallal et al., 2021a; Ledford et al., 2021; Kulkarni & Hormiga, 2021).

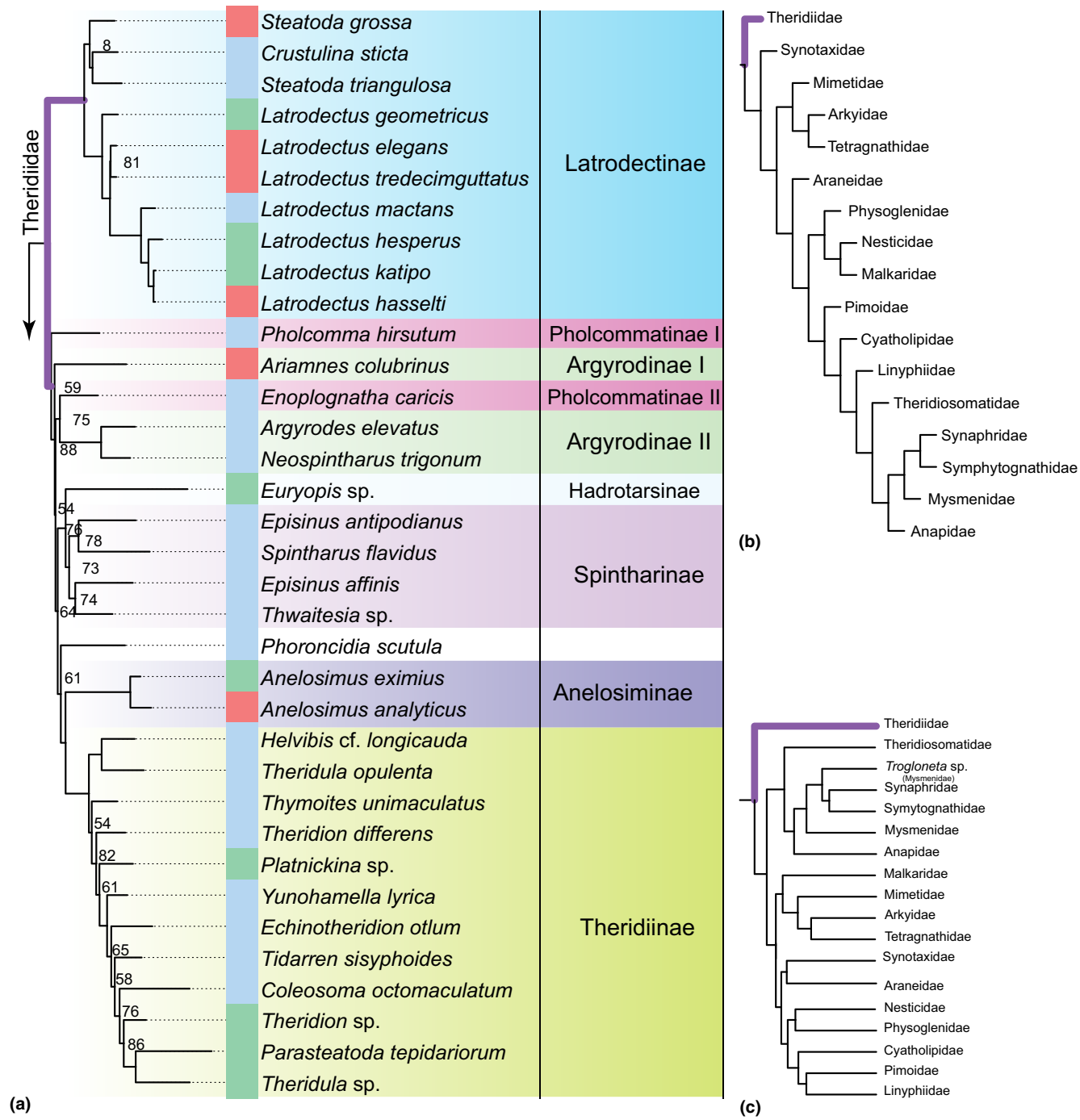

Fig. 8. Phylogenetic interrelationships of the family Theridiidae: (a) maximum-likelihood phylogeny derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset; (b) A phylogeny of Araneoidea collapsed to family level reconstructed using parsimony; and (c) maximum-likelihood (same topology at A). Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

Leptonetidae and Archoleptonetidae

Leptonetidae is a family of 22 genera grouping 375 described species distributed exclusively in the Holarctic region. Many of these species are cave-dwelling, and construct small and delicate sheet webs. Cave-adapted species show troglomorphic morphologies such as reduction of eyes, poor pigmentation and elongation

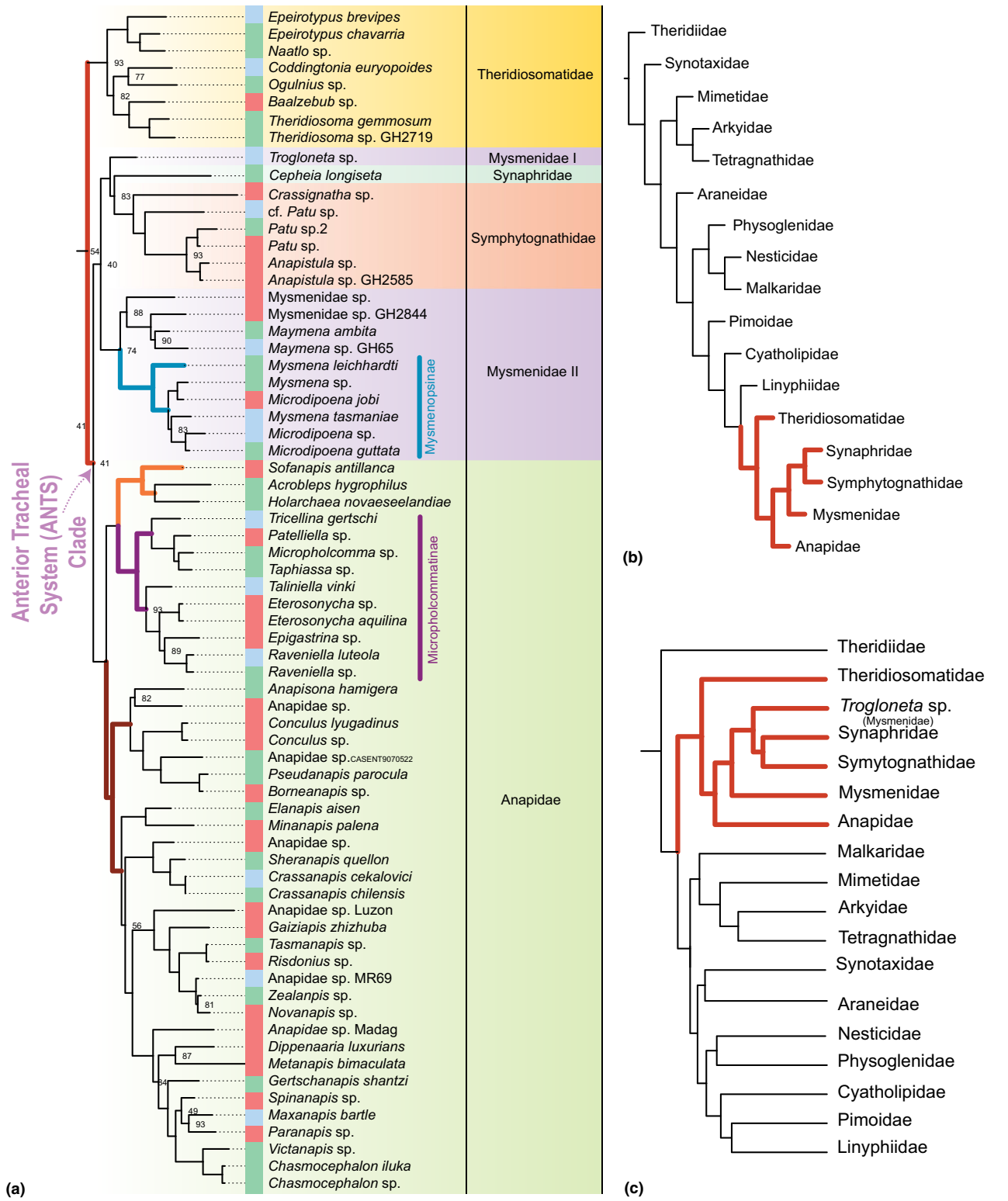

Fig. 9. Phylogenetic relationships of the symphytognathoid families: (a) maximum-likelihood phylogeny derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset; (b) phylogeny of Araneoidea collapsed to family level reconstructed using parsimony; and (c) maximum-likelihood (same topology at a). Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

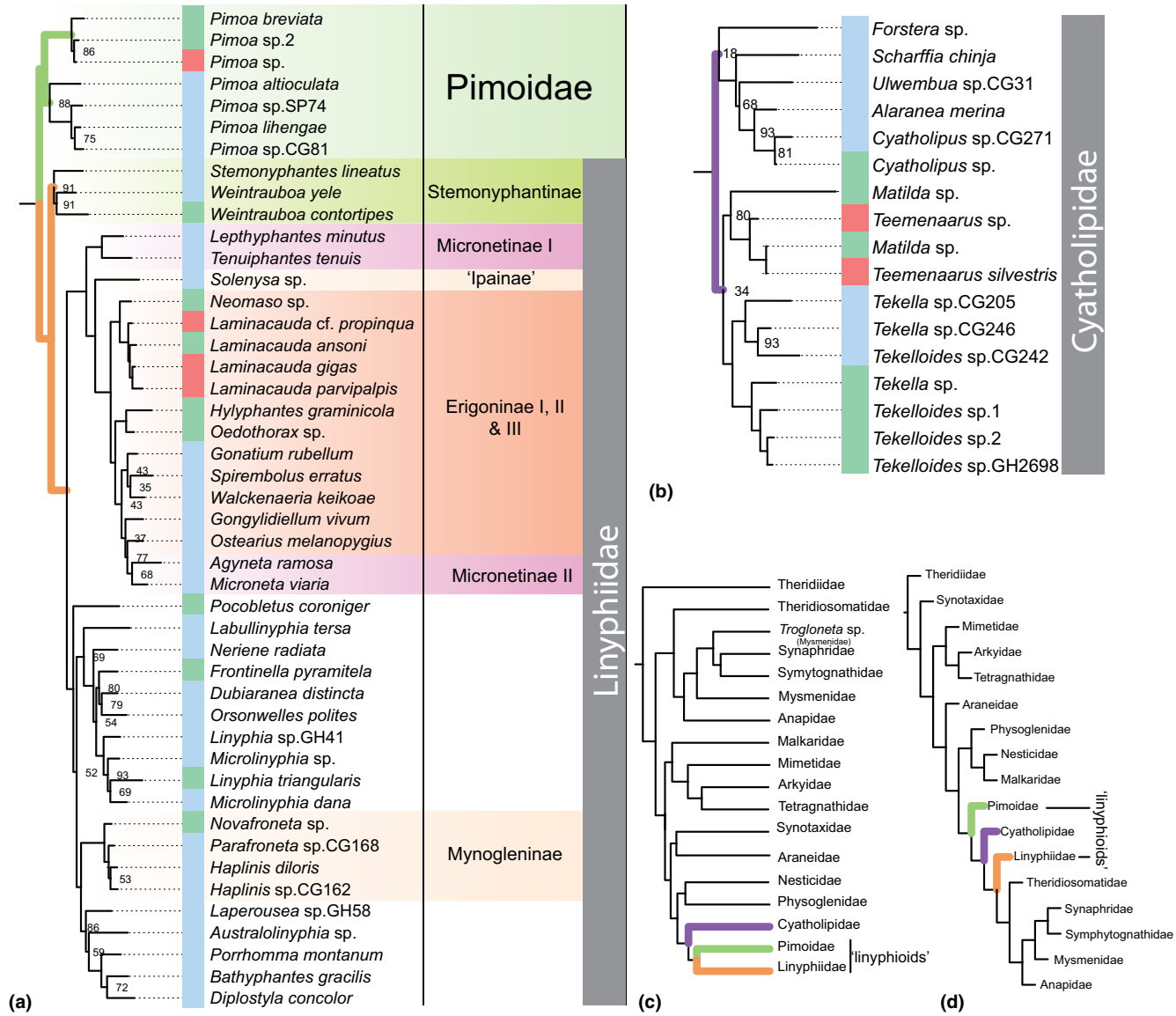

Fig. 10. Phylogenetic relationships of a part of Araneoidea families: (a) Pimoidae and Linyphiidae ("linyphioids") and (b) Cyatholipidae. A phylogeny of Araneoidea, (c) derived using maximum-likelihood (same as a) and (d) using parsimony. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Subfamilies that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

of appendages (Ledford & Griswold, 2010; Ledford et al., 2012; Mammola & Isaia, 2017).

The relationship of leptonetids to other groups have been tangled since the discovery of a functional cribellum in *Archoleptoneta* (the organ is absent in other Leptonetidae). Researchers have cast doubt on its placement within Leptonetidae (Ledford & Griswold, 2010; Ledford et al., 2011) and suggested that this family could be paraphyletic, but without making any change in the classification. Later, Wheeler et al. (2017) did recover a polyphyletic Leptonetidae. An analysis of UCE-derived data suggested that the subfamily Archoleptonetinae (which includes only two genera, the cribellate *Archoleptoneta* and the ecribellate *Darkoneta*) do not nest within the clade containing other leptonetids (Ramírez et al., 2021). This subfamily then was elevated to family rank as Archoleptonetidae by Ledford et al. (2021). This phylogenetic placement seems to be sensitive to data class and/or taxon sampling because, the transcriptomic data treated as amino acids, with three genera sampled, suggest that *Archoleptoneta* (Archoleptonetidae), *Calileptoneta* and *Leptoneta* (both Leptonetidae) form a clade (Kallal et al., 2021a). Likewise, our UCE dataset representing two Archoleptonetidae and 12 Leptonetidae genera recovered a clade including the two families (Fig. S3). In our Combined dataset with more

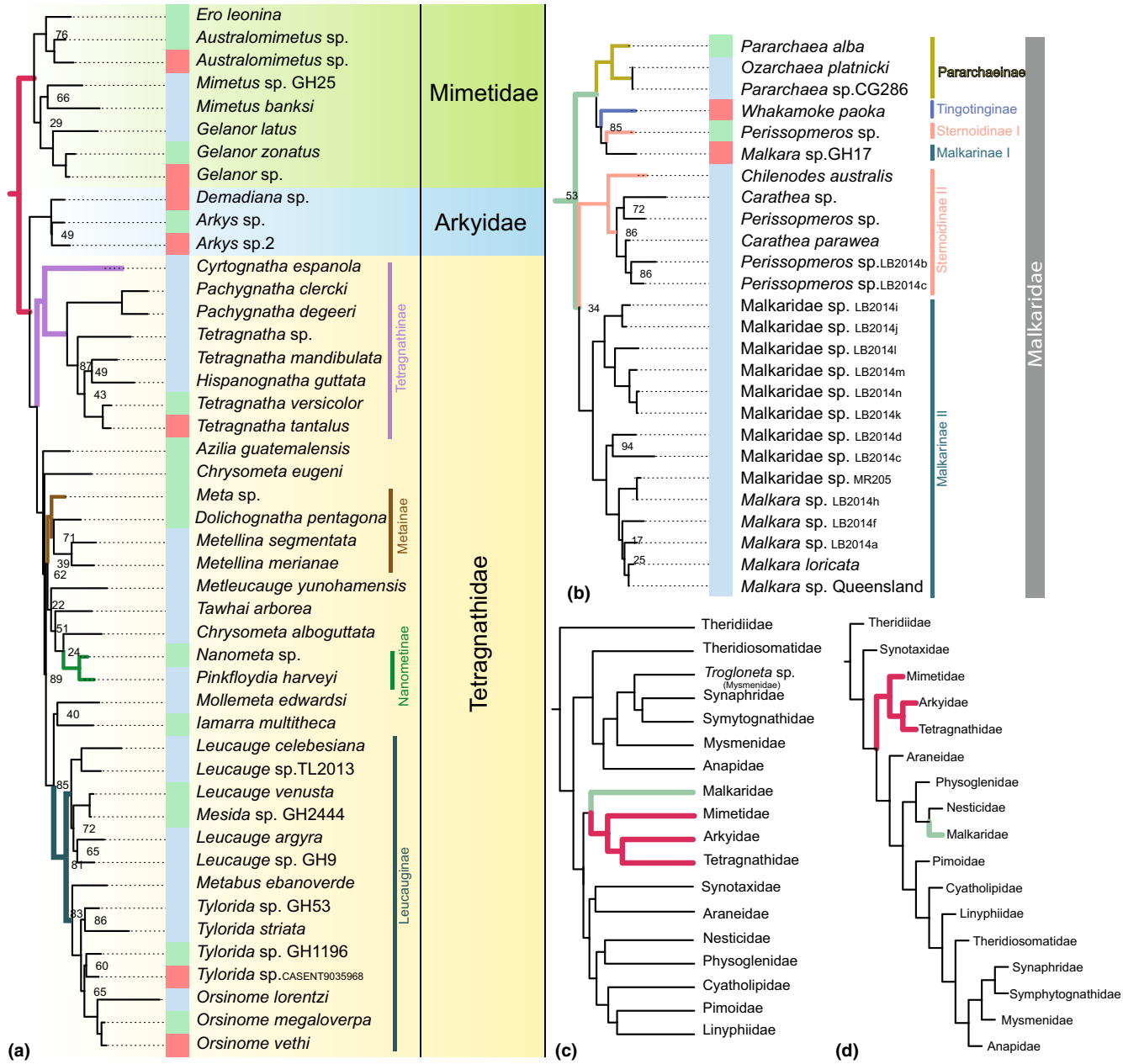

Fig. 11. Phylogenetic relationships of a sample of Araneoidea families: (a) Tetragnathidae, Arkyidae and Mimetidae ("tetragnathoids") and (b) Malkaridae, A phylogeny of Araneoidea, (c) derived using maximum-likelihood (same as a) and (d) using parsimony. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Subfamilies that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

archoleptonetids (five terminals), Archoleptonetidae was the sister group to a clade including the Austrochiloidea+Leptonetidae clade (Fig. 6d).

Palpimanoidea

Palpimanoids are a group of spiders known for their unusual chelicerae and carapace morphologies and associated predatory behaviours, many of which forage predominantly on other spiders using a variety of predatory tactics (see Wood et al., 2012). This group consists of five extant families which occur primarily in the Southern Hemisphere: Archaeidae, Huttoniidae, Mecysmaucheniidae, Palpimanidae and Stenochilidae. Palpimanoids have peg teeth on the pro-margin of the paturon, a cheliceral gland mound, and most have dense scopulae on the first pair of legs (Wood et al., 2012). Before this, Forster & Platnick (1984) had proposed a

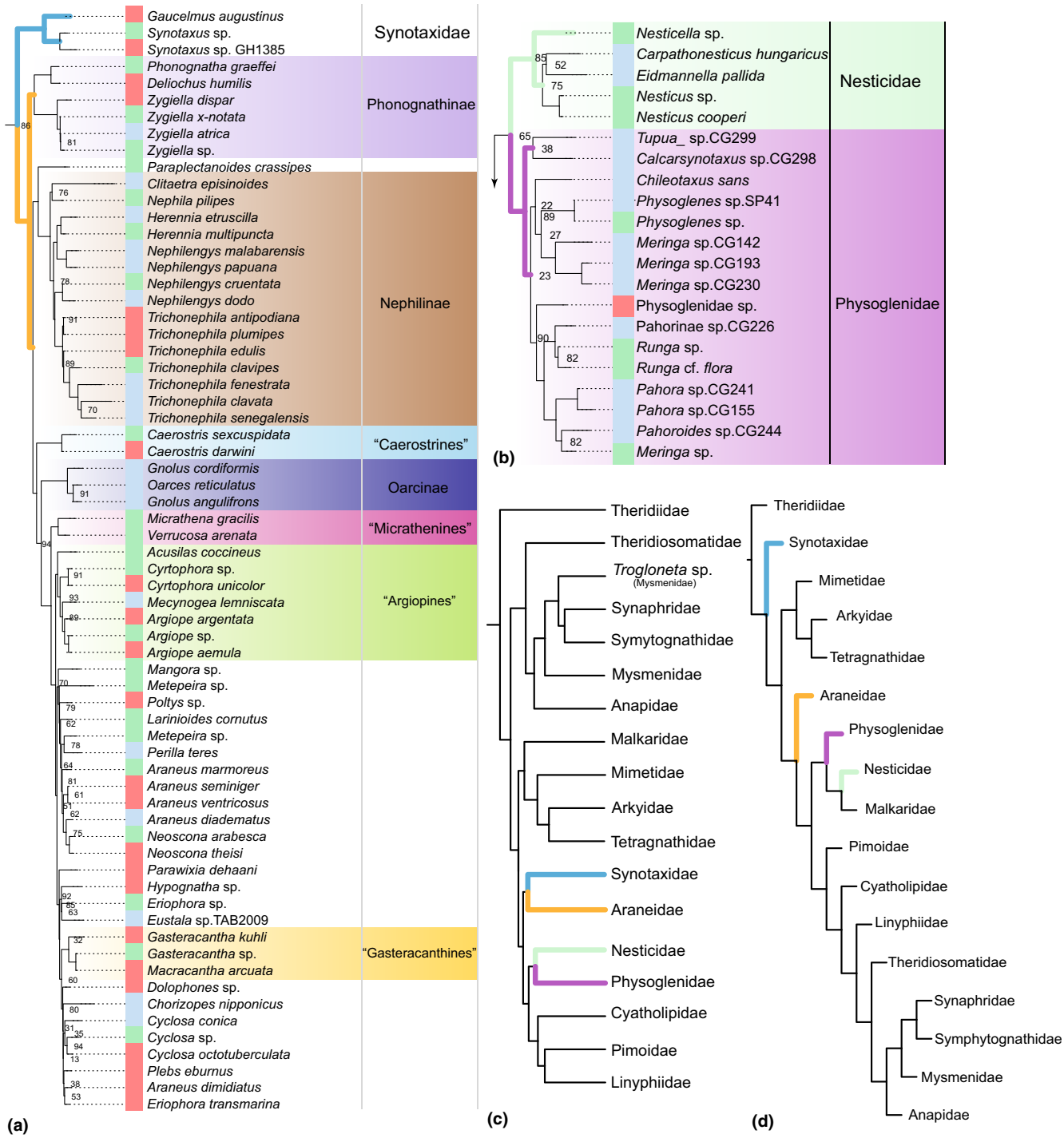

Fig. 12. Phylogenetic relationships of a sample of Araneoidea families (a) Synotaxidae and Araneidae, (b) Nesticidae and Physoglenidae, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. A phylogeny of Araneoidea, (c) derived using maximum-likelihood (same as a) and (d) using parsimony. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

larger grouping of Palpimanoidea which included Pararchaeidae, Holarchaeidae, Micropholcommatidae and Textricellidae (all were families at the time) and Mimetidae in addition to the present members of this superfamily. This expanded view of Palpimanoidea was based on the presence of cheliceral peg teeth and

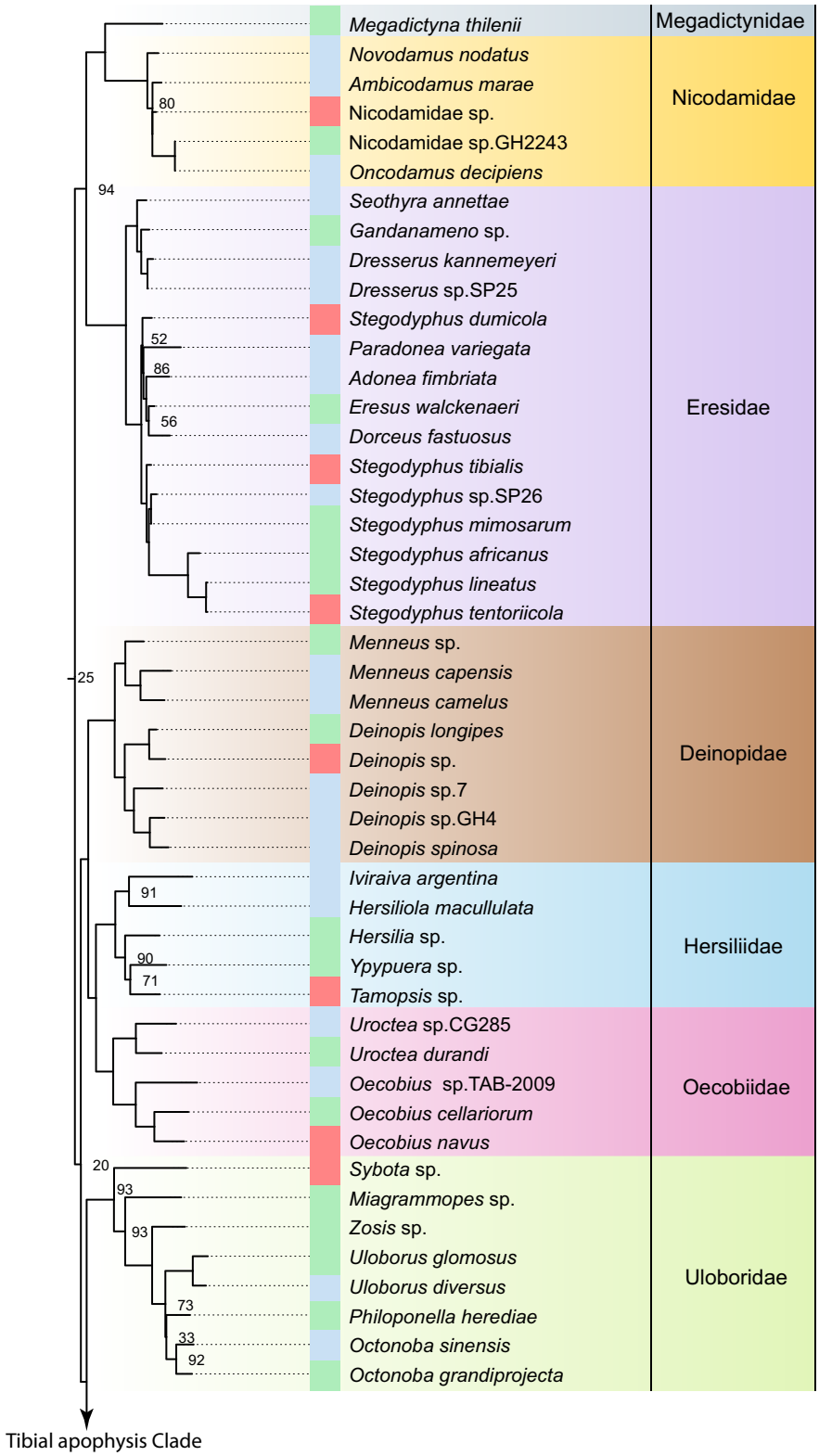

Fig. 13. Phylogenetic relationships of the Nicodamoidea (Nicodamidae and Megadictynidae), Eresidae and the UDOH grade families, Uloboridae, Deinopidae, Oecobiidae and Hersiliidae derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

