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Phylogeny of the orb-weaving spider family Araneidae (Araneae: Araneoidea)

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Abstract

We present a new phylogeny of the spider family Araneidae based on five genes (28S, 18S, COI, H3 and 16S) for 158 taxa, identified and mainly sequenced by us. This includes 25 outgroups and 133 araneid ingroups representing the subfamilies Zygiellinae Simon, 1929, Nephilinae Simon, 1894, and the typical araneids, here informally named the "ARA Clade". The araneid genera analysed here include roughly 90% of all currently named araneid species. The ARA Clade is the primary focus of this analysis. In taxonomic terms, outgroups comprise 22 genera and 11 families, and the ingroup comprises three Zygiellinae and four Nephilinae genera, and 85 ARA Clade genera (ten new). Within the ARA Clade, we recognize ten informal groups that contain at least three genera each and are supported under Bayesian posterior probabilities (≥ 0.95): "Caerostrines" (*Caerostris*, *Gnolus* and *Testudinaria*), "Micrathenines" (*Acacesia*, *Micrathena*, *Ocrepeira*, *Scoloderus* and *Verrucosa*), "Eriophorines" (*Acanthepeira*, *Alpaida*, *Eriophora*, *Parawixia* and *Wagneriana*), "Backobourkiines" (*Acroaspis*, *Backobourkia*, *Carepalxis*, *Novakiella*, *Parawixia*, *Plebs*, *Singa* and three new genera), "Argiopines" (*Arachnura*, *Acusilas*, *Argiope*, *Cyrtophora*, *Gea*, *Lariniaria* and *Mecynogea*), "Cyrtarachnines" (*Aranoethra*, *Cyrtarachne*, *Paraplectana*, *Pasilobus* and *Poecilopachys*), "Mastophorines" (*Celaenia*, *Exechocentrus* and *Mastophora*,), "Nuctenines" (*Larinia*, *Larinioides* and *Nuctenea*), "Zealaraneines" (*Colaranea*, *Cryptaranea*, *Paralarinia*, *Zealaranea* and two new genera) and "Gasteracanthines" (*Augusta*, *Acrosomoides*, *Austracantha*, *Gasteracantha*, *Isoxya*, *Macracantha*, *Madacantha*, *Parmatergus* and *Thelacantha*). Few of these groups are currently corroborated by morphology, behaviour, natural history or biogeography. We also include the large genus *Araneus*, along with *Aculepeira*, *Agalenatea*, *Anepsion*, *Araniella*, *Cercidia*, *Chorizopes*, *Cyclosa*, *Dolophones*, *Eriovixia*, *Eustala*, *Gibbaranea*, *Hingstepeira*, *Hypognatha*, *Kaira*, *Larinia*, *Mangora*, *Metazygia*, *Metepeira*, *Neoscona*, *Paraplectanoides*, *Perilla*, *Poltys*, *Pycnacantha*, *Spilasma* and *Telaprocera*, but the placement of these genera was generally ambiguous, except for *Paraplectanoides*, which is strongly supported as sister to traditional Nephilinae. *Araneus*, *Argiope*, *Eriophora* and *Larinia* are polyphyletic, *Araneus* implying nine new taxa of genus rank, and *Eriophora* and *Larinia* two each. In *Araneus* and *Eriophora*, polyphyly was usually due to north temperate generic concepts being used as dumping grounds for species from southern hemisphere regions, e.g. South-East Asia, Australia or New Zealand. Although Araneidae is one of the better studied spider families, too little natural history and/or morphological data are available across these terminals to draw any strong evolutionary conclusions. However, the classical orb web is reconstructed as plesiomorphic for Araneidae, with a single loss in "cyrtarachnines"–"mastophorines". Web decorations (collectively known as stabilimenta) evolved perhaps five times. Sexual dimorphism generally results from female body size increase with few exceptions; dimorphic taxa are not monophyletic and revert to monomorphism in a few cases.

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Introduction

Few spider families have been the object of so much general interest and research as Araneidae, perhaps because many of its members are large, conspicuous (Fig. 1), abundant and often build conspicuous geometric orb webs (Fig. 2). The family therefore figures prominently in popular works (e.g. McCook, 1889; Nielsen, 1932; Kaston, 1948; Bristowe, 1958; Brunet, 1994; Forster and Forster, 1999; Bradley, 2012; Brunetta and Craig, 2012) and its species have been the target of considerable research on sexual size dimorphism (SSD) (Elgar et al., 1990; Elgar, 1991; Hormiga et al., 2000; Foellmer and Moya-Laraño, 2007; Cheng and Kuntner, 2014), behaviour (e.g. Herberstein et al., 2000; Hesselberg, 2015; Xavier et al., 2017), ecology (Turnbull, 1973), material science (e.g. Kluge et al., 2008; Agnarsson et al., 2010; Blackledge, 2012), genomics (Babb et al., 2017), pharmacology and medicine (e.g. Rash and Hodgson, 2002; Liberato et al., 2006; Fachim et al., 2011; Pineda et al., 2017), and it has been a popular object for phylogenetic speculations (e.g. Simon, 1892; Kaston, 1964; Lehtinen, 1978; Levi, 1978; Heimer and Nentwig, 1983; Levi and Coddington, 1983; Eberhard, 1990; Coddington and Levi, 1991; Shear, 1994). A search on Google Scholar revealed 13 200 publications in which the word Araneidae is included (exclusive citations), and a search on Thomson Web of Science revealed more than 1000 research papers, reflecting the scientific attention to the family.

One fundamental way to assess knowledge of araneid diversity is to measure the rate at which scientists encounter araneid lineages over time. In this sense, the

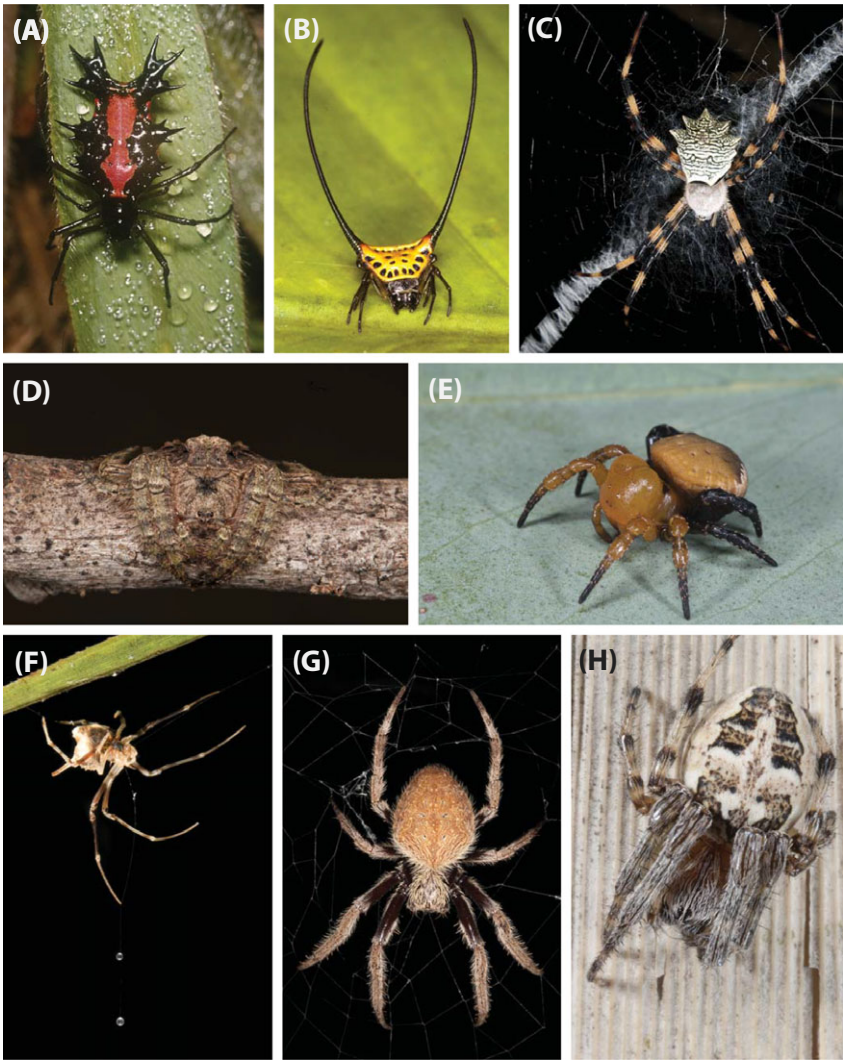


Fig. 1. Samples from Araneidae body forms. (A) *Micrathena lepidoptera* Mello-Leitão, 1941. (B) *Macracantha arcuata* (Fabricius, 1793). (C) *Argiope levii* Bjørn, 1997. (D) *Dolophones* sp. (E) *Paraplectanoides crassipes* Keyserling, 1886. (F) *Exechocentrus lancearius* Simon, 1889. (G) *Plebs eburnus*. (Keyserling, 1886). (H) *Larinioides* sp. Photos: J. A. Coddington (A); T. Szűts (H); N. Scharff (B–G).

