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Webs of intrigue: museum genomics elucidate relationships of the marronoid spider clade (Araneae)

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Relationships among spider families that lack support through other lines of evidence (e.g., morphology) have recently been uncovered through molecular phylogenetics. One such group is the "marronoid" clade, which contains about 3,400 described species in 9 families. Marronoids run the gamut of life history strategies, with social species, species producing a variety of silk types, and species occurring in a range of extreme environments. Despite recognition of the ecological variability in the group, there remains uncertainty about family- level relationships, leaving diverse ecologies without an evolutionary context. The phylogenies produced to date have relatively low nodal support, there are few defined morphological synapomorphies, and the internal relationships of many families remain unclear. We use 93 exemplars from all marronoid families and ultraconserved element loci captured in silico from a combination of 48 novel low-coverage whole genomes and genomic data from the Sequence Read Archive (SRA) to produce a 50% occupancy matrix of 1,277 loci from a set of ultraconserved element probes. These loci were used to infer a phylogeny of the marronoid clade and to evaluate the familial relationships within the clade, and were combined with single-locus (Sanger) legacy data to further increase taxonomic sampling. Our results indicate a clearly defined and well-supported marronoid clade and provide evidence for both monophyly and paraphyly within the currently defined families of the clade. We propose taxonomic changes in accordance with the resulting phylogenetic hypothesis, including elevating Cicurinidae (**restored status**) and Macrobunidae (**new rank**).

Key words: low-coverage whole genome sequencing, phylogenetics, Cicurinidae, Macrobunidae, ultraconserved element

Introduction

The use of multilocus genetic data in phylogenetics has allowed for the resolution of long-standing questions regarding the higher-level phylogenetic relationships of spiders. The first molecular phylogeny of all spider families (Araneae excluding Synotaxidae Simon, 1895) was recently published, supporting the monophyly of many major groups (Wheeler et al. 2017). This seminal study also identified dark nodes within the spider tree of life—novel relationships among families or groups of families without clearly discernible morphological synapomorphies. One such dark node is the "marronoid" clade, a group coined by Wheeler et al. (2017) from the Spanish word for brown (*marrón*), a reference to the fact that an overwhelming number of species in the clade are brown and generally morphologically nondescript. This moniker also serves as a statement to how little attention this group has received historically—brown is the most appropriate identifier. Whereas the marronoids include some families that have been grouped together in superfamilies (Fig. 1; e.g., the Amaurobioidea and Dictynoidea; sensu Lehtinen

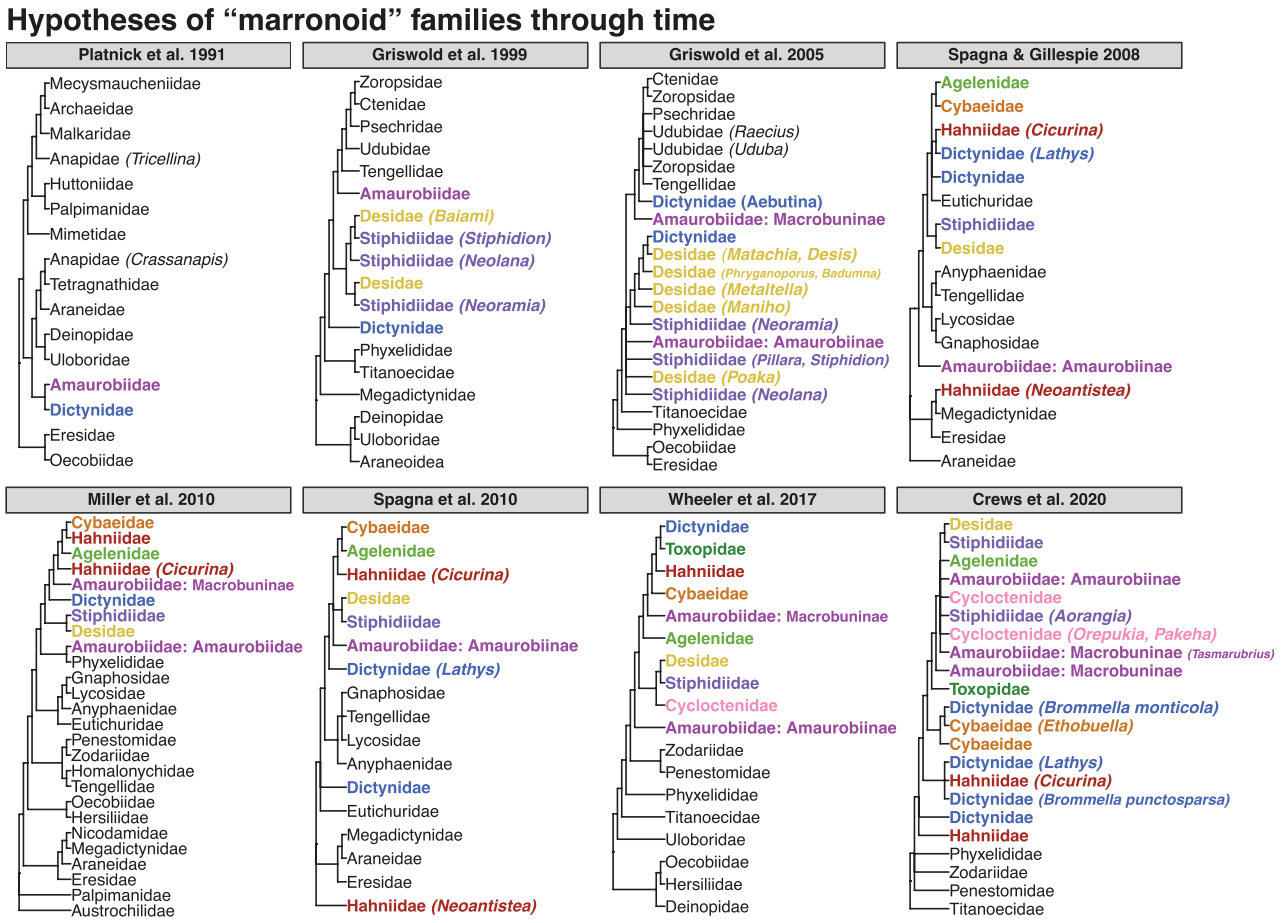

Fig. 1. Recent phylogenetic hypotheses of family relationships within the marronoid clade (in color) from 1991 to 2020 (Platnick et al. 1991, Griswold et al. 1999, 2005, Spagna and Gillespie 2008, Miller et al. 2010, Spagna et al. 2010, Wheeler et al. 2017, Crews et al. 2020).

1967, Forster and Wilton 1973, Griswold et al. 1999, 2005), the specific combination of families to the exclusion of other families previously hypothesized to be morphologically associated was a novel hypothesis (Wheeler et al. 2017), corroborated by Crews et al. (2020). In subsequent studies using genomic data, the marronoids were also recovered as a clade, sister to the Sparassidae Bertkau, 1872(Kulkarni et al. 2020, Kallal et al. 2021, Azevedo et al. 2022), and part of the speciose retrolateral tibial apophysis (RTA) clade (Coddington and Levi 1991).

The Marronoid Clade: A Cryptic Lineage with a Messy History

In part, the uncertainty among the relationships of marronoids relates to the seemingly endless rearrangement of lineages within its families that has occurred throughout the history of spider taxonomy (Fig. 2, and for a written summary of the changes illustrated in this figure, see the Supplementary Material). One of the driving factors for this messy history is that this clade contains both cribellate and ecribellate members. Cribellate spiders are defined by the presence of a cribellum, a spinning organ on the abdomen from which silk is combed out via a calamistrum, a structure on the metatarsus of the fourth leg. Ecribellate spiders lack this structure and may instead have a colulus, thought to be a vestige of the cribellum. There are implications for the type of silk spiders can produce with and without a cribellum: in cribellate spiders, the capture thread, though dry, is elastic and has mechanical adhesive properties through entanglement, while in ecribellate spiders, glue assists the silk in prey capture. It has been suggested the loss of the cribellum has led to a reduced dependency on a prey capture web (Forster and Wilton 1973), and it is possible this lessened dependency has led to greater diversity in many clades, such as the most speciose spider family, the Salticidae Blackwall 1841. Marronoids, while they contain ecribellate and cribellate species, do not make orb webs, placing them at a potentially interesting evolutionary transition. The idea that closely related spiders could be both ecribellate and cribellate was initially suggested by Lehtinen (1967) and upended much of spider taxonomy to that point. Until this hypothesis was raised, the designation of being either cribellate or ecribellate was considered of key importance for distinguishing major groups of spiders. It is now hypothesized that the cribellum (and therefore, cribellate silk) is ancestral to araneomorphs and was subsequently lost in many lineages (Blackledge et al. 2009, Spagna and Gillespie 2008). However, within the marronoid clade, the presence and absence of a cribellum is so varied that in some cases it is the main delimiter between sister species, such as in the genus *Mahura* Forster & Wilton, 1973 (Forster and Wilton 1973). Four marronoid families contain both cribellate and ecribellate members (Dictynidae O. Pickard-Cambridge, 1871, Desidae Pocock, 1895, Toxopidae Hickman, 1940, Stiphidiidae Dalmas, 1917). Additionally, the only unifying morphological characters for marronoids proposed to date are the presence of 3 tarsal claws and an RTA, which are not synapomorphies. In the absence of concrete, unifying morphological