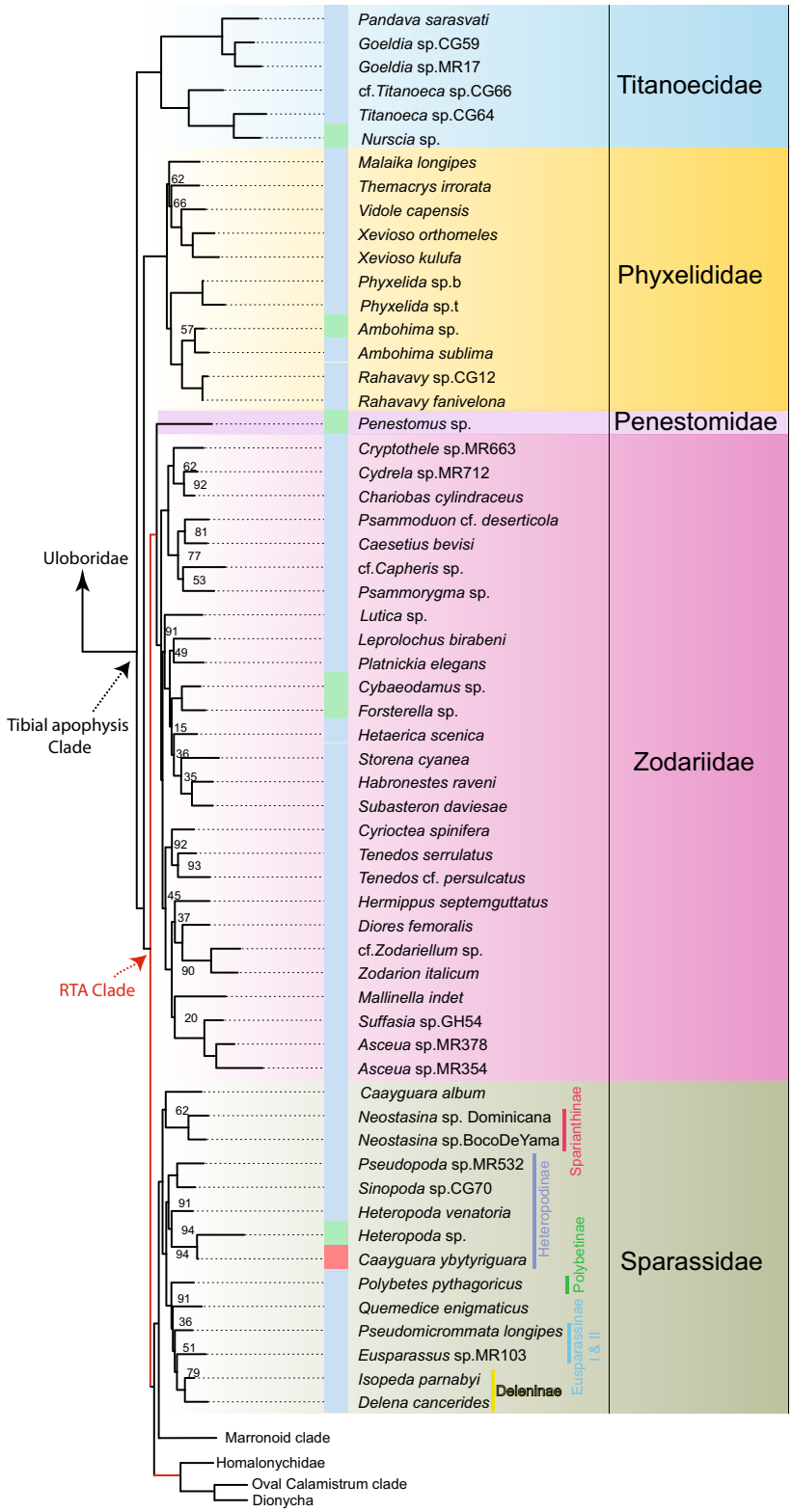

Fig. 14. Phylogenetic relationships of a sample of the Tibial apophysis clade (TA clade) excluding the Marronoid, Oval Calamistrum, Dionycha clades and Homalonychidae, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Subfamilies that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

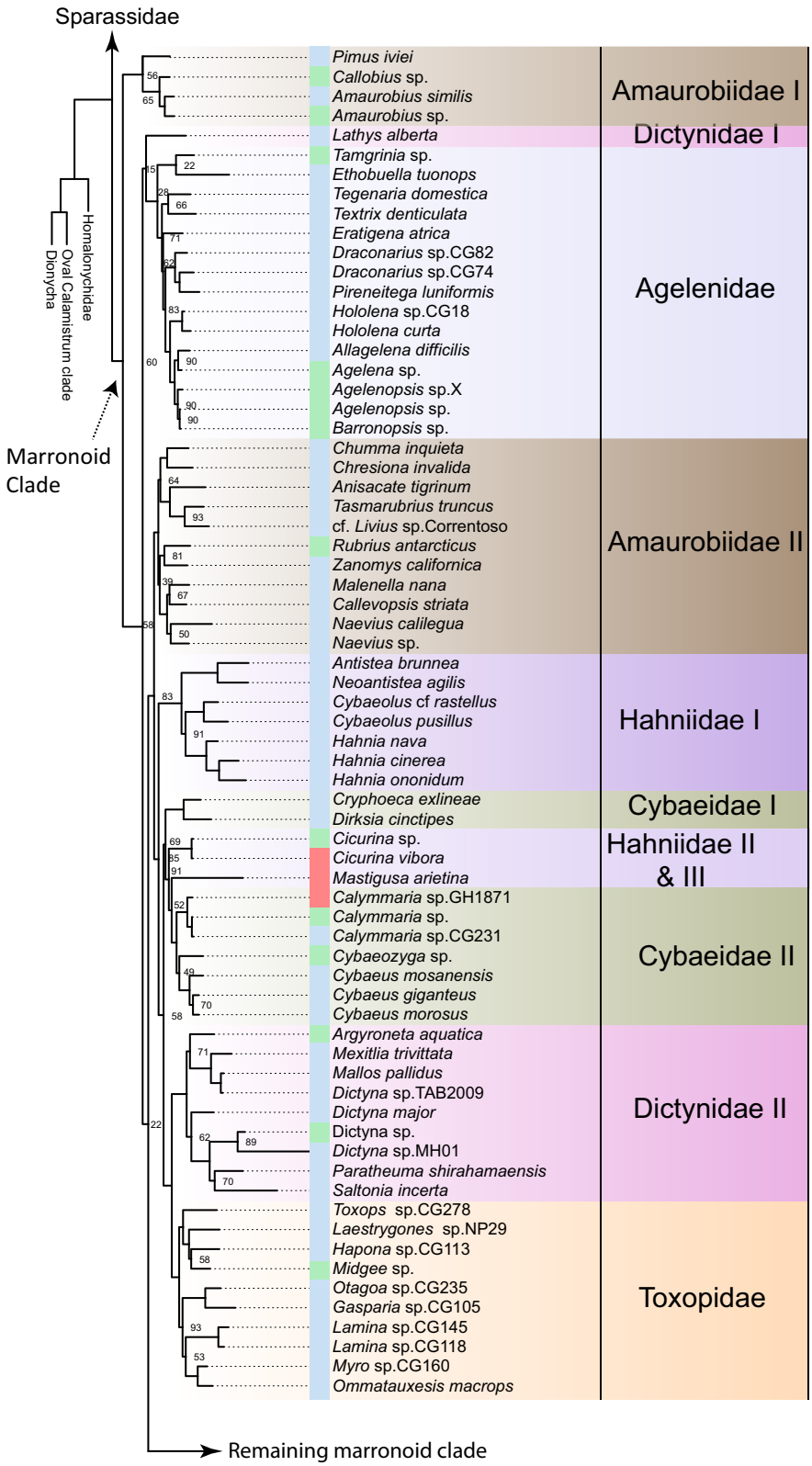

Fig. 15. Phylogenetic relationships of a sample of the Marronoid families, derived using a combination of the 25% occupancy dataset of the ultra-conserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

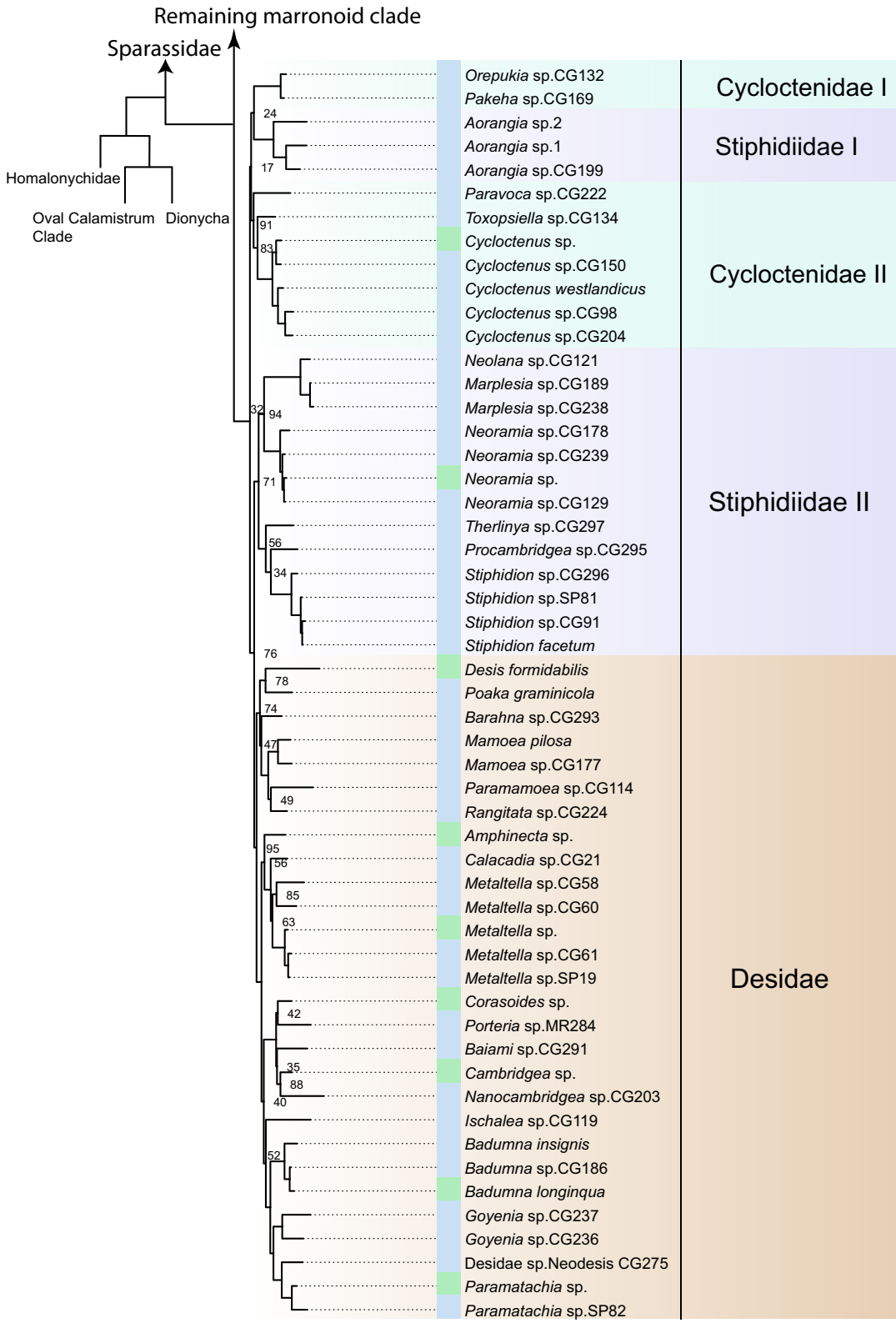

Fig. 16. Phylogenetic relationships of a sample of the Marronoid families, derived using a combination of the 25% occupancy dataset of the ultra-conserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

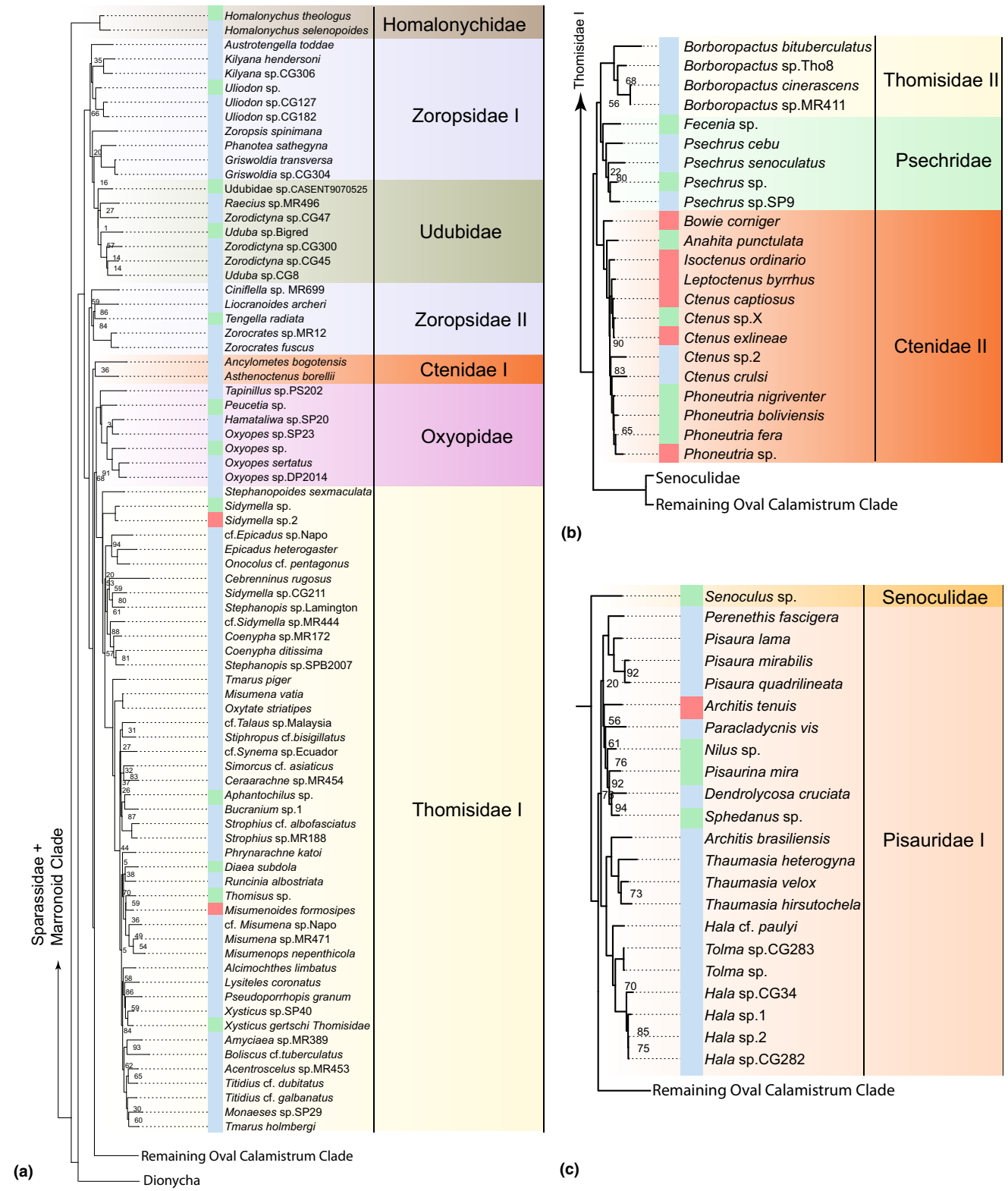

Fig. 17. Phylogenetic relationships of Homalonychidae family and a sample of the Oval Calamistrum clade families, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

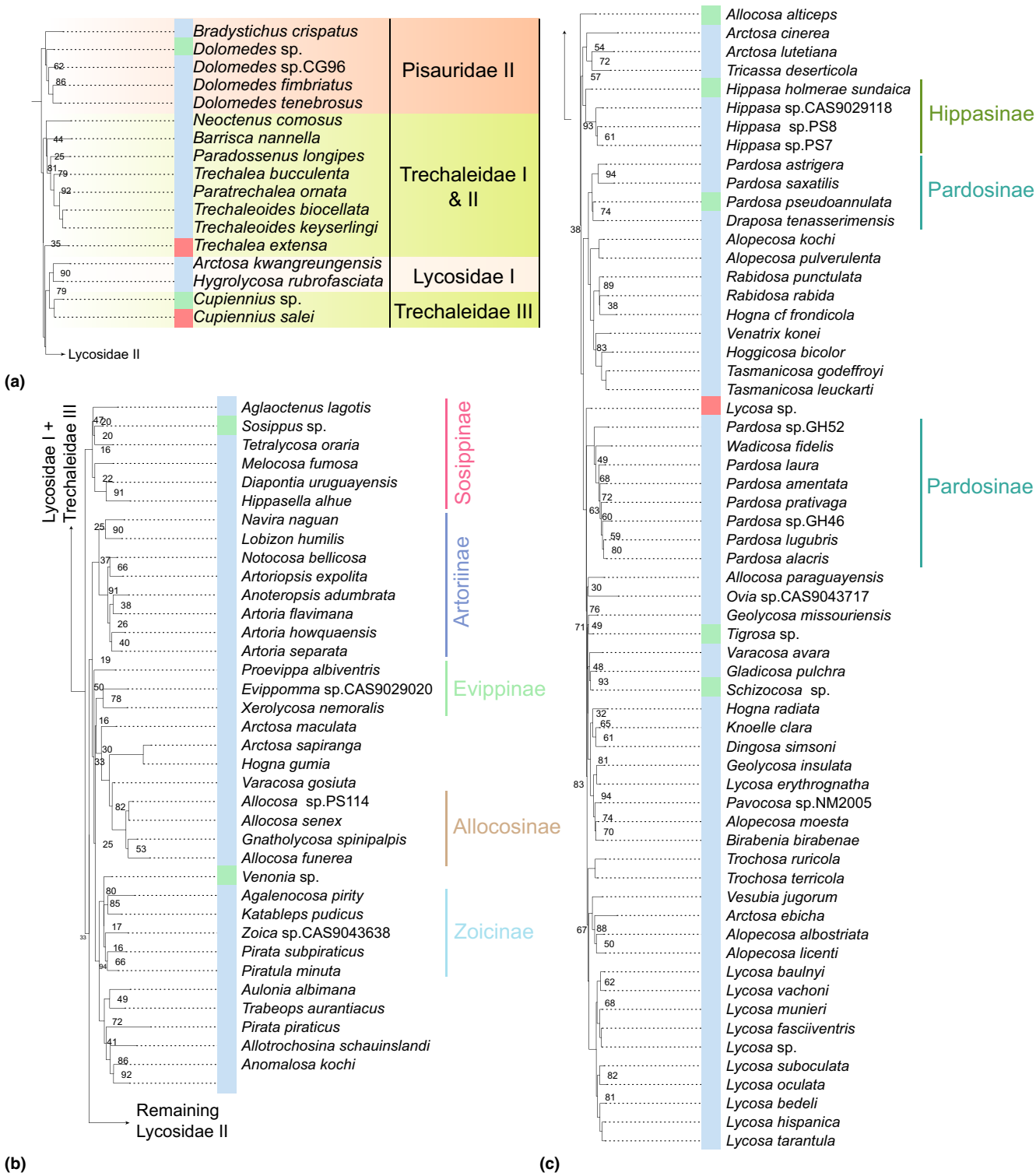

Fig. 18. Phylogenetic relationships of a sample of the Oval Calamistrum clade families, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

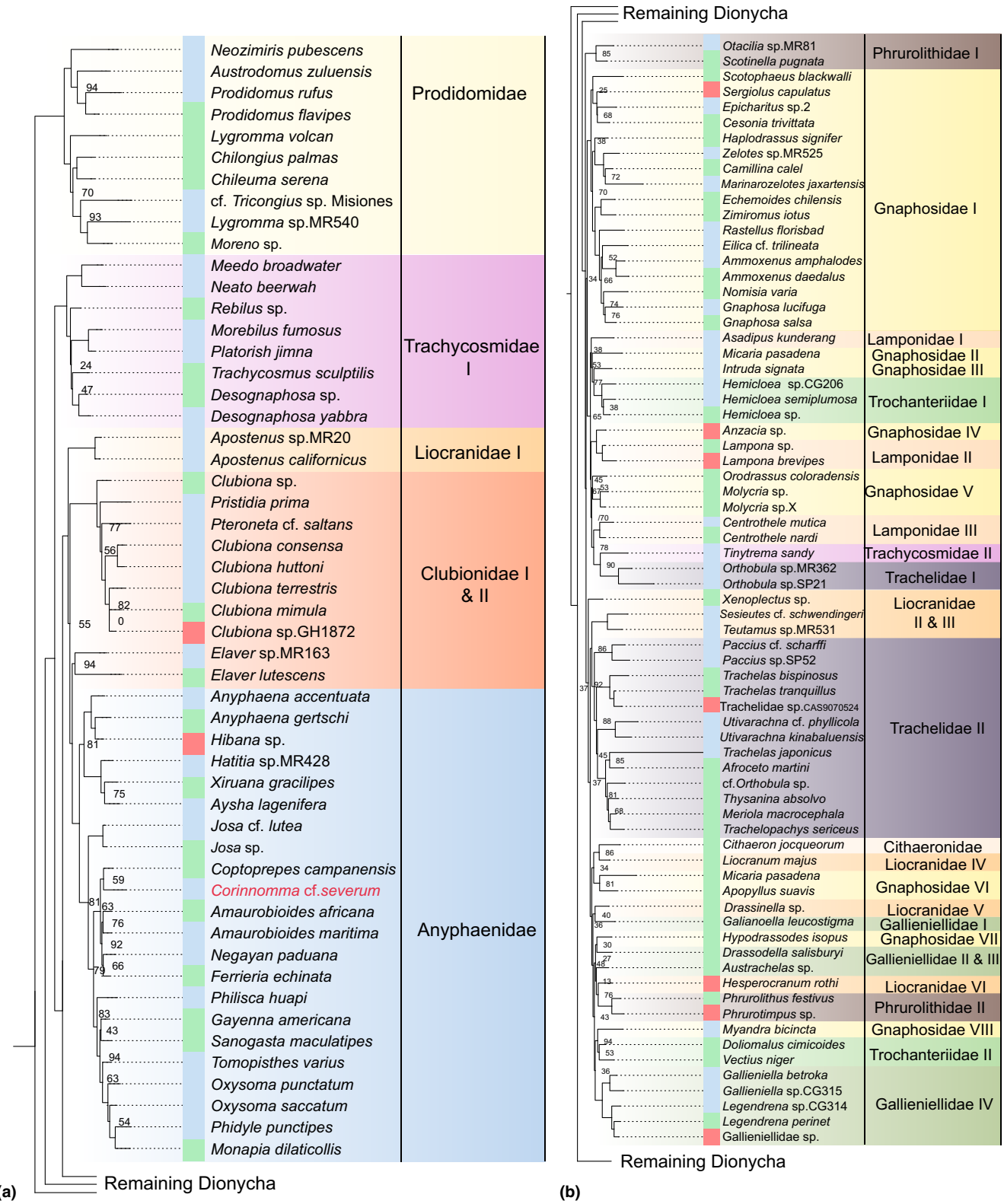

Fig. 19. Phylogenetic relationships of a sample of the Dionycha clade families, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger + UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%.