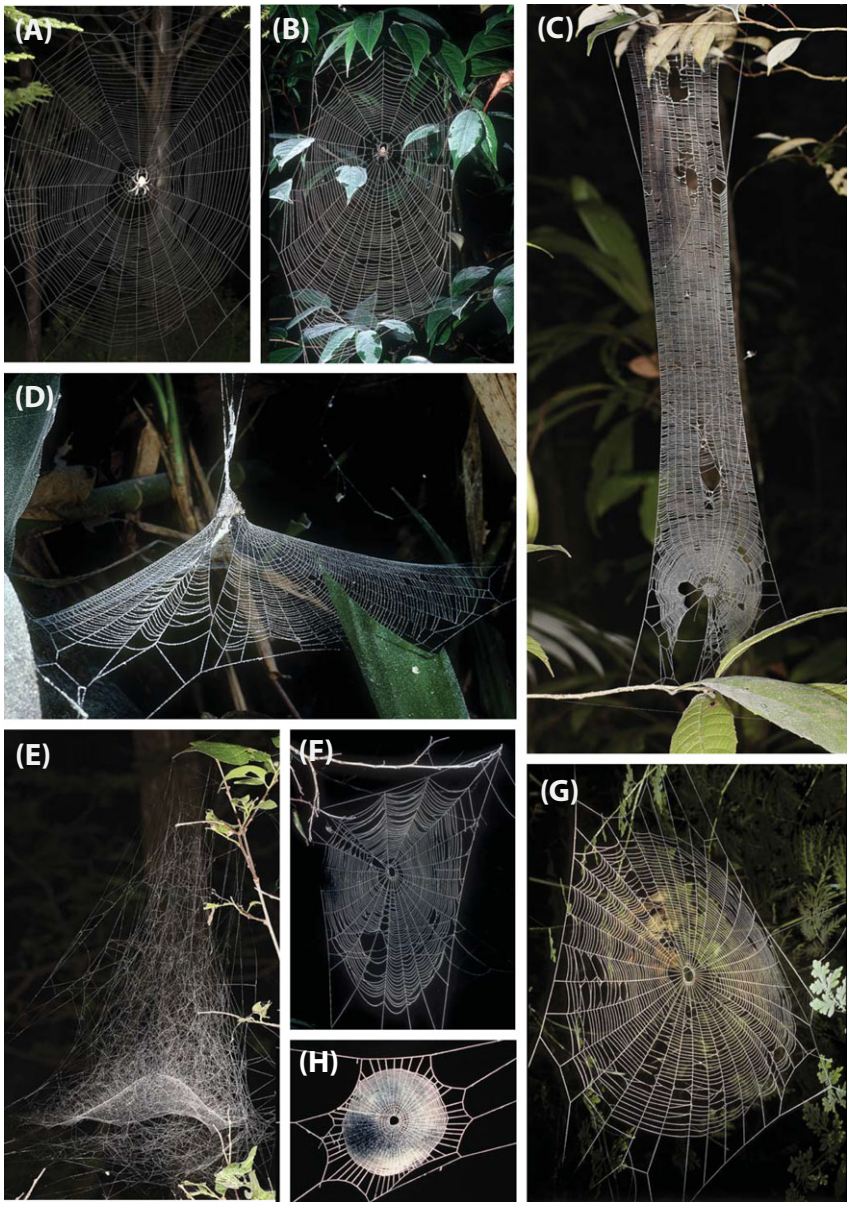


Fig. 2. Webs of Araneidae. (A) "*Eriophora*" *biapicata*. (B) *Eriophora ravilla* (C. L. Koch, 1844). (C) *Scoloderus* sp. (D) *Spilasma* sp. (E) *Mecynogea* sp. (F) *Wagneriana* sp. (G) *Macracantha arcuata* (Fabricius, 1793). (H) *Micrathena gracilis* (Walckenaer, 1805). Photos: N. Scharff (A, G); J.A. Coddington (B–F, H).

discovery, or encounter date, of a lineage such as a genus is approximately the earliest date of description of a species now included in it. More precisely, it should be the earliest collection date of a specimen assigned to the lineage, but such dates are difficult to compile, and the earliest species description date, acknowledging almost 300 years of scientific fieldwork and classification, is an acceptable proxy.

Discovery differs from phylogenetic knowledge, which will no doubt continue to increase for a long time. In phylogeny, species are moved among genera, and new genera are created or synonymized as necessary (we identify ten such candidates here). However, the species involved were usually first encountered decades if not centuries ago. For araneids, the rate of species discovery, as in most large spider families, continues to accelerate (Fig. 3c). The rate of genus discovery, in contrast, is sigmoidal, with an upper inflection point around 1915 and thereafter constant or decelerating. For spiders generally (Agnarsson et al., 2013), the rate of discovery of new species in the last 100 years has accelerated. The same is true for araneids (Fig. 3c), due principally to the work of H. W. Levi from the 1970s onwards—however, all such

graphs are bedevilled by the sparsity of taxonomists at any one time. That the encounter rate of genus-level clades may be slowing in most parts of the world suggests our awareness of the deeper branches of araneid diversity is approaching an asymptote. This being said, only North and South America had their araneid fauna properly revised and many new araneid genera may therefore turn up when the araneid faunas of other continents are revised. For example, in connection with an ongoing revision of the Australian araneid fauna, V.W. Framenau and N. Scharff (unpublished data) estimate that approximately 30 new genera will be described.

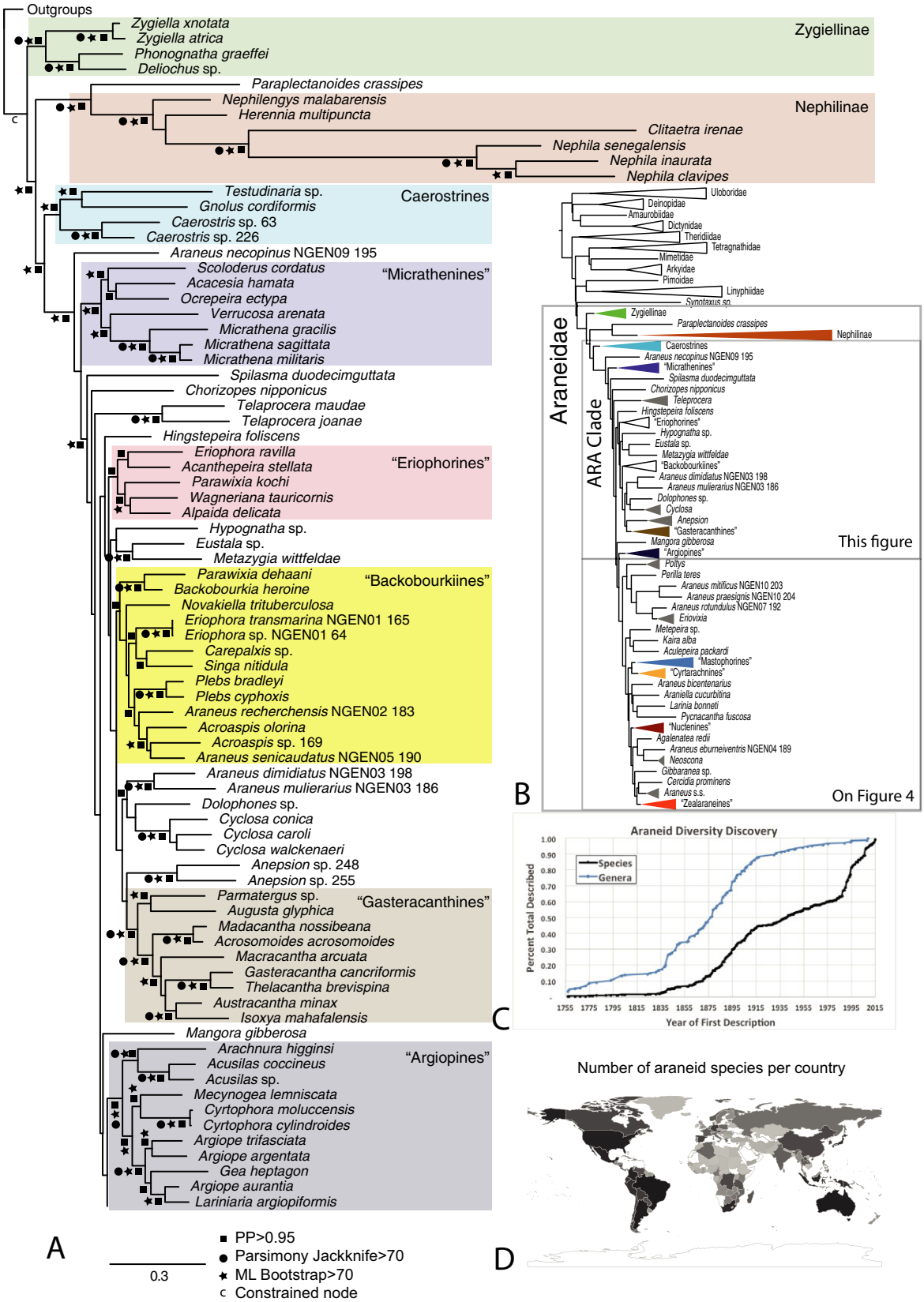
Since Simon (1893), the family Araneidae has been considered a "natural group", although its taxonomic composition has changed considerably through time. Because spiders in this family are so diverse in biology and habitus (Fig. 1), it has been difficult to diagnose it adequately. Morphological synapomorphies are hard to find. The last comprehensive classification of the family is that of Simon (1895), who changed his definition of the family between different pages in his "Histoire naturelle de Araignées". Since then no one has seriously tried to re-classify the family. As no modern classification exists, we provide a reference table to track how included genera have been classified previously (Table S1).

Over the years the family has grown to more than 3100 species in 175 genera (World Spider Catalog, 2019) and new species are constantly added, especially from the southern hemisphere. Simon's concept of Araneidae (which he called Argiopidae) was more similar to the modern-day superfamily Araneoidea than modern-day Araneidae, and until recently, Araneidae included present-day Tetragnathidae, Arkyidae, Linyphiidae and Theridiosomatidae. These were removed to make the family easier to diagnose (Coddington and Levi, 1991; Dimitrov et al., 2017). In fact, most work to circumscribe the family after Simon's seminal volumes has been done by re-delimitation and re-definitions. The placement of some genera has been particularly troublesome, with many different family associations. The genus *Arkys* Walckenaer, 1837 is a good example. Originally associated with Thomisidae and Philodromidae (Walckenaer, 1837), it was then moved to Araneidae (Simon, 1864), and further on to Mimetidae by Simon (1889) and Heimer (1984). Davies (1988) moved *Arkys* to Tetragnathidae and Scharff and Coddington (1997) moved it back to Araneidae. More recently, Blackledge et al. (2009) suggested *Arkys* as sister to Tetragnathidae and subsequently, a new family Arkyidae was established to hold *Arkys* and *Demadiana*, as sister to Tetragnathidae (Dimitrov et al., 2017). The placements suggested by Scharff and Coddington (1997), Blackledge et al. (2009) and Dimitrov et al. (2017) are all based on phylogenetic analyses, and the sister group relationships found in the two latter studies have high support.

The genus *Nephila* and related genera in the subfamily Nephilinae Simon, 1894 (*Nephila*, *Nephilengys*, *Nephilingis*, *Herennia* and *Clitaetra*) have also been difficult to place within Araneoidea. Kuntner et al. (2018) found *Nephila* to be polyphyletic, resurrected an old genus (*Trichonephila*) name to apply to the non-*Nephila* moiety, and another (*Indoetra*) for the sister to *Clitaetra*, resulting in seven nephiline genera. For most of the 20th century and before, *Nephila* and its relatives were considered as a subfamily of Araneidae until Levi (1986) suggested a placement within Tetragnathidae. Since then *Nephila* and its relatives have been moved back and forth between Tetragnathidae and Araneidae, or placed in their own family, Nephilidae (Kuntner, 2006). The latest phylogenetic and phylogenomic analyses placed *Nephila* and its relatives as sister to Araneidae (Dimitrov et al., 2012; Garrison et al., 2016; Wheeler et al., 2017; Fernández et al., 2018; Kuntner et al., 2018) or nested within Araneidae (Kuntner et al., 2013; Dimitrov et al., 2017; Kallal et al., 2018). Kallal and Hormiga (2018) included the araneid genus *Paraplectanoides* and found strong support for a sister-group relationship to nephilines. The association of nephilines with Araneidae is strongly supported in all analyses (see also Bond et al., 2014).