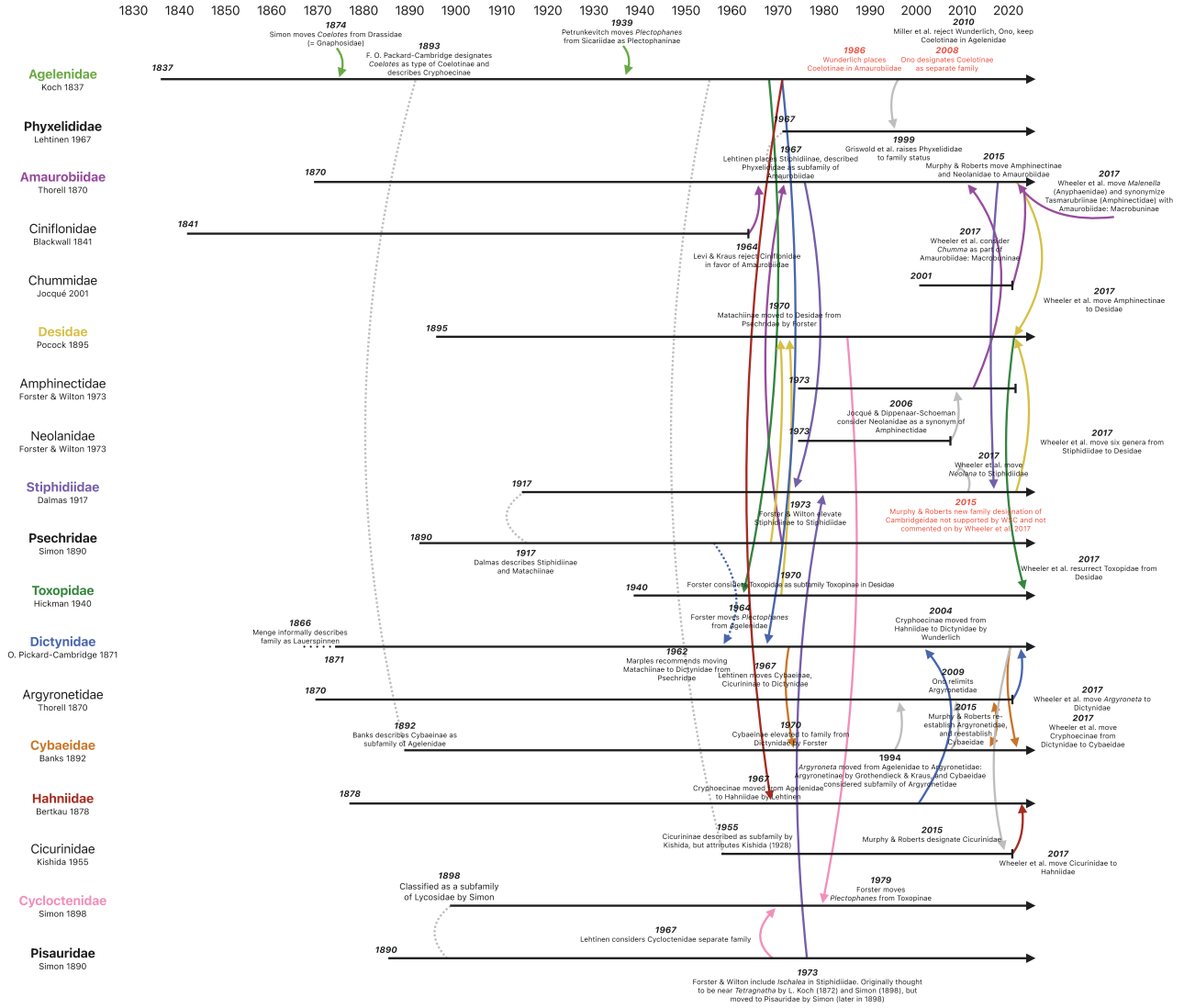

Fig. 2. Timeline depicting significant rearrangements in the marronoid clade from the inception of each family. Families currently contained in the marronoid clade are indicated by the same colors as in Fig. 1. Solid lines indicate movements by the indicated author, arrows, and colors indicate the destination family. Dotted lines indicate families originally described as subfamilies, or taxonomic suggestions that did not result in a formal taxonomic action. Movements in red indicate taxonomic changes that were not accepted by subsequent authors. Positions are illustrative and not to scale. Any papers referenced in this figure and not in the main text are referenced in Appendix A.

characteristics beyond simple descriptors, or a well-resolved phylogenetic backbone, the marronoids collectively represent RTA spider families, many of which have historically served as a taxonomic waste bin for generally small, and usually brown, spiders.

Families currently considered to be part of the marronoid clade include Agelenidae C.L. Koch 1837, Amaurobiidae Thorell 1869, Cybaeidae Banks 1892, Cyclocteninae Simon 1898, Desidae, Dictynidae, Hahniidae Bertkau 1878, Stiphidiidae, and Toxopidae. Although the marronoid clade was recovered in all constrained inferences in Wheeler et al. (2017), support was consistently very low (constrained maximum likelihood tree bootstrap value = 28), and unconstrained maximum likelihood inferences additionally included Sparassidae. It is important to note, however, that the Bayesian unconstrained inference in Wheeler et al. (2017) recovered a marronoid clade with high support (posterior probability = 0.9853). Castellucci et al. (2023) subsequently inferred a phylogeny of marronoid spiders, but used extensive backbone constraints from Wheeler et al. (2017), such that no major conclusions could be made about family-level relationships, the monophyly of the marronoids, or the internal relationships of the group. In an unconstrained tree in Castellucci et al. (2023), the marronoid clade was not recovered as monophyletic, with multiple families within also paraphyletic. While higher support for the clade has been recovered in other subsequent phylogenomic analyses (Kulkarni et al. 2020, Kallal et al. 2021, both ≥95% ultrafast bootstrap (UFBoot) support sensu Hoang et al. 2018), its monophyly has not been evaluated at a genomic level with taxonomic coverage comparable to that of the most representative Sanger locus phylogeny in Crews et al. (2020).

Interfamilial Relationships of the Marronoid Clade

Kishida (1930) was the first to propose any association of marronoid families, and classified Hahniidae, Agelenidae, Lycosidae Sundevall, 1833 (including *Cyclocteninae* L. Koch, 1878), and Argyronetidae Thorell, 1870 in the Argiopoidea (now considered Araneoidea) and Psechridae Simon, 1990 (including subfamilies Matachiinae

Dalmas, 1917 and Stiphidiinae), Dictynidae, and Amaurobiidae in the Amaurobioidea. At this point, marronoid families were still split between distinct superfamilies that also contained many non-marronoid families.

When Lehtinen (1967) reviewed the classification of the araneomorphae, a form of the present marronoid clade was established within what he referred to as the "branch" Amaurobiides, the superfamily Amaurobioidea, including the following families: Miturgidae Simon, 1886 (including Tengellidae Dahl, 1908, now a synonym of Zoropsidae Bertkau, 1882), Amaurobiidae (including Stiphidiidae, Phyxelididae Lehtinen, 1967, and Desidae), Liocranidae Simon, 1897, Agelenidae, Dictynidae (including Cybaeidae), Hahniidae, and Toxopidae. Other superfamilies of the "branch" Amaurobiides include Lycosoidea (including Lycosidae, Cycloctenidae, Dolomedidae Lehtinen, 1967 [now Pisauridae Simon, 1890], Zoridae F.O. Pickard-Cambridge, 1893 [now Miturgidae], Ctenidae Keyserling, 1877, and Selenopidae Simon, 1897), Pisauroidea (including Pisauridae Simon, 1890, Oxyopidae Thorell, 1869, Senoculidae Simon, 1890, and Homalonychidae Marx, 1891), Sparassoidea (including Sparassidae and Clubionidae Wagner, 1887), and Gnaphosoidea (including Gnaphosidae Banks, 1892, Platoridae Simon, 1897 [a synonym of Trochanteriidae Karsch, 1879], and Prodidomidae Simon, 1884), as well as unassigned families Titanoecidae Lehtinen, 1967, Anyphaenidae Bertkau, 1878, and Psechridae. Lehtinen (1967) observed that many characteristics used traditionally to distinguish taxa were uninformative for taxa found outside of Europe. Lehtinen (1967) further commented that "limitation of taxa at a family group level in Amaurobiides is more of a matter of opinion than in any other group treated in this paper…", and considered them an "exceptionally homogeneous group". Regarding the extensive taxonomic changes made in this work, Lehtinen (1967) commented that many of his families now included both ecribellate and cribellate species, in effect "dissolving the course of evolution of the cribellum".

The next taxonomic treatment of the group was in 1973, when Forster and Wilton (1973) identified 2 superfamilies: Dictynoidea (consisting of Dictynidae, Hahniidae, Desidae, Cybaeidae, Argyronetidae, Amaurobioididae, and Anyphaenidae) and the Amaurobioidea (consisting of Amaurobiidae, Agelenidae, Stiphidiidae, Amphinectidae Forster & Wilton, 1973, Neolanidae Forster & Wilton, 1973, Psechridae, Ctenidae, and Cycloctenidae). The genus *Aorangia* Forster & Wilton 1973 established in this work is considered *incertae sedis* but allied with Amphinectidae. Forster and Wilton (1973) emphasized that, consistent with Lehtinen (1967), every family placement contained both ecribellate and cribellate genera and that the cribellate phase had reverted to ecribellate many times, so much so that sometimes this character is the main way to distinguish closely related species of the same genus. Further reading of the history of family-level classification of spiders in the marronoid clade may be found in Appendix A of the Supplementary Material.

The Ecology of Spiders in the Marronoid Clade

The marronoids are distributed worldwide, with certain clades, such as the Fused Paracribellar Clade (FPC; Griswold et al. 1999, Spagna and Gillespie 2008), restricted to, or primarily found in a certain region of the world (i.e., the FPC is primarily Australasian in distribution). Marronoids can occur in a variety of specialized microhabitats including tundra, deserts, caves, intertidal areas (including coral reef habitats), salt flats, and seasonally flooded regions (Lee and Baust 1985, Blest and Taylor 1995, Baehr et al. 2017). Despite the confusion regarding phylogenetic placement and relationships of the marronoid clade within the spider tree of life, many species within the group are of particular interest due to their diverse ecological adaptations. For example, Crews et al. (2020), using a Sanger-locus dataset and the broadest sampling of dictynids and closely related marronoids, identified multiple independent origins of aquatic associations. If any single descriptor could be assigned to marronoids, it would be that they are extreme: including specialization in extreme temperatures (high and low) along huge latitudinal and elevational ranges, and along both aquatic and saline gradients (Crews and Gillespie 2014, Crews et al. 2020). For example, the genus *Cicurina* Bertkau, 1878 contains several eyeless cave specialists, with 3 species listed as Federally Endangered according to the US Fish & Wildlife Service (Endangered Species List 2023). All of these adaptations make the marronoids an excellent candidate model-clade for understanding the mechanisms allowing them to live in such novel environments (Sanger and Rajakumar 2019). Aside from the range of silk and web-behaviors in marronoids, there are also several species in 4 marronoid families that exhibit some degree of social behavior: Agelenidae (*Agelena consociata* Denis, 1965, *Coelotes terrestris* (Wider 1834), *Eratigena atrica* (C.L. Koch, 1843)), Amaurobiidae (*Amaurobius fenestralis* (Ström, 1768), *A. ferox* (Walckenaer, 1830), *A. similis* (Blackwall, 1861)), Desidae (*Badumna socialis* (Rainbow, 1905), *Phryganoporus candidus* (L. Koch, 1872)), and Dictynidae (*Aebutina binotata* Simon, 1892, *Dictyna albopilosa* Franganillo, 1936, *D. calcarata* Banks, 1904, *D. follicola* Bösenberg & Strand, 1906, *Mallos gregalis* (Simon, 1909), *Mexitlia trivittata* (Banks, 1901)) (Jackson 1979, Riechert et al. 1986, Avilés 1993, Yip and Rayor 2014).