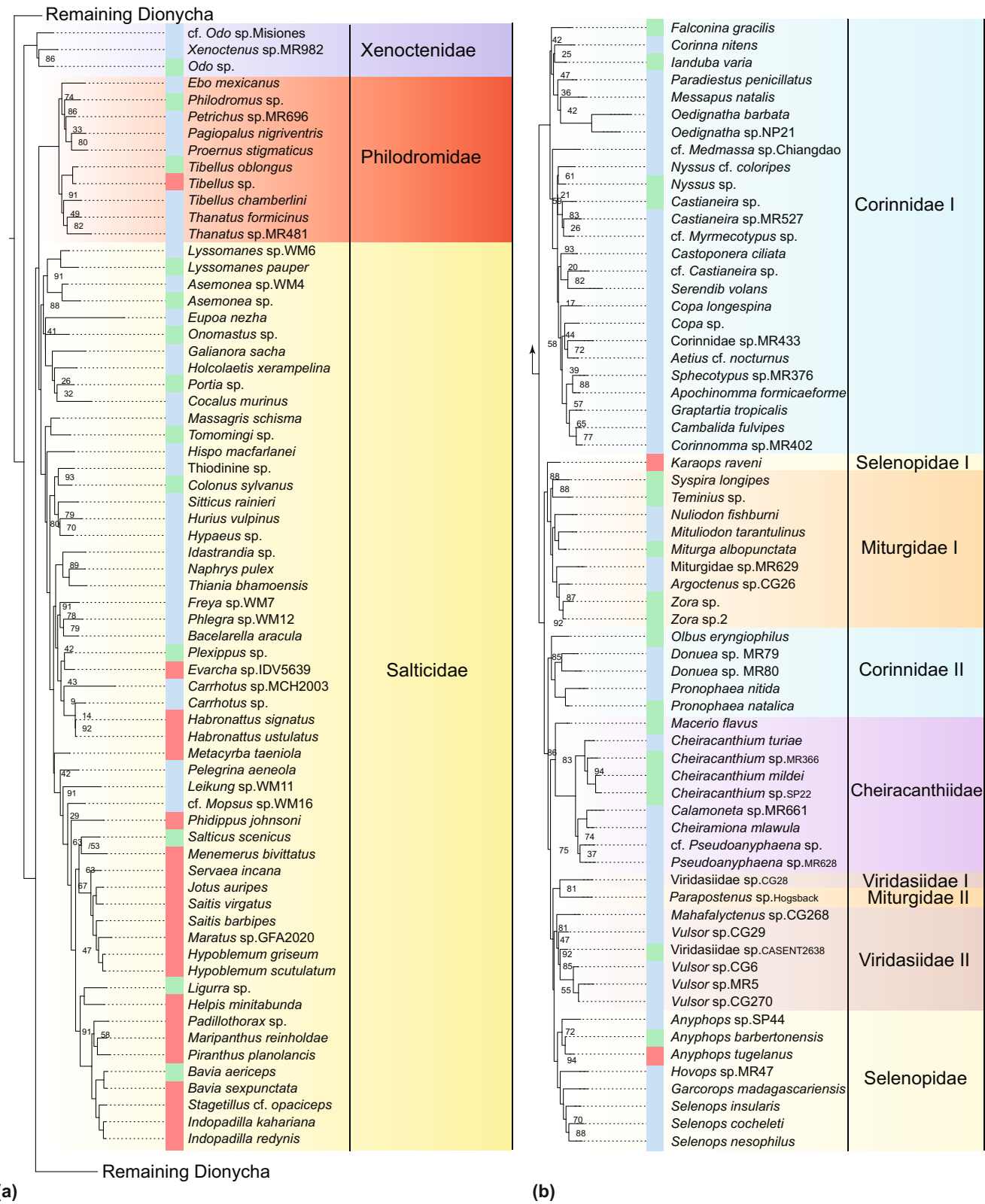

Fig. 20. Phylogenetic relationships of a sample of the Dionycha clade families, derived using a combination of the 25% occupancy dataset of the ultraconserved elements (UCEs) and the Sanger-sequenced dataset. Annotated boxes indicate family or subfamily. Coloured squares at tips indicate the following data classes that they represent: blue, Sanger data only; red, UCE data only; green, Sanger+UCE data. Families that are paraphyletic or polyphyletic are appended with Roman numerals. Ultrafast bootstrap values are indicated at nodes except when they were >95%. [Correction added on 31 October 2023, after first online publication: Figure 20 and figure legend have been updated.]

gland mounds in Mimetidae and Pararchaeidae, both characters reduced in Holarchaeidae, Micropholcommatidae and Textricellidae, chelicerae originating from a sclerotized foramen in the carapace in Pararchaeidae, a convex carapace in Micropholcommatidae and Textricellidae, with Holarchaeidae having an intermediate state between the two (Forster & Platnick, 1984). All these taxa are now placed in Araneoidea as follows: Pararchaeinae (Malkaridae), *Holarchaea*, Textricellini and Micropholcommatinae (Anapidae) based on multiple phylogenetic studies (Schütt, 2000; Rix & Harvey, 2010a; Lopardo et al., 2011; Dimitrov et al., 2017).

A combination of morphology and four Sanger-sequenced genetic markers strongly supported the monophyly of Palpimanoidea. However, six genetic markers (without morphology) recovered a poorly supported paraphyletic grouping for Palpimanoidea (Wheeler et al., 2017). In our UCE phylogeny, Palpimanoidea was monophyletic and formed a sister group to entelegyne spiders with strong support (Figs 3 and 4). This placement of Palpimanoidea within the spider phylogeny and its interfamilial relationships were previously recovered in the transcriptome-based analyses of Fernández et al. (2018a) and Kallal et al. (2021a), the UCE-based analyses of Wood et al. (2018), Kulkarni et al. (2020) and Ramírez et al. (2021), and in analyses combining UCEs and transcriptomic datasets (Kulkarni et al., 2021). This relationship is of interest because the Entelegynae spiders contain the bulk of araneomorph spider species diversity, while palpimanoids contain only *c*. 300 species (World Spider Catalog, 2023). The extensive fossil record of palpimanoids indicates that this group and Synspermiata were once dominant in the Mesozoic, with faunal turnover giving way to dominance of other Araneomorphae clades, Araneoidea and the RTA-clade, in the Cenozoic (Magalhaes et al., 2021).

Within Palpimanoidea, Palpimanidae is the sister group to the remaining four families (Fig. 7), a result also found by Wood et al. (2018). However, transcriptomes analysed as amino acids recover Palpimanidae plus Stenochilidae as a clade (Kallal et al., 2021a). Huttonidae + Mecysmaucheniidae diverged next and are the sister group to a clade containing Archaeidae + Stenochilidae (Fig. 7), contradicting the results of Wood et al. (2018). Our UCE data recovered Archaeidae as the sister group to Mecysmaucheniidae and Stenochilidae + Huttonidae.

Alternative placements have been obtained in other UCE and transcriptome-based studies. For example, on the one hand, the Huttonidae plus Stenochilidae clade was recovered using UCE data in Wood et al. (2018) and Kulkarni et al. (2021), yet this branch was poorly supported in both studies. On the other hand, morphology alone recovers Archaeidae and Mecysmaucheniidae as sister groups, that are sister to Palpimanidae + Stenochilidae, and with Huttoniidae the earliest diverging total evidence analysis results in Mecysmaucheniidae as the earliest diverging and Archaeidae + Stenochilidae sister to Huttoniidae + Palpimanidae (Wood et al., 2012).

Entelegynae

The araneomorph lineages which are a sister group to the Palpimanoidea clade form the Entelegynae clade (>80% of spider diversity). The entelegyne male genitalia, in general, is relatively more complex than haplogyne genitalia, and has distinct sclerites (sclerite morphology generally serves as synapomorphies for many entelegyne spider groups) and the female genitalia has a "flow-through" system, with separate copulatory and fertilization ducts (Griswold et al., 2005). The early diverging araneomorph groups such as Hypochilidae, Filistatidae, Synspermiata and Palpimanoidea have haplogyne genitalia. It is noteworthy that at least three reversals to the haplogyne condition are known to have occurred in the Entelegynae—in some tetragnathids, uloborids and anapids (Lopardo & Hormiga, 2015). Recently, Michalik et al. (2019) inferred that the entelegyne condition has evolved at least six times independently in the Synspermiata families, Pholcidae, Tetrablemmidae, Oonopidae, Ochyroceratidae and Trogloraptoridae.

Molecular phylogenies consistently support the monophyly of Entelegynae (Garrison et al., 2016; Wheeler et al., 2017; Fernández et al., 2018a; Kulkarni et al., 2020, 2021; Kallal et al., 2021a), including our study (Figs 3 and 4). Our phylogeny suggests that Araneoidea is a sister group to a clade that includes all the remaining entelegynes. In the latter clade, Nicodamoidea + Eresidae are sister to a large lineage that includes the UDOH grade (see below) and the retrolateral tibial apophysis clade (RTA clade). This topology is corroborated by the UCE-based phylogeny of Kulkarni et al. (2020) and the *AllUCEs* dataset (nucleotide data of UCEs + transcriptomes) of Kulkarni et al. (2021). The recent transcriptomic analysis of Kallal et al. (2021a) suggested that UDOH grade + RTA clade is a sister group to the remaining entelegyne spiders. In that study, Eresidae was a sister group to the Nicodamoidea + Araneoidea clade.

Araneoidea

This lineage of 17 ecribellate spider families includes the largest diversity of web architectures, a few examples of which include the orbicular web (Araneidae, "symphytognathoids", Tetragnathidae), the cob web (Theridiidae, Nesticidae) and the sheet web (Cyatholipidae, Linyphiidae, Pimoidae), along with several instances of foraging web loss (these spiders are instead active or sit-and-wait hunters) (e.g. Mimetidae,

Malkaridae, Arkyidae). Orbicular webs (webs with distinct radii and spiral) also are built by two other families outside Araneoidea—Deinopidae and Uloboridae (both cribellate)—which belong to the UDOH grade assemblage (see UDOH grade section below).

Untangling the relationships among the araneoid spiders families has been a challenging task (reviewed in Hormiga & Griswold 2014), because various data types such as morphology (Coddington, 1990), morphology and behaviour (Griswold et al., 1998), Sanger-sequencing-based on six markers (Dimitrov et al., 2012, 2017; Wheeler et al., 2017; Scharff et al., 2020), transcriptomes (Fernández et al., 2014, 2018a, b; Kallal et al., 2021a) and UCEs (Kulkarni et al., 2020, 2021) have recovered some conflicting phylogenetic relationships. For example, the placement of Araneidae varies across datasets: morphological data recover the family as sister group to the remaining araneoids (Griswold et al., 1998), Sanger-based sequences as sister group to Theridiosomatidae + Synotaxidae (Dimitrov et al., 2017) or Synotaxidae (Scharff et al., 2020, Theridisomatidae was not sampled) or as a sister group to Theridiosomatidae with transcriptomes (Fernández et al., 2018a; Kallal et al., 2021a), and UCEs sequences place araneids as the sister group to Synotaxidae (Kulkarni et al., 2020, 2021). Another example is provided by the miniature orb-weaving spiders (the "symphythognathoids"; see section below): morphological data suggested that these families are grouped in a clade (Coddington, 1986b; Griswold, 1990; Schütt, 2003; Lopardo & Hormiga, 2008; Lopardo et al., 2011), a hypothesis rejected by the analyses of Sanger-based sequences and transcriptomes, but supported by UCE data (Kulkarni et al., 2020, 2021).

Araneoidea includes spiders with a characteristic configuration of spigots on the posterior lateral spinnerets—one flagelliform gland and two aggregate gland spigots, a synapomorphy of the group (Coddington, 1989; Griswold et al., 1998). The flagelliform and aggregate glands work in tandem to produce the sticky thread (Kovoor, 1977; Coddington, 1989) of the capture spiral.

These araneoid triplet spigots may be reduced in some spiders such as *Cepheia longiseta* (Simon, 1881) (Synaphridae) (Lopardo & Hormiga, 2008) or absent (Mimetidae) (Platnick & Shadab, 1993). All genome-scale based phylogenies recover Theridiidae as a sister group to a lineage that includes all remaining araneoid families (Garrison et al., 2016; Fernández et al., 2018a; Shao & Li, 2018; Kulkarni et al., 2020, 2021; Kallal et al., 2021a) (Fig. 4). The transcriptome-based phylogeny of Fernández et al. (2018a) placed Theridiidae as the sister group to Anapidae.

However, the inclusion of Symphytognathidae representatives in the transcriptomic dataset of Kallal et al. (2021a) placed Anapidae as sister to Symphytognathidae, similar to the results of the UCE-based phylogeny of Kulkarni et al. (2021). Our parsimony analysis recovered Theridiidae as a sister group to the remaining araneoids; monophyly of symphytognathoids and tetragnathoids were recovered, yet the Pimoidae + Linyphiidae clade was not recovered (Figs 8–1 and S4).

Theridiidae

Theridiids or cobweb spiders are the third largest family (after Linyphiidae and Araneidae) in Araneoidea with >2500 species grouped in 125 genera distributed worldwide (World Spider Catalog, 2023). The black widow spider genus *Latrodectus* known for its sexual cannibalism (Andrade, 1996) and potent toxicity (Clarke et al., 2014), and the common house spider *Parasteatoda tepidariorum* (C. L. Koch, 1841) are members of this family. *Parasteatoda tepidariorum* has been widely studied in research on evolutionary and developmental biology, and is considered as a model organism (reviewed in Oda and Akiyama-Oda, 2020). Theridiids are of interest beyond taxonomy and systematics because of their ecological diversity, perhaps the largest among spider families, as illustrated by diversity of web architectures (e.g. Eberhard et al., 2008a, b) and the independent evolution of kleptoparasitism (e.g. Vollrath, 1979), sociality (e.g. Agnarsson et al., 2006), and myrmecophagy (e.g. Líznarová & Pekár, 2019).

Theridiid spiders also are known as "comb-footed" spiders owing to the presence of a row of bristled setae on their fourth tarsus used to direct and manipulate viscid sticky silk to entangle the prey. A similar tarsal comb has independently evolved in another Araneoidea family, Nesticidae, and in the non-araneoid Pholcidae (Huber & Fleckenstein, 2008).

Lehtinen & Saaristo (1980) placed Nesticidae and Theridiidae in different superfamilies claiming that these setae are "purely adaptive", thus suggesting convergent evolution of this trait. However, Coddington (1989) grouped Theridiidae and Nesticidae together based on the enlarged aggregate spigots and the presence of the fourth tarsal comb and its association with the behaviour of prey capture. Griswold et al. (1998) proposed synapomorphies for Theridiidae plus Nesticidae (which they called "theridioids") that included presence of a 'theridiid tegular apophysis' (a sclerite of the male pedipalp), fourth tarsal comb, enlarged aggregate gland spigots on the posterior lateral spinnerets, and the construction of gumfoot webs. However, to date, no molecular analysis has ever supported the monophyly of theridioids (Dimitrov et al., 2012, 2017; Wheeler et al., 2017).

The morphological hypothesis about the internal relationships of Theridiidae recovered Hadrotarsinae (minute ant specialist theridiids with reduced/no webs)

as a sister group to a clade composed of Latrodectinae (a monophyletic subfamily) plus remaining theridiids (Agnarsson, 2004). Arnedo et al. (2004) reconstructed the first molecular phylogeny of the family Theridiidae. In their molecular phylogeny, a clade including the subfamily Latrodectinae and the genera *Anelosimus* (in part *Selkirkiella*), *Pholcomma* and *Robertus*, were a sister group to the remaining theridiids. An incremental taxon sampling of Liu et al. (2016) recovered Latrodectinae as a sister clade to the remaining theridiid lineages.

Our UCE-based phylogeny recovered Latrodectinae as the sister group to a clade including all remaining theridiids, which were represented by nine genera (15 terminals) (Figs 8b, S3 and S4). Our Combined phylogeny, however, recovered a larger clade which included a monophyletic Latrodectinae as a sister group to paraphyletic Pholcommatinae (*Enoplognatha* and *Pholcomma*) and Argyrodinae (*Ariamnes*, *Argyrodes* and *Neospintharus*) and other theridiids (Fig. 8). The "lost colulus" clade, which includes Theridiinae and Anelosiminae [a grouping proposed by Agnarsson (2004) based on the absence of a colulus and colular setae], was also recovered in our Combined analysis (Fig. 8). In the UCE phylogeny, *Euryopis* (Hadrotarsinae) was a sister group to the Theridiinae + Anelosiminae clade with high support (99% UB) (Fig. 8).

Symphytognathoid clade

This clade includes four or five families of minute spiders (<2 mm) known as the "symphytognathoids" (an informal group name proposed by Coddington, 1986b): Anapidae, Mysmenidae, Symphytognathidae and Theridiosomatidae, most of which construct orb-webs (Eberhard, 1986) with various degrees of architectural modifications. Lopardo et al. (2011) added Synaphridae to this group based on a phylogenetic analysis combining morphological and molecular data. Symphytognathoid webs are architecturally quite diverse ranging from typical orb webs to a multitude of variation such as irregular webs and sheet webs. Some symphytognathoids are kleptoparasites that do not build any foraging webs, but instead occupy the webs of their host spider. Most mysmenids build spherical or planar orbs, symphytognathids build a two-dimensional horizontal orb web, theridiosomatids build orb webs (although some of them are highly modified, e.g. sticky lines connected to water surface), anapids build orb webs with out of plane radii, and at least some synaphrids build sheet or irregular webs (Coddington, 1986b; Coddington and Valerio, 1980; Eberhard 1986; Rix and Harvey, 2010b; Lopardo et al., 2011, Cotoras et al., 2021). In each of these "symphytognathoid" families (except Synaphridae), there is at least one genus with a kleptoparasitic lifestyle, accompanied by loss of the foraging web, in all its constituent species. For example, *Mysmenopsis furtiva* Coyle & Meigs, 1989 (Mysmenidae) and *Curimagua bayano* Forster & Platnick, 1977 (Symphytognathidae) live in the webs of diplurid spiders (Griswold et al., 1998; Vollrath, 1978), and *Sofanapis antillanca* Platnick & Forster, 1989 (Anapidae) live in the sheet webs of austrochilids (Ramírez & Platnick, 1999).

The genealogical relationships of the symphytognathoids themselves have an interesting history. The monophyly of "symphytognathoids" has been supported by morphological and behavioural characters (Coddington, 1986b; Eberhard, 1986; Griswold et al., 1998; Schütt, 2003; Lopardo & Hormiga, 2008; Lopardo et al., 2011; Hormiga & Griswold, 2014), but they have appeared as either paraphyletic or polyphyletic in molecular phylogenies using the six Sanger-based markers (Dimitrov et al., 2012, 2017; Wheeler et al., 2017) or transcriptomes (Fernández et al., 2018a; Kallal et al., 2021a). Dimitrov et al. (2017) obtained Anapidae as paraphyletic with "Anapidae I" (represented by *Anapis*, one micropholcommatine genus (*Taphiassa*) and *Holarchaea*) as sister to Theridiidae and "Anapidae II" (represented by *Gerstchanapis*, *Maxanapis* and *Chasmocephalon*) as sister to Cyatholipidae. The "Anapidae II" plus Cyatholipidae clade was sister to the Symphytognathidae lineage. Lopardo et al.'s (2011) extensive Sanger-based dataset supported "symphytognathoid" monophyly only when the nucleotide data were analysed in combination with phenotypic data. It is noteworthy that transcriptomic data, analysed as amino acids in a maximum-likelihood framework, recovered polyphyletic origins of "symphytognathoids" (Fernández et al., 2018a; Kallal et al., 2021a). In a parsimony analysis, Kallal et al. (2020) recovered Theridiosomatidae as sister to Araneidae, while the other "symphytognathoid" families formed a monophyletic group. An analysis of UCEs using a small sample of symphytognathoids (16 species in all families except Synaphridae and representatives of all other araneoid families) provided the first empirical support for symphytognathoid monophyly using molecular data alone, with the analysed low occupancy datasets (Kulkarni et al., 2020). A further integrated sampling obtained by extracting UCEs from transcriptomes found that Synaphridae too are nested within symphytognathoids (Kulkarni et al., 2021, 2023). All prior molecular analyses, including Sanger-sequencing-based six markers and amino acid data from transcriptomes, rejected the monophyly of symphytognathoids. Interestingly, the polyphyly of this group received high ultrafast bootstrap support by transcriptomes. This paradox of highly supported but incongruent relationships across phylogenomic datasets was explored through

analyses of exons, ultraconserved loci, a combination of these data as amino acids and nucleotides which recovered monophyly of "symphytognathoids" (Kulkarni et al., in 2021). This discordance resulting from nucleotide (rendering monophyly) and amino acid data (recovering polyphyly) between the position of symphytognathoids within Araneoidea was also observed in the 99-target enrichment study of Shao et al. (2023). This paradox is not unique to these spiders, but also has been observed in snakes (e.g. Klein et al., 2021), birds (e.g. Cloutier et al., 2019) and other arachnids (e.g. Ballesteros et al., 2021). A recent study by Kulkarni et al. (2023) focused on symphytognathoid phylogenomics using UCEs and a combination with six standard markers recovered monophyly of this group. This placement rendered transformation of anterior tracheae to book lungs and the reduction and loss of the posterior tracheae multiple times. The symphytognathoid ancestral orb was lost four times and transformed to sheet web once (Kulkarni et al. 2023).

Our UCE and Combined datasets recovered the symphytognathoids clade (Figs 3, 4, 9, S3 and S4). Theridiosomatidae formed a sister group to the remaining symphytognathoids, a lineage referred to as the "Anterior tracheal system clade" by Lopardo et al. (2011). Interestingly, *Trogloneta*, an unusual mysmenid with fused chelicerae (Schütt, 2003) similar to Symphytognathidae spiders, was placed as a sister group to Synaphridae + Symphytognathidae with high support (95% UB; Fig. 9). This genus has been placed within Mysmenidae (Lopardo et al., 2011, Lopardo and Hormiga, 2015). Among Anapidae, both UCEs and the Combined dataset recovered micropholcommatines nested with Anapidae (Fig. 9), similar to the total evidence analysis of Lopardo et al. (2011).

Linyphioids clade

This clade was informally named by Hormiga (1994a, 2000) to group the families Linyphiidae and Pimoidae. The monophyly of linyphioids is supported by the following synapomorphies: cheliceral stridulatory striae, patella-tibia autospasy, enlargement of the peripheral cylindrical spigot base on the posterior lateral spinnerets, a 9 + 0 axonemal pattern in the sperm and an ectal cymbial process in the male palp (Hormiga, 1993, 1994a, b; Michalik and Hormiga, 2010; Hormiga et al., 2021).

Linyphiidae is the second largest family of spiders and the largest in Araneoidea with *c*. 4850 species classified in 636 genera. About 10% of all described spiders are linyphiids (World Spider Catalog, 2023). Although the ancestral web of Araneoidea probably was an orb (Fernández et al., 2018a; Kallal et al., 2021a), linyphiids build sheet webs of varying degrees of complexity (Hormiga & Eberhard, 2023). These spiders are distributed globally, but are more abundant at higher elevations, particularly in temperate regions (Hormiga, 1994b), contrary to the typical biological pattern of increasing species diversity towards the equator (Lomolino, 2004).

Linyphiids have been found on most oceanic islands, far away from continental masses, such as Saint Helena, Tristan da Cunha and the Juan Fernández islands. In the latter archipelago 15 endemic species of *Laminacauda* and ten species of *Neomaso* occur, suggesting their long dispersal abilities (Arnedo & Hormiga 2021). Linyphiidae have been classified into several subfamilies (Mynogleninae, Dubiaraneinae, Erigoninae, Linyphiinae, Micronetinae, Ipainae and Stemonyphantinae) although no comprehensive phylogenetic classification exists for the family and only some of the existing subfamilies have been corroborated as clades (e.g. Stemonyphantinae and Mynogleninae), whereas others have never been repeatedly shown not to be monophyletic (e.g. Dubiraneinae or Micronetinae) (Hormiga, 2000; Miller & Hormiga, 2004; Arnedo et al., 2009; Frick & Scharff, 2018; Wang et al., 2015; Hormiga et al., 2021). In our combined analysis, Stemonyphantinae and Mynogleninae were monophyletic whereas Erigoninae, and Micronetinae were polyphyletic (Fig. 10a).

Wunderlich (1986) suggested that *Pimoa* was the sister group to Linyphiidae and accommodated it in a new subfamily (Pimoinae), which Hormiga (1993) elevated to family rank. Hormiga (1994a) monographed Pimoidae, and added new species to *Pimoa*. Subsequently, the genera *Weintrauboa* (Hormiga 2003), *Nanoa* (Hormiga et al., 2005), and *Putaoa* (Hormiga & Tu 2008) were placed in Pimoidae based on morphology-based cladistic analyses. However, molecular phylogenies using the six markers, transcriptomes and UCEs recovered a paraphyletic Pimoidae with *Weintrauboa* and *Putaoa* nesting in Linyphiidae (Dimitrov et al., 2012, 2017; Wang et al., 2015; Wheeler et al., 2017; Fernández et al., 2018a; Kallal et al., 2021a). More recently, Hormiga et al. (2021) addressed the placement of *Weintrauboa* and *Putaoa* using Sanger-sequencing data and formalized the transfer of *Weintrauboa* and *Putaoa* to linyphiid subfamily Stemonyphantinae. The remaining two genera, *Nanoa* and *Pimoa* were hypothesized to be sister groups based on their male genitalic morphology (Hormiga et al., 2005), which was corroborated by molecular data (Dimitrov et al., 2012, 2017; Hormiga et al., 2021). Our study also placed *Weintrauboa* and *Putaoa* in Stemonyphantinae, and *Pimoa* and *Nanoa* form the Pimoidae clade (Fig. 10a). Currently, Pimoidae includes 86 species classified in two genera with *Nanoa* (with the single species *N. enana*) from the United States and *Pimoa* with 85 species distributed in the Holarctic region (World Spider Catalog, 2023).

Cyatholipidae

This is a meso-diverse family with 58 species classified into 23 genera distributed in Africa, Madagascar, Australia and New Zealand where they construct sheet webs generally in moist forests or mesic forests (Griswold, 1987, 2001; World Spider Catalog, 2023). Griswold (2001) proposed the first phylogenetic hypothesis using morphology. In our Combined dataset, *Tekella* and *Tekelloides* form a clade similar to Griswold (2001), yet the genera were not monophyletic (Fig. 10b). The genera *Alaranea*, *Cyatholipus*, *Scharffia* and *Ulwembua* formed a clade, whereas in Griswold's (2001) analysis these genera did not form a clade.

Malkaridae + "tetragnathoids" clade

Malkaridae is a family of 57 species classified in 13 genera distributed in the southern hemisphere with a monotypic genus known from Chile and Argentina (*Chilenodes)* and the remaining from Australia, New Zealand and New Caledonia (World Spider Catalog, 2023). They are web-less, active hunters that live in the leaf litter and mosses of temperate and tropical wet forests (Platnick & Forster, 1987; Rix, 2006; Rix & Harvey, 2010a; Hormiga & Scharff, 2020). These spiders are relatively difficult to find leading to few specimens in natural history collections and scarce information. Furthermore, some of their morphological features made it difficult to understand their affinities. For example, in one clade (Pararchaeniae) the presence of peg teeth on the chelicerae and the unusual shape of the carapace suggested an affinity with the palpimanoids, specifically Archaeidae and Mecysmaucheniidae (Forster and Platnick, 1984).

However, molecular sequencing removed pararchaeines from the Palpimanoidea and firmly placed it with the araneoid Malkaridae (Forster, 1949; Rix, 2006; Wood et al., 2012; Dimitrov et al., 2017). Thus, Pararchaeinae is an example of convergence with Mecysmaucheniidaes—both lineages have similar morphologies in order to produce "trap-jaw" predatory strikes with their highly manueverable chelicerae (Kallal et al., 2021b). Recently Hormiga and Scharff (2020) revised the non-pararchaeine malkarids of New Zealand and proposed a phylogenetic hypothesis for the family which now includes four subfamilies: Malkarinae, Pararchaeinae, Tingotinginae and Sternoidinae.