Scharff and Coddington (1997) presented the first comprehensive phylogenetic hypothesis for the family Araneidae based on 82 morphological characters. Their character matrix included representatives of 57 araneid genera and 13 outgroup taxa, selected to represent 19 of Simon's 25 groupings of Araneidae. They presented just one of 16 most parsimonious trees as their preferred tree, and warned that their matrix was sensitive to inclusions or exclusions of characters and taxa, and therefore was quite unstable. The aim of their phylogenetic study was to infer basic phylogenetic structure of the family by detecting major lineages and their interrelationships. More than 20 years

Fig. 3. (A) Results from the MB analyses (outgroups not shown) summarizing nodal supports including those from the ML and MP analyses. The ML and MP results with the corresponding support values are shown in Figs S1–S3 and results from all analyses are available also as supplementary tree files. (B) Results from the MB analyses showing a summary of the complete tree including outgroups. (C) The rate of species (n = 3123) and genus (n = 174) discovery since 1757. The "discovery date" of a genus is defined as that of its earliest species description. (D) Number of araneid species per country (data from GBIF, see text for discussion), where darker colour corresponds to higher species number. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.


Outgroups
Zygiella xnotata
Zygiella atrica
Phonognatha graeffei
Deliochus sp.
Zygiellinae
Paraplectanoides crassipes
Nephilengys malabarensis
Herennia multipuncta
Clitaetra irenae
Nephila senegalensis
Nephila inaurata
Nephila clavipes
Nephilinae
c
Testudinaria sp.
Gnolus cordiformis
Caerostris sp. 63
Caerostris sp. 226
Caerostrines
Araneus necopinus NGEN09 195
Scoloderus cordatus
Acacesia hamata
Ocrepeira ectypa
Verrucosa arenata
Micrathena gracilis
Micrathena sagittata
Micrathena militaris
"Micrathenines"
Spilasma duodecimguttata
Chorizopes nipponicus
Telaprocera maudae
Telaprocera joanae
Hingstepeira foliscens
Eriophora ravilla
Acanthepeira stellata
Parawixia kochi
Wagneriana tauricornis
Alpaida delicata
"Eriophorines"
Hypognatha sp.
Eustala sp.
Metazygia wittfeldae
Parawixia dehaani
Backobourkia heroine
Novakiella trituberculosa
Eriophora transmarina NGEN01 165
Eriophora sp. NGEN01 64
Carepalxis sp.
Singa nitidula
Plebs bradleyi
Plebs cyphoxis
Araneus recherchensis NGEN02 183
Acroaspis olorina
Acroaspis sp. 169
Araneus senicaudatus NGEN05 190
"Backobourkiines"
Araneus dimidiatus NGEN03 198
Araneus mulierarius NGEN03 186
Dolophones sp.
Cyclosa conica
Cyclosa caroli
Cyclosa walckenaeri
Anepsion sp. 248
Anepsion sp. 255
Parmatergus sp.
Augusta glyphica
Madacantha nossibeana
Acrosomoides acrosomoides
Macracantha arcuata
Gasteracantha cancriformis
Thelacantha brevispina
Austracantha minax
Isoxya mahafalensis
"Gasteracanthines"
Mangora gibberosa
Arachnura higginsi
Acusilas coccineus
Acusilas sp.
Mecynogea lemniscata
Cyrtophora moluccensis
Cyrtophora cylindroides
Argiope trifasciata
Argiope argentata
Gea heptagon
Argiope aurantia
Lariniaria argiopiformis
"Argiopines"
A
0.3
PP>0.95
Parsimony Jackknife>70
ML Bootstrap>70
c Constrained node
Uloboridae
Deinopidae
Amaurobiidae
Dictynidae
Theridiidae
Tetragnathidae
Mimetidae
Arkyidae
Pimoidae
Linyphiidae
Synotaxus sp.
Araneidae
ARA Clade
Zygiellinae
Paraplectanoides crassipes
Nephilinae
Caerostrines
Araneus necopinus NGEN09 195
"Micrathenines"
Spilasma duodecimguttata
Chorizopes nipponicus
Teleprocera
Hingstepeira foliscens
"Eriophorines"
Hypognatha sp.
Eustala sp.
Metazygia wittfeldae
"Backobourkiines"
Araneus dimidiatus NGEN03 198
Araneus mulierarius NGEN03 186
Dolophones sp.
Cyclosa
Anepsion
"Gasteracanthines"
Mangora gibberosa
"Argiopines"
Pollys
Perilla teres
Araneus mitificus NGEN10 203
Araneus praesignis NGEN10 204
Araneus rotundulus NGEN07 192
Eriovixia
Metepeira sp.
Kaira alba
Aculepeira packardi
"Mastophorines"
"Cyrtarachnines"
Araneus bicentenarius
Araniella cucurbitina
Larinia bonneti
Pycnacantha fuscosa
"Nuctenines"
Agalenatea redii
Araneus eburneiventris NGEN04 189
Neoscona
Gibbaranea sp.
Cercidia prominens
Araneus s.s.
"Zealaraneines"
This figure
On Figure 4
B
Araneid Diversity Discovery
Species
Genera
Percent Total Described
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
1755 1775 1795 1815 1835 1855 1875 1895 1915 1935 1955 1975 1995 2015
Year of First Description
C
Number of araneid species per country
D

later, this study is still the most comprehensive phylogenetic study available for Araneidae. Several subsequent phylogenetic studies have used the matrix of Scharff and Coddington (1997) to place particular genera within Araneidae (Tanikawa, 2000—*Eriophora*; Kuntner, 2002—*Perilla*; Kuntner and Hormiga, 2002—*Singafrotypa*; Smith, 2006—*Poltys*; Harmer and Framenau, 2008—*Telaprocera*; Schmidt and Scharff, 2008—*Acusilas*; Framenau et al., 2010a—*Backobourkia*; Framenau et al., 2010b—*Demadiana*; Framenau, 2011—*Lariniophora*; Magalhães and Santos, 2012—*Micrathena*), but a new comprehensive phylogeny based on a broader selection of taxa and characters (morphological, behavioural or molecular) has not been developed. However, a new study (Kallal et al., 2018) based on transcriptomic data, and including 18 araneid genera, found strong support for the monophyly of Araneidae and some core araneid lineages (zygiellines, nephilines, argiopines, cyrtophorines and gasteracanthines).

All araneoid spiders, except theridiids, have a fixed basal paracymbium on the male pedipalp and a "triad" consisting of two aggregate gland spigots and one flagelliform spigot on the posterior lateral spinnerets, responsible for producing the sticky silk that characterizes araneoid spiders (Wheeler et al., 2017). These are morphological synapomorphies for Araneoidea (Griswold et al., 1998) and the monophyly of this clade is well supported by all recent analyses, including molecular studies (Blackledge et al., 2009; Dimitrov et al., 2012, 2017; Garrison et al., 2016; Wheeler et al., 2017; Fernández et al., 2018). There is thus strong support for the inclusion of Araneidae within Araneoidea, and in the most recent phylogenomic analyses of araneoid relationships (Fernández et al., 2018) most interfamilial relationships are well supported. When Scharff and Coddington (1997) conducted their phylogenetic analysis, they found araneids to be sister to other araneoids (Griswold et al., 1998) but none of the recent molecular phylogenies supports such a basal position of Araneidae. A sister group relationship between Araneidae (including Nephilinae) and a clade consisting of Synotaxidae and Theridiosomatidae has been suggested (Dimitrov et al., 2017) as well as Araneidae sister to a clade consisting of Symphytognathidae and Anapidae (Wheeler et al., 2017). An earlier study by Dimitrov et al. (2012) suggested a sister group relationship between Araneidae and a clade consisting of Linyphiidae, Pimoidae and Cyatholipidae. None of the suggested sister group relationships was well supported (e.g. Gregorič et al., 2015). Recent phylogenomic studies have placed Araneidae sister to Linyphiidae + Pimoidae and Nesticidae (Garrison et al., 2016), or to Theridiosomatidae (Fernández et al., 2018), but it is hard to compare the two studies. The latter has more representatives of araneoids and the former did not include the family Theridiosomatidae. Overall they agree on the interfamilial relationships, except for the placement of Nesticidae. The study by Fernández et al. (2018) is the most recent and most comprehensive study of araneoid relationships. They place the family Araneidae as sister to Theridiosomatidae.

Beginning in 1968, Herbert W. Levi published more than 60 revisionary papers on Araneidae (Leibensperger, 2016), mainly from the Americas, and his revisionary work revealed many character systems that have later been used for testing morphology-based phylogenetic hypotheses (Scharff and Coddington, 1997). Levi also resolved the taxonomy of many American araneid genera and thereby facilitated work with araneids in many other disciplines. However, for the rest of the world, very little modern revisionary work has been conducted on the family and many genera are therefore weakly defined and probably not monophyletic. A good example is the genus *Araneus* Clerck, 1757 with 641 described species (World Spider Catalog, 2019), many of which probably do not belong there. The number of described *Araneus* species is probably a historical artefact. The sheer diversity of *Araneus*-like araneids probably baffled early explorers, who placed such species in *Araneus*. This taxonomic mess is particularly pronounced in areas of the southern hemisphere where early European taxonomists explored and described the araneid fauna and placed new species in European genera. For instance, approximately 100 Australian araneid species are currently placed in the genus *Araneus* (a senior synonym of *Epeira*, where they were originally placed), even though the genus does not occur there (Framenau et al., 2010a).

Araneids also include some of the largest known spiders (e.g. *Nephila komaci*, Kuntner and Coddington, 2009) along with diminutive species (e.g. *Mangora*, *Singa*, *Hypsosinga*, *Colphepeira*). Interestingly, large body sizes are found mostly in females while males are usually small and show much less variation in body size. Such striking sexual dimorphism has attracted attention and it has been suggested that the differences in size between sexes are mostly due to an increase in female body size (Coddington et al., 1997; Hormiga et al., 2000; Kuntner and Elgar, 2014; Kuntner and Cheng, 2016). Here, we revisit this question in order to test if this conclusion remains valid given the topological differences between our molecular phylogeny and the supertree used by Hormiga et al. (2000).