There exists a contradiction in that the natural history and ecology of marronoids is a wellspring, yet there remains a poor understanding of the systematics of the clade. This contrast is best described by Lehtinen (1967), who when referring to his concept of the Amaurobioidea (to which many families now considered marronoids belong), described the group as being "characterized by conservatism as regards general appearance", but noted that the "structural variation in some details…is exceptionally large… and the range of habitats occupied by [the] Amaurobioidea is… wider than the ecological amplitude of any other superfamily of Araneomorpha". Understanding the evolution of this group to better understand this broad "ecological amplitude" is of paramount importance in spider biology.

Hypotheses about Potential Areas of Diversification in the Marronoid Tree of Life

While the ecology of marronoids is not fully understood, there are several species that have aquatic habitat associations, including the only fully aquatic spider, *Argyroneta aquatica* (Clerck, 1757) (Dictynidae). Previous work has suggested that aquatic dictynids may share some degree of evolutionary history and may even form a clade, but thus far the evidence for this has been inconclusive (Spagna et al. 2010, Crews et al. 2020). In addition to the dictynids, aquatic associations occur in other marronoids, such as *Desis* Walckenaer, 1837 (Baehr et al. 2017). If aquatic-associated clades occur across the marronoids, we hypothesize that this association may correspond to a rate shift (or shifts) because of expansion into a novel niche space. Bayesian Analysis of Macroevolutionary Mixtures (BAMM) permits the inference of diversification rates on phylogenetic trees (Rabosky 2014, Rabosky et al. 2014). Paired with a strong understanding of the biology, biogeography, or ecology of a clade, these analyses can provide additional context. As an example, Garrison et al. (2016), found that BAMM indicated the highest rates of diversification occurred within the RTA clade.

Museum Genomics as a Solution

Museums serve as libraries of biodiversity on Earth. How this library is utilized has changed with advanced imaging technologies and the internet, permitting widespread digitization and dissemination of data. Similarly sequencing technology has revealed potential to unlock the genetic biodiversity in these collections, often in cases when the specimens were not collected with genetic data in mind (Yeates et al. 2016). The utility of museum specimens for phylogenetics has been widely recognized since Sanger sequencing of individually amplified loci began to be used as a tool in phylogenetics (Wandeler et al. 2007). This has led to efforts such as the Barcode of Life Database to generate a DNA sequence barcode (in metazoans, cytochrome c oxidase subunit I, or COI) for every species, with a corresponding specimen vouchered (Ratnasingham and Hebert 2007), though often these initiatives have relied heavily on freshly collected material. High-throughput sequencing technologies have further allowed for rapid, and comparatively less expensive, sequencing of whole genome data (in some cases from museum specimens), providing finer resolution for phylogenetic study (Young and Gillung 2020). Over the past decade, pipelines using archival museum specimens have been developed for a variety of types of genomic data useful in phylogenomics, including restriction-site associated digest sequencing and sequence capture approaches (such as anchored hybrid enrichment (AHE) and ultraconserved elements (UCEs) (Tin et al. 2014, Derkarabetian et al. 2019, Zhang et al. 2019b)). In many cases, destructive sampling is necessary to obtain DNA. By obtaining whole-genome data from museum specimens, instead of a few loci using Sanger sequencing, we are able to maximize the data we can access from these specimens. Zhang et al. (2019a) proposed harvesting ultraconserved elements in silico (computationally) from low-coverage whole genome sequencing data and provided an example with hexapods. We propose and hypothesize that this approach will provide a model for successfully extracting UCE loci and legacy Sanger loci in tandem, from archival arachnid specimens preserved in ethanol, further allowing for future use of genomic information like functional genes under selection that may not be used for phylogenetic inference.

Methods

Using an exemplar approach, 1–15 representatives from the following families were selected for sequencing: Agelenidae, Amaurobiidae, Desidae, Cybaeidae, Cycloctenidae, Dictynidae, Hahniidae, Stiphidiidae, and Toxopidae. These specimens were selected from a combination of availability of holdings at the California Academy of Sciences, recency of collection (to improve concentration of DNA extracted), and were sought to represent the diversity across the families, including taxa known to render some families paraphyletic in previous analyses such as Wheeler et al. (2017) and Crews et al. (2020). This study contains 48 newly sequenced taxa (Supplementary Table S1), and paired-end raw Illumina reads are available under BioProject PRJNA996962 from the National Center for Biotechnology Information (NCBI) SRA. An additional 56 terminals (taxa) were downloaded from the SRA in split read format using the SRA Toolkit version 3.0.0, and original accession numbers are provided in Supplementary Table S2 (Fernández et al. 2014, Garrison et al. 2016, Carlson and Hedin, 2017, Starrett et al. 2017, Wood et al. 2018, Wu et al. 2020, Kallal et al. 2021, Arakawa et al. 2022, Azevedo et al. 2022, Li et al. 2022). Sanger loci for COI, H3, 12S ribosomal RNA (12SrRNA), 16S ribosomal RNA (16SrRNA), 18S ribosomal RNA (18SrRNA), 28S ribosomal RNA (28SrRNA) were downloaded from GenBank (Supplementary Table S3; Croucher et al. 2004, Bi et al. 2005, Ratnasingham and Hebert 2007, Spagna and Gillespie 2008, Blackledge et al. 2009, Copley et al. 2009, Miller et al. 2010, Spagna et al. 2010, Arabi et al. 2012, Bayer and Schönhofer 2013, Bolzern et al. 2013, Telfer et al. 2015, Blagoev et al. 2016, Okumura et al. 2017, Sikes et al. 2017, Wheeler et al. 2017, Crews et al. 2020, Macías-Hernández et al. 2020, Walker et al. 2020, Domènech et al. 2022, Gorneau et al. 2022, Kuralt et al. 2022, Roslin et al. 2022, Castellucci et al. 2023) and integrated into a combined UCE and Sanger locus matrix as described below.

Depending on the physical size of the sample and availability of tissue from the specimen, anywhere from a single leg fragment to all 4 legs on one side were removed for extraction, with all legs on one side generally removed from smaller specimens to maximize DNA yield. Legs were placed directly in 180 µl of ATL buffer with no maceration of the tissue performed. DNA was extracted using the QIAGEN QIAamp Micro DNA extraction kit (Hilden, Germany) modifying the standard protocol by increasing the proteinase K from 20 µl to 60 µl and including the optional step of adding 1 µl of 1 ng/µl carrier RNA. The first soak in proteinase K and ATL buffer was completed overnight in a VWR thermomixer (Radnor, PA, USA) at 900 rpm at 56 °C. Extracted DNA was eluted using the AE elution buffer provided by the extraction kit in a single elution of 50–55 µl. DNA was quantified using the High Sensitivity Assay Kit on a Qubit Fluorometer, and quality for some samples was assessed using 260/280 and 260/230 ratios with a Nanodrop spectrophotometer (both from ThermoFisher Scientific, Waltham, MA, USA). Starting DNA inputs ranged from 27.7 to 5,280 ng. For 41 samples, extracted DNA was sent to MedGenome (Hayward, CA, USA) for library preparation and Illumina NovaSeq 2 x 150 (paired-end) low-coverage whole genome sequencing (lcWGS). Seven samples, CASENT9024965 (*Penestomus egazini* Miller, Griswold & Haddad, 2010), CASENT9031755 and CASENT9031736 (*Saltonia incerta* (Banks, 1898)), CASENT9112234 (*Cybaeolus pusillus* Simon, 1884), CASENT9081477 and CASENT9118873 (*Brommella punctosparsa* (Oi, 1957)), and CASENT9112257 (*Funny valentine* Lin & Li, 2022) (Lin et al. 2022), were part of a library made using the NEBNext UltraTM II DNA Library Prep Kit (New England BioLabs, Ipswich, MA, USA) and sequenced by Novogene (West Coast: Sacramento, CA, USA) for Illumina NovaSeq 2 x 150 (paired-end) lcWGS. For all samples except *P. egazini*, the standard library preparation protocol was modified to include 12–20 cycles of PCR and an additional 0.9× bead wash.

Illumina raw reads were run through the program fastp version 0.22.0 in compressed format (Chen et al. 2018) to remove adapters, oligos, and perform a quality check. All reads were then assembled de novo (i.e., without a reference genome) using the program SPAdes version 3.14.1 (Bankevich et al. 2012). These reads were then converted to 2bit format using the tool FaToTwoBit (Kent 2002).

Our UCE dataset included 93 ingroup terminals and eleven outgroups from the families Uloboridae Thorell, 1869, Deinopidae C.L. Koch 1850, Oecobiidae Blackwall, 1862, Hersiliidae Thorell, 1869, Titanoecidae, Zodariidae Thorell, 1881, and Sparassidae, based on previously recovered putative relationships for a final UCE matrix of 104 terminals. Ultraconserved elements were harvested from the assembled low-coverage genomes using PHYLUCE version 1.7.1 (Faircloth 2016), with the UCE probe set for spiders designed by Kulkarni et al. (2020), heretofore referred to as spider probes, and the UCE probe set for spiders in the RTA clade designed by Zhang et al. (2023), heretofore referred to as RTA probes. To accomplish this, the following commands were run sequentially: phyluce_probe_run_multiple_lastzs_sqlite, phyluce_probe_slice_sequence_from_genomes (from PHYLUCE Tutorial III: Harvesting

UCE Loci From Genomes), and then the process returned to the extracting UCE loci step at phyluce_assembly_match_contigs_to_probes, phyluce_assembly_get_match_counts, and phyluce_assembly_get_fastas_from_match_counts, (from PHYLUCE Tutorial I: Extracting UCE loci). The UCEs were then assembled and aligned in MAFFT (Katoh and Standley 2013) using internal trimming in GBlocks version 0.91b (Castresana 2000, Talavera and Castresana 2007) as recommended by the PHYLUCE documentation for lineages >50 mya divergence using phyluce_align_seqcap_align, phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed, and phyluce_align_get_align_summary_data. Aligned UCE loci were then cleaned using phyluce_align_remove_locus_name_from_files. Final data matrices of 25% and 50% gene occupancy (the percent of terminals with sequence data for each locus) were created using phyluce_align_get_only_loci_with_min_taxa, and concatenated using phyluce_align_concatenate_alignments.