Tetragnathidae is a relatively large family with 990 species classified in 45 genera distributed globally except Antarctica (World Spider Catalog, 2023). The majority construct typical orb webs similar to other orb-weaving members of Araneoidea (e.g. Araneidae), yet their webs usually have open hubs (Álvarez-Padilla & Hormiga, 2011). Some have adopted a web-less, active hunter or cursorial lifestyle (e.g. Berger et al., 2021). Some tetragnathid genera such as *Tetragnatha* are secondarily-haplogyne whereas most of them have entelegyne genitalia (Griswold et al., 1998; Álvarez-Padilla & Hormiga, 2011). The taxonomy and systematics of various tetragnathid groups has a convoluted history (see Álvarez-Padilla and Hormiga, 2011), which has now settled on grouping genera into four subfamilies, namely Tetragnathinae, Nanometinae, Metainae and Leucauginae (Kallal et al., 2018; Álvarez-Padilla et al., 2020; Ballesteros & Hormiga 2021).

Arkyidae is a relatively small family with two genera and 38 species known from New Guinea, Australia and New Caledonia (World Spider Catalog, 2023). They do not construct foraging webs and instead are sit-and-wait or ambush predators. Arkyids have a field of short dense macrosetae on the prolateral surface of the first tarsus in males and have enlarged aggregate gland spigots on the posterior lateral spinnerets. This family was recently elevated from subfamily Arkyinae (Araneidae) to its own family by Dimitrov et al. (2017). Before being in Araneidae, arkyids were placed in Thomisidae, Mimetidae (which at the time was considered to be a palpimanoid family based on the presence of cheliceral peg teeth and gland mounds) and Tetragnathidae (Forster & Platnick, 1984; reviewed in Framenau et al., 2010).

Mimetidae is a family of araneophagic spiders, which has earned them the name "pirate spiders". They include 159 species classified in eight genera distributed globally except Antarctica (World Spider Catalog, 2023). Similar to arkyids, they do not construct any foraging web and instead have developed a sophisticated method of aggressive mimicry for hunting spiders in webs. They mimic the behaviour of ensnared prey on the web of other spiders, or the courtship vibrations of their prey's conspecific male by plucking on the web of their prey, to lure the prey spider from their web and then attack and feed on them (Cutler, 1972; Jackson & Whitehouse, 1986). Mimetids have a conspicuous line of raptorial macrosetae on the prolateral surfaces of the tibiae and metatarsi of first two legs (Platnick & Shadab, 1993), which presumably assists in prey capture (similar macrosetae are found in many malkarids). The taxonomy and systematics of this family was recently revised by Benavides et al. (2017) and Benavides & Hormiga (2020).

Based on a highly supported clade including the families Arkyidae, Mimetidae and Tetragnathidae, Hormiga (2017) named this grouping as "tetragnathoids". This clade is perhaps the only grouping within Araneoidea that is robust to Sanger sequencing (Dimitrov et al., 2017, Hormiga, 2017; Wheeler et al., 2017), transcriptomes (Garrison et al., 2016 (Arkyidae not

sampled), Fernández et al., 2018a; Kallal et al., 2021a) and UCEs (Kulkarni et al., 2020, 2021).

Malkaridae has been recovered as a sister group to the tetragnathoids using Sanger-sequencing data (Dimitrov et al., 2017; Hormiga, 2017; Wheeler et al., 2017) and UCEs (Kulkarni et al., 2020, 2021), yet transcriptomes suggest Mysmenidae as a sister group to Malkaridae (Kallal et al., 2021a) or Mysmenidae as a sister group to tetragnathoids (Garrison et al., 2016, Fernández et al., 2018a) (Fig. 11). In Tetragnathidae, the Tetragnathinae, Metainae, Nanometinae and Leucauginae subfamilies were recovered monophyletic using our combined dataset (Fig. 11a). In Malkaridae, Pararchaeinae and Tingotinginae were monophyletic, yet Sternoidinae and Malkarinae were polyphyletic (Fig. 11b).

Araneidae + Synotaxidae

Araneidae is the second most speciose family within Araneoidea (after Linyphiidae), with *c*. 3125 species classified in 189 genera distributed worldwide (World Spider Catalog, 2023) and the third most speciose family (after Salticidae and Linyphiidae). Some of the largest species and cosmopolitan web-building spider genera such as *Nephilengys* and *Nephila* belong to this family. Most araneids construct typical orb webs, whereas some genera such as cyrtarachnines and mastophorines (also known as bolas spiders) dispel this phenomenon. Scharff & Coddington (1997) carried out the first large-scale cladistic analysis using morphological and behavioural characters. Several of the groups supported by that study continue to be recognized (such as gasteracanthines or cyrtophorines), while others have been placed elsewhere, such as the arkyines ("Arciinae") which are now placed in their own family, Arkyidae. Multiple molecular data classes (six Sanger-sequenced markers, transcriptomes and UCEs) have consistently placed the lineage of *Nephila* and its close relatives in Araneidae (Dimitrov et al., 2012, 2017; Scharff et al., 2020; Kallal et al., 2021a; Kulkarni et al., 2021), where it is now classified as a subfamily (Kallal et al., 2020). Although recently Araneidae has been split into several families (Kuntner et al. 2023), we reject such classification as premature in the absence of more thorough and extensive phylogenetic hypothesis of the family. In this study, we follow the classification of Dimitrov et al. (2017), Scharff et al. (2020) and Kallal et al. (2021a). Synotaxidae was until recently a monogeneric family with 11 species known from South America (World Spider Catalog, 2023): *Synotaxus* species construct "chicken-wire" shaped webs (Eberhard, 1977) and are identifiable based on a stout patellar apophysis in the male palp (Exline & Levi, 1965, Santos & Rheims, 2005). Recent phylogenetic work (Ramírez et al., 2022) has expanded the circumscription of Synotaxidae to include the genera *Tekellina* Levi, 1957 (formerly in Theridiidae) and *Hamus* Lin, Ballarin & Li, *Nescina* Lin, Ballarin & Li, *Gaucelmus* Keyserling, 1884 (formerly in Nesticidae).

Our UCE phylogeny using maximum-likelihood recovered Synotaxidae as the sister group to Araneidae, similar to other UCE-based studies (Kulkarni et al., 2020, 2021); however, with parsimony Synotaxidae was a sister group to all Araneoidea families except Theridiidae (Figs 4, 12, S3 and S4). Sanger-based markers recover Theridiosomatidae + Synotaxidae (Dimitrov et al., 2017) or Synotaxidae (Scharff et al., 2020; Theridisomatidae not sampled) whereas Theridiosomatidae is the sister group to Araneidae with transcriptomes (Fernández et al., 2018a; Kallal et al., 2021a). Interestingly, UCEs extracted from transcriptomes analysed as nucleotides recover Synotaxidae as the sister group to Araneidae (Kulkarni et al., 2021). However, transcriptomic data analysed as amino acids recover Theridiosomatidae or Synotaxidae + Theridiosomatidae as the sister group to Araneidae (Kulkarni et al., 2021: supplementary figures). No morphological analysis has suggested close affinities between araneids and synotaxids and we do not know of any morphological features that could be putative synapomorphies of such a clade. In the Combined phylogeny, we found that Synotaxidae (including *Gaucelmus* as recently transferred by Ramírez et al., 2022) are nested within the sister clade of Araneidae (Fig. 12a).

Nicodamoidea and Eresidae

Nicodamoidea clade includes the families Megadictynidae and Nicodamidae, a superfamily rank that was established by Dimitrov et al. (2017). Megadictynidae are cribellate entelegyne spiders with two monotypic genera (*Megadictyna* and *Forstertyna*), both from New Zealand.

Nicodamidae includes ecribellate entelegyne spiders with seven genera and 27 species distributed in Australia and New Guinea (Harvey, 1995; Dimitrov et al., 2017). The sister group to Nicodamoidea in our phylogeny was Eresidae, which was recovered with high support (100% UB; Figs 3, 4 and 13). This finding is consistent with other UCE-based phylogenies (Kulkarni et al., 2020, 2021). However, this contrasts with transcriptome-based phylogeny where the data are treated as amino acids, Nicodamoidea is a sister group to Araneoidea (Fernández et al., 2018a; Kallal et al., 2021a).

Eresidae (velvet spiders) includes nine genera of which the genus *Stegodyphus* includes of three subsocial species—*S. sarasinorum* (South Asia), and *S. dumicola* and *S. mimosarum* (Africa) (Kraus & Kraus, 1988;

Johannesen et al., 2007). *Stegodyphus* constructs extensive aerial cribellate sheet webs (Miller et al., 2010a). The social species share building and maintaining their webs, attack and capture prey together, and provide maternal care to the brood cooperatively (Kullmann, 1972; Agnarsson et al., 2006). Interestingly, the close relatives of the social species of Eresidae are solitary species. Sociality has been estimated to have evolved independently about 18 times in spiders (Agnarsson et al., 2006) in various families such as Oxyopidae and Theridiidae. Recent studies have found convergent expressions of certain gene families in the social spider species (Tong et al., 2022). A stable placement of Eresidae is thus important to understand the evolution of social behaviour in spiders.

A phylogeny using five Sanger-sequencing markers suggested Eresidae as a sister group to the UDOH grade families Hersiliidae + Oecobiidae and the RTA clade (Miller et al., 2010a). Eresidae is a sister group to Nicodamoidea recovered with UCE data, but a sister group to the Araneoidea + Nicodamoidea clade with transcriptomes. The Sanger-based six-marker phylogeny of Wheeler et al. (2017) recovered Eresidae as a sister group to the UDOH grade plus RTA clade, similar to Miller et al. (2010a).

UDOH grade

UDOH grade is a paraphyletic assemblage (named by Fernández et al., 2018a) containing the spider families Uloboridae, Deinopidae, Oecobiidae and Hersiliidae. Uloboridae and Deinopidae are cribellate orb-weaving groups, whereas all other orb-weaving spider families are ecribellate and cluster into a monophyletic group (Araneoidea). Uloboridae includes 19 genera with 288 species with worldwide distribution. Typically, uloborids construct an orbicular web with radii, frame threads and hub using nonsticky threads, and a sticky spiral using cribellar silk. Some genera depart from this behaviour, a few examples of which include only spirals in *Philoponella*, (Opell & Eberhard, 1984), a triangular orb web in *Hyptiotes* (Marples & Marples, 1937), and a single silk line of *Miagrammopes* partially covered with cribellate silk and few additional lines of support (Lubin et al., 1978). A recent study demonstrated a catapult-like mechanism used by *Hyptiotes* to capture prey. This spider stretches the web, thereby storing elastic energy, by extending an additional anchor line and releases it on sensing contact of prey with the web. The resulting jerk caused by the release of stored energy entraps and wraps the prey (Han et al., 2019). Deinopidae members are commonly called "ogre-faced" spiders due to the large posterior median eyes of some species. Deinopids have a unique behaviour of waiting for prey hanging upside down with a highly modified orbicular web held in anterior legs. They cast the web towards the prey to capture it (Robinson & Robinson, 1971) which has earned them the name of "net casting" spiders. It includes 68 described species classified into three genera (*Asianopis*, *Deinopis* and *Menneus*) distributed worldwide (World Spider Catalog, 2023). Oecobiidae includes six genera represented by 120 species distributed globally, with some widely distributed synanthropic species (Santos & Gonzaga, 2003; World Spider Catalog, 2023). The small webs of *Oecobius* (used as a shelter) are commonly seen in houses. Oecobiidae includes taxa that are both cribellate (such as *Oecobius*) and ecribellate (such as *Uroctea*) (Shear, 1970). Hersiliidae includes 188 described species classified into 16 genera with global distribution (World Spider Catalog, 2023). Most hersiliids are arboreal, constructing their non-foraging webs close to tree bark or wall surface on which they move swiftly for prey capture or escaping. Oecobiidae and Hersiliidae (together called "Oecobiioids" by Miller et al., 2010a) are characterized by a unique prey attack behaviour of wrapping the prey by circling around it (Crome, 1957; op. cit. after Lehtinen, 1967, p. 305; Coddington and Levi, 1991).

Resolving the relationships among the UDOH families with their diverse foraging behaviour (with and without web use) is crucial, as it affects the hypothesis about the evolutionary history of the web architecture and foraging behaviour in spiders. In our study, all families of this group were monophyletic, including Oecobiidae (represented by the cribellate *Oecobius* and ecribellate *Uroctea*) in the combined phylogeny (Fig. 13). This placement is different from the prevailing hypotheses, as described below. A morphology-based cladogram recovered a monophyletic Deinopoidea which included Deinopidae and Uloboridae; however, this was refuted by Sanger-sequencing-based phylogenies (Dimitrov et al., 2012, 2017; Wheeler et al., 2017). The close relatives of the UDOH families are the Tibial apophysis clade, consistently recovered with the six Sanger-based markers, transcriptomes and UCEs. Transcriptomes recover Deinopidae as a sister group to the RTA + Phyxelididae-Titanoecidae (PT) clade (Garrison et al., 2016; Fernández et al., 2018a; Kallal et al., 2021a) with high support. In the UCE phylogeny, Deinopidae was a sister group to Hersiliidae + Oecobiidae clade. Some morphology-based phylogenetic studies (for example, Griswold et al., 1999) inferred Oecobiioidea as a sister group to Eresidae (together called Eresoidea). In our study, the Oecobiioidea + Deinopidae clade was a sister group to a clade including Uloboridae + RTA + PT clade (Figs 3, 4 and 13), similar to thephylogenetic hypothesis of Wheeler et al. (2017).

The Tibial Apophysis clade

This large clade is united by the presence of a tibial apophysis on the male pedipalp. At least two types of tibial apophyses are known—dorsal and retrolateral. Titanoecidae and Phyxelididae are early diverging families in this clade that have a dorsal tibial apophysis (Griswold et al., 1999, 2005). Griswold et al. (1999) removed the subfamily Phyxelidinae from Amaurobiidae and elevated it to family rank, and proposed the informal name "Titanoecoidea" for grouping the families Phyxelididae and Titanoecidae clade based on their cladistic analysis of morphological data. The phyxelidid genus *Vytfutia* bears both types of tibial apophyses (TA)—a dorsal and a retrolateral apophysis on the male pedipalps—while the remaining phyxelidids only have a retrolateral tibial apophysis (Griswold et al., 2005); conjunction implies that these two tibial apophyses are not homologous. In Griswold et al. (2012b), the single terminal of *Vytfutia* was sister to *Goeldia* (Titanoecidae) plus Phyxelididae. *Vytfutia* was not sampled in either Wheeler et al. (2017) or our UCE sampling. With our current taxon sampling, Titanoecoidea was not monophyletic; instead, Titanoecidae was a sister group to the Phyxelididae + RTA clade (Figs 3, 4 and 14). Synapomorphies of Phyxelididae include palpal femur thorns in both sexes, modified male metatarsus I, and long, narrow, densely placed and laterally flattened paracribellar spigots on the posterior median spinnerets (Griswold, 1990; Griswold et al., 1999). It is noteworthy here that a retrolateral tibial apophysis also is present in the other groups such as the linyphiid subfamily Erigoninae, suggesting convergent evolution (Araneoidea) (Hormiga, 1994b).

Retrolateral Tibial Apophysis (RTA) clade

As mentioned previously, the presence of a retrolateral tibial apophysis on male pedipalp is characteristic to this large group of spiders (Coddington & Levi, 1991; Griswold et al., 2005). Our UCE phylogeny recovered a highly supported RTA clade (100% UB) (Figs 3 and 4). Two lineages, the Oval calamistrum clade and Dionycha (two-clawed spiders), make up the bulk of species richness in the RTA clade. These are mostly cursorial spiders including the common jumping spiders (Salticidae) which is the most speciose spider family with more than 6700 species belonging to the Dionycha clade (Figs 4 and 20). Most of these RTA clade members with two-claws do not construct foraging webs, but instead are active hunters and their third middle claw has been replaced with clusters of specialized adhesive setae, called scopulae, that are positioned beneath the two superior claws. The third tarsal claw is used by spiders to trace silk lines on webs, but also is present in some spiders that do not construct foraging webs (Ramírez, 2014). It has been suggested that the scopulae have evolved as a substitute for the use of silk for foraging, yet some exceptions also exist (Wolff et al., 2013). For example, most salticid spiders construct silk retreats and some Lycosidae spiders construct webs, and both have adhesive setae.

Zodariidae and Penestomidae

Penestomidae is a small family including one genus (*Penestomus*) with nine species known from South Africa, one of which also is recorded from Lesotho (Miller et al., 2010b). Miller et al. (2010a) inferred that Penestomidae nested within the RTA clade and based on this placement they elevated this group to family rank by removing it from a subfamily within Eresidae. Before this, Lehtinen (1967) had shown that male penestomids have an RTA which is typical of the RTA clade member and not found in any eresid spider. Zodariids are mostly nocturnal, ground-dwelling, wandering spiders, many of which feed on ants. The synapomorphies of this family are absence of serrula on the endites and a rounded prolateral tibial process fitting in a metatarsal pouch (Jocqué & Henrard, 2015).

In the UCE phylogeny, the Zodariidae + Penestomidae clade is the sister group to the remaining RTA clade families with high support (100% UB). The monophyly of Zodariidae (two terminals) and Penestomidae (one terminal) was also highly supported in this UCE tree (Fig. 4) as well as in the Combined phylogeny, with one terminal of Penestomidae and 27 terminals of Zodariidae. In Miller et al. (2010a), Penestomidae (two *Penestomus* species) is the sister group to Zodariidae (*Zodarion* and cf. *Aschema*).

A formal grouping called Zodarioidea, proposed by Miller et al. (2010a), includes the families Homalonychidae, Penestomidae and Zodariidae was. However, the Sanger-based phylogeny of Wheeler et al. (2017) found this group to be polyphyletic. In their phylogeny, Homalonychidae was a sister group to the Oval calamistrum + Dionycha clade. Wheeler et al. (2017) point out that this grouping may be imposed by the constraints of the backbone transcriptomic phylogeny of Garrison et al. (2016) that they used. However, multiple transcriptomic phylogenies (Fernández et al., 2018a; Shao & Li, 2018; Kallal et al., 2021a) and various other genomic data classes (UCEs, transcriptomes as nucleotides, amino acids) (Kulkarni et al., 2021) have placed Homalonychidae as sister group to the Oval calamistrum + Dionycha clade with high support (UB >95%). This suggests that Zodarioidea may need to be recircumscribed to only include Zodariidae + Penestomidae; however, we do not formally make any nomenclatural changes in this study.

Sparassidae

The members of this family with close to 1500 species classified in 96 genera includes spiders with laterigrade legs (positioned similar to the legs of a crab) (Jäger, 2001; World Spider Catalog, 2023) and fleshy, trilobate membranes at the distal region of the metatarsi, an indented tip of the claw tuft setae, membranous extensions of tarsi on the side of claw tuft plates, and the trichobothrial setae lacking the bumps on their bases (Jäger, 1998; Ramírez, 2014). These spiders are cursorial hunters and some species can be quite large (≤40 mm in body size), with very long legs. Our UCE phylogeny placed Sparassidae as a sister group to the marronoid clade with high support (100% UB; Figs 4 and 14), similar to the results of the previous transcriptomic (Fernández et al., 2018a; Shao & Li 2018; Kallal et al., 2021a) and UCE (Kulkarni et al., 2021) phylogenies. Morphological data suggest the placement of Sparassidae within the Dionycha clade (Ramírez, 2014), whereas Sanger-sequencing data suggest multiple alternative placements (see Moradmand et al., 2014; Wheeler et al., 2017). The subfamilies Sparianthinae, Heteropodinae, Polybetinae and Delninae were monophyletic whereas Eusparassinae was paraphyletic (Fig. 14). A more recent and more comprehensive study reconstructed a sparassid phylogeny using four Sanger-sequenced markers (Gorneau et al., 2022) and recovered similar relationships (including paraphyly of Eusparassinae) for these subfamilies.

Marronoid clade

The Marronoid clade groups several spider families that are mostly brown coloured, without any prominent colour pattern [Hormiga coined the informal name of this clade, which was first introduced in print by Wheeler et al. (2017)]. Marronoids are one of the major taxonomic problems in spider classification because, as Lehtinen (1967) noted, there are many closely related groups with and without a cribellum, making it difficult to group them and define diagnoses. Marronoids include the families Amaurobiidae, Agelenidae, Hahniidae, Cybaeidae, Dictynidae, Toxopidae, Cycloctenidae and Stiphiididae (sensu Wheeler et al., 2017). Our UCE phylogeny recovered a monophyletic assemblage of all the marronoid families with high support (100% UB). All these families except Hahniidae were monophyletic (Fig. 4). In the combined phylogeny, Amaurobiidae, Cycloctenidae, Dictynidae, Desidae, Hahniidae and Toxopidae were either paraphyletic or polyphyletic (Figs 15 and 16); however, some alternative relationships were recovered using the marronoid dataset (Fig. S5). We attempt to delve further into the reasons for each of these relationships below.

Hahniidae

These small-sized spiders have a distinctly transverse arrangement of the spinnerets in one row and an advanced position of the tracheal spiracle (Lehtinen, 1967). Hahniids are represented by 357 described species classified into 24 genera distributed worldwide except Antarctica and Madagascar (World Spider Catalog, 2023). In an unpublished dissertation, Catley (1996) suggested that the position of tracheal spiracles is highly variable among species, but instead loss of true lateral tracheae may be a synapomorphy of the family. Their linearly arranged spinnerets resemble a comb and therefore they also are called “comb-tailed spiders”. Hahniids live in the leaf litter or under bark, where they construct small sheet webs. Lehtinen (1967) placed Hahniidae in his superfamily Amaurobioidea (Miturgidae, Amaurobiidae, Liocranidae, Agelenidae and Dictynidae), whereas Forster (1970) considered it to be a member of the superfamily Dictynoidea (Dictynidae, Neolanidae, Desidae, Cybaeidae, Argynonetidae and Anyphaenidae).

Our UCE phylogeny included three Hahniidae terminals, two *Cicurina* and one *Mastigusa* species. The inclusion of the six-marker dataset added another four hahniid genera—*Antistea*, *Cybaeolus*, *Hahnia* (the type genus) and *Neoantistea*. In both datasets, Hahniidae was as polyphyletic. The *Cicurina* clade was recovered as a sister group to *Mastigusa* + Cybaeidae II clade, whereas the remaining hahniids including *Hahnia* formed a sister group to a larger clade including Toxopidae, Dictynidae (excluding *Lathys*), Cybaeidae I & II, *Mastigusa* and *Cicurina*. The monophyly of Hahniidae I was strongly supported (100% UB; Fig. 15). Interestingly, the marronoid dataset recovered a monophyletic Hahniidae except *Mastigusa* which was a sister group to Cybaeidae (35% UB; Fig. S5). Cybaeidae I and II formed a clade, yet a poorly supported branch of *Ethobuella* (Agelenidae) nested with this clade (61% UB; Fig. S5). A recent study by Castellucci et al., (2023) based on Sanger sequencing data, classified *Mastigusa* in the Cybaeidae, a placement that is congruent with our results (Fig. 15).

In Wheeler et al. (2017), one terminal of *Cicurina* was the sister group to Hahniidae (albeit with a moderate support of 67% UB) and was formally moved from Dictynidae to Hahniidae based on this phylogenetic placement. It should be noted that *Cicurina* in the phylogeny of Spagna & Gillespie (2008) was a sister group to *Lathys* (Dictynidae). In the phylogeny of entelegyne spiders using Sanger-sequenced markers, *Cicurina* was

recovered as a sister group to Hahniidae (including *Hahnia*) + Agelenidae clade (Miller et al., 2010a). The Sanger-sequencing-based three-marker phylogeny of Crews et al. (2020) also recovered *Cicurina* not nested within Hahniidae. The placement of remaining Hahniidae also is poorly studied and is awaiting revision.

Amaurobiidae

In these spiders, the median apophysis of the male palp is a sclerotized plate-like structure (Paquin et al., 2010). The monophyly and affinities of amaurobiids have a long and controversial history (see Lehtinen, 1967; Miller et al., 2010a, for details). In its current circumscription, both cribellate (such as *Amaurobius*) and ecribellate taxa (such as *Macrobunus*) are included. In our UCE phylogeny, Amaurobiidae was polyphyletic. *Amarobius* and *Callobius* formed a clade which was a sister group to the remaining marronoid families whereas *Rubrius antracticus* was a sister group to a clade including Toxopidae + Dictynidae + Hahniidae + Cybaeidae families (Fig. 4). In our Combined phylogeny, a clade comprising *Amaurobius*, *Callobius* and *Pimus* (Amaurobiidae I in Fig. 15) was a sister group to the remaining marronoid families which included the clade of other amaurobiid genera. The latter clade (Amaurobiidae II in Figs 15 and S5) received high support (96% UB), and represents the subfamily Macrobuninae.

Cycloctenidae

This family includes eight genera—six from New Zealand, one both New Zealand and Australia and one from Indonesia—totalling 80 described species (World Spider Catalog, 2023). Forster (1979) extensively treated the taxonomy of cycloctenids and provided a long list of diagnostic characters, perhaps the most prominent being the absence of claw tufts and scopulae.

In the UCE phylogeny, *Cycloctenus* (the single cycloctenid terminal included) was the sister group to the clade including Stiphiididae + Desidae (Fig. 4). Our Combined dataset included five cycloctenid genera, each with one species of *Orepukia*, *Pakeha*, *Paravoca*, *Toxopsiella* and five species of *Cycloctenus*. In the resulting phylogeny from this dataset, *Orepukia* and *Pakeha* formed a clade that was a sister group to *Aorangia* (Stiphidiidae) (Fig. 16). The remaining Cycloctenidae terminals formed a sister group to a clade that included the *Aorangia* (Stiphiididae) + *Orepukia* and *Pakeha* clade (Fig. 16). In the phylogeny of Wheeler et al. (2017), the *Orepukia* + *Pakeha* clade was a sister group to the remaining cycloctenids with poor support (61% UB). Based on this phylogenetic placement both *Orepukia* and *Pakeha* were transferred, from Agelenidae and Amaurobiidae respectively, to Cycloctenidae by Wheeler et al. (2017). This placement of a monophyletic Cycloctenidae was recovered by our marronoid dataset (Fig. S5).

Dictynidae

Dictynidae includes spiders occupying diverse habitats such as dry, arid and even aquatic, semi-aquatic, seashore, freshwater and salt-flat (Spagna et al., 2010). It includes the aquatic spider *Argyroneta aquatica*, which constructs a silk-tube (called "diving bell") among aquatic vegetation and resurfaces periodically to capture an air bubble around its opisthosoma.