Our main goal is to elucidate intrafamilial relationships of araneids to provide a comparative framework for the study of evolution and diversification within the family, and to determine the implications for the classification of Araneidae. The study builds on molecular data and includes many more araneid genera than

the study by Scharff and Coddington (1997). The latter taxon sample was heavily skewed towards northern hemisphere taxa. This study adds representatives of araneids from the southern hemisphere (especially Africa, Madagascar, South America, South-East Asia, Australia and New Zealand) to better represent overall araneid diversity, to test the monophyly of the family and to explore the evolution of web architecture and male and female sizes within the family.

Materials and methods

Taxon sampling

In total, 158 taxa were sampled, 133 of which belong to the in-group and represent 83 described araneid genera and, implied by this analysis, ten to be described. This taxon sampling aimed at providing a balanced representation of northern and southern hemisphere taxa and poorly studied lineages. In groups such as *Araneus*, where extreme polyphyly was suspected (Framenau et al., 2010a), we sampled as many putative lineages at the generic level as we could source. The full list of species along with locality, specimen depository and GenBank accession numbers information is available in Table S2.

The choice of out-groups was guided by recent phylogenetic results focused on higher level orb-weaver relationships (Blackledge et al., 2009; Dimitrov et al., 2012, 2017; Gregorič et al., 2015; Garrison et al., 2016; Fernández et al., 2018; Kallal and Hormiga, 2018) and includes representatives of major araneoid lineages (Theridiidae, Linyphiidae, Pimoidae, Mimetidae, Synotaxidae, Arkyidae and Tetragnathidae), the RTA-clade (Amaurobiidae, Dictynidae) and the cribellate orb weavers (Uloboridae, Deinopidae). Because the focus of this paper was the phylogeny of Araneidae, we constrained all analyses to duplicate the family-level topology (see Supplementary Material) as found by Fernández et al. (2018).

Sequences and sequencing methods

Almost all sequences used here were generated as part of this study in laboratories at the University of Akron, University of California Riverside, Ohio State University and the Natural History Museum of Denmark. Similar protocols were used at each laboratory. Genomic DNA was extracted from ethanol-preserved spiders using Qiagen DNeasy Tissue Kits. For most species, legs were removed from one side of the body but for smaller species or older specimens whole bodies were sometimes used. We then sequenced fragments of two mitochondrial cytochrome *c* oxidase I (COI) and the 16S rRNA (16S), and three nuclear 28S rDNA (28S) 18S rDNA, (18S) and histone 3 (H3) loci to provide roughly 4150 bp of data per taxon.

PCRs (50 μL) were prepared using ~0.5–1 μL of genomic DNA, 1 μL dNTP mix, 0.5 μL of each primer, ~0.25 μL Invitrogen *Taq* polymerase, 6.5 μL of buffer and 41 μL of distilled H_2O. Up to 3 μL of additional MgCl was added to poorly amplifying reactions. Amplifications typically involved 40–50 cycles with 48–52 °C annealing temperatures. PCR products were either cleaned with Montage PCR filter units (Millipore Cidra Inc., Billerica, MA, USA) and sequenced at the Genomics Core Instrumentation Facility (University of California Riverside) or sent directly to Macrogen USA for cleaning and sequencing. Sequences were edited and curated in BioEdit v7.2.5 (Hall, 1999).

Alignments

After contig assembly and editing, sequences for each gene fragment were subjected to multiple sequence alignment using the online version of MAFFT v.7 (Katoh and Standley, 2013). Protein coding genes were aligned using the L-INS-i method. Resulting alignments were translated into amino acids and checked for stop codons as an additional quality control step. Multiple sequence alignments of ribosomal genes are not trivial due to the higher number of insertions and/or deletions, especially in the rDNA loop regions. Here we align rDNA sequences using the Q-INS-i method as this approach takes into consideration the rRNA secondary structure and uses an advanced four-way consistency objective function (Katoh and Toh, 2008).

Phylogenetic analyses

Best fit models of molecular evolution were selected using jModelTest v.2 (Darriba et al., 2012). Maximum likelihood (ML) analyses were carried out in the program RaxML v.8.0.26 (Stamatakis, 2014) on the Abel cluster at the University of Oslo. Data were partitioned by gene with 28S split into two based on its variability and particularly the number of inferred gaps: one variable (more gappy) and one conserved partition. Because of the limited number of models implemented in RaxML we did not use the best-fit models selected by the jModelTest for the ML analyses. Instead, in RaxML, we applied the GTRCAT model for the fast bootstrap replicates and GRTGMMA for the optimal topology searches. To reduce computational time, bootstrap and optimal trees were reconstructed in the same run using the –fa option and 1000 bootstrap replicates.

Bayesian inference (BI) analyses were carried out using Mr Bayes v.3.2.2 (Ronquist and Huelsenbeck,

2003) on the Abel cluster at the University of Oslo. Data were partitioned as in the ML analyses. Mr Bayes implements a variety of substitution models and here we used the best-fit models of molecular evolution from the jModelTest analyses. Analyses were run for 40 million generations and convergence was assessed by monitoring the average standard deviation of split frequencies and evaluation effective sampling size of all parameters after burnin in Tracer v.1.6.0 (Rambaut and Drummond, 2007).

Maximum-parsimony (MP) analyses were carried out in the program TNT v.1.1 (Goloboff et al., 2008). We used both traditional and new technology (Goloboff, 1999) search strategies varying the intensity of searches in each run. Under traditional search we used: collapsing rule (default = rule 1), hold 500 000, DNA data format, gaps as missing, number of replications = 1000, trees saved per replication = 500, TBR swapping. Under new technology we used: all different algorithms = Sect., Search, Rachet, Drift and Tree fusing with default settings—get trees from driven search with initial addseqs = 20, find minimum length trees 20 times, stabilize consensus 20 times.

Support for nodes was assessed using jackknife (Farris, 1997) with 1000 pseudoreplicates and character removal probability equal to 36% under the new technology search.

Dating and calibration points

Molecular dating was carried out in the program BEAST v.2.4.2 (Bouckaert et al., 2014) using both uncorrelated lognormal (ULC) and uncorrelated exponential (UCE) clock models (Bouckaert et al., 2014). The mitochondrial gene markers were treated as a single locus and clock and site models for all other markers were unlinked. All analyses were run with linked trees and a birth–death model for the tree prior. Tree topology was constrained as outlined in the previous section, and an ultrametric starting tree that complies with both the dating and the topological constraints was generated with the program treePL v.1.0 (Smith and O'Meara, 2012). In order to calibrate the phylogeny, we implemented node constraints based on the fossil record of orbicularian spiders. Several recent papers have evaluated the orb weaver fossil record (e.g. Dimitrov et al., 2012, 2017; Kuntner et al., 2013, 2018) trying to identify fossils that can be reliably placed in known groups and can be used for molecular dating. We chose fossil constraints based on these discussions and on our own review of the literature. The Araneidae stem minimum age was constrained to 115 Ma based on *Mesozygiella dunlopi* described from Lower Cretaceous amber from Spain (Penney and Ortuño, 2006). The Linyphiidae minimum age was constrained as 125 Ma based on a linyphiine species described from Lebanese amber (as "Linyphiinae" incertae sedis, Penney and Selden, 2002). Another Lebanese amber fossil, *Palaeomicromenneus lebanensis* (Penney, 2003), was used to constrain the minimum age of Deinopidae (125 Ma). Finally, the stem age of *Nephila* was constrained to a minimum of 16 Ma based on *Nephila* fossils described from Dominican amber (Wunderlich, 1986). Several fossils suggested to belong in Araneidae have been described (e.g. Dunlop et al., 2018) but most of them are either members of extinct genera with uncertain placement or have been placed in *Araneus*, which is highly polyphyletic (see Taxonomic Results and Discussion below). In addition, given the ambiguous morphological diagnosis of Araneidae, interpretation of the fossil morphological evidence is even more ambiguous. Thus, we have not been able to use these araneid fossils in our analyses. All fossil constraints were applied as log-normal minimum age priors. We used the *Mean in Real Space* when specifying the prior on the expected mean of the lognormal distribution and implemented hyperpriors on these means to reflect the uncertainty associated with the actual placement of the fossils along the branches of the phylogeny. All mean hyperpriors were implemented using uniform distribution. The final set of fossil calibration points and the relevant BEAST settings are listed in Table S3.

Comparative analyses

To study the evolution of web types, web stabilimentum and SSD we used the methodological approaches described by Dimitrov et al. (2017) and the R packages ape (Paradis, 2012) and phytools (Revell, 2012). Web architecture and presence of stabilimentum were scored for all taxa with documented webs, using the character concept for web types of Blackledge et al. (2009) and Dimitrov et al. (2017). Two character states ("brushed sheet" and "terminal line") do not occur in these data. We also modified the interpretation of "no foraging web" to "foraging web lost" because in this dataset it is reasonably clear that absence of webs is secondary. To accommodate variation in Araneidae, we added three new states (see Table S4). "Spanning thread" codes for *Pasilobus*, *Cyrtarachne*, *Poecilopachys* and *Paraplectana* (reviewed by Stowe, 1986). "*Paraplectanoides*" codes for *Paraplectanoides* (web described by Hickman, 1975). "Trapeze" codes for *Celaenia*, *Kaira* and *Pycnacantha*, because all these species build a loop, or trapeze, of silk from which they hang and attack prey (moths) with their front legs (Dippenaar-Schoeman and Leroy, 1996). Species which do not build webs or for which we lack observations were not scored for stabilimentum. For the analyses of SSD origins and evolution in araneids we used the dataset of males' and females'

body sizes of araneoid spiders of Hormiga et al. (2000). Because some genera, notoriously *Araneus*, are found to be polyphyletic in our analyses we evaluated all such cases when matching the genus-level data of Hormiga et al. (2000) to our dataset. Taxa that are currently placed in the same genus but were found to belong to different lineages compared with those scored by Hormiga et al. (2000) were excluded from the analyses. All comparative analyses were carried out with the dated topology inferred in the BEAST analyses.