The RTA probe alignment produced a matrix of 104 taxa with 1,277 loci at 50% gene occupancy. For the matrix representing 25% gene occupancy, RTA probe alignment produced a matrix of 104 taxa with 3,164 loci. The spider probe alignment produced a matrix of 104 taxa with 515 loci at 50% gene occupancy. For the matrix representing 25% gene occupancy, the spider probe alignment produced a matrix of 104 taxa with 1,225 loci.

The partition file was converted to NEXUS format and was input along with the PHYLIP matrix for phylogenetic inference in IQ-TREE2 version 2.1.2 (Nguyen et al. 2015). Models of molecular evolution were selected using the built-in program ModelFinder for each locus (Kalyaanamoorthy et al. 2017). An IQ-TREE2 maximum likelihood phylogeny was inferred with 10,000 UFboot (Nguyen et al. 2015, Hoang et al. 2018) and SH-like approximate likelihood ratio test (SH-aLRT) replicates using the command iqtree2 -s [PHYLIP matrix here] -p [NEXUS partition here] -bb 10000 -alrt 10000. For the 50% taxa represented per locus phylogeny, gene and site concordance factors (gene concordance factor (gCF) and site concordance factor (sCF), respectively) were calculated in IQ-TREE2 as in Minh et al. (2020). For the sCF analysis, the assumed species tree (the maximum likelihood tree inferred in IQ-TREE2), is compared with the alignment file to identify the fraction of phylogenetically informative sites that support a particular node using the command iqtree2 -te [maximum likelihood tree here] -s [PHYLIP matrix here] --scfl 100 --prefix concord. For the gCF analysis, individual trees for each locus were recovered using the command iqtree2 -s [PHYLIP matrix here] -S [NEXUS partition here] --prefix loci -T AUTO, which models each locus using ModelFinder (Kalyaanamoorthy et al. 2017) and infers a maximum likelihood tree using IQ-TREE2 from this. Each individual locus tree was then compared with the assumed species tree (the maximum likelihood tree inferred) using the command iqtree2 -t [maximum likelihood tree here] --gcf loci.treefile --prefix concord.

To broaden taxon representation, legacy Sanger loci were harvested from the lcWGs. Sanger sequences of *Agelenopsis pennsylvanica* (C.L. Koch, 1843) were downloaded for the following loci: COI (accession number KY017545), H3 (accession number KY018083), 12SrRNA (accession number KY015266), 16SrRNA (accession number KY01569), 18SrRNA (accession number KY016263), 28SrRNA (accession number KY016881), and used as reference sequences. A single FASTA file with these sequences, as well as every contigs.fasta file for each SPAdes assembly was input into Geneious Prime (2023) version 2023.0.2. The function "Map to Reference" in Geneious was then used to map the contigs.fasta sequences to the *A. pennsylvanica* sequences, with all default parameters maintained (i.e., Mapper set at Geneious, Sensitivity set at Highest Sensitivity/Slow, Fine Tuning set at None (fast/read mapping)). Once all Sanger data were harvested from the genomic data, these data were exported as a FASTA file and integrated with a FASTA file containing 97 terminals with Sanger-only data downloaded from GenBank (Supplementary Table S3). These sequences were then aligned using the program AliView (Larsson 2014) which employs MUSCLE (Edgar 2004), and the program GBlocks version 0.91b (Castresana 2000) for the rRNA sequences. Alignments were exported as a FASTA file for each gene and then imported to Mesquite (Maddison and Maddison 2021) for concatenation. These files were exported in PHYLIP format for concatenation of the Sanger dataset and the UCE dataset in Geneious, and a concatenated file was exported from Geneious for analysis in IQ-TREE2. The partition file was amended to include the partition information regarding the additional 6 Sanger loci. The combined UCE and Sanger datasets resulted in 201 terminals (189 ingroup taxa), and was analyzed using the same parameters as for the UCE-only dataset above, including model optimization using ModelFinder (Kalyaanamoorthy et al. 2017).

To identify heterogeneous patterns in evolutionary rates, BAMM v. 2.5.0 was implemented (Rabosky 2014), consistent with the methods of Bond et al. (2020). The program requires an ultrametric tree, which was converted from the resulting maximum likelihood tree using the chronos function in the R package ape (Paradis and Schliep 2019). Priors were set using the function setBAMMprior, which requires an input ultrametric tree and the total number of taxa used in the clade. For the total number of taxa, a conversion of current family-level species counts from the World Spider Catalog with the taxonomy reflected by this work as well as as the supplementary material and methods of Gorneau et al. (2023) to calculate an estimate of the species diversity of each family were used.A control file specifying inputs included the following specifications: 100,000,000 Markov chain Monte Carlo generations, expected shifts = 1.0. Specific, clade-level species estimates at the family level were used to determine the amount of missing representatives in the phylogeny, and involved 2 methods: (i) direct counts from species in the World Spider Catalog (2023) for each family, and (ii) estimates of described plus undescribed species for each family adapted from Gorneau et al. (2023). Two metrics were calculated to evaluate the effect of these 2 methods on the rate shifts inferred. Analyses were conducted using both the maximum likelihood tree from the RTA probe plus Sanger locus analysis, and a tree with Sanger only terminals dropped, for a total of 4 analyses. The program was run in the command line and outputs were visualized using BAMMtools version 2.1.10 in RStudio (Rabosky et al. 2014), using the command getBestShiftConfiguration. R code is available from Zenodo [https://doi.org/10.5281/zenodo.8360942].

Results

Of the newly generated sequence data, a median value of 985.5 UCEs were recovered (mean 880.4), ranging from 6 to 1,121 UCEs per sample for the spider probes. From the RTA probes, a median value of 2,541 UCEs were recovered (mean 2,280.9), ranging from 23 to 2,920 UCEs per sample. Of the 56 remaining samples downloaded from the SRA, a median value of 456.5 UCEs was recovered (mean 448.8), ranging from 11 to 833 UCEs per sample from the spider probes. From the RTA probes, a median value of 954.5 UCEs were recovered (mean 952.5), ranging from 29 to 1,771 UCEs per sample. Overall, for the spider probes, a median value of 619 UCEs was recovered (mean 648), ranging from 6 to 1,121 UCEs per sample. For the RTA probes, a median value of 1,323 UCEs was recovered (mean

1,565.6), ranging from 23 to 2,920 UCEs per sample. Counts per sample are available in Supplementary Table S4.

Phylogeny Inferred from UCEs

Rooted with the "UDOH grade" (Fernández et al. 2018), Sparassidae + the marronoids were recovered as monophyletic (Figs. 3 and 4, RTA probe UFBoot = 100, spider probe UFBoot = 100), and marronoids were recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100). Within the marronoids, the Amaurobiidae was recovered as paraphyletic with the subfamily Amaurobiinae recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100) and sister to the rest of the marronoids, and the Macrobuninae Lehtinen, 1967 recovered as monophyletic and sister to the hahniids, cybaeids, toxopids, and dictynids (RTA probe UFBoot = 100, spider probe UFboot = 100). Agelenidae was recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100), with *Tamgrinia* Lehtinen, 1967 sister to the rest of the agelenids, and subfamilies Ageleninae, less *Eratigena* Bolzern, Burckhardt & Hänggi, 2013, (RTA probe UFBoot = 100, spider probe UFBoot = 100) and Coelotinae F.O. Pickard-Cambridge (RTA probe UFBoot = 100, spider probe UFBoot = 100) were also recovered as monophyletic. The Cycloctenidae were recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100). A group containing Stiphidiidae and Desidae was recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100), though neither the stiphidiids nor the desids are reciprocally monophyletic. Rather, *Aorangia* Forster & Wilton, 1973 is recovered as sister to all other stiphidiids and desids. Within this clade, we recover a primarily stiphidiid monophyletic grouping containing *Neoramia* Forster & Wilton, 1973, *Stiphidion*, *Forsterina* Lehtinen, 1967, and *Taurongia* Hogg, 1901 and a primarily desid monophyletic grouping containing *Desis* (Desinae) as sister to all other desids (RTA probe UFBoot = 100, spider probe UFBoot = 100). Within the desids, Ischaleinae Davies, 1990 (here *Badumna* Thorell, 1890, *Paramatachia* Dalmas, 1918, and *Ischalea* L. Koch, 1872) was rendered paraphyletic by the inclusion of the Metaltellinae Lehtinen, 1967 (*Metaltella simoni* Keyserling, 1878, RTA probe UFBoot = 100, spider probe UFBoot = 100) and the monophyletic Amphinectinae (here *Amphinecta* and *Mamoea* Forster & Wilton, 1973, RTA probe UFBoot = 100, spider probe UFBoot = 100). A clade containing *Badumna*, cf. *Badumna*, *Otagoa* Forster, 1970, cf. *Desis*, and *Paramatachia* was recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100). The Porteriinae Lehtinen, 1967 was recovered as monophyletic (here *Porteria* Simon, 1904, *Cambridgea* L. Koch, 1872, and *Corasoides* Butler, 1929, RTA probe UFBoot = 100, spider probe UFBoot = 100). A primary clade of Hahniidae was recovered as monophyletic to the exclusion of *Cicurina* and *Mastigusa* Menge, 1854 (Koch and Berendt 1854) (RTA probe UFBoot = 100, spider probe UFBoot = 100). *Mastigusa* was recovered within the Cybaeidae with the spider probes (UFBoot = 66), but sister to the Toxopidae and Dictynidae and with low support in the RTA probes (UFBoot = 42). Cybaeidae, excluding *Mastigusa*, was recovered as monophyletic (here *Blabomma* Chamberlin & Ivie, 1937, *Cybaeozyga* Chamberlin & Ivie, 1937, *Cybaeus* L. Koch, 1868, and *Calymmaria* Chamberlin & Ivie, 1937, RTA probe UFBoot = 100, spider probe UFBoot = 100). A group containing *Cicurina* (currently Hahniidae)