Dictynidae includes *c*. 474 described species classified in 53 genera distributed worldwide except Antarctica (World Spider Catalog, 2023). In its current circumscription, both cribellate and ecribellate species are included in Dictynidae. The cribellate dictynids formed a clade in some analyses (Griswold et al., 2005), yet the family is rendered polyphyletic when the ecribellate members are included (Spagna et al., 2010).

Lathys, which is currently placed in Dictynidae, was recovered as a sister group to Agelenidae, albeit with poor support (15% UB), and the other dictynids formed a clade which was sister group to Toxopidae (Fig. 15). Our marronoid dataset recovered *Lathys* as a sister group to the Toxopidae + Dictynidae clade (Fig. S5). Multiple alternative placements of *Lathys*, such as a sister group to *Cheiracanthium* (Cheiracanthiidae), were recovered using single and combined Sanger-sequencing-based trees (see Spagna et al., 2010). In Wheeler et al. (2017), *Lathys* was a sister to the remaining Dictynidae with low support (11% UB). The Sanger-sequencing-based phylogenies of Spagna & Gillespie (2008) and Miller et al. (2010a) recovered a polyphyletic Dictynidae with *Lathys* as a sister group to *Cicurina* (currently placed in Hahniidae) and the remaining Dictynidae formed a clade. Lehtinen (1967) had already stated that Cybaeidae and Cicurininae (both were subfamilies within Dictynidae at the time) "perhaps they could be united in a single, monophyletic family".

Desidae

Desidae includes about 325 species classified in 63 genera with most species in Australia, New Zealand, and New Caledonia, and some species in south-east Asia and Africa (World Spider Catalog, 2023). Desidae has both cribellate and ecribellate species. Some desids (whose natural history is known), such as *Cambridgea* from New Zealand, construct a large sheet web with a tube-like retreat (Forster & Forster, 1999). *Desis* live inside silken retreats and inhabit intertidal

zones, for example hiding inside barnacles or among kelp, and for that reason are also known as "intertidal spiders" (Baehr et al., 2017). Desidae was monophyletic in all datasets including the UCE, Combined and marronoid datasets (Figs 4, 15 and S5).

Toxopidae

Toxopidae includes more than 80 species classified in 14 genera, distributed in New Zealand and Australia, and some islands in the Southern Hemisphere such as Crozet Islands and Kerguelen Islands (World Spider Catalog, 2023). In our UCE phylogeny, the single terminal of this family (*Midgee* sp.) formed a sister group to Dictynidae (Fig. 4). In the Combined and marronoid phylogeny, with nine genera (ten terminals), Toxopidae was monophyletic and formed a sister group to Dictynidae (excluding *Lathys*) (Figs 15 and S5).

Homalonychidae

Homalonychus, the single genus of this family, includes only two species, both known from the southern United States and northern Mexico. Homalonychids are wandering spiders that live in the desert where they can throw sand on their body to bury themselves, which is hypothesized to be a defensive behaviour (Domínguez & Jiménez, 2005). This family was monophyletic (both species of *Homalonychus* sampled in the Combined dataset) and was recovered as a sister group to the clade including Oval Calamistrum and Dionycha clades (Figs 3, 4 and 17), similar to the findings of Wheeler et al. (2017), Fernández et al. (2018a), Kulkarni et al. (2021) and Kallal et al. (2021a).

Oval calamistrum (OC) clade

The Oval calamistrum (OC) clade was described by Polotow et al. (2015) and includes spiders with a calamistrum with several rows of setae. In our UCE phylogeny, the *Uliodon* (Zoropsidae) + Udubidae clade formed a sister lineage to the remaining OC clade taxa. The other zoropsid in our UCE analysis, *Tengella*, was a sister group to the lycosoid families (Fig. 4). In the Combined phylogeny, two groupings of Zoropsidae were recovered (polyphyletic), one of which was a sister group to (Udubidae) and the other one was a sister group to the lycosoid families similar to the UCE phylogeny (Fig. 17). As Wheeler et al. (2017) stated, the placement of Zoropsidae is unstable and requires further attention.

Ctenidae

This family includes about 600 species classified in 49 genera distributed on all continents except Antarctica (World Spider Catalog, 2023). They are nocturnal, wandering spiders and are mostly ground-dwelling, with a few arboreal species (Polotow & Brescovit, 2008). Members of this family have a typical "ctenid eye pattern" of 2-4-2 eyes arranged in three rows of which anterior lateral eyes are smallest. The "ctenid eye pattern" has evolved convergently seven times in the RTA clade (Griswold, 1993; Hazzi & Hormiga, 2023). Most ctenids are ecribellate, but some genera such as *Acanthoctenus* have retained the cribellum (Griswold et al., 2005). Additional diagnostic characters of the family are eyes with a grate-shaped tapetum, teeth on the fang furrow and chelicerae with a boss (Griswold et al., 2005). The highly venomous and medically important spiders of the genus *Phoneutria* belong to this family (Lucas, 1988; Foelix, 2010).

In the morphological phylogeny of Silva-Dávila (2003), Ctenidae was monophyletic and a sister group to Miturgidae. In a more recent morphological study, Polotow & Brescovit (2014) recovered a monophyletic Ctenidae. However, only two outgroups (*Zoropsis* and *Tengella*, both Zoropsidae) were used in the latter study, so its close relatives in the RTA clade could not be identified. Recently, Hazzi & Hormiga (2023) published the most comprehensive phylogeny of Ctenidae representing 28 of the current 49 described genera, using nine Sanger-sequenced markers where the family was monophyletic. In our UCE phylogeny, Ctenidae was monophyletic (Fig. 4) and was a sister group to Psechridae similar to the transcriptomic phylogeny of Cheng & Piel (2018). In the combined phylogeny, however, *Ancylometes* (not sampled in UCE phylogeny) was recovered as a sister group to all lycosoid families with moderate support (93% UB; Fig. 17a), a finding that is similar to Wheeler et al. (2017). In the phylogeny of Piacentini and Ramírez (2019), *Ancylometes* was a sister terminal to Oxyopidae with poor support (39% posterior probability; see supplementary tree of Piacentini and Ramírez, 2019). The placement of *Ancylometes* varied across analyses in Hazzi & Hormiga (2023) including a placement as sister to Oxyopidae. The current taxonomic placement of *Anyclometes* within Ctenidae is unusual because it is the only group within ctenids that constructs a nursery web (Merret, 1988; Santos, 2007), a behaviour that is found primarily in Pisauridae. Another nursery web-building spider outside Pisauridae is *Cupiennius*. It was recently transferred from Ctenidae to Trechaleidae by Piacentini & Ramírez (2019) based on its highly supported phylogenetic placement. Our UCE phylogeny also recovered *Cupiennius* nested within Trechaleidae (Fig. 4). Interestingly, a phylogenetic analysis based solely on the CO1 marker recovered both non-pisaurid nursery web-building spiders *Anyclometes* and *Cupiennius* in a clade (Gámez Vargas, 2019).

Thomisidae

Spiders of this family are called "crab spiders" owing to the laterigrade orientation of their legs, their posture superficially resembling that of a crab. Thomisidae includes >2100 species classified in 171 genera distributed globally (World Spider Catalog, 2023). They are sit-and-wait predators and do not construct foraging webs. Many species have cryptic body coloration and can even change the body colour (Weigel, 1941). Some thomisids can mimic twigs (e.g. *Tmarus*), ants (e.g. *Aphantochilus*) or bird droppings (e.g. *Phrynarachne*) (Benjamin et al., 2008; Benjamin, 2011; Teixeira et al., 2013; Ileperuma-Arachchi and Benjamin, 2019).

Thomisidae was recovered as polyphyletic with one clade of most thomisid representatives (45 terminals), including the type genus *Thomisus*, as a sister group to Oxyopidae in our Combined phylogeny (Fig. 17a). The other clade included *Borboropactus*, which was the sister group to Psechridae, albeit with moderate support (56% UB; Fig. 17b).

Borboropactus is unusual because it has a canoe-shaped tapetum, whereas all other thomisid genera have a grate-shaped tapetum (Homann, 1934; Benjamin, 2011). This genus is one of the few thomisid genera found fossilized in the amber (Wunderlich, 2004). *Borboropactus* has a characteristic behaviour of digging and covering itself with soil particles. A similar behaviour is found in *Stephanophis* (Thomisidae), *Cryptothele* (Zodariidae), *Sicarius* (Sicariidae) and even some mygalomorphs such as *Paratropis* (Paratropidae). Based on this unusual behaviour, in addition to some morphological characters, Wunderlich (2004) erected a new family (Borboropactidae) to accommodate extant and fossil *Borboropactus* species. Benjamin et al. (2008) used three Sanger-sequencing-based markers and found that *Borboropactus* is sister group to the remaining Thomisidae and, thus, rejected Borboropactidae, which was synonymized with Thomisidae. Morphology recovered *Borboropactus* nested within the *Stephanopis* clade (Benjamin, 2011). In Wheeler et al. (2017), *Borboropactus* was the sister group to remaining thomisids with poor support (35% UB). In some of the Wheeler et al. 2017) analyses *Borboropactus* did not nest within Thomisidae, and the authors preferred *"to keep the more traditional Thomisidae* sensu lato *with weak support"* noting that their results were *"also compatible with the split of a robust Thomisidae* sensu stricto *and a separate Borboropactidae as proposed by* Wunderlich (2004)."

Pisauridae and Dolomedes

Pisauridae includes about 360 species classified in 52 genera distributed globally (World Spider Catalog, 2023). Many pisaurids show a peculiar courtship behaviour which involves a "nuptial gift" consisting of a prey wrapped in silk as studied in *Pisaurina mirabilis* (Clerck, 1757). If a female accepts the prey, it means that she is receptive for mating (van Hasselt, 1884; Stålhandske, 2001). A similar behaviour has been observed in some spiders of the family Trechaleidae (Costa-Schmidt et al., 2008). Female pisaurids construct a tent-like silk structure when the spiderlings are about to emerge from the egg sacs. This web is called a "nursery web" and is a synapomorphy of Pisauridae (Piacentini & Ramírez, 2019). Similar nursery webs have convergently evolved in other spiders such as *Peucetia* (Oxyopidae), *Cupiennius* (Trechaleidae) and *Ancylometes* (Ctenidae) (Merret, 1988; Sierwald, 1997; Piacentini & Ramírez, 2019).

In our UCE phylogeny, Pisauridae was paraphyletic, with most of Pisauridae (in part) as sister group to a clade that includes *Dolomedes* (Pisauridae) and the Trechaleidae + Lycosidae clade (Fig. 4). In the combined phylogeny, *Dolomedes* (four terminals) + *Bradystichus* were the sister group to a clade that included Trechaleidae and Lycosidae (Figs 17 and 18). Wheeler et al. (2017) and Piacentini & Ramírez (2019) recovered the *Dolomedes* + *Bradystichus* clade as sister to the remaining Pisauridae clade. Likewise, the eight-marker phylogeny of Albo et al. (2017) also recovered *Dolomedes* not nesting within Pisauridae. However, the transcriptomic analysis of Fernández et al. (2018a), Cheng & Piel (2018) and Kallal et al. (2021a) recovered a monophyletic Pisauridae with *Dolomedes* as a sister group to the remaining Pisauridae.

Lycosidae and Trechaleidae

Lycosidae are a large family including close to 2500 species classified in 132 genera and distributed globally (World Spider Catalog, 2023). Lycosids are wandering, agile hunters that chase their prey, earning them the vernacular name of "wolf spiders". Most lycosids do not construct foraging webs and some, such as *Geolycosa*, dig and live in burrows (Marshall, 1995). Lycosid females carry their egg sac attached to their spinnerets and on hatching, the spiderlings move to the mother's abdomen and are carried by her, where they cling to modified abdominal setae. The lycosid genus *Schizocosa* has been extensively studied for visual and vibratory signalling during courtship. Male *Schizocosa* use their tibial bristles and dark pigmentation on first legs for visual display. They also use vibrational signals by stridulating, drumming of pedipalps or even bouncing their body (Hebets et al., 1996; Stratton, 2005). Although the family Lycosidae is nested in the RTA clade, lycosid males lack a retrolateral tibial apophysis (Polotow et al., 2015; Poy et al., 2020).

Trechaleidae is a relatively small family with 133 species classified in 17 genera, distributed in Central

and South America and one species in Japan (World Spider Catalog, 2023). Most trechaleids live close to water bodies and have long and flexible tarsi, a character which is hypothesized to be an adaptation for walking on the water surface (da Silva et al., 2008).

Lycosidae was recovered as the sister group to Trechaleidae in the UCE phylogeny (Fig. 4), similar to the results from Sanger-sequencing analyses (Albo et al., 2017; Wheeler et al., 2017; Piacentini & Ramírez, 2019), yet both families were polyphyletic in the Combined phylogeny (Fig. 18). We integrated Piacentini & Ramírez (2019)'s and Wheeler et al. (2017)'s Lycosidae sequences to assess if increased taxon sampling rendered monophyly of these families. However, the trechaleid *Trechalea* (one terminal) formed a sister group to a clade that included *Cupiennius* (two terminals), *Arctosa kwangreungensis* Paik & Tanaka, 1986 and *Hygrolycosa rubrofasciata* (Ohlert, 1865) (Lycosidae I) and the remaining Lycosidae. The Lycosidae I branch was moderately supported (79% UB) in its placement as a sister group to the *Cupiennius* clade (Fig. 18). The remaining Lycosidae (Lycosidae II) placed as sister clade to this includes Lycosidae 98 terminals. In the Sanger-sequencing-based phylogeny of Piacentini & Ramírez (2019), *A. kwangreungensis* did not nest with other *Arctosa* species, but instead was a sister group to *Hygrolycosa rubrofasciata* and *Melocosa fumosa* (latter nesting within Lycosidae in this study, see Fig. 18).

Dolejš (2013) suggested that *Arctosa fujiii* Tanaka, 1985, (closely related to *A. kwangreungensis*), *H. rubrofasciata* and *Hygrolycosa umidicola* Tanaka, 1978 use an empty egg sac to carry their spiderlings. This behaviour is characteristic of Trechaleidae, whereas most lycosids carry spiderlings on their abdomen. Furthermore, Dolejš (2013) suggests that *A. kwangreungensis* and *Arctosa ebicha* Yaginuma, 1960 (both from China and Korea) do not belong to *Arctosa*, but may be an undescribed genus. Interestingly, *A. ebicha* nested within Lycosidae in our Combined phylogeny (Fig. 18). The inclusion of *A. fujiii* and *A. hikosanensis* in our Combined dataset will be useful to further investigate the placement of this group.

Dionycha

Dionychans are characterized by having a reduced or secondarily lost third claw in their leg tarsi (Coddington & Levi, 1991; Ramírez, 2014). They represent *c*. 30% of all described spider species classified into 19 families (World Spider Catalog, 2023). There are, however, other spider families such as some Dysderidae, Palpimanidae and Ctenidae, which also have convergently evolved the two-claw condition (Ramírez, 2014). Dionychans were monophyletic with high support in both the UCE phylogeny and the Combined phylogeny (both with 100% UB). The Dionycha clade is divided into three subclades: Prodidomidae, Dionycha A and Dionycha B. Dionycha A clade is supported by one unambiguous synapomorphy: the cylindrical gland spigots (Cy) on the posterior median spinnerets are clustered posteriorly and isolated from the other spigots (Azevedo et al., 2022).

Prodidomidae

This family was recently restored from a subfamily within Gnaphosidae by Azevedo et al. (2022) and currently includes 192 species classified in 23 genera (World Spider Catalog, 2023). This family is united by the shaft of the minor ampullate gland spigots being reduced to a needle-like extension of the base (Platnick, 1990). A morphological cladistic analysis by Rodrigues & Rheims (2020) recovered Prodidominae (sensu Rodrigues and Rheims, 2020) as a sister group to Molycriinae (Gnaphosidae). However, our UCE and Combined phylogeny recovered Prodidomidae as a sister group to remaining Dionycha (Figs 4, 19 and S6), similar to the results of Azevedo et al. (2022).

Trachycosmidae

This family was recently elevated by Azevedo et al. (2022) to circumscribe the Australian genera formerly placed in Gallieniellidae (*Meedo*, *Neato*, *Oreo*, *Peeto* and *Questo*) based on the phylogenetic placement recovered from a Combined dataset of UCEs, Sanger-sequenced markers and phenotypic data. In our UCE, Combined and Dionychan phylogenies, Trachycosmidae was monophyletic (Figs 4, 19 and S6), with the exception of *Tinytrema* which was placed as the sister group to Trachelidae (in part) or Gnaphosidae (in part). *Tinytrema* was placed in a similar way in Wheeler et al.'s (2017) analysis, but was not sampled in the more rigorous analysis of Azevedo et al. (2022).

Azevedo et al. (2022) provided the following diagnosis for Trachycosmidae: anterior lateral spinnerets with a complete distal article and lacking inflatable area, separated by their diameter or more; the presence of two major ampullate gland spigots in males and females; epigynal field formed by an undivided plate, usually with an atrium at the copulatory openings; lens of the anterior lateral eyes are convex, juxtaposed from surrounding cuticle (compared to flat lens of Trochanteriidae).

Clubionidae

This family includes more than 650 species classified in 18 genera. In our UCE, Combined and Dionychan phylogenies, Clubionidae was polyphyletic with *Elaver* as a sister group to Anyphaenidae and this clade as the sister group to the remaining Clubionidae (Figs 4, 19 and S6). In the morphological cladogram of

Ramírez (2014), *Clubiona* and *Elaver* formed a clade which represent the loss of the cylindrical gland spigots. Anyphaenidae and Clubionidae are closely related families (Platnick, 1974), so the placement of *Elaver* recovered in our study is perhaps not surprising.

[Correction added on 31 October 2023, after first online publication: The last sentence has been deleted in this paragraph.]

Anyphaenidae

This family includes *c*. 635 species classified in 58 genera (World Spider Catalog, 2023). Anyphaenids have an advanced tracheal spiracle and their large and complex tracheal system extends into the prosoma and legs (Platnick, 1974; Ramírez, 2014). The morphological cladogram of Ramírez (2014) included four genera, *Amaurobioides*, *Gayenna*, *Xiruana* and *Anyphaena*, which formed a clade. Our UCE and Combined phylogenies recovered a monophyletic Anyphaenidae (Figs 4 and 19). In the Combined phylogeny, *Corinnomma* cf. *severum* (Corinnidae) nested with Anyphaenidae, albeit with poor support (59% UB). However, with the Dionychan dataset, *Corinnomma* cf. *severum* nested within Corinnidae, rendering Anyphaenidae monophyletic (Fig. S6).

Gnaphosidae

This is a large family of ground spiders with >2445 species classified in 147 genera and distributed globally. Gnaphosids are easily identified by the enlarged, cylindrical, widely separated anterior lateral spinnerets (Murphy, 2007). Many gnaphosids have enlarged piriform gland spigots of anterior lateral spinnerets compared to the major ampullate gland spigots (Platnick, 1990). In the gnaphosid subfamily Molycriinae, the anterior lateral spinnerets are extremely elongated and placed further anteriorly near middle of the abdomen, away from the remaining spinnerets (Platnick & Baehr, 2006). This configuration of spinnerets is hypothesized to be an adaptation for efficient use of piriform silk in prey capture (Wolff et al., 2017). Another well-studied gnaphosid, *Micaria sociabilis* Kulczyński, 1897 mimics the arboreal *Liometopum microcephalum* (Panzer, 1798) ants using kairomones (a chemical substance produced by *Liometopum* and detected by *Micaria*) (Pekár, 2020). The same species also shows reverse cannibalism where male spiders cannibalized older female spiders and showed preference for young females for mating (Sentenská & Pekár 2013). Another gnaphosid, *Drassodes cupreus* (Blackwall, 1834), is known to track polarized light as a compass using its posterior median eyes to navigate to its retreat after foraging trips (Dacke et al., 1999, 2001).

In our UCE phylogeny, one terminal of *Lampona* (Lamponidae) nested within a clade of four terminals that included three Gnaphosidae taxa (Fig. 4). In the Combined and Dionychan phylogenies Gnaphosidae are polyphyletic, although with poor support (<95% UB) (Figs 19, 20 and S6). Recent phylogenetic studies using molecular data focused on systematics of Gnaphosidae also obtained this family as polyphyletic (Azevedo et al., 2018; Rodrigues & Rheims, 2020). Our study recovered relationships similar to the study of Wheeler et al. (2017) because 14 of 16 taxa representing this family contained six markers, two taxa included UCEs and one with both data.

Lamponidae

This family includes close to 200 species classified in 23 genera (World Spider Catalog, 2023) characterized by unisegmented anterior lateral spinnerets (Platnick, 2000). The first cladistic based classification of Lamponidae was proposed by Platnick (2000) using several generic representations, and recovered *Lampona*, *Centrothele* and *Asadipus* nested within the family. Ramírez (2014) revised some characters and *Centrothele* and *Lampona* to be monophyletic. The molecular phylogeny of Wheeler et al. (2017) recovered a polyphyletic Lamponidae similar to the most recent study of Azevedo et al. (2022). However, in our UCE phylogeny rendered a polyphyletic Lamponidae with a clade including *Lampona* (type genus) as a sister group to *Anzacia* (Gnaphosidae) and *Centrothele nardi* (Lamponidae) as a sister group to other Gnaphosidae (Fig. 4). Likewsie, in our Combined phylogeny, the *Centrothele* (two terminals) clade was a sister group to Trachycosmidae II, whereas *Lampona* (type genus) were a sister group to *Anzacia* (Fig. 19, but see Fig. S6). Azevedo et al. (2022) recently pointed out that *Anzacia* (SRR6997629) may be a lamponid, but requires examination of the vouchers. The systematics of Lamponidae needs revision and it is possible that a rapid radiation of Lamponidae and Gnaphosidae is rendering noise in the phylogenetic signal (Azevedo et al., 2022).

Trochanteriidae

This is a small family with about 50 species classified in six genera (World Spider Catalog, 2023). These spiders have a flattened body and laterigrade legs with greatly elongated posterior trochanters. In our Combined and Dionychan phylogenies, this family was polyphyletic with one clade including *Hemicloea* (three terminals) sister group to *Intruda* (Gnaphosidae), and

the other clade including *Doliomalus* and *Vectius* (one terminal each) (Fig. 19).

Trachelidae

This family includes cl*c*. 265 species classified in 20 genera (World Spider Catalog, 2023). Ramírez (2014) provided a diagnosis for this family as follows: claw tufts made of heavily folded setae, a claw tuft clasper and reduce leg spination on posterior legs and, dorsally on all femora and lacking median apophysis similar to Phrurolithidae, but distinguished by the absence of ventral distal hook on the male palpal femur. In our UCE phylogeny, Trachelidae was monophyletic (Fig. 4), yet in the Combined phylogeny it was polyphyletic with two terminals of *Orthobula* sister to *Tinytrema* (Trachycosmidae) (Fig. 19). Interestingly, our Dionychan phylogeny recovered a monophyletic Trachelidae (Fig. S6). In the UCE phylogeny of Azevedo et al. (2022), Trachelidae was a sister group to Phrurolithidae, yet addition of legacy markers data and phenotypic data refuted this placement.

Gallieniellidae

This is a relatively small family with 41 species classified in five genera that are distributed in the Southern hemisphere, Argentina (*Galianoella*), South Africa (*Austrachelas*, *Drassodella*), Madagascar (*Gallieniella*, *Legendrena*) and the Comoros (*Gallieniella*). Platnick (1984) diagnosed the family based on sclerotized anterior spinnerets, obliquely depressed endites, and flattened oval posterior median eyes.

Gallieniellids were represented by five terminals in our UCE phylogeny which recovered a polyphyletic Trachelidae (Fig. 4). In the Combined and Dionychan phylogenies, the increment of three taxa recovered a clade including *Gallieniella* and *Legendrena* (Figs 19 and S6). Cladograms in Platnick (2002), Ramírez (2014) and Azevedo et al. (2022) included some gallieniellid genera. In the latter study, this family was a sister group to Phrurolithidae. In our combined phylogeny, *Galianoella* was recovered as a sister group to *Drassinella* (Liocranidae), *Drassodella* as a sister branch of *Hypodrassodes* (Gnaphosidae) and *Austrachelas* of *Hesperocranum* (Liocranidae). The remaining gallieniellids formed a sister group to Trochanteriidae.

Liocranidae

This family includes *c*. 340 species classified in 35 genera (World Spider Catalog, 2023). Lehtinen (1967) stated that the presence of a secondary conductor in the male palpus is the key characteristic of Liocranidae. The cladistic analysis of Ramírez (2014) recovered a polyphyletic Liocranidae. In all of our phylogenetic analyses, this family was polyphyletic, also similar to Wheeler et al. (2017). The type genus representative *Liocranum* was a sister group to Cithaeronidae (Figs 4, 19 and S6). Although the preferred hypothesis of Azevedo et al. (2022) recovered a monophyletic Liocranidae, although they state that another analysis suggests that nonmonophyly of this family is equally likely. We recovered a monophyletic *Teutamus* group (sensu Ramírez, 2014) which was represented by *Teutamus* and *Sesieutes* in our Combined and Dionycha datasets (Figs 19 and S6).

Phrurolithidae

This family includes *c*. 366 species classified in 24 genera (World Spider Catalog, 2023). Ramírez (2014) diagnosed this family as follows: claw tufts made of heavily folded setae, a claw tuft clasper and reduce leg spination on posterior legs and, dorsally on all femora and lacking median apophysis similar to Trachelidae, but distinguished by modifications on the ventral median apophysis and usually a ventral apical hook, a globose receptacle on the epigynum, in addition to the primary and secondary spermathecae. Our UCE phylogeny recovered a monophyletic Phrurolithidae as a sister group to *Xenoplectus* (Liocranidae) (Fig. 4), yet addition of *Otacilia* in the Combined phylogeny recovered a polyphyletic placement (Fig. 19). Interestingly, the Dionychan dataset recovered a monophyletic Phrurolithidae (Fig. S6). The taxon sample of Azevedo et al. (2022) was similar to our UCE dataset and they recovered a monophyletic Phrurolithidae as a sister group to Trachelidae; however, the placement was not robust to addition of legacy marker or phenotypic dataset.