Taxonomic Results

Scharff and Coddington (1997) and Kallal et al. (2018) were the most recent authors to analyse quantitatively the internal phylogenetic structure of the family Araneidae. The former study, based on morphology and behaviour, included 57 genera. The latter, based primarily on phylogenomic transcriptome data, included 18 genera, 13 in common with the former. Both of these studies owe much to the late Herbert W. Levi, who devoted more than 40 years to the study of Araneidae. He periodically struggled to make sense of the existing taxonomy of subfamilies and tribes, but many of his generic concepts are supported here. All of these works built on the largest and most formal treatment of araneid relationships by Eugène Simon (1895) who proposed 28 family group names within the modern concept of Araneidae. Simon's taxonomic hypotheses—all proposed before phylogenetic theory developed—still retain intuitive validity and therefore provide the basic hypothesis with which we compare our results.

Araneidae *sensu lato*, as delimited by Dimitrov et al. (2017), is supported. It contains three strongly supported monophyletic groups, Zygiellinae (ZYG), a clade consisting of *Paraplectanoides* + classical Nephilinae (NEP), and a large clade including all remaining araneids (here informally named "the ARA Clade", Fig. 3). Araneidae *sensu lato* has few obvious morphological synapomorphies, such as the presence of modified setae (sustentaculum) on the tip of the fourth tarsi and the presence of a radix in the embolic division of the male palp (Dimitrov et al., 2017). The same is true for some of its component subfamilies. Classical Zygiellinae contains at least four genera: *Deliochus*, *Leviellus, Phonognatha* and *Zygiella*. Without *Paraplectanoides*, classical Nephilinae is well defined morphologically and contains at least *Nephila*, *Clitaetra*, *Herennia*, *Nephilengys* and *Nephilingis*. *Paraplectanoides* (Fig. 1E) is here strongly supported as sister to classical Nephilinae. Kallal and Hormiga (2018) also placed *Paraplectanoides* as sister to classical Nephilinae. Previous authors proposed that *Paraplectanoides* was related to araneines (Davies, 1988) or *Anepsion* and *Aspidolasius* (Simon, 1895; Anepsieae). The type species of *Paraplectanoides*, *P. crassipes* (Fig. 1E) from coastal southern Australia and Tasmania, is a diurnally reclusive, size-dimorphic animal that spins highly unconventional webs for orb weavers—a closed ovoid covered with detritus (Hickman, 1975) that somewhat resembles the web design of the mygalomorph purse web spider *Sphodros rufipes* (Atypidae) (W. G. Eberhard, pers. com.). The second species currently placed in *Paraplectanoides*, *P. kochi*, only known from its type specimen collected in tropical eastern Australia, is probably a member of *Demadiana* in the family Arkyidae based on its original description (Pickard-Cambridge, 1887). Using a combination of hybrid and classical genetic markers and a smaller sample of taxa, Kuntner et al. (2018) found support for the same three basal monophyletic groups mentioned above, but they did not include *Paraplectanoides*. Given our results for *Paraplectanoides*, also supported by Kallal and Hormiga (2018), the more narrowly defined Araneidae suggested by Kuntner et al., 2018 (Araneidae *sensu stricto*) and the current classification of Araneidae (World Spider Catalog, 2019) renders Araneidae *sensu stricto* polyphyletic and Nephilidae *sensu* Kuntner et al. (2018) paraphyletic and we therefore maintain Araneidae *sensu lato* as currently circumscribed in the World Spider Catalog (2019).

We recovered Zygiellinae, *Paraplectanoides* + classical Nephilinae and the ARA Clade with the former as sister to the latter two (Fig. 3) with strong support, as did Dimitrov et al. (2017), Kallal and Hormiga (2018), Kallal et al. (2018) and Kuntner et al. (2018). Gregorič et al. (2015) and Kallal and Hormiga (2018) studied the internal structure of Zygiellinae and included more genera than here. Our topology for Zygiellinae agrees with theirs. Our results for classical Nephilinae agree with those of Kuntner et al. (2013) and Kallal and Hormiga (2018) except for the placement of *Herennia*. Kuntner et al. (2018) studied the phylogeny of classical nephilines using phylogenomic data with a larger nephiline taxon sample, but a smaller ARA Clade sample. They argue that by priority Phonognathidae (based on Phonognatheae Simon, 1894) is the correct name for Zygiellinae (based on Zygielleae Simon, 1929, a younger family group name), and resurrect Nephilidae, and a more narrowly defined Araneidae (but see comment above on Araneidae *sensu stricto*). They also recover a different nephiline internal topology, but agree that nephilines and the ARA Clade are sisters.

The ARA Clade contains most of araneid diversity with 165 described genera, of which 83 are included here (Figs 3a and 4a, Figs S1–S4 and supplementary tree files). Of the spiders included in this study, we

expect that at least ten new genera, mainly from Australia and formerly included in the polyphyletic genera *Eriophora* and *Araneus*, will require taxonomic description in addition to new genera that were not included here. Even with these exclusions *Araneus* itself still clearly remains polyphyletic, but a cluster of Holarctic species, including *A. diadematus*, *A. marmoreus*, *A. cavaticus* and *A. gemmoides*, is monophyletic and highly supported (Fig. 4a) and morphologically and biogeographically similar to the type species, *Araneus angulatus*. Unfortunately, we could not include *A. angulatus* in this study due to a lack of adequately preserved tissue samples in any collection, and ambiguous identity of sequences available in GenBank, but

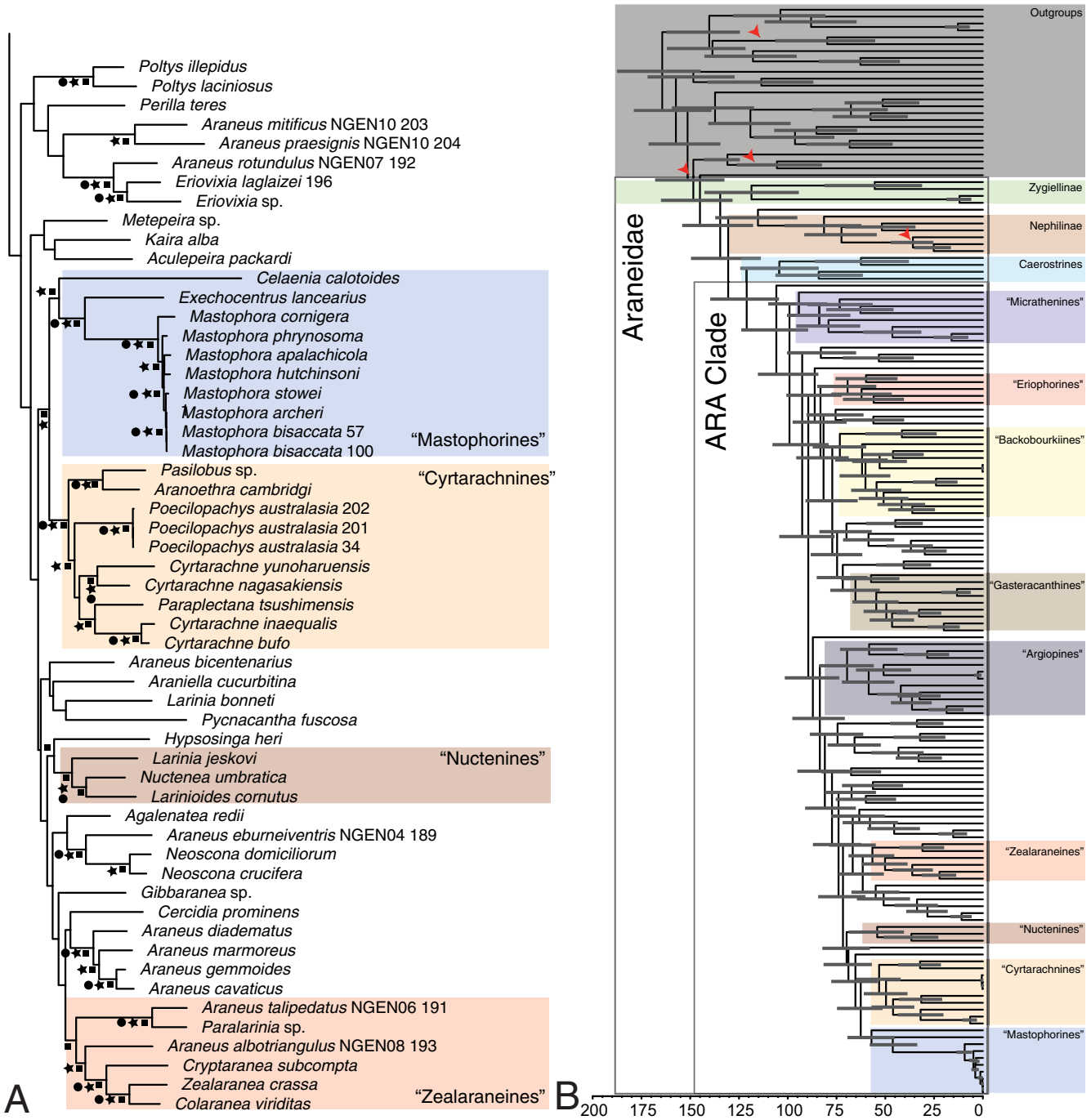


Fig. 4. (A) Results from the MB analyses (continues from Fig. 3A) summarizing nodal supports including those from the ML and MP analyses. (B) Results from molecular dating in BEAST. Red arrows point to the places where fossil constraints were applied; bars show the 95% highest posterior density for the age estimates at the corresponding nodes. The full tree with confidence intervals is shown in Fig. S8.

because it anchors phylogenetically the genus name *Araneus*, the family name Araneidae and the ordinal name Araneae (all Clerck, 1757), it is a urgent priority for phylogenetic evaluation (see below).

Several previous studies have included araneids in molecular dating analyses (Dimitrov et al., 2012, 2017; Kuntner et al., 2013; Bond et al., 2014; Garrison et al., 2016; Fernández et al., 2018; Kallal and Hormiga, 2018) and most of them suggest that araneids diverged from their sister group about 115–125 Ma with the exception of Garrison et al. (2016) who found younger ages for that clade—61 Ma (21–116 Ma)—and Kuntner et al. (2018) who found much older ages for araneids (about 285 Ma) and for the other two araneoid families included in their analyses (stem tetragnathids and mimetids are estimated to have originated about 320 Ma). Our dating analysis resulted in an estimate of the age of stem Araneidae of 145 Ma (128–164) (Fig. 4b), slightly older under a UCE model, 152 Ma (128–181) (Fig. S5).