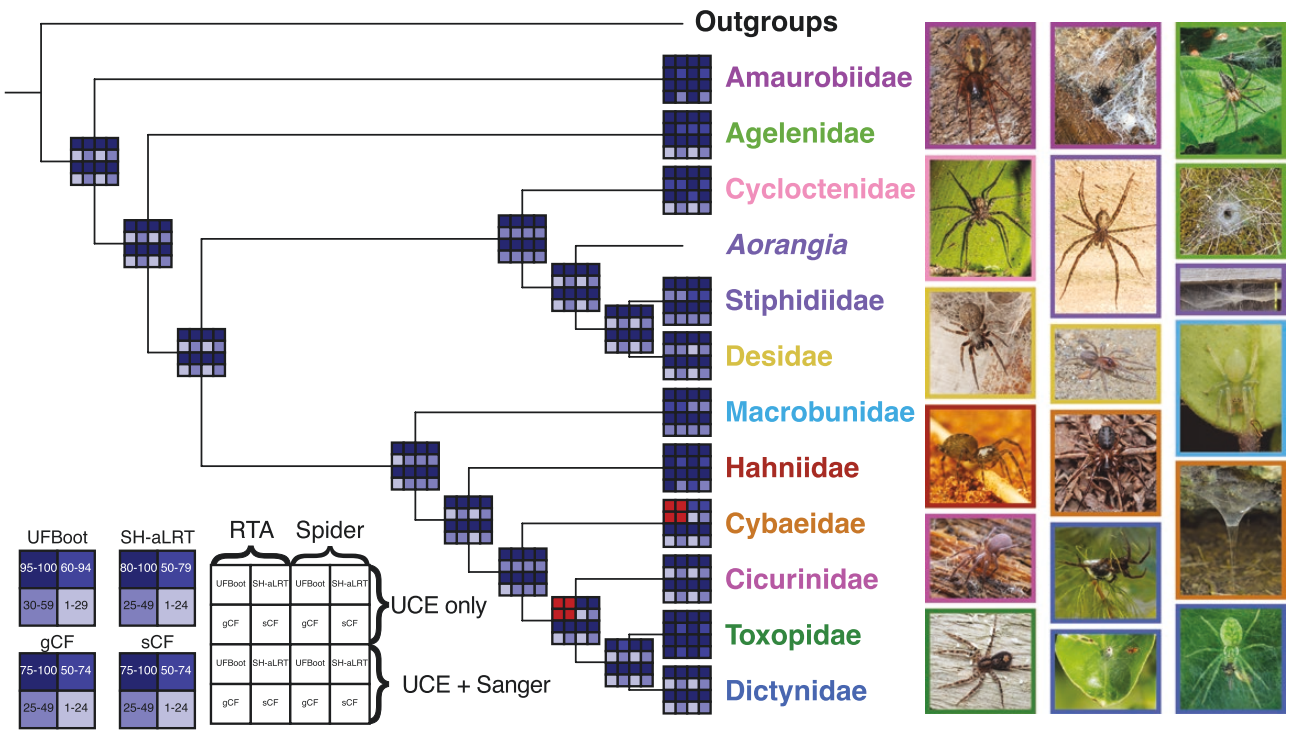

Fig. 3. Summary tree of marronoid families from maximum likelihood inference in IQ-TREE2 of UCE loci, and UCE locicombined with legacy Sanger loci. Grids at the nodes correspond to support values in various analyses as indicated in the legend to the lower left. Images to the right of the phylogeny are of marronoid spiders observed on iNaturalist, used with permission from contributors. First column, top to bottom: *Amaurobius fenestralis* by iNaturalist user wp-polzin, *Cycloctenus* sp. by Dustin LaMont, *Badumna longinqua* by Andrès Costa, *Neoantistea magna* by Ruan Booysen, *Cicurina cicur* by Julien C., *Toxopsoides huttoni* by Cameron Rodda. Second column, top to bottom: *Amaurobius ferox* in typical web by Caveman, *Stiphidion facetum* by Linda Coster, *Desis martensi* by Marcus F.C. Ng, *Cybaeus* sp. by Tony Iwane, *Argyroneta aquatica* by Ben Williams, *Nigma puella* male and female in web by David Gil Pérez. Third column, top to bottom: *Agelena labyrinthica* by Sabine Gasparitz, *Agelena labyrinthica* web by Lenni Gottlieb, *Stiphidion facetum* web by iNaturalist user davidkaipatiki, *Malenella nana* by Matías Gargiulo, *Calymmaria persica* in web by Candice Talbot, *Nigma walckenaeri* by Ewelina Oszust.

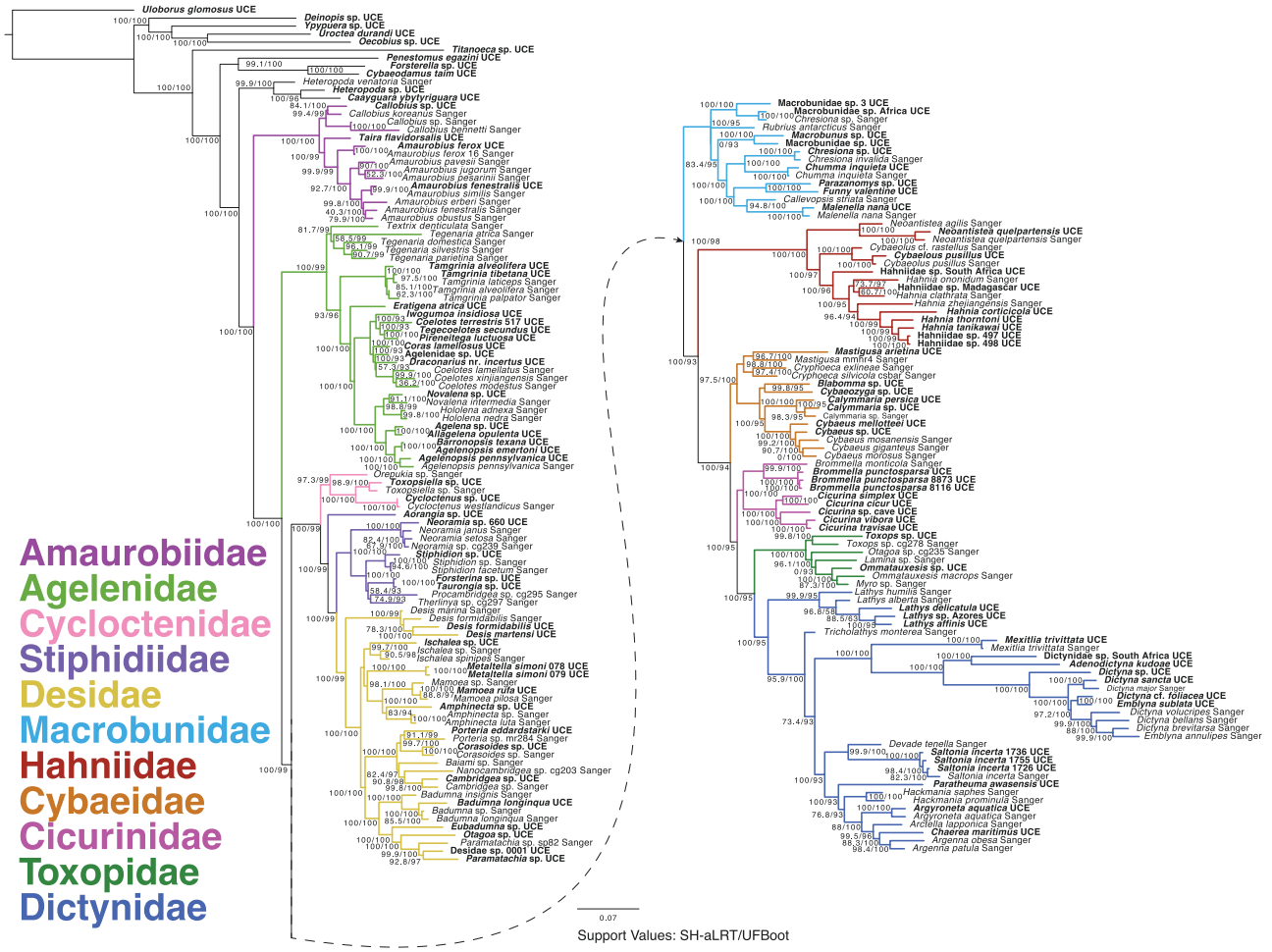

Fig. 4. Phylogeny of the marronoids from IQ-TREE2 maximum likelihood inference after 10,000 UFboot replicates (support are UFboot values) for 50% gene occupancy matrix of RTA spider probes combined with Sanger loci (COI, H3, 12SrRNA, 16SrRNA, 18SrRNA, 28SrRNA). Tips with data for UCE and Sanger loci in bold, and tips with only legacy Sanger loci not in bold. Families in the marronoid clade are indicated by color. Numbers at nodes correspond to SH-aLRT value/UFBoot value.

and *Brommella* (currently Dictynidae; RTA probe UFBoot = 100, spider probe UFBoot = 100) was also recovered as monophyletic. A group of Toxopidae + Dictynidae was recovered as monophyletic (RTA probe UFBoot = 100, spider probe UFBoot = 100). Toxopidae and Dictynidae were both recovered as reciprocally monophyletic (to the exclusion of *Brommella*, RTA probe UFBoot = 100, spider probe UFBoot = 100). The genus *Lathys* Simon, 1884 is recovered as sister to all other dictynids (RTA probe UFBoot = 100, spider probe UFBoot = 100).

The results from the 25% taxa represented per locus matrix had a nearly concordant topology with the 50% matrix for both the RTA and spider probes described above (see Appendix B, Supplemenatary Figures S1 and S2 comparison).

Integrated UCE and Sanger Phylogeny

The matrix integrating the 50% gene occupancy matrix of UCEs with Sanger data resulted in a topology largely congruent with that of the UCE-only trees. The additional sampling effort resulted in expanded taxon sampling in support of subfamilial relationships and additional taxon sampling for Stiphidiidae, as well as confidently placing *Mastigusa* in Cybaeidae with high support (Figs. 3 and 4, Sanger and RTA probe UFBoot = 100, Sanger and spider probe UFBoot = 100).

Results of SH-aLRT, sCF, gCF Analysis

Except for the movement of *Mastigusa* in some analyses, and the relative position of Toxopidae and Dictynidae in 1 analysis, all SH-aLRT values at each familial and backbone node were greater than 85%.

For the RTA and spider probe 50% occupancy matrix trees, the sCF analysis resulted in a median value of 46.25% (mean: 49.8%) with the highest value (97%) at the node containing both representatives of *Metaltella simoni*, and the lowest for a subset of *Saltonia incerta* (sample numbers 1746 and 1726, 0%). The gCF analysis for these trees resulted in a median value of 50% (mean: 51.1%) with the highest value (100%) at the node containing all *Saltonia incerta* and the lowest for the genus *Amaurobius* C.L. Koch 1837 (0%).