Xenoctenidae

This is a relatively small family with 33 species classified in four genera distributed mostly in South America and Australia (World Spider Catalog, 2023). The cladistic analysis of Silva-Dávila (2003) recovered a monophyletic group consisting of *Odo* and *Xenoctenus*. Ramírez (2014) obtained an addition of *Paravulsor* in this clade which he called the *Xenoctenus* group. This group was established formally as a family by Ramírez & Silva-Dávila (2017) in the Wheeler et al. (2017) study. Xenoctenids are diagnosed as being similar to viridasiids and some miturgids owing to two recurved eye rows with grate-shaped tapetum, two claws and well-developed scopulae and claw tufts in some spiders. It is distinguishable by the distal divide in the tegulum in the region where the embolus emerges (Wheeler et al., 2017). In all of our analyses, Xenoctenidae was monophyletic (Figs 4, 20 and S6), yet the

placement of Miturgidae as its sister group, as in Azevedo et al. (2022), was never recovered.

Philodromidae

Commonly called as running crab spiders, this family includes more than 500 species classified in 29 genera (World Spider Catalog, 2023). These spiders lack tapeta on the anterior lateral and the posterior eyes (Azevedo et al., 2022). The first cladistic analysis of Philodromidae by Muster (2009) recovered the family monophyletic. Ramírez (2014) inferred that the claw tuft of tenent setae in the male and female pedipalps as an unambiguous synapomorphy of Philodromidae. In all of our datasets, Philodromidae was a sister group to Salticidae (Figs 4, 20 and S6) similar to Wheeler et al. (2017) and Azevedo et al. (2022). This is one of the most robustly supported grouping by molecular data among the Dionychan spider families.

Salticidae

Salticids (jumping spiders) are the largest family of spiders comprising close to 6600 species (*c*. 12% of all described spiders) classified in 674 genera distributed globally (World Spider Catalog, 2023). They are easily recognizable by their large anterior median eyes, which likely contribute to their documented ability to learn and solve problems (Jackson, 2002). A great diversity of biological features has been documented for jumping spiders, including courtship, foraging behaviours, extreme sexual dimorphism and aggressive mimicry (reviewed in Richman & Jackson, 1992). Salticidae includes some highly specialized species, such as ant mimics (Ceccarelli & Crozier, 2007), specialists of other spiders, like *Portia* (Jackson & Wilcox, 1998), and even specialization on mosquitoes that have recently had a blood meal (Jackson & Cross, 2015). An examplar of their charismatic courtship behaviours, peacock spider, genus *Maratus*, males have brightly coloured abdomens that enlarge during courtship, and they combine vibrational cues with the visual cues from the abdomen during courtship (Girard et al., 2011).

In our UCE and Combined phylogenies with 31 and 54 taxa, respectively (Figs 4 and 20), this family was monophyletic, which has been supported by all previous molecular analyses (e.g. Maddison & Hedin, 2003; Maddison et al., 2014, 2017; Maddison, 2015).

Maddison et al. (2017) provided the most updated phylogenetic hypothesis of salticid relationships using anchored hybrid enrichment data. They recovered the Asemoneinae + Lyssomaninae clade as the sister group to remaining salticids, similar to our study (Fig. 20). The internal relationships within Salticinae varied in comparison with Maddison et al. (2017), but it could be attributed to the difference with the taxon sampling in both studies. The baviines were monophyletic in our study similar to Maddison et al. (2020).

Corinnidae

This family includes about 850 species classified in 76 genera (World Spider Catalog, 2023). In all of our datasets, this family was polyphyletic. In the Dionycha and Combined phylogenies, the "*Pronophaea* group" (sensu Wheeler et al. 2017) was recovered as a sister group of a clade including Viridasiidae, Selenopidae, Cheiracanthiidae and Miturgidae (in part) (Figures 20, S6). The remaining Corinnidae taxa (26 terminals) were monophyletic (Fig. S6).

[Correction added on 31 October 2023, after first online publication: This sentence has been revised.]

Azevedo et al. (2022) recovered *Pronophaea* group within Corinnidae, yet our taxon sample differed from their study and therefore this result could not be tested. Instead, our UCE phylogeny obtained a strongly supported *Pronophaea* group (two terminals) as a sister group to the Viridasiidae + Selenopidae + Cheiracanthiidae clade (Fig. 4).

Selenopidae

These cursorial spiders include nine genera and 281 species distributed globally, however with a large diversity in the southern hemisphere (World Spider Catalog, 2023). Selenopids are dorsoventrally flat and extremely agile predators (Crews et al., 2008), and have their posterior median eyes placed within the row of anterior eyes (Ramírez, 2014). In Wheeler et al. (2017), Selenopidae was a sister group to Viridasiidae. In our UCE and Combined phylogenies, Selenopidae was polyphyletic with the Australian endemic genus placed as a sister group to Miturgidae and the other group (which included the type genus *Selenops*) as a sister group to Viridasiidae (Figs 4 and 20). The four gene phylogeny of Crews & Gillespie (2010) included *Karaops* (listed as "New Genus Australia") which nested within Selenopidae, albeit with poor support.

Miturgidae

This family includes *c*. 136 species classified into 28 genera (World Spider Catalog, 2023). Miturgidae was monophyletic in our UCE phylogeny placed as a sister group to *Karaops* (Selenopidae); however, the addition of *Parapostenus* in the Combined and Dionycha datasets rendered the family polyphyletic (Fig. S6). *Parapostenus* was placed as a sister branch to Viridasiidae (in part). Wheeler et al. (2017) mention a possibility that *Parapostenus* may be either a miturgid or a viridiasiid. Although Ramírez (2014) and Azevedo et al. (2022) recovered Miturgidae as a sister group to

Xenoctenidae, none of our analyses recovered this placement.

Cheiracanthiidae

This family includes 362 species classified in 14 genera with a cosmopolitan distribution (World Spider Catalog, 2023). They are diagnosed by the conical and contiguous anterior lateral and posterior median spinnerets, an elongated article on posterior lateral spinnerets distally, eyes occupying the caput and curved setae on the opisthosoma (Ramírez, 2014). The cladogram of Ramírez (2014) inferred that Eutichuridae (former name of Cheiracanthiidae, as discussed in the same paper) was a sister group to a clade including Miturgidae, Sparassidae, Philodromidae, Salticidae and Thomisidae. With the six-marker dataset, Eutichuridae was a sister group to Viridasiidae and Selenopidae, similar to Azevedo et al. (2022), and our UCE and Combined phylogenies, except that with the Combined data, the sister group to Cheiracanthiidae included *Parapostenus* sp. (Miturgidae) (Figs 4 and 20).

Viridasiidae

Viridasiidae is a small family including seven species classified into three genera (*Mahafalytenus*, *Viridasius* and *Vulsor*) primarily distributed in Madagascar and nearby islands, with one species in Brazil. The natural history of these spiders is poorly known; however, Bauer et al. (2018) and Bauer (2021) reported that in captivity, these spiders constructed silken retreats and a pendulous egg sac covered with debris. In our Combined analysis, *Mahafalytenus* (formerly in Ctenidae) nested within Viridasiidae (Fig. 20), similar to the result of Wheeler et al. (2017). The recent Azevedo et al. (2022) also recovered this placement and formally transferred *Mahafalytenus* to Viridasiidae.

Conclusions

1. The classification of spiders and the hypotheses about their phylogenetic relationships have significantly changed in the last decades. Several morphological features that have been traditionally used to circumscribe higher taxa have evolved or been lost multiple times independently. For example, higher taxa are no longer grouped strictly by presence or absence of cribellum, and several families such as Oecobiidae and Udubidae have both cribellate and ecribellate members. It is clear that this character, which once weighed over spider classification, has been lost multiple times during the evolution of this group. Although haplogyne spiders are not a clade, a general trend from the haplogyne to the entelegyne condition is suggested by the recent literature, even in the face of multiple convergences both ways. Although the question of whether the orb weavers are a monophyletic group or not seems to have converged onto a stable answer (Orbiculariae is not a clade), the hypothesis of a single origin of the orbweb remains debated. The scattering of orb weaving groups in the spider tree of life offers a great challenge for hypothesizing a single origin of the orb web using phylogenetic comparative methods. Thus, in spiders the story tends to be one of groups being defined by a single character, that is later undone and the defining character turns out to be homoplasious. Large-scale analyses of genomic data have contributed to a better understanding of both spider phylogeny and the evolution of their morphological features and spinning products. Phylogenetic hypotheses at the interfamilial level have changed in most families, whereas the intergeneric relationships remain poorly and insufficiently understood.
2. Using a combination of newly generated and publicly available genome-scale data and Sanger-sequencing-based six-marker datasets, we produced the most comprehensive phylogenomic inference of the spider tree of life in terms of taxa (128 spider families ~97% sampling, 1362 terminals). The analyses recovered some highly supported placements that reject the monophyly of certain families, for example, the placement of Gnaphosidae. However, previous studies indicated similar placements based on morphology or molecular data. The subsetting of the Combined dataset to Marronoid and Dionychan datasets rendered some polyphyletic families such as Trachelidae as monophyletic, which reveals an interesting phenomenon that needs further exploration. We are aware of and emphasize the limitations of our dataset and therefore resorted to only review these phylogenetic placements; we do not make any formal taxonomic changes.
3. Our results covered several taxonomic hierarchical levels, cemented various hypotheses on important family-level relationships and allowed us to identify the stable phylogenetic relationships across the spider tree of life. We identified the unstable areas of the cladogram and discussed the conflicting hypotheses resulting from various classes of data such as morphology, Sanger-sequencing-based markers, and genomic-scale data such as transcriptomes and UCEs. We recognize that future studies are warranted to focus on certain groups of the spider tree of life (e.g. RTA clade, marronoid clade, Hahniidae and Araneoidea). Our review can help to design studies targeting taxonomic groups in need of systematic revisions.
4. Some clades supported by morphological characters are corroborated by molecular data (such as in the

case of symphytognathoids), whereas some novel groupings have made arachnologists review their classifications over again (such as polyphyly of theridioids). Many new spider phylogenetic studies are published every year, thus recalibrating and refining the synapomorphies of those groups. These continued efforts are helping us to better understand how evolutionary processes have shaped the diversification of spiders. Spider systematics and phylogenetics have never been this close to visualizing a highly comprehensive picture of their evolutionary history at the family level.

5. Sequencing technologies continue to be increasingly more cost-effective, and museum specimens are now widely used for both morphology and molecular sequencing. The tools to study morphology have greatly advanced too, such as micro-computed-tomography (microCT) scanning. We are now able to see internal anatomical structures in a three-dimensional view (e.g. Michalik and Lipke, 2013; Wood & Parkinson, 2019), when previously morphologists were restricted to histological sectioning or dissection, typically resulting in a two-dimensional photograph or illustration. MicroCT is a great advantage to observing fossils (e.g. Penney et al., 2007), which is a morphology-based endeavour, and allows for hidden structures to be revealed. This technique also allows for creating 3D digital objects and was recently used to study the evolution of carapace and cheliceral shapes across spiders, with a focus on Araneoidea (Kallal & Wood, 2022).

Taxon sampling has grown comprehensively for molecular data-based phylogeny and fossils, informed by their morphology and ages, provide calibration points for these phylogenies. Beyond the utility of dating phylogenies at nodes, fossils also are used as taxa to be placed in a phylogeny, a method known as "tip-dating". Wood et al. (2013) used tip-dating to show that Palpimanoidea diversification was shaped by the break-up of Pangaea in the Mesozoic. Recently, using morphology observed under microCT, Magalhaes et al. (2022) discovered that the holotype of *Loxosceles aculicaput* Wunderlich, 2004 (Sicariidae) is actually a misidentified Drymusidae, which was the first fossil from the latter family and placed in a phylogeny. Fossils are also useful in reconstructing trait evolution. Morphology also provides observable ontogenetic information in the light of gene regulatory networks, which is detectable to a certain extent in molecular data by the timing and location of gene expression.

Although it is apparent that molecular data are dominating phylogenetic studies, it is likely that this skewed pattern will soon reach a tipping point. The advent of the World Spider Trait database (Pekár et al., 2021) has an enormous potential and will facilitate the study of the evolution of a variety of characters across the spider tree of life. Without morphological, behavioural and natural history data, phylogenetic trees have limited value because their explanatory power is based on their ability to interpret phenotypic and other biological observations. Both morphology and molecules are gradually converging to unravel a more precise understanding of evolutionary history. It is perhaps the most exciting time so far for advancing our knowledge about the evolution of spiders.

Acknowledgements

This study was funded by the following grants/fellowships: a Weintraub fellowship, Harlan fellowship, Smithsonian Predoctoral fellowship, Mortensen grant, Oscar and Jan Francke Student Research grant, two Lakeside grants and a National Geographic Society Early Career grant EC-54674R-18, Columbia College Dean's Dissertation Completion grant to SK; National Science Foundation DEB 1457300, 1457539 grants to GH and Gonzalo Giribet, DEB 1754289 to GH, and from an Exploratory Award (year 2016) from the Global Genome Initiative (National Museum of Natural History, Smithsonian Institution) to HMW and Michael Lloyd. Authors are grateful to Charles Griswold, Darrel Ubick and Lauren Esposito for the curation of material and their help during our visit to the California Academy of Sciences. Fieldwork was made possible as a result of the generous help of Miquel Arnedo and Robert Raven in Australia, and Milenko Aguilera and participation of Darko Cotoras in Chile. We also thank Charles Griswold, Bob Kallal, Chuy Ballesteros, Nicolas Hazzi, Thiago da Silva-Moreira, Dimitar Dimitrov, Miquel Arnedo, Alex Pyron, Jimmy Saw, Sarah Crews, Joseph Koh, Suresh Benjamin, Petr Dolejš and Prashant Sharma for discussions that helped in improving this manuscript. The authors are deeply grateful to the editor Martín Ramírez and reviewers for their time and effort on this manuscript. We acknowledge the computing resources, Pegasus and Hydra made available to us by The George Washington University and the Smithsonian Institution, respectively.

Conflict of interest

None declared.

Data availability statement

Raw sequence reads are available from the NCBI Sequence Read Archive, under BioProject accession PRJNA991600. Any additional information required

to reanalyze the data reported in this paper is available from the corresponding author upon request.

References

Agnarsson, I., 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zool. J. Linn. Soc. 141, 447–626.

Agnarsson, I., Aviles, L., Coddington, J.A. and Maddison, W.P., 2006. Sociality in theridiid spiders: Repeated origins of an evolutionary dead end. Evolution 60, 2342–2351.

Agnarsson, I., Coddington, J.A. and Kuntner, M., 2013. Systematics: progress in the study of spider diversity and evolution. In: Penney, D. (Ed.), Spider Research in the 21st Century: Trends and Perspectives. Siri Sci. Press, Manchester, pp. 58–111.

Alberti, G. and Weinmann, C., 1985. Fine structure of spermatozoa of some labidognath spiders (Filistatidae, Segestriidae, Dysderidae, Oonopidae, Scytodidae, Pholcidae; Araneae; Arachnida) with remarks on spermiogenesis. J. Morphol. 185, 1–35.

Albo, M.J., Bidegaray-Batista, L., Bechsgaard, J., da Silva, E.L.C., Bilde, T. and Pérez-Miles, F., 2017. Molecular phylogenetic analyses show that Trechaleidae and Lycosidae are sister groups. Arachnology 17, 169–176.

Álvarez-Padilla, F. and Hormiga, G., 2011. Morphological and phylogenetic atlas of the orb-weaving spider family Tetragnathidae (Araneae: Araneoidea). Zool. J. Linn. Soc. 162, 713–879.

Álvarez-Padilla, F., Kallal, R.J. and Hormiga, G., 2020. Taxonomy and Phylogenetics of Nanometinae and other Australasian orb-weaving spiders (Araneae: Tetragnathidae). Bull. Am. Mus. Nat. Hist. 2020, 1–108.

Andrade, M.C.B., 1996. Sexual selection for male sacrifice in the Australian redback 986 spider. Science 271, 70–72.

Arakawa, K., Kono, N., Malay, A.D., Tateishi, A., Ifuku, N., Masunaga, H., Sato, R., Tsuchiya, K., Ohtoshi, R., Pedrazzoli, D., Shinohara, A., Ito, Y., Nakamura, H., Tanikawa, A., Suzuki, Y., Ichikawa, T., Fujita, S., Fujiwara, M., Tomita, M., Blamires, S.J., Chuah, J.-A., Craig, H., Foong, C.P., Greco, G., Guan, J., Holland, C., Kaplan, D.L., Sudesh, K., Mandal, B.B., Norma-Rashid, Y., Oktaviani, N. A., Preda, R.C., Pugno, N.M., Rajkhowa, R., Wang, X., Yazawa, K., Zheng, Z. and Numata, K., 2022. 1000 spider silkomes: Linking sequences to silk physical properties. Sci. Adv. 8, eabo6043. https://doi.org/10.1126/sciadv.abo6043

Arnedo, M.A. and Hormiga, G., 2021. Repeated colonization, adaptive radiation and convergent evolution in the sheet-weaving spiders (Linyphiidae) of the South Pacific archipelago of Juan Fernández. Cladistics 37, 317–342.

Arnedo, M.A., Coddington, J., Agnarsson, I. and Gillespie, R.G., 2004. From a comb to a tree: Phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. Mol. Phylogenet. Evol. 31, 225–245.

Arnedo, M.A., Hormiga, G. and Scharff, N., 2009. Higher-level phylogenetics of linyphiid spiders (Araneae, Linyphiidae) based on morphological and molecular evidence. Cladistics 25, 231–262.

Azevedo, G.H.F., Griswold, C.E. and Santos, A.J., 2018. Systematics and evolution of ground spiders revisited (Araneae, Dionycha, Gnaphosidae). Cladistics 34, 579–626.

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

Babb, P.L., Lahens, N.F., Correa-Garhwal, S.M., Nicholson, D.N., Kim, E.J., Hogenesch, J.B., Kuntner, M., Higgins, L., Hayashi, C.Y., Agnarsson, I. and Voight, B.F., 2017. The *Nephila clavipes* genome highlights the diversity of spider silk genes and their complex expression. Nat. Genet. 49, 895–903.

Baehr, B.C., Raven, R. and Harms, D., 2017. "High tide or low tide": *Desis bobmarleyi* sp. n., a new spider from coral reefs in Australia's sunshine state and its relative from Sāmoa (Araneae, Desidae, *Desis*). Evol. Syst. 1, 111–120.

Ballesteros, J.A. and Hormiga, G., 2021. Molecular phylogeny of the orb-weaving spider genus *Leucauge* and the intergeneric relationships of Leucauginae (Araneae, Tetragnathidae). Invertebr. Syst. 35, 922–939.

Ballesteros, J.A., Setton, E.V., Santibánez-López, C.E., Arango, C.P., Brenneis, G., Brix, S., Corbett, K.F., Cano-Sánchez, E., Dandouch, M., Dilly, G.F. and Eleaume, M.P., 2021. Phylogenomic resolution of sea spider diversification through integration of multiple data classes. Mol. Biol. Evol. 38, 686–701.

Bauer, T., 2021. The camouflaged silken retreat of *Viridasius* sp. (Araneae: Viridasiidae). J. Arachnol. 48, 339–342.

Bauer, T., Raub, F. and Höfer, H., 2018. Notes on the behavior and the pendulous egg-sacs of *Viridasius* sp.(Araneae: Viridasiidae). J. Arachnol. 46, 155–158.

Benavides, L. and Hormiga, G., 2020. A morphological and combined phylogenetic analysis of "pirate spiders" (Araneae, Mimetidae): Evolutionary relationships, taxonomy and character evolution. Invertebr. Syst. 34, 144–191.

Benavides, L., Giribet, G. and Hormiga, G., 2017. Molecular phylogenetic analysis of pirate spiders (Araneae, Mimetidae) with the first description of maternal care behavior in the family and a new African genus. Cladistics 33, 375–405.

Benjamin, S.P., 2011. Phylogenetics and comparative morphology of crab spiders (Araneae: Dionycha, Thomisidae). Zootaxa 3080, 1–108.

Benjamin, S.P., Dimitrov, D., Gillespie, R.G. and Hormiga, G., 2008. Family ties: Molecular phylogeny of crab spiders (Araneae: Thomisidae). Cladistics 24, 708–722.

Benjamini, Y. and Speed, T.P., 2012. Summarizing and correcting the GC content bias in high-throughput sequencing. Nucleic Acids Res. 40, e72.

Berger, C.A., Brewer, M.S., Kono, N., Nakamura, H., Arakawa, K., Kennedy, S.R., Wood, H.M., Adams, S.A. and Gillespie, R.G., 2021. Shifts in morphology, gene expression, and selection underlie web loss in Hawaiian *Tetragnatha* spiders. BMC Ecol. Evol. 21, 1–17.

Bertkau, P., 1882. Über das Cribellum und Calamistrum. Ein Beitrag zur Histologie, Biologie und Systematik der Spinnen. Arch. Naturgesch. 48, 316–362.

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

Bond, J.E., Hendrixson, B.E., Hamilton, C.A. and Hedin, M., 2012. A reconsideration of the classification of the spider infraorder Mygalomorphae (Arachnida: Araneae) based on three nuclear genes and morphology. PloS One 7, e38753.

Bond, J.E., Garrison, N.L., Hamilton, C.A., Godwin, R.L., Hedin, M. and Agnarsson, I., 2014. Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. Curr. Biol. 24, 1765–1771.

Breitling, R., 2022. On the taxonomic rank of the major subdivisions of the extant segmented spiders (Arachnida: Araneae: Mesothelae: Liphistiidae s. lat.). Misc. Araneol. 2022, 1–4.

Bristowe, W.S., 1976. A contribution to the knowledge of liphistiid spiders. J. Zool. 178, 1–6.

Burger, M., 2013. Genital morphology of female goblin spiders (Arachnida: Araneae: Oonopidae) with functional implications. Acta Zool. 92, 280–290.

Burger, M., Nentwig, W. and Kropf, C., 2003. Complex genital structures indicate cryptic female choice in a haplogyne spider (Arachnida, Araneae, Oonopidae, Gamasomorphinae). J. Morphol. 255, 80–93.

Burger, M., Izquierdo, M. and Carrera, P., 2010. Female genital morphology and mating behavior of *Orchestina* (Arachnida: Araneae: Oonopidae). Fortschr. Zool. 113, 100–109.

Capella-Gutiérrez, S., Silla-Martínez, J.M. and Gabaldón, T., 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25, 1972–1973.

Castellucci, F., Scharff, N. and Luchetti, A., 2023. Molecular systematics and phylogenetics of the spider genus Mastigusa Menge, 1854 (*Araneae, Cybaeidae*). Mol. Phylogenet. Evol. 107833.

Catley, K.M., 1996. The systematics of the hahniid spiders of austral South America (Araneae, Hahniidae). Cornell University. Cornell University ProQuest Dissertations Publishing, 1996. 9639563. pp. 388.

Ceccarelli, F.S. and Crozier, R.H., 2007. Dynamics of the evolution of Batesian mimicry: Molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. J. Evol. Biol. 20, 286–295.

Cheng, D.-Q. and Piel, H.W., 2018. The origins of the Psechridae: Web-building lycosoid spiders. Mol. Phylogenet. Evol. 125, 213–219.

Christensen, K.D., Dukhovny, D., Siebert, U. and Green, R.C., 2015. Assessing the costs and cost-effectiveness of genomic sequencing. J. Pers. Med. 5, 470–486.

Clarke, T.H., Garb, J.E., Hayashi, C.Y., Haney, R.A., Lancaster, A.K., Corbett, S. and Ayoub, 1065 N.A, 2014. Multi-tissue transcriptomics of the black widow spider reveals expansions, co-options, and functional processes of the silk gland gene toolkit. BMC Genomics 15, 365.

Clerck, C., 1757. Aranei Svecici. Svenska spindlar, uti sina hufvud-slågter indelte samt under några och sextio särskildte arter beskrefne och med illuminerade figurer uplyste. Laurentius Salvius, Stockholmiae [= Stockholm], 154 pp.

Cloutier, A., Sackton, T.B., Grayson, P., Clamp, M., Baker, A.J. and Edwards, S.V., 2019. Whole-genome analyses resolve the phylogeny of flightless birds (Palaeognathae) in the presence of an empirical anomaly zone. Syst. Biol. 68, 937–955.

Coddington, J.A., 1986a. The monophyletic origin of the orb web. In: Shear, W.A. (Ed.), Spiders: Webs, Behavior and Evolution. Stanford University Press, Stanford, pp. 319–363.

Coddington, J.A., 1986b. The genera of the spider family Theridiosomatidae. Smithson. Contrib. Zool. 422, 1–96.

Coddington, J.A., 1989. Spinneret silk spigot morphology: Evidence monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. J. Arachnol. 17, 71–95.

Coddington, J.A., 1990. Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithson. Contrib. Zool. 496, 1–52.

Coddington, J.A. and Levi, H.W., 1991. Systematics and evolution of spiders (Araneae). Annu. Rev. Ecol. Syst. 22, 565–592.

Coddington, J. and Valerio, C., 1980. Observations on the web and behavior of *Wendilgarda* spiders (Araneae: Theridiosomatidae). Psyche 87, 93–105.

Coddington, J.A., Agnarsson, I., Hamilton, C.A. and Bond, J.E., 2019. Spiders did not repeatedly gain, but repeatedly lost, foraging webs. PeerJ 7, e6703.

Costa-Schmidt, L.E., Carico, J.E. and de Araújo, A.M., 2008. Nuptial gifts and sexual behavior in two species of spider (Araneae, Trechaleidae, *Paratrechalea*). Naturwissenschaften 95, 731–739.

Cotoras, D.D., Suenaga, M. and Mikheyev, A.S., 2021. Intraspecific niche partition without speciation: Individual level web polymorphism within a single island spider population. Proc. R. Soc. Biol. Sci. 288, 20203138.

Crews, S.C. and Gillespie, R.G., 2010. Molecular systematics of *Selenops* spiders (Araneae: Selenopidae) from north and Central America: Implications for Caribbean biogeography. Biol. J. Linn. Soc. 101, 288–322.

Crews, S.C., Wienskoski, E. and Gillespie, R.G., 2008. Life history of the spider *Selenops occultus* Mello-Leitão (Araneae, Selenopidae) from Brazil with notes on the natural history of the genus. J. Nat. Hist. 42, 2747–2761.