ARA Clade groups

Ten groups within the ARA Clade have either Bayesian (PP) support values ≥ 0.95 or ML support values (BS) ≥ 70 (or both) and contain at least three genera: "Caerostrines", "Micrathenines", "Eriophorines", the "Backobourkiines", "Gasteracanthines", "Argiopines", "Cyrtarachnines", "Mastophorines", "Nuctenines" and the "Zealaraneines". "Gasteracanthines", "Cyrtarachnines" and "Mastophorines" are also supported by maximum parsimony (GC) values > 70.

"Caerostrines" includes at least *Caerostris*, *Gnolus* and *Testudinaria* (Fig. 3a) and started to diversify about 121 Ma (84–123, Fig. 4B); 94 Ma (68–124, Fig. S5) under UCE. This clade includes genera that are not easily recognized as araneids based on morphology. The male pedipalp of *Testudinaria* and *Gnolus* does not have a radix (Levi, 2005), which is otherwise one of the few putative synapomorphies for Araneidae, and the male pedipalp sclerites of *Caerostris* are hard to homologize. Scharff and Coddington (1997) and Kuntner and Agnarsson (2010) considered the radix to be absent in *Caerostris*. Furthermore, the male pedipalp of *Caerostris* does not have a paracymbium and the somatic morphology is unusual for an araneid, for example flattened tibiae and metatarsi, modified clypeus and modified macrosetae on femur IV (Scharff and Coddington, 1997; Gregorič et al., 2015). Levi (2005) was in doubt about the family associations of *Testudinaria* (either Araneidae or Theridiidae) and several species of *Testudinaria* were originally placed in *Gnolus* (Levi, 2005). Until recently, *Gnolus* was placed in the family Mimetidae, but more recent molecular phylogenies places it as basal within Araneidae (Dimitrov et al., 2012; Gregorič et al., 2015). No known morphological synapomorphies confirm this group, but the Bayesian (PP = 0.99) and ML (BS = 77) support values for the monophyly and interrelationships of this group are high (Fig. 3A). Simon (1895) considered that each of these genera exemplified a distinct group (Caerostreae, Gnoleae, and Testudinareae), but our evidence supports all as one closely related group, for which we propose the informal name "Caerostrines", pending further evidence for its monophyly. Caerostrines are strongly supported as the basal lineage within and sister to the rest of the ARA Clade.

"Micrathenines." Simon (1895) operated with two groups of spiny orb-weavers (Micratheneae and Gasteracantheae) and subsequent authors have divided the spiny orb-weavers into New World (Micratheninae) and (mostly) Old World (Gasteracanthinae) spiny orb-weavers (Dahl, 1914; Roewer, 1942; Emerit, 1973). Both groups have been considered formal subfamilies. However, the taxonomic composition of the groups varies between authors. Levi (1985) placed the genera *Micrathena* (Fig. 1A), *Chaetacis* and *Gasteracantha* in the subfamily Gasteracanthinae because all these genera have a sclerotized ring around the spinnerets, which is otherwise only known from the genera *Enacrosoma* and *Xylethrus*, and therefore suggested that these genera could also belong in Gasteracanthinae. We do not find support for a monophyletic spiny orb-weaver clade including Old World gasteracanthines and New World micrathenines. Simon (1895) included *Micrathena*, *Chaetacis*, *Enacrosoma* and *Pronous* in his Micratheneae, but this group was shown to be polyphyletic by Scharff and Coddington (1997) who also suggested that *Micrathena* could be paraphyletic with respect to *Chaetacis*. This paraphyly was later confirmed by Magalhães and Santos (2012). We did not include *Enacrosoma* and *Pronous* in the current matrix, so we cannot confirm the finding of Scharff and Coddington (1997), but we recovered *Micrathena* in a well-supported clade also including *Verrucosa*, *Ocrepeira*, *Acacesia* and *Scoloderus* (Fig. 3A). This clade has diverged from its sister group some 94 Ma (80–109, Fig. 4B; 63 Ma, 45–81, under UCE, Fig. S5) and is currently restricted to the New World with some very species-rich genera (e.g. *Micrathena*, *Verrucosa* and *Ocrepeira*). None of these genera has previously been associated with *Micrathena*, and there are no known morphological synapomorphies that confirm this group, but the Bayesian (PP = 1.00) and the ML (BS = 99) support values for the monophyly and interrelationships of this group are high (Fig. 3A). We use the informal name "Micrathenines".

"Eriophorines" includes at least *Acanthepeira*, *Eriophora*, *Parawixia*, *Alpaida* and *Wagneriana* (Fig. 3A) and is estimated to be about 83 Ma old (70–97, Fig. 4B; 46 Ma, 35–60, under UCE, Fig. S5). Three

nominal *Eriophora* species have been included in this study, two from Australia and *E. ravilla*, the type species, from South America. *Eriophora* is polyphyletic. *Eriophora ravilla* is related to the New World *Acanthepeira*, *Parawixia*, *Alpaida* and *Wagneriana*. Levi (1985) mentioned the presence of a paramedian apophysis as a possible synapomorphy for this group of genera, but as shown by Scharff and Coddington (1997), the paramedian apophysis has developed several times independently within Araneidae. Thus, no known morphological synapomorphies confirm this group, but the Bayesian (PP = 1.00) support value is high. The same clade with the same interrelationships (Fig. 3a) is also recovered in the ML analyses, but without support. Levi (1976) considered *Eriophora* to be related to *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Alpaida* and *Scoloderus*, although he did not provide explicit homologies as support.

"Backobourkiines" includes at least *Backobourkia*, *Parawixia*, *Novakiella*, *Carepalxis*, *Singa*, *NGEN01*, *Plebs* (Fig. 1G), *NGEN02*, *NGEN05* and *Acroaspis* (Fig. 3A). Many of the Australian species currently listed in *Araneus* (and a host of undescribed species) appear to belong in this clade and the generic diversity is much higher than reflected here (V.W. Framenau and N. Scharff unpublished data). Not all nodes within this group are strongly supported but the group as a whole is. The group includes species of many phenotypes and behaviours, but a uniting feature appears to be the presence of a single macroseta on the male pedipalp patella. This group includes a number of common, iconic Australian species currently placed in European and North American genera. These placements have never been tested by rigorous phylogenetic methods and our analysis demonstrates that these placements do not reflect their true systematic position. Recent revisionary work has clarified the taxonomy of some of the more common Australian members of the "Backobourkiines", for example the treatments of *Plebs* (Fig. 1G) and *Backobourkia* (Framenau et al., 2010a; Joseph and Framenau, 2012), but species such as *Eriophora transmarina* and *Eriophora_sp_64* represent a new Australian genus (*NGEN01*). No known morphological synapomorphies currently confirm this group, but the Bayesian (PP = 0.98) support value is high. The same monophyletic clade (Fig. 3A) is also recovered in the ML analysis, but without support. The inferred age of this lineage is 77 Ma (64–90, Fig. 4B; 41 Ma, 31–53 under UCE, Fig. S5) which, as in the case of the "Zealaraneines" (see below), suggest that these taxa have diversified after the breakup of Australia from Antarctica some 85 Ma ago (Fig. 4B). *Novakiella trituberculosa* occurs both in southern Australia and New Zealand (Court and Forster, 1988), but our analysis suggests a biogeographic origin in Australia and subsequent dispersal to New Zealand. This is consistent with the presence of at least one undescribed species of *Novakiella* in Australia (V.W. Framenau and N. Scharff, unpublished data).

The Oriental-Australian *Parawixia dehaani* forms part of the Backobourkiine clade, but this species is probably misattributed to *Parawixia*, a putative Neotropical genus (Levi, 1992), based on considerable morphological differences in the sclerites of the male pedipalp, specifically the paramedian and median apophyses (see Levi, 1992, figs 7–8; and Song et al., 1999, fig. 182H). The species was probably transferred to *Parawixia* due to superficial similarities of the female epigyne to those of Neotropical *Parawixia*. *Parawixia dehaani* probably belongs to a new genus, together with other species in the *dehaani*-group as defined by Yin et al. (1997).

The inclusion of *Singa nitidula*, a Palearctic species in the Backobourkiines, requires further investigation. However, other species of the Backobourkiines putatively dispersed into South-East Asia and the Indian subcontinent after Australia collided with the Sunda shelf, for example in the genus *Plebs*, which has highest diversity in Australia (Joseph and Framenau, 2012).

"Gasteracanthines" includes at least *Augusta*, *Parmatergus*, *Acrosomoides*, *Madacantha*, *Macracantha* (Fig. 1B), *Austracantha*, *Isoxya*, *Gasteracantha* and *Thelacantha* (Fig. 3A). Simon (1895) included the Old World spiny orb-weavers *Augusta*, *Aetrocantha*, *Austracantha*, *Gasteracantha*, *Macracantha*, *Isoxya* and *Togocantha* and the New World *Encyosaccus* in his Gasteracantheae. Scharff and Coddington (1997) confirmed the monophyly of Gasteracanthines including Simon's Old World genera plus *Gastroxya* but excluding the New World genus *Encyosaccus*. In the current study, we found high support (PP = 1.00, BS = 97 and GC = 84) for a monophyletic "Gasteracanthines" including the genera *Augusta*, *Parmatergus*, *Acrosomoides*, *Madacantha*, *Macracantha*, *Austracantha*, *Isoxya*, *Gasteracantha* and *Thelacantha*. Putative morphological synapomorphies are the presence of a paramedian apophysis on the male pedipalp, the shape of the female carapace (broader than long and square-shaped) and perhaps the sclerotized ring around the spinnerets. This clade is well supported and conforms to previous definitions. We propose the informal name "Gasteracanthines". Our analyses estimate the age of "Gasteracanthines" around 71 Ma (59–84, Fig. 4B; 35 Ma, 26–45, under UCE, Fig. S5).