For the Sanger-RTA and Sanger-spider probe 50% occupancy matrix trees, the sCF analysis resulted in a median value of 42.15% (mean: 47.5%) with the highest value (98.1%) at the node containing an *Amaurobius fenestralis* and *Am. similis*, and the lowest for 2 Sanger-only representatives of *Ischalea* and a node containing *Mamoea rufa* (Berland, 1931) and *M. pilosa* (Bryant, 1935) (0%). The gCF analysis for these trees resulted in a median value of 41.7% (mean: 44.9%) with multiple nodes represented by each the highest value (100%) and the lowest value (0%).

BAMM

The BAMM analysis detected a single rate shift in the family Agelenidae, less *Tegenaria* Latreille, 1804 and *Textrix* Sundevall, 1833, in all analyses (Fig. 5, Appendix B, Supplementary Figures S3 and S4) except the RTA plus Sanger analysis where the proportion of missing taxa was based on species estimates from Gorneau et al. (2023) (Appendix B, Supplementary Figure S5).

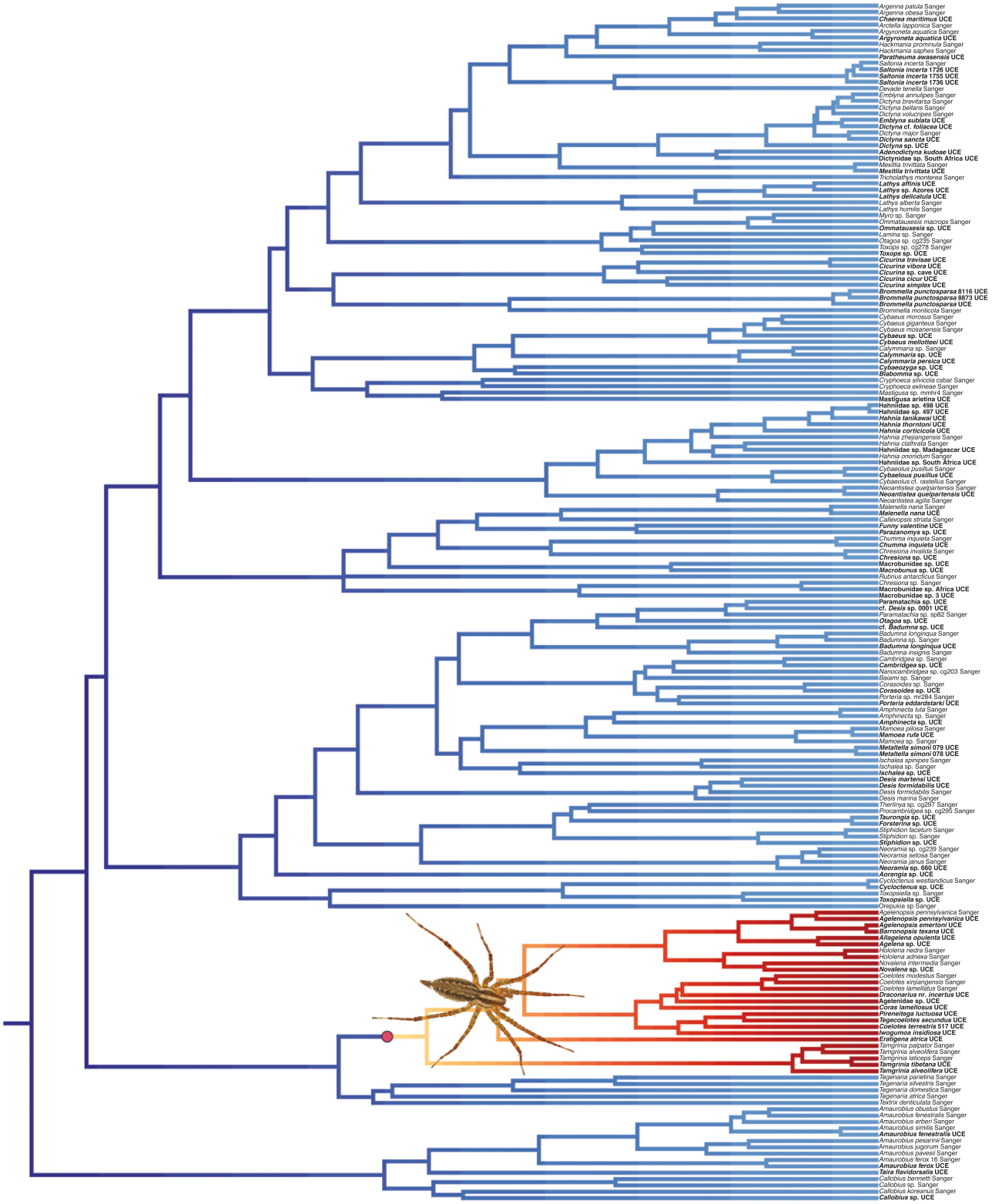

Fig. 5. Result of BAMM inference best rate shift configuration for the RTA probe plus Sanger loci maximum likelihood tree with sampling estimates based on species totals from the World Spider Catalog (2023), plotted in BAMMtools. Red indicates significant evolutionary rate shifts. Photo of *Agelenopsis* sp. uploaded to Flickrby Judy Gallagher, used with permission.

Taxonomy

Family Amaurobiidae Thorell, 1869 (**new circumscription**)

Type genus. *Amaurobius* C. L. Koch, 1837 (type species: *Aranea fenestralis* Ström, 1768).

Diagnosis. Amaurobiidae can be distinguished by having a "pseudocalamistrum" (Wheeler et al. 2017, Lehtinen 1967, Jocqué and Dippenaar-Schoeman 2006 (Figure 8F)); the trichobothrial bases are transversely ridged (Griswold et al. 2005 (Figures 147B, 156D)); the conductor short, usually hyaline or partially sclerotized; at least 1 tegular apophysis plus a tegular median apophysis, and a cribellum usually divided into 2 fields of strobilate spigots (Griswold et al. 2005 (Figures 88A, 96A–B)).

Composition. After removing Macrobuninae, 4 subfamilies remain in Amaurobiidae: Altellopsinae Lehtinen, 1967 (Neotropical), Amaurobiinae Thorell, 1869 (Holarctic), Arctobiinae Leech, 1972 (Holarctic), and Ovtchinnikoviinae Marusik, Kovblyuk, & Ponomarev, 2010 (Palearctic).

Remarks. See Wheeler et al. (2017).

List of included subfamilies and genera:

Altellopsinae Lehtinen, 1967: *Altellopsis* Simon, 1905, *Yacolla* Lehtinen, 1967, *Neuquenia* Mello-Leitão, 1940, *Rhoicinaria* Exline, 1950, *Tugana* Chamberlin, 1948.
Amaurobiinae Thorell, 1869: *Amaurobius* C. L. Koch, 1837, *Auhunga* Forster & Wilton, 1973, *Callobius* Chamberlin, 1947, *Cybaeopsis* Strand, 1907, *Dardurus* Davies, 1976, *Daviesa* Koçak & Kemal, 2008, *Ecurobius* Zamani & Marusik, 2021, *Himalmartensus* Wang & Zhu, 2008, *Maloides* Forster & Wilton, 1989 (Platnick 1989), *Muritaia* Forster & Wilton, 1973, *Otira* Forster & Wilton, 1973, *Oztira* Milledge, 2011, *Pimus* Chamberlin, 1947, *Storenosoma* Hogg, 1900, *Taira* Lehtinen, 1967, *Tymbira* Mello-Leitão, 1944, *Virgilus* Roth, 1967, *Wabarra* Davies, 1996, *Waitetola* Forster & Wilton, 1973.
Arctobiinae Leech, 1972: *Arctobius* Lehtinen, 1967.
Ovtchinnikoviinae Marusik, Kovblyuk, & Ponomarev, 2010: *Ovtchinnikovia* Marusik, Kovblyuk & Ponomarev, 2010.

Family Macrobunidae Petrunkevitch, 1928 (**new rank**)

Type genus: *Macrobunus* Tullgren, 1901 (type species: *Myro backhauseni* Simon, 1896).

Diagnosis. Macrobunidae **new rank** can be distinguished from other families by usually having multiple apophysis (e.g., VTA, RvTA, RdTA, DTA) on the male palpal tibiae, including an RTA bearing an internal branch related to a stridulatory area at the cymbium; reduced anterior median eyes (Griswold et al. 2005, Almeida-Silva et al. 2015 (Figures 1A, 2A–B), Wheeler et al. 2017); retromarginal side of cheliceral fang furrow with 1 to several differential denticles (Griswold et al. 2005, Almeida-Silva et al. 2015); chilum, when present, entire or divided; single row of tarsal trichobothria with bases smooth to longitudinally striate (Griswold et al. 2005 (Figure 151C, 156E), Almeida-Silva et al. 2015), except in *Chumma* Jocqué, 2001 in which it is transversely striate; one or more tegular apophyses plus a tegular median apophysis, and in some cases an embolar apophysis. Additionally, some genera have an enlarged male palpal tibiae, sometimes bearing an internal gland suspected to be connected to an opening on the DTA (Wheeler et al. 2017). Typical cribellate Macrobunidae have an entire cribellum; however, in some representatives, the cribellum is divided into 2 fields of strobilate spigots (Griswold et al. 2005 (Figures 88A, 96A–B)). In the ecribellate Macrobunidae, the cribellum is lost and a colulus is present (e.g., *Emmenomma* Simon, 1884, *Chresiona* Simon, 1903, *Chumma*, *Hicanodon* Tullgren, 1901, some *Macrobunus*, *Neoporteria* Mello-Leitão, 1943, *Naevius* Roth, 1967, *Rubrius* Simon, 1887, *Urepus* Roth, 1967, and some *Yupanquia* Lehtinen, 1967).

Composition. As in Macrobuninae, sensu Wheeler et al. (2017).

Remarks. Wheeler et al. (2017) refer to the author of Macrobuninae as Lehtinen 1967, but in Lehtinen (1967, p. 333), it is attributed to Petrunkevitch (1928). Almeida-Silva (2013, unpublished thesis) provided diagnostic characters and putative synapomorphies to allow the definition of Macrobuninae in Wheeler et al. (2017) and suggested a provisional position within Amaurobiidae. Our phylogeny strongly supports the new rank of Macrobunidae, and we incorporate diagnostic characters from Griswold et al. (2005), Wheeler et al. (2017), and Almeida-Silva et al. (2013, unpublished thesis; 2015).