Crews, S.C., Garcia, E.L., Spagna, J.C., Van Dam, M.H. and Esposito, L.A., 2020. The life aquatic with spiders (Araneae): Repeated evolution of aquatic habitat association in Dictynidae and allied taxa. Zool. J. Linn. Soc. 189, 862–920.

Crome, W., 1957. Bau und Funktion des Spinnapparates und Analhügels, Ernährungsbiologie und allgemeine Bemerkungen zur Lebensweise von *Uroctea durandi* (Latreille) (Araneae, Urocteidae). Zool. Jahrb. Abt. Syst. 85, 501–672.

Cutler, B., 1972. Notes on the biology of *Mimetus puritanus* Chamberlin (Araneae: Mimetidae). Am. Midl. Nat. 87, 554–555.

Dacke, M., Nilsson, D.-E., Warrant, E.J., Blest, A.D., Land, M.F. and O'Carroll, D.C., 1999. Built-in polarizers form part of a compass organ in spiders. Nature 401, 470–473.

Dacke, M., Doan, T.A. and O'Carroll, D.C., 2001. Polarized light detection in spiders. J. Exp. Biol. 204, 2481–2490.

Decae, A. and Cardoso, P., 2006. *Iberesia*, a new genus of trapdoor spiders (Araneae, Nemesiidae) from Portugal and Spain. Rev. Ibérica Aracnol. 12, 3–11.

Dimitrov, D. and Hormiga, G., 2020. Spider diversification through space and time. Annu. Rev. Entomol. 66, 225–241.

Dimitrov, D., Lopardo, L., Giribet, G., Arnedo, M.A., Alvarez-Padilla, F. and Hormiga, G., 2012. Tangled in a sparse spider web: Single origin of orb weavers and their spinning work unravelled by denser taxonomic sampling. Proc. R. Soc. Bio. Sci. 279, 1341–1350.

Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G., Griswold, C.E., Scharff, N. and Hormiga, G., 2017. Rounding up the usual suspects: A standard target-gene approach for resolving the interfamilial relationships of ecribellate orb-weaving spiders with a new family-rank. Cladistics 33, 221–250.

Dolejš, P., 2013. Do really all wolf spiders carry spiderlings on their opisthosomas? The case of *Hygrolycosa rubrofasciata* (Araneae: Lycosidae). Arachnol. Mitt. 45, 30–35.

Domínguez, K. and Jiménez, M.L., 2005. Mating and self-burying behavior of *Homalonychus theologus* Chamberlin (Araneae, Homalonychidae) in Baja California Sur. J. Arachnol. 33, 167–174.

Eberhard, W.G., 1977. 'Rectangular orb' webs of *Synotaxus* (Araneae: Theridiidae). J. Nat. Hist. 11, 501–507.

Eberhard, W.G., 1986. Web-building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). J. Arachnol. 14, 339–356.

Eberhard, W., 2020. Spider Webs: Behavior, Function, and Evolution. University of Chicago Press, Chicago, IL.

Eberhard, W.G., Agnarsson, I. and Levi, H.W., 2008a. Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): Chaos from order. Syst. Biodiv. 6, 415–475.

Eberhard, W.G., Barrantes, G. and Madrigal-Brenes, R., 2008b. Vestiges of an orb-weaving ancestor? The "biogenetic law" and ontogenetic changes in the webs and building behavior of the black widow spider *Latrodectus geometricus* (Araneae Theridiidae). Ethol. Ecol. Evol. 20, 211–244.

Exline, H. and Levi, H.W., 1965. The spider genus *Synotaxus* (Araneae: Theridiidae). Trans. Am. Microsc. Soc. 84, 177–184.

Faircloth, B.C. and Glenn, T.C., 2012. Not all sequence tags are created equal: Designing and validating sequence identification tags robust to indels. PloS One 7, e42543.

Faircloth, B.C., Branstetter, M.G., White, N.D. and Brady, S.G., 2015. Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. Mol. Ecol. Resour. 15, 489–501.

Fernández, R., Hormiga, G. and Giribet, G., 2014. Phylogenomic analysis of spiders reveals nonmonophyly of orb weavers. Curr. Biol. 24, 1772–1777.

Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G. and Hormiga, G., 2018a. Phylogenomics, diversification dynamics, and comparative transcriptomics across the spider tree of life. Curr. Biol. 28, 1489–1497.

Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G. and Hormiga, G., 2018b. Phylogenomics,

diversification dynamics, and comparative transcriptomics across the spider tree of life (correction). Curr. Biol. 28, 2190–2193.
Foelix, R., 2010. Biology of Spiders, 3rd edition. Oxford University Press, New York, NY.
Forster, R., 1949. New Zealand spiders of the family Archaeidae. Rec. Canterb. Mus. 5, 193–203.
Forster, R., 1970. The spiders of New Zealand, III. Otago Mus. Bull. 3, 1–184.
Forster, R.R., 1979. The spiders of New Zealand. Part V. Cycloctenidae, Gnaphosidae, Clubionidae. Otago Mus. Bull. 5, 1–95.
Forster, R.R. and Forster, L., 1999. Spiders of New Zealand and their Worldwide Kin. Otago University Press, Dunedin, vii+270 pp.
Forster, R.R. and Platnick, N.I., 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). Bull. Am. Mus. Nat. Hist. 178, 1–106.
Forster, R.R., Platnick, N.I. and Gray, M.R., 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). Bull. Am. Mus. Nat. Hist. 185, 1–116.
Framenau, V.W., Scharff, N. and Harvey, M.S., 2010. Systematics of the Australian orb-weaving spider genus *Demadiana* with comments on the generic classification of the Arkyinae (Araneae: Araneidae). Invertebr. Syst. 24, 139–171.
Frick, H. and Scharff, N., 2018. Description of one new genus and four new species of mynoglenine spiders from Africa (Araneae: Linyphiidae: Mynogleninae). Eur. J. Taxon. 415, 1–27.
Gámez Vargas, A.F., 2019. Divergencia por los Andes: vicarianza en las poblaciones de Ancylometes bogotensis (Araneae: Ctenidae). Doctoral dissertation, Universidad del Rosario. https://doi.org/10.48713/10336_20734.
Garrison, N.L., Rodriguez, J., Agnarsson, I., Coddington, J.A., Griswold, C.E., Hamilton, C.A., Hedin, M., Kocot, K.M., Ledford, J.M. and Bond, J.E., 2016. Spider phylogenomics: Untangling the spider tree of life. PeerJ 4, e1719.
Gertsch, W.J., 1958. The spider family Hypochilidae. Am. Mus. Novitates 1912, 28.
Girard, M.B., Kasumovic, M.M. and Elias, D.O., 2011. Multimodal courtship in the peacock spider, *Maratus volans* (O.P.-Cambridge, 1874). PloS One 6, e25390.
Goloboff, P. and Catalano, S., 2016. TNT, version 1.5, with a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238.
Gorneau, J.A., Rheims, C.A., Moreau, C.S. and Rayor, L.S., 2022. Huntsman spider phylogeny informs evolution of life history, egg sacs, and morphology. Mol. Phylogenet. Evol. 27, 107530.
Griswold, C.E., 1987. A review of the southern African spiders of the family Cyatholipidae Simon, 1894 (Araneae: Araneomorphae). Ann. Natal Mus. 28, 499–542.
Griswold, C.E., 1990. A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobiidae). Bull. Am. Mus. Nat. Hist. 196, 1–206.
Griswold, C.E., 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithson. Contrib. Zool. 539, 1–39.
Griswold, C.E., 2001. A monograph of the living world genera and Afrotropical species of cyatholipid spiders (Araneae, Orbiculariae, Araneoidea, Cyatholipidae). Mem. Calif. Acad. Sci. 26, 1–251.
Griswold, C.E., Coddington, J.A., Hormiga, G. and Scharff, N., 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zool. J. Linn. Soc. 123, 1–99.
Griswold, C.E., Coddington, J.A., Platnick, N.I. and Forster, R.R., 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). J. Arachnol. 27, 53–63.
Griswold, C.E., Ramírez, M.J., Coddington, J.A. and Platnick, N.I., 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. Proc. Calif. Acad. Sci. 56(Suppl. II), 1–324.
Griswold, C.E., Audisio, T. and Ledford, J.M., 2012a. An extraordinary new family of spiders from caves in the Pacific northwest (Araneae, Trogloraptoridae, new family). ZooKeys 215, 77–102.
Griswold, C.E., Wood, H.M. and Carmichael, A.D., 2012b. The lace web spiders (Araneae, Phyxelididae) of Madagascar: Phylogeny, biogeography and taxonomy. Zool. J. Linn. Soc. 164, 728–810.
Hamilton, C.A., Lemmon, A.R., Lemmon, E.M. and Bond, J.E., 2016. Expanding anchored hybrid enrichment to resolve both deep and shallow relationships within the spider tree of life. BMC Evol. Biol. 16, 1–20.
Han, S.I., Astley, H.C., Maksuta, D.D. and Blackledge, T.A., 2019. External power amplification drives prey capture in a spider web. Proc. Natl. Acad. Sci. U. S. A. 116, 12060–12065.
Harvey, M.S., 1995. The systematics of the spider family Nicodamidae (Araneae: Amaurpbioidea). Invertebr. Syst. 9, 279–386.
Harvey, M.S., 2013. Whip Spiders of the World, Version 1.0. Western Australian Museum, Perth. http://www.museum.wa.gov.au/catalogues/whip-spiders.
van Hasselt, A.W.M., 1884. Waarnemingen omtrent anomaliën van de geslachtsdrift bij spinnen-mares. Tijdschr. Entomol. 27, 197–206.
Haupt, J., 2003. The Mesothelae – A monograph of an exceptional group of spiders (Araneae:Mesothelae). Fortschr. Zool. 154, 1–102.
Hausdorf, B., 1999. Molecular phylogeny of araneomorph spiders. J. Evol. Biol. 12, 980–985.
Hazzi, N.A. and Hormiga, G., 2023. Molecular phylogeny of the tropical wandering spiders (Araneae, Ctenidae) and the evolution of eye conformation in the RTA clade. Cladistics 39, 18–42.
Hebets, E.A., Stratton, G.E. and Miller, G.L., 1996. Habitat and courtship behavior of the wolf spider *Schizocosa retrorsa* (Banks) (Araneae, Lycosidae). J. Arachnol. 24, 141–147.
Hedin, M. and Bond, J.E., 2006. Molecular phylogenetics of the spider infraorder Mygalomorphae using nuclear rRNA genes (18S and 28S): Conflict and agreement with the current system of classification. Mol. Phylogenet. Evol. 41, 454–471.
Hedin, M., Derkarabetian, S., Ramírez, M.J., Vink, C. and Bond, J.E., 2018. Phylogenomic reclassification of the world's most venomous spiders (Mygalomorphae, Atracinae), with implications for venom evolution. Sci. Rep. 8, 1636.
Hedin, M., Derkarabetian, S., Alfaro, A., Ramírez, M.J. and Bond, J.E., 2019. Phylogenomic analysis and revised classification of atypoid mygalomorph spiders (Araneae, Mygalomorphae), with notes on arachnid ultraconserved element loci. PeerJ 7, e6864.
Hoang, D.T., Vinh, L.S., Flouri, T., Stamatakis, A., von Haeseler, A. and Minh, B.Q., 2018. MPBoot: Fast phylogenetic maximum parsimony tree inference and bootstrap approximation. BMC Evol. Biol. 18, 11.
Homann, H., 1934. Beiträge zur Physiologie der Spinnenaugen. Z. Vgl. Physiol. 20, 420–429.
Hormiga, G., 1993. Implications of the phylogeny of Pimoidae for the systematics of linyphiid spiders (Araneae, Araneoidea, Linyphiidae). Mem. Queensl. Mus. 33, 533–542.
Hormiga, G., 1994a. A revision and cladistic analysis of the spider family Pimoidae (Araneae: Araneoidea). Smithson. Contrib. Zool. 549, 1–105.
Hormiga, G., 1994b. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). Zool. J. Linn. Soc. 111, 1–71.
Hormiga, G., 2000. Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). Smithson. Contrib. Zool. 609, 1–160.
Hormiga, G., 2003. *Weintrauboa*, a new genus of pimoid spiders from Japan and adjacent islands, with comments on the monophyly and diagnosis of the family Pimoidae and the genus *Pimoa* (Araneoidea, Araneae). Zool. J. Linn. Soc. 139, 261–281.
Hormiga, G., 2017. The discovery of the orb-weaving spider genus *Pinkfloydia* (Araneae, Tetragnathidae) in eastern Australia with description of a new species from New South Wales and comments on the phylogeny of Nanometinae. Zootaxa 4311, 480–490.

Hormiga, G. and Griswold, C.E., 2014. Systematics, phylogeny, and evolution of orb-weaving spiders. Annu. Rev. Entomol. 59, 487–512.
Hormiga, G. and Eberhard, W.G., 2023. Sheet webs of linyphioid spiders (*araneae: linyphiidae, pimoidae*): the light of diversity hidden under a linguistic basket. Bull. Mus. Comp. Zool. 163, 279–415.
Hormiga, G. and Scharff, N., 2020. The malkarid spiders of New Zealand (Araneae: Malkaridae). Invertebr. Syst. 34, 345–405.
Hormiga, G. and Tu, L., 2008. On *Putaoa*, a new genus of the spider family Pimoidae (Araneae) from China, with a cladistic test of its monophyly and phylogenetic placement. Zootaxa 1792, 1–21.
Hormiga, G., Buckle, D.J. and Scharff, N., 2005. *Nanoa*, an enigmatic new genus of pimoid spiders from western North America (Pimoidae, Araneae). Zool. J. Linn. Soc. 145, 249–262.
Hormiga, G., Kulkarni, S., Da Silva Moreira, T. and Dimitrov, D., 2021. Molecular phylogeny of pimoid spiders and the limits of Linyphiidae, with a reassessment of male palpal homologies (Araneae, Pimoidae). Zootaxa 5026, 71–101.
Huang, D., Hormiga, G., Xia, F., Cai, C., Yin, Z., Su, Y. and Giribet, G., 2018. Origin of spiders and their spinning organs illuminated by mid-Cretaceous amber fossils. Nat. Ecol. Evol. 2, 623–627.
Huber, B.A. and Fleckenstein, N., 2008. Comb-hairs on the fourth tarsi in pholcid spiders (Araneae, Pholcidae). J. Arachnol. 19, 232–240.
i5K Consortium, 2013. The i5K initiative: Advancing arthropod genomics for knowledge, human health, agriculture, and the environment. J. Hered. 104, 595–600.
Ileperuma-Arachchi, I.S. and Benjamin, S.P., 2019. Twigs that are not twigs: Phylogenetic placement of crab spiders of the genus *Tmarus* of Sri Lanka with comments on the higher-level phylogeny of Thomisidae. Invertebr. Syst. 33, 575–595.
Jackson, R.R., 2002. Trial-and-error derivation of aggressive-mimicry signals by *Brettus* and *Cyrba*, spartaeine jumping spiders (Araneae: Salticidae) from Israel, Kenya, and Sri Lanka, New Zealand. J. Zool. 29, 95–117.
Jackson, R.R. and Cross, F.R., 2015. Mosquito-terminator spiders and the meaning of predatory specialization. J. Arachnol. 43, 123–142.
Jackson, R.R. and Whitehouse, M.E.A., 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): Aggressive mimicry, araneophagy and prey specialization. J. Zool. Ser. A 210, 279–303.
Jackson, R.R. and Wilcox, R.S., 1998. Spider-eating spiders: Despite the small size of their brain, jumping spiders in the genus *Portia* outwit other spiders with hunting techniques that include trial and error. Am. Sci. 86, 350–357.
Jäger, P., 1998. First results of a taxonomic revision of the SE Asian Sparassidae (Araneae). In: Selden, P.A. (Ed.), Proceedings of the 17th European colloquium of arachnology, Edinburgh 1997. British Arachnological Society, Burnham Beeches.
Jäger, P., 2001. Diversität der Riesenkrabbenspinnen im Himalaya: Über eine Radiation zweier Gattungen in den Schneetropen. (Araneae: Sparassidae: Heteropodinae) Cour. Forsch. Senck. 232, 1–136.
Jocqué, R. and Henrard, A., 2015. The new spider genus *Palindroma*, featuring a novel synapomorphy for the Zodariidae (Araneae). Eur. J. Taxon. 152, 1–33.
Johannesen, J., Lubin, Y., Smith, D.R., Bilde, T. and Schneider, J.M., 2007. The age and evolution of sociality in *Stegodyphus* spiders: A molecular phylogenetic perspective. Proc. R. Soc. B: Biol. Sci. 274, 231–237.
Juberthie, C., 1985. Cycle vital de *Telema tenella* dans la Grotte-Laboratoire de Moulis et strategies de reproduction chez les Araignees cavernicoles. Mém. Biospéol. 12, 77–89.
Kallal, R.J. and Wood, H.M., 2022. High-density three-dimensional morphometric analyses reveal predation-based disparity and evolutionary modularity in spider 'jaws'. Evol. Biol. 49, 389–402.
Kallal, R.J., Fernández, R., Giribet, G. and Hormiga, G., 2018. A phylotranscriptomic backbone of the orb-weaving spider family Araneidae (Arachnida, Araneae) supported by multiple methodological approaches. Mol. Phylogenet. Evol. 126, 129–140.
Kallal, R.J., Dimitrov, D., Arnedo, M.A., Giribet, G. and Hormiga, G., 2020. Monophyly, taxon sampling, and the nature of ranks in the classification of orb-weaving spiders (Araneae: Araneoidea). Syst. Biol. 69, 401–411.
Kallal, R.J., Kulkarni, S.S., Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G. and Hormiga, G., 2021a. Converging on the orb: Denser taxon sampling elucidates spider phylogeny and new analytical methods support repeated evolution of the orb web. Cladistics 37, 298–316.
Kallal, R.J., Elias, D.O. and Wood, H.M., 2021b. Not so fast: Strike kinematics of the araneoid trap-jaw spider *Pararchaea alba* (Malkaridae: Pararchaeinae). Integr. Org. Biol. 3, obab027.
Kalyaanamoorthy, S., Minh, B.-Q., Wong, T.K.F., von Haeseler, A. and Jermiin, L.S., 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nat. Methods 14, 587–589.
Katoh, K. and Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol. Biol. Evol. 30, 772–780.
Kent, W.J., 2002. BLAT—The BLAST-like alignment tool. Genome Res. 12, 656–664.
Klein, C.G., Pisani, D., Field, D.J., Lakin, R., Willis, M.A. and Longrich, N.R., 2021. Evolution and dispersal of snakes across the Cretaceous-Paleogene mass extinction. Nat. Commun. 12, 5335.
Kovoor, J., 1972. Etude histochimique et cytologique des glandes sericigenes de quelques Argiopidae. Ann. Sci. Nat. Zool. 14, 1–40.
Kovoor, J., 1977. La soie et les glandes séricigènes des Arachnides. Ann. Biol. 16, 97–171.
Kraus, O. and Kraus, M., 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origin of social living. Verh. Nat.wiss. Ver. Hamburg (NF) 30, 151–254.
Kuhn-Nentwig, L., Stöcklin, R. and Nentwig, W., 2011. Venom composition and strategies in spiders: Is everything possible? In: Casas, J. (Ed.), Advances in Insect Physiology Spider Physiology and Behaviour. Academic Seminal Review of the Composition of Spider Venoms, Burlington, MA, pp. 1–86.
Kulkarni, S. and Hormiga, G., 2021. Hooroo mates! Phylogenomic data suggest that the closest relatives of the iconic Tasmanian cave spider *Hickmania troglodytes* are in Australia and New Zealand, not in South America. Invertebr. Syst. 35, 850–856.
Kulkarni, S.S., Wood, H.M., Lloyd, M. and Hormiga, G., 2020. Spider-specific probe set for ultraconserved elements offers new perspectives on the evolutionary history of spiders (Arachnida, Araneae). Mol. Ecol. Resour. 20, 185–203.
Kulkarni, S., Kallal, R.J., Wood, H., Dimitrov, D., Giribet, G. and Hormiga, G., 2021. Interrogating genomic-scale data to resolve recalcitrant nodes in the spider tree of life. Mol. Biol. Evol. 38, 891–903.
Kulkarni, S., Wood, H.M. and Hormiga, G., 2023. Phylogenomics illuminates the evolution of orb webs, respiratory systems and the biogeographic history of the world's smallest orb-weaving spiders (Araneae, Araneoidea, Symphytognathoids). Mol. Phylogenet. Evol. 186, 107855.
Kullmann, E.J., 1972. The convergent development of orb-webs in cribellate and ecribellate spiders. Am. Zool. 12, 395–405.
Kuntner, M., Čandek, K., Gregorič, M., Turk, E., Hamilton, C.A., Chamberland, L., Starrett, J., Cheng, R.C., Coddington, J.A., Agnarsson, I. and Bond, J.E., 2023. Increasing information content and diagnosability in family-level classifications. Syst. Biol. 72, 964–971.
Ledford, J.M. and Griswold, C.E., 2010. A study of the subfamily Archoleptonetinae (Araneae, Leptonetidae) with a review of the morphology and relationships for the Leptonetidae. Zootaxa 2391, 1–32.
Ledford, J., Paquin, P., Cokendolpher, J., Campbell, J. and Griswold, C., 2011. Systematics of the spider genus *Neoleptoneta* Brignoli, 1972 (Araneae: Leptonetidae) with a discussion of the

morphology and relationships for the North American Leptonetidae. Invertebr. Syst. 25, 334–388.
Ledford, J., Paquin, P., Cokendolpher, J., Campbell, J. and Griswold, C., 2012. Systematics, conservation and morphology of the spider genus *Tayshaneta* (Araneae, Leptonetidae) in Central Texas caves. ZooKeys 167, 1–102.
Ledford, J., Derkarabetian, S., Ribera, C., Starrett, J., Bond, J.E., Griswold, C. and Hedin, M., 2021. Phylogenomics and biogeography of leptonetid spiders (Araneae: Leptonetidae). Invertebr. Syst. 35, 332–349.
Lehtinen, P.T., 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool. Fenn. 4, 199–468. [second pdf: index and outline by V. D. Roth (unpubl.)].
Lehtinen, P.T. and Saaristo, M.I., 1980. Spiders of the Oriental-Australian region. II. Nesticidae. Ann. Zool. Fenn. 17, 47–66.
Li, S.Q., 2022. On the taxonomy of spiders of the suborder Mesothelae. Acta Arachnol. Sin. 31, 71–72.
Lin, Y. and Li, S., 2020. Taxonomic studies on the genus *Ectatosticta* (Araneae, Hypochilidae) from China, with descriptions of two new species. ZooKeys 954, 17–29.
Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius, Holmiae [= Stockholm], 821 pp. (Araneae, pp. 619–624).
Liu, J., May-Collado, L.J., Pekár, S. and Agnarsson, I., 2016. A revised and dated phylogeny of cobweb spiders (Araneae, Araneoidea, Theridiidae): A predatory Cretaceous lineage diversifying in the era of the ants (Hymenoptera, Formicidae). Mol. Phylogenet. Evol. 94, 658–675.
Líznarová, E. and Pekár, S., 2019. Trophic niche and capture efficacy of an ant-eating spider, *Euryopis episinoides* (Araneae: Theridiidae). J. Arachnol. 47, 45–51.
Lomolino, M.V., 2004. Conservation biogeography. In: Lomolino, M.V. and Heaney, L.R. (Eds.), Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates; Sunderland, Massachusetts, pp. 293–296.
Lopardo, L. and Hormiga, G., 2008. Phylogenetic placement of the Tasmanian spider *Acrobleps hygrophilus* (Araneae, Anapidae) with comments on the evolution of the capture web in Araneoidea. Cladistics 24, 1–33.
Lopardo, L. and Hormiga, G., 2015. Out of the twilight zone: Phylogeny and evolutionary morphology of the orb-weaving spider family Mysmenidae, with a focus on spinneret spigot morphology in symphytognathoids (Araneae, Araneoidea). Zool. J. Linn. Soc. 173, 527–786.
Lopardo, L., Giribet, G. and Hormiga, G., 2011. Morphology to the rescue: Molecular data and the signal of morphological characters in combined phylogenetic analyses—A case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. Cladistics 27, 278–330.
Lubin, Y.D., Eberhard, W.G. and Montgomery, G.G., 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche 85, 1–23.
Lucas, S., 1988. Spiders in Brazil. Toxicon 26, 759–772.
Lüddecke, T., Herzig, V., von Reumont, B.M. and Vilcinskas, A., 2022. The biology and evolution of spider venoms. Biol. Rev. 97, 163–178.
Maddison, W.P., 2015. A phylogenetic classification of jumping spiders (Araneae: Salticidae). J. Arachnol. 43, 231–292.
Maddison, W.P. and Hedin, M.C., 2003. Jumping spider phylogeny (Araneae: Salticidae). Invertebr. Syst. 17, 529–549.
Maddison, W., Li, D., Bodner, M., Zhang, J., Xin, X., Liu, Q. and Liu, F., 2014. The deep phylogeny of jumping spiders (Araneae, Salticidae). ZooKeys 440, 57–87.
Maddison, W.P., Evans, S.C., Hamilton, C.A., Bond, J.E., Lemmon, A.R. and Lemmon, E.M., 2017. A genome-wide phylogeny of jumping spiders (Araneae, Salticidae), using anchored hybrid enrichment. ZooKeys 695, 89.
Maddison, W.P., Beattie, I., Marathe, K., Ng, P.Y., Kanesharatnam, N., Benjamin, S.P. and Kunte, K., 2020. A phylogenetic and taxonomic review of baviine jumping spiders (Araneae, Salticidae, Baviini). ZooKeys 1004, 27–97.
Magalhaes, I.L.F. and Ramírez, M.J., 2017. Relationships and phylogenetic revision of *Filistatinella* spiders (Araneae: Filistatidae). Invertebr. Syst. 31, 665–712.
Magalhaes, I.L.F. and Ramírez, M.J., 2019. The crevice weaver spider genus *Kukulcania* (Araneae: Filistatidae). Bull. Am. Mus. Nat. Hist. 426, 1–151.
Magalhaes, I.L., Azevedo, G.H., Michalik, P. and Ramírez, M.J., 2020. The fossil record of spiders revisited: Implications for calibrating trees and evidence for a major faunal turnover since the Mesozoic. Biol. Rev. 95, 184–217.
Magalhaes, I.L.F., Pérez-González, A., Labarque, F.M., Carboni, M., Hammel, J.U., Kunz, R., Ramírez, M.J. and Solórzano-Kraemer, M.M., 2022. Revision of recluse spiders (Araneae: Sicariidae: *Loxosceles*) preserved in Dominican amber and a total-evidence phylogeny of Scytodoidea reveal the first fossil Drymusidae. Arthropod Syst. Phylogeny 80, 541–559.
Mammola, S. and Isaia, M., 2017. Spiders in caves. Proc. R. Soc. B Biol. Sci. 284, 20170193.
Marples, M.J. and Marples, B.J., 1937. Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica*. Proc. Zool. Soc. Lond. A107, 213–221.
Marshall, S.D., 1995. Natural history, activity patterns, and relocation rates of a burrowing wolf spider: *Geolycosa xera archboldi* (Araneae, Lycosidae). J. Arachnol. 23, 65–70.
Marx, G., 1888. On a new and interesting spider. Entomol. Am. 4, 160–162.
Merret, P., 1988. Notes on the biology of the Neotropical pisaurid, *Ancylometes bogotensis* (Keyserling) (Araneae: Pisauridae). Bull. Br. Arachnol. Soc. 7, 197–201.
Michalik, P. and Hormiga, G., 2010. Ultrastructure of the spermatozoa in the spider genus *Pimoa* new evidence for the Monophyly of Pimoidae plus Linyphiidae (Arachnida: Araneae). Am. Mus. Novit. 2010, 1–17.
Michalik, P. and Lipke, E., 2013. Male reproductive system of spiders. In: Spider Ecophysiology. Springer, Berlin, Heidelberg, pp. 173–187.
Michalik, P. and Ramírez, M.J., 2014. Evolutionary morphology of the male reproductive system, spermatozoa and seminal fluid of spiders (Araneae, Arachnida)–current knowledge and future directions. Arthropod Struct. Dev. 43, 291–322.
Michalik, P., Kallal, R., Dederichs, T.M., Labarque, F.M., Hormiga, G., Giribet, G. and Ramirez, M.J., 2019. Phylogenomics and genital morphology of cave raptor spiders (Araneae, Trogloraptoridae) reveal an independent origin of a flow-through female genital system. J. Zoolog. Syst. Evol. Res. 57, 737–747.
Miller, J.A. and Hormiga, G., 2004. Clade stability and the addition of data: A case study from erigonine spiders (Araneae: Linyphiidae, Erigoninae). Cladistics 20, 385–442.
Miller, J.A., Carmichael, A., Ramírez, M.J., Spagna, J.C., Haddad, C.R., Rezac, M., Johannesen, J., Kral, J., Wang, X. and Griswold, C.E., 2010a. Phylogeny of entelegyne spiders: Affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). Mol. Phylogenet. Evol. 55, 786–804.
Miller, J.A., Griswold, C.E. and Haddad, C.R., 2010b. Taxonomic revision of the spider family Penestomidae (Araneae, Entelegynae). Zootaxa 2534, 1–36.
Millot, J., 1949. Classe des Arachnides: Morphologie generale et anatomie inteme; Ordre des Araneides. In: Grasse, P.-P. (Ed.), Traite de Zoologie, Vol. 6. Masson et Cie Editeurs, Libraires de l'Académie de Médecine, Paris, pp. 263–320, 589–743.
Miranda, G.S., Giupponi, A.P., Prendini, L. and Scharff, N., 2021. Systematic revision of the pantropical whip spider family Charinidae Quintero, 1986 (Arachnida, Amblypygi). Eur. J. Taxon. 772, 1–409.