"Argiopines" includes at least *Arachnura*, *Acusilas*, *Mecynogea*, *Cyrtophora*, *Argiope* (Fig. 1c), *Gea* and *Lariniaria* (Fig. 3A). Classically, authors have also recognized Arachnurines (*Arachnura*, *Acusilas*), Cyrtophorines (*Mecynogea*, *Cyrtophora*) and Argiopines *sensu stricto* [*Argiope*, *Gea*, e.g. Simon (1895;

Argiopeae, Cyrtophoreae and Arachnureae)] as distinct groups but this is the first analysis to place *Lariniaria* with Argiopines. Cyrtophorines could easily include *Kapogea* and *Manogea* (Levi, 1997), but their monophyly is untested and, at first glance, may be paraphyletic with respect to *Mecynogea*. There is strong support (PP = 0.99; BS = 0.90) for the inclusion of *Gea heptagon* and *Lariniaria argiopiformis* in the *Argiope* clade, thereby rendering the genus *Argiope* polyphyletic. *Lariniaria argiopiformis* is the type species of the monotypic *Lariniaria*, so our results suggest that *Lariniaria* should be synonymized with *Argiope*. The type species of *Gea* is *G. spinipes*, so we cannot conclude anything about the genus *Gea*, but the results suggest that *Gea heptagon* should be transferred to *Argiope*. Bayesian (PP = 1.00) and ML support (BS = 0.90) are high. The age of this lineage according to our results is 83 Ma (74–101, Fig. 4B; 53 Ma, 43–70, under UCE, Fig. S5). This relatively young age and their broad distribution suggest that many species in this lineage are capable of long-distance dispersal and that dispersal has been important in shaping the current diversity and distribution patterns of argiopine species (Agnarsson et al., 2016). We propose the informal name "Argiopines".

"Cyrtarachnines" include at least *Aranoethra*, *Cyrtarachne*, *Paraplectana*, *Pasilobus* and *Poecilopachys* (Fig. 4A). Simon (1895) included the same five genera in his Cyrtarachneae and this clade is strongly supported (PP = 1.00; BS = 98; GC = 95). It includes spiders that build so-called "spanning-thread webs". These webs are horizontal, reduced orb webs, with a small number of radii and widely spaced non-spiral viscid threads. Our result supports those of Tanikawa et al. (2014), who only included three genes and much fewer outgroup taxa and did not include *Aranoethra*. They also found strong support for a sister group relationship to mastophorines, but because they only included *Gasteracantha kuhli* as the outgroup in their study, the validity of the sister group relationship remained to be tested. Our results, including a much larger taxon selection of araneids, strongly support a sister group relationship between "cyrtarachnines" and "mastophorines" (PP = 99; BS = 81) (Fig. 4A). Such sister group relationships have already been argued based on behavioural characters (Eberhard, 1980; Robinson, 1982; Stowe, 1986) and Scharff and Coddington (1997) also found support for such a sister group relationship when using these behavioural characters in their phylogenetic matrix. The combined clade "cyrtarachnines" + "mastophorines" is characterized by a tendency towards web reduction and for those species where we know the hunting strategy, chemical mimicry seems to have evolved as a compensation for the reduced web (Scharff and Coddington, 1997). We propose the informal name "Cyrtarachnines".

"Mastophorines" include at least *Celaenia*, *Exechocentrus* (Fig. 1F) and *Mastophora* (Fig. 4a). Simon (1895) placed these three genera in separate groups: Celaenieae with *Celaenia* and *Taczanowskia* (not included here), Exechocentreae with *Exechocentrus* and *Coelossia* (not included here), and Glyptocranieae (= Mastophoreae) with *Mastophora*, *Ordgarius* and *Cladomelea* (the last two not included here). In addition to strong support for a clade including all three genera from molecular data (PP = 1.0; BS = 89), all these genera have lost the orb web. They all produce pheromones that attract male moths and catch their prey with their front legs (*Celaenia*) or with a single silk line provided with one or more extremely viscid droplet(s) (bolas spiders; *Mastophora*—Levi, 2003; *Exechocentrus*—Scharff and Hormiga, 2012; Fig. 1F). Our results support those of Tanikawa et al. (2014), who did not include *Exechocentrus* from Madagascar, but included the Australian *Ordgarius*. *Mastophora* is a large New World genus of 50 species, and, unusually, is most diverse in north and south temperate rather than tropical regions (Levi, 2003). Our sample includes seven species from the eastern USA all of which radiated unusually rapidly (Fig. 4B).

"Cyrtarachines" and "Mastophorines" are sister to each other and have diverged from their most recent common ancestor about 62 Ma (71–74, Fig. 4B; 32 Ma, 24–40, under UCE, Fig. S5) but despite some common traits, such as their reduced webs, both clades show different macroevolutionary patterns. In Cyrtarachines, genera and species seem to have accumulated gradually through time while in Mastophorines an important part of the diversity is a result of radiation in the genus *Mastophora* within the last 9 Ma (5–13) (even younger in the UCE estimates, ca. 3 Ma, Fig. S5) that belongs to an otherwise old lineage 46 Ma (34–57) (ca. 19 Ma under UCE, Fig. S5).

"Zealaraneines" include at least *Colaranea*, *Cryptaranea*, *NGEN06* ("*Araneus*" *talipedatus*), *NGEN08* ("*Araneus*" *albotriangulus*), *Paralarinia* and *Zealaranea* (Fig. 4A). No known morphological synapomorphies confirm this group, but the Bayesian support value is high (PP = 1.00; Fig. 4A). *Colaranea*, *Cryptaranea* and *Zealaranea* are monophyletic and endemic to New Zealand. Similar to the "Backobourkiines" (see above), the inferred age of this clade, 61 Ma (51–73, Fig. 4B; younger under UCE ca. 33 Ma, Fig. S5), suggests that it has probably diversified after Australia and New Zealand split from Antarctica, and hence supports the "Goodbye Gondwana paradigm" (McGlone, 2005; Giribet and Boyer, 2010). In fact, this clade may be even younger than the split of Australia and New Zealand about 60 Ma (Harvey et al., 2017). It appears that this clade diversified following dispersal events into New Zealand from outside

Australia, as it has (albeit poorly supported) closer affinities to Northern Hemisphere taxa (e.g. true *Araneus*) than to the Australian "Backobourkiines". This seems to be confirmed by morphological data, as many of the New Zealand endemic genera appear more closely related to *Araneus* than to species in the "Backobourkiines" (Court and Forster, 1988). The pre-Oligocene diversification time of the clade clearly refutes the "Drowned New Zealand" hypothesis (Waters and Craw, 2006; Chousou-Polydouri et al., 2019) and implied recolonization from Australia.

"Nuctenines" includes at least *Larinia*, *Larinioides* (Fig. 1H) and *Nuctenea* (Fig. 4A). No known morphological synapomorphies confirm this group, but the Bayesian (PP = 1.00) and ML (BS = 86) support values for this group are high (Fig. 4A). *Larinia*, *Larinioides* and *Nuctenea* do share certain genitalic features (a female epigynal scape and details of the male palpal sclerites, N. Scharff and J. A. Coddington, unpublished data), but such features may be homoplasious. "Nuctenines" are a relatively young clade, 54 Ma (40–68) (Fig. 4B) (or less under UCE clock, ca. 33 Ma), yet some of its genera (e.g. *Larinia*) have very broad distribution, suggesting good long-distance dispersal abilities similarly to "Argiopines". We propose the informal name "Nuctenines".

Additional noteworthy results

Araneinae has for many years been a core taxonomic concept in Araneidae, originated by Simon (1895) in his group Araneae. It includes, of course, the type genus *Araneus*. Scharff and Coddington (1997) interpreted the name as denoting one of two major lineages of araneids—the other being Argiopinae (Simon, 1890, 1892). They included, from the point of view of the results here, a heterogenous set of genera that certainly do not form a monophyletic group. The backbone of the ARA Clade in our preferred tree (Figs 3 and 4) lacks strong support at almost all nodes. Numerous subclades (see above) do have strong support and warrant informal, if not formal, recognition. Nothing that corresponds to the classical concept of Araneinae, containing genera with highly complex male and female genitalia but otherwise conventional morphology, basically nocturnal, spinning vertical sticky orb webs, is strongly supported here.

Arkys and *Archemorus* were synonymized by Heimer (1984), and placed in Araneidae by Scharff and Coddington (1997). Dimitrov et al. (2017) transferred them to Arkyidae. In this analysis, two *Archemorus* species group together and *Arkys* and *Demadiana* are sisters (Figs S1 and S2). Because our taxon sample is small we do not formally remove *Archemorus* from synonymy but highlight the issue for future work.

Araneus is notably polyphyletic in this analysis. With 641 species, *Araneus* is the largest spider genus, and is the basionym of the family and the order Araneae. Its delimitation is therefore nomenclaturally and taxonomically important. To test its monophyly we included 11 *Araneus* from the Austral region. This small, targeted sample chosen to test polyphyly suggests seven new genera. On the other hand, a set of four North American and European species (*diadematus*, *cavaticus*, *gemmoides* and *marmoreus*) are monophyletic by Bayesian (PP = 1.00), ML (BS = 97) and parsimony (GC = 99) criteria. Quite surprisingly, the otherwise typical North American *Araneus bicentenarius* does not group with this core *Araneus* set, but is weakly supported in a clade including *Araniella*, *Larinia* and *Pycnacantha*, thus implying an unexpected instance of north temperate *Araneus* polyphyly. Finally, although we were unable to obtain tissue samples of the type species *Araneus angulatus* when the sequencing for this project occurred, multiple gene sequences for *angulatus* have since appeared on GenBank and BOLD, and their implications are not simple to interpret. *Araneus angulatus* may be more than one species, and its parts may not group with the set of species including *diadematus*. Insofar as *angulatus* is the type of *Araneus*, itself the basionym of the order Araneae, the identity of *Araneus angulatus* and its relatives should be an urgent research priority. Regardless of issues surrounding its type species, *Araneus* (and its junior synonym *Epeira*) has been a dumping ground for vaguely similar species from many parts of the globe, and no doubt more instances of polyphyly will surface.

Araneae of Simon (1895) included *Araneus*, *Scoloderus*, *Carepalxis* and *Acroaspis*. As mentioned above, the genus *Araneus* is seriously polyphyletic. We also included the other three genera and none of them grouped together, indicating a polyphyletic Araneae *sensu* Simon. *Scoloderus* is part of the well-supported "Micrathenines", and included in a highly supported subclade that also includes *Acacesia* and *Ocrepeira*. The genus *Acroaspis* from Australia and New Zealand is placed in a clade with mainly Australian taxa ("Backobourkiines"), but support for this is low. Within this clade, there is high Bayesian support (PP = 0.99) for a subclade including *Acroaspis*, *Plebs*, and two potential new Australian genera, *Araneus recherchensis NGEN02* and *Araneus senicaudatus NGEN05*. We included two species of *Acroaspis*, including the type species *Acroaspis olorina*, and the genus is polyphyletic, unless we include *Araneus senicaudatus NGEN05*, thereby suggesting that this species should be transferred to *Acroaspis*. The same topology is found by ML, but without significant support (Fig. S2). The genus *Carepalxis* is situated in the "Backobourkiines" but in another highly supported

subclade (PP = 0.99) in the Bayesian tree. This subclade includes *Eriophora transmarina* and *Eriophora_*64 (both representing a potential new Australian genus, *NGEN01*) and the Euro-Asian *Singa nitidula*. The ML tree does not recognize the same topology and has low support for the placement of *Carepalxis* within the Backobourkiines (Fig. S2).