List of included genera:

Anisacate Mello-Leitão, 1941, *Auximella* Strand, 1908, *Callevopsis* Tullgren, 1902, *Cavernocymbium* Ubick, 2005, *Chresiona* Simon, 1903, *Chumma* Jocqué, 2001, *Emmenomma* Simon, 1884, *Funny* Lin & Li, 2022, *Hicanodon* Tullgren, 1901, *Livius* Roth, 1967, *Macrobunus* Tullgren, 1901, *Malenella* Ramírez, 1995, *Naevius* Roth, 1967, *Neoporteria* Mello-Leitão, 1943, *Obatala* Lehtinen, 1967, *Parazanomys* Ubick, 2005, *Pseudauximus* Simon, 1902, *Retiro* Mello-Leitão, 1915, *Rubrius* Simon, 1887, *Tasmarubrius* Davies, 1998, *Tasmabrochus* Davies, 2002, *Teeatta* Davies, 2005, *Urepus* Roth, 1967, *Yupanquia* Lehtinen, 1967, *Zanomys* Chamberlin, 1948.

Family Desidae Pocock, 1895 (**new circumscription**)

Type genus: *Desis* Walckenaer, 1837 (type species: *Desis dysderoides* Walckenaer, 1837; syn. of *Desis maxillosa* (Fabricius, 1793)).

Diagnosis. Following Wheeler et al. (2017), representatives of Desidae have 3 claws, tarsal trichobothria, and also comprise cribellate or ecribellate genera. Additionally, the palpal tibia of the male can have a complex RTA (e.g., Matachiinae with multiple, separate processes; Metaltellinae and Amphinectinae [in part] with distal and proximal processes).

Composition. Current circumscription in Wheeler et al. (2017), less *Forsterina* and *Taurongia* (transferred to Stiphidiidae), and with the inclusion of the Cedicinae Marusik, Zonstein & Koponen, 2023 to include 3 genera previously included in Cybaeidae (*Cedicus* Simon, 1875, *Cedicoides* Charitonov, 1946, *Paracedicus* Fet, 1993).

Remarks. See Wheeler et al. (2017).

List of included subfamilies and genera:

Amphinectinae Forster & Wilton, 1973: *Amphinecta* Simon, 1898, *Barahna* Davies, 2003, *Mamoea* Forster & Wilton, 1973, *Maniho* Marples, 1959, *Paramamoea* Forster & Wilton, 1973, *Rangitata* Forster & Wilton, 1973.

Cedicinae Marusik, Zonstein & Koponen, 2023: *Cedicus* Simon, 1875, *Cedicoides* Charitonov, 1946, *Paracedicus* Fet, 1993.
Desinae Walckenaer, 1837: *Desis* Walckenaer, 1837, *Poaka* Forster & Wilton, 1973.
Ischaleinae Davies 1990: *Bakala* Davies, 1990, *Ischalea* L. Koch, 1872, *Manjala* Davies, 1990.
Porteriinae Lehtinen, 1967: *Baiami* Lehtinen, 1967, *Cambridgea* L. Koch, 1872, *Corasoides* Butler, 1929, *Nanocambridgea* Forster & Wilton, 1973, *Porteria* Simon, 1904.
Matachiinae Lehtinen, 1967: *Badumna* Thorell, 1890, *Goyenia* Forster, 1970, *Paramatachia* Dalmas, 1918, *Matachia* Dalmas, 1917, *Notomatachia* Forster, 1970, *Nuisiana* Forster & Wilton, 1973.
Metaltellinae Lehtinen, 1967: *Austmusia* Gray, 1983, *Buyina* Davies, 1998, *Calacadia* Exline, 1960, *Cunnawarra* Davies, 1998, *Jalkaraburra* Davies, 1998, *Keera* Davies, 1998, *Magua* Davies, 1998, *Metaltella* Mello-Leitão, 1931, *Penaoola* Davies, 1998, *Quemusia* Davies, 1998.

Family Stiphidiidae Dalmas, 1917 (**new circumscription**)

Type genus *Stiphidion* Simon, 1902 (type species: *Stiphidion facetum* Simon, 1902).

Diagnosis. Following the inconclusive diagnosis of Wheeler et al. (2017), Stiphidiidae can be distinguished from other marronoids by having a simple posterior respiratory system of 4 tubes and may be cribellate or ecribellate; the cribellate taxa have posterior median spinneret paracribellars with multiple shafts arising from single, enlarged bases. We recovered Stiphidiidae as paraphyletic, and more thorough molecular sampling will be necessary to further delimit the family. *Aorangia* Forster & Wilton, 1973 is an ecribellate taxon, with trochanters deeply notched; the tarsal organ subdistal; the trichobothria in a double row on the tibia and a single row on the metatarsi and tarsi; with 2 retromarginal teeth, and usually 2 promarginal teeth; and the male palp with processes on the distal retrolateral surface of the tibia. Cymbium pointed distally, without median apophysis well developed (see Forster and Wilton 1973).

Composition. Current conscription + *Taurongia* Hogg, 1901 and *Forsterina* Lehtinen, 1967 from Desidae. The position of *Aorangia* remains dubious, and it is currently sister to Stiphidiidae and Desidae.

Remarks. See Wheeler et al. (2017).
List of included genera:

Aorangia Forster & Wilton, 1973, *Asmea* Gray & Smith, 2008, *Borrala* Gray & Smith, 2004, *Carbinea* Davies, 1999, *Couranga* Gray & Smith, 2008, *Elleguna* Gray & Smith, 2008, *Forsterina* Lehtinen, 1967, *Jamberoo* Gray & Smith, 2008, *Kababina* Davies, 1995, *Karriella* Gray & Smith, 2008, *Malarina* Davies & Lambkin, 2000 (Davies and Lambkin 2000a), *Marplesia* Lehtinen, 1967, *Neolana* Forster & Wilton, 1973, *Neoramia* Forster & Wilton, 1973, *Pillara* Gray & Smith, 2004, *Procambridgea* Forster & Wilton, 1973, *Stiphidion* Simon, 1902, *Tartarus* Gray, 1973, *Taurongia* Hogg, 1901, *Therlinya* Gray & Smith, 2002, *Tjurunga* Lehtinen, 1967, *Wabua* Davies, 2000 (Davies and Lambkin 2000b).

Family Cybaeidae Banks, 1892 (**new circumscription**)

Type genus: *Cybaeus* L. Koch, 1868 (type species: *Amaurobius tetricus* C.L. Koch, 1839)

Diagnosis. Cybaeidae, Cicuriniidae **new rank**, Toxopidae, and Dictynidae form a monophyletic group characterized by the presence of a complex conductor that usually surrounds the embolus and articulates with the tegulum by means of medial hematodochae. Cybaeidae can be distinguished from all other spider families by having 3 claws and lacking a cribellum (Bennett 1991, Griswold et al. 2005, Wheeler et al. 2017); a single row of tarsal trichobothria (Bennett 1991), and a very short distal segment of the posterior lateral spinnerets (Bennett 1991), with the spigots clustered (separated into 2 long vertical lines in Agelenidae).

Composition. Cybaeidae sensu Wheeler et al. (2017) and *Mastigusa* Menge, 1854 (Koch and Berendt 1854), with 3 genera previously included in Cybaeidae (*Cedicus* Simon, 1875, *Cedicoides* Charitonov, 1946, *Paracedicus* Fet, 1993) moved to Desidae in accordance with Marusik et al. (2023).

Remarks. See Wheeler et al. (2017).
List of included genera:

Allocybaeina Bennett, 2020 (Bennett et al. 2020), *Blabomma* Chamberlin & Ivie, 1937, *Calymmaria* Chamberlin & Ivie, 1937, *Cryphoeca* Thorell, 1870, *Cryphoecina* Deltshev, 1997, *Cybaeina* Chamberlin & Ivie, 1932, *Cybaeota* Chamberlin & Ivie, 1933, *Cybaeozyga* Chamberlin & Ivie, 1937, *Cybaeus* L. Koch, 1868, *Dirksia* Chamberlin & Ivie, 1942, *Ethobuella* Chamberlin & Ivie, 1937, *Neocryphoeca* Roth, 1970, *Pseudocybaeota* Bennett, 2022 (Bennett et al. 2022), *Sincybaeus* Wang & Zhang, 2022, *Symposia* Simon, 1898, *Tuberta* Simon, 1884, *Vagellia* Simon, 1899, *Willisus* Roth, 1981, *Yorima* Chamberlin & Ivie, 1942.

Family Cicurinidae Kishida, 1955 (**restored status**)

Type genus: *Cicurina* Menge, 1871 (type species: *Aranea cicurea* Fabricius, 1793).

Diagnosis. *Cicurinidae* **restored status** can be distinguished from other marronoids, including Dictynidae and Hahniidae, in lacking a cribellum and instead having a reduced colulus with several setae; 3 tarsal claws, and legs without scopulae or claw tufts (Murphy and Roberts 2015); the male palp with a variable retroventral tibial apophysis in proximal position (RvTA); and the RTA enlarged (in some case as long as the cymbium length), usually with an RTA-conductor.

Composition. Genera *Cicurina*, *Brommella* Tullgren, 1948, and *Chorizomma* Simon, 1872 (based on morphology).

Remarks. Lehtinen (1967; p. 222) considered *Chorizomma* a junior synonym of *Cicurina* and part of the tribe Chorizommatini, (Dictynidae: Cicurininae), to include *Chorizomma sylvicolus* (now *Blabomma sylvicola* (Chamberlin & Ivie, 1937), Cybaeidae). de Blauwe (1973) re-established *Chorizomma*, and it was then transferred by Murphy and Roberts (2015) to Cicurinidae. Wheeler et al. (2017) transferred all *Cicurina* to Hahniidae because an undetermined Holarctic *Cicurina* was found moderately supported as sister to all Hahniidae. Neither *Brommella* nor *Chorizomma* were included or mentioned in Wheeler et al. (2017) so the movement of *Cicurina* puts the placement of the non-type genera of the Cicuriniinae, *Brommella* and *Chorizomma*, into question. The first inclusion of *Brommella* in a molecular phylogeny suggested an unsupported relationship with *Cicurina* and *Lathys* (see Crews et al. 2020). Previously, *Brommella* was originally placed in Cicurininae with *Cicurina* and

Lathys and several genera now placed in Cybaeidae (Lehtinen 1967, Crews et al. 2020). Our phylogeny strongly supports the monophyly of *Brommella* + *Cicurina* and the new rank of Cicurinidae.