Miranda, G.S., Kulkarni, S.S., Tagliatela, J., Baker, C.M., Giupponi, A.P., Labarque, F.M., Gavish-Regev, E., Rix, M.G., Carvalho, L.S., Fusari, M.L., Wood, H.M. and Sharma, P.P., 2022. The rediscovery of a relict unlocks the first global phylogeny of whip spiders (Amblypygi). *bioRxiv*. https://doi.org/10.1101/2022.04.26.489547.

Moradmand, M., Schönhofer, A.L. and Jäger, P., 2014. Molecular phylogeny of the spider family Sparassidae with focus on the genus *Eusparassus* and notes on the RTA-clade and 'Laterigradae'. Mol. Phylogenet. Evol. 74, 48–65.

Murphy, J.A., 2007. Gnaphosid Genera of the World. British Arachnological Society, St Neots, Cambridgeshire.

Muster, C., 2009. Phylogenetic relationships within Philodromidae, with a taxonomic revision of *Philodromus* subgenus *Artanes* in the western Palearctic (Arachnida: Araneae). Invertebr. Syst. 23, 135–169.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. and Minh, B.-Q., 2015. IQTREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. 32, 268–274.

Oda, H. and Akiyama-Oda, Y., 2020. The common house spider *Parasteatoda tepidariorum*. EvoDevo 11, 1–7.

Opatova, V., Hamilton, C.A., Hedin, M., De Oca, L.M., Král, J. and Bond, J.E., 2020. Phylogenetic systematics and evolution of the spider infraorder Mygalomorphae using genomic scale data. Syst. Biol. 69, 671–707.

Opell, B. and Eberhard, W.G., 1984. Resting postures of orb-weaving uloborid spiders (Araneae, Uloboridae). J. Arachnol. 18, 205–234.

Pekár, S., 2020. Ant-mimicking spider actively selects its mimetic model (Araneae: Gnaphosidae; hymenoptera: Formicidae). Myrmecol. News. 30, 103–129.

Pekár, S. and Toft, S., 2015. Trophic specialisation in a predatory group: The case of prey-specialised spiders (Araneae). Biol. Rev. 90, 744–761.

Pekár, S., Bočánek, O., Michálek, O., Petráková, L., Haddad, C.R., Šedo, O. and Zdráhal, Z., 2018. Venom gland size and venom complexity—Essential trophic adaptations of venomous predators: A case study using spiders. Mol. Ecol. 2018, 4257–4269.

Pekár, S., Wolff, J.O., Černecká, Ľ., Birkhofer, K., Mammola, S., Lowe, E.C., Fukushima, C.S., Herberstein, M.E., Kučera, A., Buzzatto, B.A., Djoudi, E.A., Domenech, M., Enciso, A.V., Piñanez Espejo, Y.M.G., Febles, S., García, L.F., Gonçalves-Souza, T., Isaia, M., Lafage, D., Líznarová, E., Macías-Hernández, N., Magalhães, I., Malumbres-Olarte, J., Michálek, O., Michalik, P., Michalko, R., Milano, F., Munévar, A., Nentwig, W., Nicolosi, G., Painting, C.J., Pétillon, J., Piano, E., Privet, K., Ramírez, M.J., Ramos, C., Řezáč, M., Ridel, A., Růžička, V., Santos, I., Sentenská, L., Walker, L., Wierucka, K., Zurita, G.A. and Cardoso, P., 2021. The world spider trait database: A centralized global open repository for curated data on spider traits. Database 2021, baab064.

Penney, D., Dierick, M., Cnudde, V., Masschaele, B., Vlassenbroeck, J., Van Hoorebeke, L. and Jacobs, P., 2007. First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-ray computed tomography. Zootaxa 1623, 47–53.

Petrunkevitch, A., 1923. On families of spiders. Ann. N. Y. Acad. Sci. 29, 145–180.

Piacentini, L.N. and Ramírez, M.J., 2019. Hunting the wolf: A molecular phylogeny of the wolf spiders (Araneae, Lycosidae). Mol. Phylogenet. Evol. 136, 227–240.

Platnick, N., 1974. The spider family Anyphaenidae in America north of Mexico. Bull. Mus. Comp. Zool. 146, 205–266.

Platnick, N.I., 1977. The Hypochiloid spiders: A cladistic analysis, with notes of the Atypoidea (Arachnida, Araneae). Am. Mus. Novit. 2627, 1–23.

Platnick, N.I., 1984. Studies on Malagasy spiders, 1. The family Gallieniellidae (Araneae, Gnaphosoidea). Am. Mus. Novit. 2801, 1–17.

Platnick, N.I., 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosoidea). Am. Mus. Novit. 2978, 1–42.

Platnick, N.I., 1994. A revision of the spider genus *Caponina* (Araneae, Caponiidae). Am. Mus. Novit. 3100, 15.

Platnick, N.I., 1999. Dimensions of biodiversity: targeting megadiverse groups. In: Cracraft, J. and Grifo, F.T. (Eds.), The Living Planet in Crisis: Biodiversity Science and Policy. Columbia University Press, New York, NY, pp. 33–52.

Platnick, N.I., 2000. A relimitation and revision of the Australasian ground spider family Lamponidae (Araneae: Gnaphosoidea). Bull. Am. Mus. Nat. Hist. 245, 1–328.

Platnick, N.I., 2020. Spiders of the World. A Natural History. Princeton University Press, Princeton, NJ, p. 256.

Platnick, N.I. and Baehr, B., 2006. A revision of the Australasian ground spiders of the family Prodidomidae (Araneae, Gnaphosoidea). Bull. Am. Mus. Nat. Hist. 298, 1–287.

Platnick, N.I. and Forster, R.R., 1987. On the first American spiders of the subfamily Sternodinae (Araneae, Malkaridae). Am. Mus. Novit. 2894, 1–12.

Platnick, N.I. and Gertsch, W.J., 1976. The suborders of spiders: A cladistic analysis (Arachnida, Araneae). Am. Mus. Novit. 2607, 1–15.

Platnick, N.I. and Goloboff, P.A., 1985. On the monophyly of the spider suborder Mesothelae (Arachnida: Araneae). J. N. Y. Entomol. Soc. 93, 1265–1270.

Platnick, N.I. and Shadab, M.U., 1993. A review of the pirate spiders (Araneae, Mimetidae) of Chile. Am. Mus. Novit. 3074, 1–30.

Platnick, N.I., Coddington, J.A., Forster, R.R. and Griswold, C.E., 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Am. Mus. Novit. 3016, 1–73.

Polotow, D. and Brescovit, A.D., 2008. Revision of the neotropical spider genus *Gephyroctenus* (Araneae: Ctenidae: Calocteninae). Rev. Brasil. Zool. 25, 705–715.

Polotow, D. and Brescovit, A.D., 2014. Phylogenetic analysis of the tropical wolf spider subfamily Cteninae (Arachnida, Araneae, Ctenidae). Zool. J. Linn. Soc. 170, 333–361.

Polotow, D., Carmichael, A. and Griswold, C.E., 2015. Total evidence analysis of the phylogenetic relationships of Lycosoidea spiders (Araneae, Entelegynae). Invertebr. Syst. 29, 124–163.

Poy, D., Ramírez, M.J., Michalik, P. and Piacentini, L.N., 2020. Copulatory mechanics in the wolf spider *Agalenocosa pirity* reveals a hidden diversity of locking systems in Lycosidae (Araneae). J. Morphol. 281, 250–257.

Ramírez, M.J., 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). J. Arachnol. 28, 149–157.

Ramírez, M.J., 2014. The morphology and phylogeny of dionychan spiders (Araneae: Araneomorphae). Bull. Am. Mus. Nat. Hist. 390, 1–374.

Ramírez, M. and Platnick, N., 1999. On *Sofanapis antillanca* (Araneae, Anapidae) as a kleptoparasite of austrochiline spiders (Araneae, Austrochilidae). J. Arachnol. 27, 547–549.

Ramírez, M.J., Magalhaes, I.L., Derkarabetian, S., Ledford, J., Griswold, C.E., Wood, H.M. and Hedin, M., 2021. Sequence capture phylogenomics of true spiders reveals convergent evolution of respiratory systems. Syst. Biol. 70, 14–20.

Ramírez, M.J., Magalhaes, I.F., Pizarro-Araya, J., Ballarin, F., Marusik, Y.M. and Eskov, K.Y., 2022. A new species of the spider genus *Tekellina* Levi, 1957 from Chile, with a broadened definition of the family Synotaxidae (Arachnida, Araneae). Zool. Anz. 301, 76–90.

Ranwez, V., Harispe, S., Delsuc, F. and Douzery, E.J.P., 2011. MACSE: Multiple Alignment of Coding SEquences accounting for frameshifts and stop codons. PloS One 6, e22594.

Raven, R.J., 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematics. Bull. Am. Mus. Nat. Hist. 182, 1–180.

Richman, D.B. and Jackson, R.R., 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bull. Br. Arachnol. Soc. 9, 33–37.

Rix, M.G., 2006. Systematics of the Australasian spider family Pararchaeidae (Arachnida: Araneae). Invertebr. Syst. 20, 203–254.
Rix, M.G. and Harvey, M.S., 2010a. The first pararchaeid spider (Araneae: Pararchaeidae) from New Caledonia, with a discussion on spinneret spigots and egg sac morphology in *Ozarchaea*. Zootaxa 2414, 27–40.
Rix, M. and Harvey, M., 2010b. The spider family Micropholcommatidae (Arachnida, Araneae, Araneoidea): A relimitation and revision at the generic level. ZooKeys 36, 1–321.
Rix, M.G., Cooper, S.J., Meusemann, K., Klopfstein, S., Harrison, S.E., Harvey, M.S. and Austin, A.D., 2017. Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae). Mol. Phylogenet. Evol. 109, 302–320.
Robinson, M.H. and Robinson, B., 1971. The predatory behavior of the Ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). Am. Midl. Nat. 85, 85–96.
Rodrigues, B.V. and Rheims, C.A., 2020. Phylogenetic analysis of the subfamily Prodidominae (Arachnida: Araneae: Gnaphosidae). Zool. J. Linn. Soc. 190, 654–708.
Sanggaard, K.W., Bechsgaard, J.S., Fang, X., Duan, J., Dyrlund, T.F., Gupta, V., Jiang, X., Cheng, L., Fan, D., Feng, Y. and Han, L., 2014. Spider genomes provide insight into composition and evolution of venom and silk. Nat. Commun. 5, 1–12.
Santos, A.J., 2007. A phylogenetic analysis of the nursery-web spider family Pisauridae, with emphasis on the genera *Architis* and *Staberius* (Araneae: Lycosoidea). Zool. Scr. 36, 489–507.
Santos, A.J. and Gonzaga, M.O., 2003. On the spider genus *Oecobius* Lucas 1846 in South America (Araneae, Oecobiidae). J. Nat. Hist. 37, 239–252.
Santos, A. and Rheims, C.A., 2005. Four new species and new records for the spider genus *Synotaxus* Simon, 1895 (Araneae: Synotaxidae) from Brazil. Zootaxa 937, 1–12.
Scharff, N. and Coddington, J.A., 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zool. J. Linn. Soc. 120, 355–434.
Scharff, N., Coddington, J.A., Blackledge, T.A., Agnarsson, I., Framenau, V., Szuts, T., Hayashi, C.Y. and Dimitrov, D., 2020. Phylogeny of the orb-weaving spider family Araneidae (Araneae, Araneoidea). Cladistics 36, 1–21.
Schmitz, A., 2013. Tracheae in spiders: respiratory organs for special functions. In: Nentwig, W. (Ed.), Spider ecophysiology. Springer, New York, NY, pp. 29–39.
Schütt, K., 2000. The limits of the Araneoidea (Arachnida: Araneae). Aust. J. Zool. 48, 135–153.
Schütt, K., 2003. Phylogeny of Symphytognathidae s.l. (Araneae, Araneoidea). Zool. Scr. 32, 129–151.
Schwager, E.E., Sharma, P.P., Clarke, T., Leite, D.J., Wierschin, T., Pechmann, M., Akiyama-Oda, Y., Esposito, L., Bechsgaard, J., Bilde, T. and Buffry, A.D., 2017. The house spider genome reveals an ancient whole-genome duplication during arachnid evolution. BMC Biol. 15, 1–27.
Selden, P.A., Shear, W.A. and Sutton, M.D., 2008. Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order. Proc. Natl. Acad. Sci. U. S. A. 105, 20781–20785.
Sentenská, L. and Pekár, S., 2013. 2013. Mate with the young, kill the old: Reversed sexual cannibalism and male mate choice in the spider *Micaria sociabilis* (Araneae: Gnaphosidae). Behav. Ecol. Sociobiol. 67, 1131–1139.
Shao, L. and Li, S., 2018. Early Cretaceous greenhouse pumped higher taxa diversification in spiders. Mol. Phylogenet. Evol. 127, 146–155.
Shao, L., Zhao, Z. and Li, S., 2023. Is phenotypic evolution affected by spiders' construction behaviors? Syst. Biol. 72, 319–340.
Sharma, P.P., Kaluziak, S.T., Pérez-Porro, A.R., González, V.L., Hormiga, G., Wheeler, W.C. and Giribet, G., 2014. Phylogenomic interrogation of Arachnida reveals systemic conflicts in phylogenetic signal. Mol. Biol. Evol. 31, 2963–2984.
Shear, W.A., 1970. The evolution of social phenomena in spiders. Bull. Br. Arachnol. Soc. 1, 65–76.
Shultz, J.W., 1987. The origin of the spinning apparatus in spiders. Biol. Rev. 62, 89–113.
Sierwald, P., 1997. Phylogenetic analysis of pisaurine nursery web spiders, with revisions of *Tetragonophthalma* and *Perenethis* (Araneae, Lycosoidea, Pisauridae). J. Arachnol. 25, 361–407.
da Silva, E.L.C., Lise, A.A. and Carico, J.E., 2008. Revision of the Neotropical spider genus *Enna* (Araneae, Lycosoidea, Trechaleidae). J. Arachnol. 36, 76–110.
Silva-Dávila, D., 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). Bull. Am. Mus. Nat. Hist. 274, 1–86.
Simmons, M.P. and Goloboff, P.A., 2014. Dubious resolution and support from published sparse supermatrices: The importance of thorough tree searches. Mol. Phylogenet. Evol. 78, 334348.
Song, L. and Florea, L., 2015. Rcorrector: Efficient and accurate error correction for Illumina RNA-seq reads. GigaScience 4, 48.
Spagna, J.C. and Gillespie, R.G., 2008. More data, fewer shifts: Molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. Mol. Phylogenet. Evol. 46, 347–368.
Spagna, J.C., Crews, S.C. and Gillespie, R.G., 2010. Patterns of habitat affinity and austral/Holarctic parallelism in dictynoid spiders (Araneae: Entelegynae). Invertebr. Syst. 24, 238–257.
Stålhandske, P., 2001. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. Behav. Ecol. 12, 691–697.
Starrett, J., Derkarabetian, S., Hedin, M., Bryson, R.W., Jr., McCormack, J.E. and Faircloth, B.C., 2017. High phylogenetic utility of an ultraconserved element probe set designed for Arachnida. Mol. Ecol. Resour. 17, 812–823.
Stratton, G.E., 2005. Evolution of ornamentation and courtship behavior in *Schizocosa*: Insights from a phylogeny based on morphology (Araneae, Lycosidae). J. Arachnol. 33, 347–376.
Teixeira, R.A., Campos, L.A. and Lise, A.A., 2013. Phylogeny of Aphantochilinae and Strophiinae sensu Simon (Araneae; Thomisidae). Zool. Scr. 43, 65–78.
Tong, C., Avilés, L., Rayor, L.S., Mikheyev, A.S. and Linksvayer, T.A., 2022. Genomic signatures of recent convergent transitions to social life in spiders. Nat. Commun. 13, 1–12.
Vollrath, F., 1978. A close relationship between two spiders (Arachnida, Araneidae): *Curimagua bayano* synecious on a *Diplura* species. Psyche 85, 347–353.
Vollrath, F., 1979. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). Anim. Behav. 27, 515–518.
Wang, C., Ribera, C. and Li, S., 2012. On the identity of the type species of the genus *Telema* (Araneae, Telemidae). Zookeys 251, 11–19.
Wang, F., Ballesteros, J.A., Hormiga, G., Chesters, D., Zhan, Y., Sun, N., Zhu, C., Chen, W. and Tu, L., 2015. Resolving the phylogeny of a speciose spider group, the family Linyphiidae (Araneae). Mol. Phylogenet. Evol. 91, 135–149.
Wang, B., Dunlop, J.A., Selden, P.A., Garwood, R.J., Shear, W.A., Muller, P. and Lei, X., 2018. Cretaceous arachnid *Chimerarachne yingi* gen. et sp. nov. illuminates spider origins. Nat. Ecol. Evol. 2, 614–624.
Weigel, G., 1941. Färbung und Farbwechsel der Krabbenspinne *Misumena vatia* (L.). Z. Vergl. Physiol. 29, 195–248.
Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramırez, M.J., Sierwald, P., Almeida-Silva, L., Alvarez-Padilla, F., Arnedo, M.A., Benavides Silva, L.R., Benjamin, S.P., Bond, J.E., Grismado, C.J., Hasan, E., Hedin, M., Izquierdo, M.A., Labarque, F.M., Ledford, J., Lopardo, L., Maddison, W.P., Miller, J.A., Piacentini, L.N., Platnick, N.I., Polotow, D., Silva-Dávila, D., Scharff, N., Szűts, T., Ubick, D., Vink, C.J., Wood, H.M. and Zhang, J., 2017. The spider tree of life: Phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. Cladistics 33, 574–616.
Wiehle, H., 1967. Meta – eine semientelegyne Gattung der Araneae. Senckenb. Biol. 48, 183–196.

Wilson, J.D., Bond, J.E., Harvey, M.S., Ramírez, M.J. and Rix, M.G., 2023. Correlation with a limited set of behavioral niches explains the convergence of somatic morphology in mygalomorph spiders. Ecol. Evol. 13, e9706.
Wolff, J.O., Nentwig, W. and Gorb, S.N., 2013. The great silk alternative: Multiple co-evolution of web loss and sticky hairs in spiders. PloS One 8, e62682.
Wolff, J.O., Řezáč, M., Krejčí, T. and Gorb, S.N., 2017. Hunting with sticky tape: Functional shift in silk glands of araneophagous ground spiders (Gnaphosidae). J. Exp. Biol. 220, 2250–2259.
Wood, H.M. and Parkinson, D.Y., 2019. Comparative morphology of cheliceral muscles using high-resolution X-ray microcomputed-tomography in palpimanoid spiders (Araneae, Palpimanoidea). J. Morphol. 280, 232–243.
Wood, H.M., Griswold, C.E. and Gillespie, R.G., 2012. Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into the evolution of the "neck" and predatory behaviours of the superfamily Palpimanoidea. Cladistics 28, 598–626.
Wood, H.M., Matzke, N.J., Gillespie, R.G. and Griswold, C.E., 2013. Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. Syst. Biol. 62, 264–284.
Wood, H.M., Gonzalez, V.L., Lloyd, M., Coddington, J.A. and Scharff, N., 2018. Next-generation museum genomics: Phylogenetic relationships among palpimanoid spiders using sequence capture techniques (Araneae: Palpimanoidea). Mol. Phylogenet. Evol. 127, 907–918.
World Spider Catalog, 2023. World Spider Catalog. Version 22.5. Natural History Museum Bern. http://wsc.nmbe.ch.
Wunderlich, J., 1986. Spinnenfauna gestern und heute: Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten. Quelle Meyer, Wiesbaden, p. 283.
Wunderlich, J., 2004. The new spider (Araneae) family Borboropactidae from the tropics and fossil in Baltic amber. Beitr. Araneol. 3, 1737–1746.
Xu, X., Liu, F., Cheng, R.C., Chen, J., Xu, X., Zhang, Z., Ono, H., Pham, D.S., Norma-Rashid, Y., Arnedo, M.A. and Kuntner, M., 2015. Extant primitively segmented spiders have recently diversified from an ancient lineage. Proc. R. Soc. B Biol. Sci. 282, 20142486.
Xu, X., Su, Y.C., Ho, S.Y., Kuntner, M., Ono, H., Liu, F., Chang, C.C., Warrit, N., Sivayyapram, V., Aung, K.P.P. and Pham, D.S., 2021. Phylogenomic analysis of ultraconserved elements resolves the evolutionary and biogeographic history of segmented trapdoor spiders. Syst. Biol. 70, 1110–1122.
Zapfe, H., 1955. Filogenia y función en *Austrochilus manni* Gertsch y Zapfe (Araneae-Hypochilidae). Trabajos Lab. Zool. Univ. Chile 2, 1–53.
Zhao, Y.J., Zeng, Y., Chen, L., Dong, Y. and Wang, W., 2014. Analysis of transcriptomes of three orb-web spider species reveals gene profiles involved in silk and toxin. Insect Sci. 21, 687–698.

Supporting Information

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

Figure S1 Percentage of GC-content of taxa in the 25% occupancy UCE dataset.

Figure S2 Percentage of missing data in the 25% occupancy UCE dataset.

Figure S3 Maximum-likelihood phylogeny reconstructed using the 25% occupancy dataset of the UCEs, collapsed to family level in Fig. 4 in the main text.

Figure S4 Parsimony cladogram constructed using TNT for the 25% occupancy UCE dataset composed of 17 Araneoidea families.

Figure S5 Maximum-likelihood phylogeny of the marronoid clade reconstructed using the 25% occupancy dataset of the UCEs.

Figure S6 Maximum-likelihood phylogeny of the Dionycha clade reconstructed using the 25% occupancy dataset of the UCEs.

[Correction added on 31 October 2023, after first online publication: Figure S6 has been updated.]

Table S1 Count of UCE loci recovered using the spider-specific Spider2Kv1 probe set.

Table S2 Accession numbers, concatenation scheme of sequences and locality data of specimens representing UCEs and six Sanger-sequence-based markers. UCEbycatch, Sanger markers were extracted from the UCE assembly of that taxon; UetS, Sanger markers were taken from publicly available repository (i.e. NCBI).

File S1 Alignment file of UCE analysis of 25% occupancy.

File S2 (A) Alignment file of UCE (25% occupancy) + legacy marker datasets. (B) Partition file used for IQ-TREE analysis.

File S3 (A) Subset of File S2 including Dionycha taxa. (B) Partition file used for IQ-TREE analysis.

File S4 (A) Subset of File S2 including marronoid taxa. (B) Partition file used for IQ-TREE analysis.

File S5 Alignment file of UCE (25% occupancy) use to reconstruct the cladogram of Araneoidea using TNT.