List of included genera:

Cicurina Menge, 1871, *Brommella* Tullgren, 1948, *Chorizomma* Simon, 1872.

Family Dictynidae O. Pickard-Cambridge, 1871 (**new circumscription**)

Type genus: *Dictyna* Sundevall, 1833 (type species: *Aranea benigna* Walckenaer, 1802).

Diagnosis. See Wheeler et al. (2017)

Composition. Dictynidae sensu Wheeler et al. (2017), less *Brommella*, moved to Cicurinidae, and *Funny*, moved to Macrobunidae.

Remarks. See Wheeler et al. (2017).

List of included genera:

Adenodictyna Ono, 2008, *Aebutina* Simon, 1892, *Ajmonia* Caporiacco, 1934, *Altella* Simon, 1884, *Anaxibia* Thorell, 1898, *Arangina* Lehtinen, 1967, *Archaeodictyna* Caporiacco, 1928, *Arctella* Holm, 1945, *Argenna* Thorell, 1870, *Argennina* Gertsch & Mulaik, 1936, *Argyroneta* Latreille, 1804, *Atelolathys* Simon, 1892, *Banaidja* Lehtinen, 1967, *Bannaella* Zhang & Li, 2011, *Brigittea* Lehtinen, 1967, *Callevophthalmus* Simon, 1906, *Chaerea* Simon, 1884, *Clitistes* Simon, 1902, *Devade* Simon, 1884, *Dictyna* Sundevall, 1833, *Dictynomorpha* Spassky, 1939, *Emblyna* Chamberlin, 1948, *Hackmania* Lehtinen, 1967, *Helenactyna* Benoit, 1977, *Hoplolathys* Caporiacco, 1947, *Iviella* Lehtinen, 1967, *Kharitonovia* Esyunin, Zamani & Tuneva, 2017, *Lathys* Simon, 1884, *Mallos* O. Pickard-Cambridge, 1902, *Marilynia* Lehtinen, 1967, *Mashimo* Lehtinen, 1967, *Mexitlia* Lehtinen, 1967, *Mizaga* Simon, 1898, *Myanmardictyna* Wunderlich, 2017, *Nigma* Lehtinen, 1967, *Paradictyna* Forster, 1970, *Paratheuma* Bryant, 1940, *Penangodyna* , *Phantyna* Chamberlin, 1948, *Qiyunia* Song & Xu, 1989, *Rhion* O. Pickard-Cambridge, 1871, *Saltonia* Chamberlin & Ivie, 1942, *Scotolathys* Simon, 1884, *Shango* Lehtinen, 1967, *Sudesna* Lehtinen, 1967, *Tahuantina* Lehtinen, 1967, *Tandil* Mello-Leitão, 1940, *Thallumetus* Simon, 1893, *Tivyna* Chamberlin, 1948, *Tricholathys* Chamberlin & Ivie, 1935, *Viridictyna* Forster, 1970.

Discussion

This work contains the broadest taxon sampling of the marronoid spiders since Crews et al. (2020), the densest sampling for phylogenomic inference, and provides a fully resolved, and well-supported backbone for the clade. The monophyly of the group is maintained, and the monophyly of Agelenidae, Cycloctenidae, Cybaeidae, and Toxopidae is supported. Other families, such as Amaurobiidae, Desidae, Dictynidae, Hahniidae, and Stiphidiidae are recovered as paraphyletic as currently defined and are herein relimited for consistency between the taxonomy and phylogeny. The relationships in this work differ in slight but significant ways from the topology of marronoids recovered by Wheeler et al. (2017). Consistent with Wheeler et al. (2017), Amaurobiinae is recovered as sister to the rest of the marronoids. Agelenidae, however, is sister to the clade containing the rest of the marronoids, except Amaurobiinae, which differs from Wheeler et al. (2017). Wheeler et al. (2017) recovered (Amaurobiinae + ((Agelenidae + (Macrobuninae + (Cybaeidae + (Hahniidae + (Toxopidae + Dictynidae))))) + (Cycloctenidae + (Stiphidiidae + Desidae)))). In short, our well-supported superfamilial groupings, along the marronoid backbone, differ from those recovered with weak support in Wheeler et al. (2017), which had single-digit bootstrap support in some cases. Combined with the expanded taxon sampling from legacy Sanger loci, the taxon sampling in each of these families is sufficient to resolve their phylogenetic position and provide a hypothesis for circumscribing families that were, prior to this study, paraphyletic.

The additional taxon sampling, and the integration of legacy Sanger loci added resolution to the paraphyly of Stiphidiidae and Desidae. *Forsterina* and *Taurongia* are recovered not as desids but instead as stiphidiids, and the position of *Aorangia* as sister to a clade containing all other Stiphidiidae and Desidae in all trees renders the genus of uncertain familial placement (*incertae sedis*). We have elected, for the moment, to keep *Aorangia* in Stiphidiidae because we had a sole representative taxon, and additional data may further clarify its placement. The alternative solution would be to synonymize Stiphidiidae with Desidae, considering all taxa sister to the Cycloctenidae as desids, but we feel this solution is too broad as it fails to fully consider the wide morphological range of diversity and phylogenetic structure represented in these families. At the other extreme, Wheeler et al. (2017) considered only retaining *Desis* in Desidae, and potentially including *Poaka* (Forster & Wilton, 1973). In this scenario, all other taxa would need to be relimited to the Amphinectidae. We refrained from doing so to avoid creating monogeneric (or nearly monogeneric) families.

As a result of this work, we re-establish the family Cicurinidae Kishida 1955 to include the genera *Brommella* (from Dictynidae), *Chorizomma*, and *Cicurina* (from Hahniidae). We also transfer the genus *Mastigusa* from Hahniidae to Cybaeidae, consistent with recent work by Castellucci et al. (2023). Macrobunidae Petrunkevitch, 1928 **n. rank** is herein elevated, and regarded as having priority over Chummidae. It was previously argued by Jocqué and Alderweireldt (2018) that Chummidae has priority over Macrobunidae, but this is incorrect. Although *Chresiona* is sister to *Chumma* in our analysis (consistent with Miller et al. 2010, Wheeler et al. 2017), rather than all other macrobunines (as in Dimitrov et al. 2017), the currently monogeneric "Chummidae" is nested within the macrobunines that have been described since Lehtinen (1967). Finally, our work indicates unquestionably that *Lathys* are reciprocally monophyletic and sister to all other dictynids. The branch length of *Lathys* further indicates that this is a derived group that warrants further investigation, but here we denote them as a dictynid subfamily Lathysinae.

The lcWG sequencing strategy implemented here is of particular note, and we suggest that it is highly effective for UCE phylogenomics, particularly for organisms with a relatively small genome size (<10 Gb) (Zhang et al. 2019). By indiscriminately sequencing genomic DNA from our samples at a target coverage of 10×, we were able to extract UCE loci in silico, extract legacy Sanger loci (including 12SrRNA, 16SrRNA, 18SrRNA, 28SrRNA, H3, and COI), and still retain the whole genome sequences for further genomic studies. This approach maximizes the utility of museum specimens, which may not have the high molecular weight DNA needed for traditional UCEs or AHE sequencing. An indiscriminate sequencing approach using short read technologies (e.g., Illumina) plays to the strengths of the fragmented archival DNA in museum collections preserved without the intent for use in DNA sequencing, as well as maximizes the "cost" of the destructive sampling often necessary for

DNA extraction. Furthermore, the UCEs recovered from this lcWGS strategy markedly exceed the available sequence data from the SRA, which variously include transcriptomic, mitochondrial genome, and other types of genomic data.

While our matrices represent a 50% gene occupancy at a maximum and 25% at a minimum (and less in cases with Sanger-only data) for both the RTA and spider probes, we are confident that the proportion of missing data has had a negligible impact on the backbone and family-level relationships and diagnoses within the group. Our evidence for this is the lack of significant differences between the 25% gene occupancy matrix and the 50% gene occupancy matrix, the fact that the Sanger-only legacy data (which in many cases include less than 6 loci) are recovered at logical positions within the phylogeny, and that previous work has highlighted that although missing data may be a problem that is not fully understood, biases against missing data may be overstated whereas the quality of the data present and the models may be more important (Philippe et al. 2004, Roure et al. 2013, Hosner et al. 2016). The analysis by Kulkarni et al. (2020) recovered consistent topologies with high support at gene occupancies as low as 10%.

The marronoid clade represents a remarkable showcase of some of the most interesting ecological and behavioral phenotypes in spiders. Our expectation, considering the amount of ecological diversity in this group and how this could contribute to potential diversification, was that we would see evidence of a rate shift in either the aquatic-associated Desidae or the aquatic-associated Dictynidae. However, we did not observe any rate shift in either of these groups. It is possible the generic sampling of the Dictynidae, as well as the sampling of aquatic species in this family, is simply too low in the present work to detect evidence of any evolutionary rate shift dynamics. This is understandable given our global sampling fraction ranges from 4.1% based on family-level species estimates adapted from Gorneau et al. (2023) or 6.8% in terms of described species for this speciose group. The rate shift in the Agelenidae was observed in 3 of the 4 analyses, though it is possible the exclusion of *Tegenaria* and *Textrix* from this rate shift was due to the fact that there were only Sanger loci available for these taxa. However, a rate shift in this group is not unreasonable given this is the most speciose group of marronoid spiders that make use of a distinctively funnel-shaped sheet web.

Prior to this study, a morphological and molecular basis for the relationships of many marronoid groups was lacking. The morphological characteristics observed across the group include non-synapomorphic traits, or traits that we currently understand to be non-monophyletic (e.g., the cribellum, see Ubick et al. 2005, Wheeler et al. 2017, the present study). This work provides, for the first time, a well-resolved phylogenetic hypothesis, as well as morphological diagnosis for each of the (now) eleven families in the clade. However, a morphological synapomorphy for the marronoid clade remains undiscovered.

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

Specimen Collection Statement

The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

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JAG (Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing—original draft; Writing—review & editing). SCC (Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing—review & editing), FCR (Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Visualization; Writing—original draft; Writing—review & editing), KOM (Data curation; Investigation; Formal analysis; Writing—review & editing), JCS (Investigation; Funding acquisition; Resources; Writing—review & editing), FB (Resources; Writing—review & editing), LMAS (Investigation; Resources; Writing—review & editing), LAE (Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing—review & editing)

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