Other polyphyletic genera include *Eriophora*, *Larinia* and *Parawixia*. For the former we included the type species, *Eriophora ravilla*, so that two Australian species, *E. transmarina* and *E.* sp. 64, probably belong to a new genus (*NGEN01*). We did not include the type of *Larinia* (*L. lineata* Lucas, 1846**)** or *Parawixia* (*P. destricta* O. Pickard-Cambridge, 1889) so we can only infer that both contain at least two relatively unrelated groups of species. *Gea* and *Lariniaria* are nested within *Argiope*.

Mangoreae of Simon (1895) included *Larinia*, *Mangora*, *Eustala*, *Spilasma*, *Prasonica* and *Acacesia* in his tribe Mangoreae. Roewer (1942) and Grasshoff (1970) referred to the tribe Mangorini, but left out *Spilasma* and *Acacesia*, and instead added *Drexelia* and *Psyllo*, and Grasshoff (1970) added another eight new genera, by mainly splitting *Larinia* into a number of new genera, and thereby providing a more narrow definition of *Larinia*. *Drexelia* has since been synonymized with *Larinia* (Levi, 1975; Harrod et al., 1990) and although most of Grasshoff's new genera are considered valid by the World Spider Catalog, recent authors have preferred a broader definition of *Larinia* (Framenau and Scharff, 2008). Our results suggest that Mangorini is highly polyphyletic. All genera are scattered throughout the trees (Figs 3 and 4). Levi (1975) suggested a close relationship between *Larinia* and *Araneus*, but this is not supported by our results. Despite the fact that *Mangora* is one of the easiest araneid genera to define (feathered trichobothria on the third tibiae) its nearest relatives are unknown. Levi (1975) considered *Mangora* "far removed from *Araneus*". Scharff and Coddington (1997) included *Mangora* in their morphological matrix, but could not resolve their relationships, and this is also the case for the current study.

Cycloseae of Simon (1895) included *Cyclosa*, *Acusilas*, *Witica* and *Nemoscolus*. We did not include *Witica* and *Nemoscolus* and did not find support for a close relationship between *Cyclosa* and *Acusilas*. In fact, the placement of *Acusilas* within "Argiopines" is strongly supported, whereas the placement of *Cyclosa* is uncertain. The monophyly of *Cyclosa* is strongly supported in this study (PP = 1.0; BS = 99; GC = 100) but the placement of the clade including *Cyclosa* within the ARA Clade is uncertain. Their sister group placement (Fig. 3A) with the (largely) Australian *Dolophones* (the highly cryptic, "wrap-around spiders", Fig. 1D) and the Australian "*Araneus*" *dimidiatus* and "*Araneus*" *mulierarius* (both representing a new genus of leaf-curling spiders, *NGEN03*) unites spiders of extremely different morphology and behaviour. However, if the relationship holds true in future analyses, it suggests an Australian origin of the cosmopolitan, or at least largely cosmotropical genus *Cyclosa*.

Xylethreae, Physioleae and Hypognatheae of Simon (1895) included single genera and because we did not include representatives of *Xylethrus* or *Physiola* (= *Witica*) we cannot comment on their relationships. We did include one species of *Hypognatha* in our analysis, but did not find any support for its phylogenetic placement. Levi (1996) considered *Hypognatha* to be related to *Gasteracantha* but this is not supported here.

Bertraneae of Simon (1895) included *Bertrana* and *Spintharidius*. We did not include representatives from this group.

Anepsieae of Simon (1895) included *Aspidolasius*, *Anepsion* and *Paraplectanoides*. Even though we did not include *Aspidolasius* in the current study, we can conclude that Anepsieae *sensu* Simon is polyphyletic. There is strong support (PP = 1.0; BS = 100) for a sister group relationship between *Paraplectanoides* and Nephilinae and *Anepsion* is sister to Gasteracanthines on our tree, but without much support (Fig. 3).

Chorizopeae of Simon (1895) included *Chorizopes* and *Artonis*. Here we only included *Chorizopes* and the phylogenetic placement of this genus differs between our trees (BI, ML and MP) and none of the placements is supported.

Dolophoneae of Simon (1895) included *Dolophones* and *Pitharatus*. Here we only included *Dolophones* (Fig. 1D), but its placement as sister to *Cyclosa* on all trees (BI, ML and MP) is not supported.

Poltyeae of Simon (1895) included *Poltys*, *Kaira*, *Pycnacantha*, *Homalopoltys* (= *Dolichognatha*, Tetragnathidae) and *Cyphalonotus*. We did not include *Cyphalonotus*, but the rest of the genera join different parts of the tree, and therefore suggest polyphyly. However, none of the placements of these three genera is significantly supported on our trees. We included two species of *Poltys*, including the type species *Poltys illepidus*, and the support for the monophyly of *Poltys* is high (PP = 1.0; BS = 100; Fig. 4A). *Poltys*, *Pycnacantha* and *Kaira* are known to feed on moths that they attract with pheromones (Stowe, 1986).

Remaining genera. We included 32 additional taxa in this analysis, either valid genera or single species that our results suggest may deserve generic status: *Aculepeira*, *Agalenatea*, *Anepsion*, *Araneus bicentenarius*, "*Araneus*" *neocopinus* (*NGEN10*), *Araniella*, *Cercidia*, *Chorizopes*, *Cyclosa*, *Dolophones*, *Eriovixia*, *Eustala*, *Gibbaranea*, *Hingstepeira*, *Hypognatha*, *Hypsosinga*,

Kaira, *Larinia*, *Mangora*, *Metazygia*, *Metepeira*, *Neoscona*, *NGEN03*, *NGEN04*, *NGEN07*, *NGEN09*, *NGEN10*, *Paraplectanoides* (see above), *Perilla*, *Poltys*, *Pycnacantha*, *Spilasma* and *Telaprocera*, but they formed no coherent pattern phylogenetically as a group or in relation to the ten groups that met our criteria for group recognition. Some of these relationships are strongly supported and others less so. Little can be concluded other than araneid phylogeny remains a work in progress to be pursued with more data and more taxa.

Finally, note also that even in the absence of a backbone constraint, the lineages discussed herein are still recovered by our dataset as can be seen from the results of unconstrained ML and BI analyses (Figs S10 and S11).

Comparative analyses

Evolution of sexual size dimorphism. Our results show that the genera that exhibit extreme sexual dimorphism (female $\geq 2\times$ male) do not form a clade (Fig. S6). In most of these cases, SSD appears to be driven by an increase in female body size while male body size changes do not follow a common trend even in closely related taxa. For example, males of *Nephila* show slight increases in body size while males of *Herennia* decrease. In a few cases, a decrease of male size does contribute towards the observed SSD (e.g. *Kaira*). There are also several cases where monomorphic taxa originate from dimorphic ancestors (Fig. S7). This is achieved by significant changes of either male (e.g. *Mecynogea*) or female (e.g. *Hypognatha*) body size or both (e.g. *Austracantha*). *Backobourkia* demonstrates that SSD may also not be a character state evolved at the genus level. Of three species, only one is sexually dimorphic (*B. collina*), and comparison with the other two species in the genus suggests that its SSD is caused by male dwarfism rather than female gigantism (Framenau et al., 2010a).

Evolution of web architecture and stabilimentum. The araneid ancestor apparently built vertical orbs (Fig. S8). There are at least three independent transitions from vertical to horizontal orbs, in Cyrtophorines, *Novakiella* and *Spilasma* (Fig. S8). Spanning thread web spiders (*Cyrtarachne*, *Paraplectana*, *Pasilobus* and *Poecilopachys*) are monophyletic and sister to the bolas spiders (*Mastophora*). The "trapeze" web evolves convergently three times (*Celaenia*, *Kaira*, *Pycnacantha*), although *Celaenia* does fall in the cyrtarachnine–mastophorine clade with other highly modified web architectures. Among araneids, webs are completely lost only in *Gnolus*.

The stabilimentum (Fig. 1c) has multiple independent origins and few reversals across the araneid tree (Fig. S9).

Discussion

Araneidae is the third most speciose family of spiders at a global scale (after Salticidae and Linyphiidae) and contains by far the largest (and probably most polyphyletic) spider genus, *Araneus*, with 641 species. At the generic level Araneidae is third largest with 175 genera. Here we treat 83 genera (including ~90% of all currently named araneid species) in Araneidae as currently recognized.

What of the 92 omitted genera? Twenty-five of these are known from three or fewer species, all described prior to the 20th century, few revised and rarely mentioned in the scientific literature after their taxonomic description. Having received little to no attention since their description, they will probably be synonymized or displace a later name when finally evaluated. As one example, *Heurodes* was described based on a single juvenile spider and a review of the Australian Araneidae suggests strongly synonymy of the genus with *Acroaspis*. As another example, *Collina* includes only a single Tasmanian species and was described based on an adult female (Urquhart, 1891). Its type specimen appears to be lost. The original description is too vague to allow identification in a country with a diverse araneid fauna and the genus is therefore probably a *nomen dubium*. An additional 23 genera contain three or fewer species and have not been mentioned taxonomically since their description, although some of these are recent, and, if tissue were available, would have been included. The remaining 39 genera are somewhere in the middle with regard to their taxonomic knowledge. Like most partially revised, large taxonomic groups, Araneidae has much historical baggage that poses a formidable obstacle to advances in phylogenetic or evolutionary biology.

How to advance in this context? One important but surprising observation is that morphology, the backbone of museum-based comparative biology, and behaviour, almost uniquely informative in orb-web weaving spiders (Eberhard, 2019), correlates poorly with molecular data. Most of the clades named in this study cannot be corroborated, as far as currently known, by non-molecular data. Molecular data accumulate rapidly, and, with some notable exceptions, have recently tended to consilience. The implication is that progress in araneid phylogeny for the foreseeable future requires molecular data, and, therefore, sequence-quality tissue. However, global biodiversity tissue resources remain poorly indexed or completely undiscoverable. The Global Genome Biodiversity Network (GGBN, 2018) is a recent data portal that attempts to mitigate the problem of genetic resource discoverability, but, tellingly, none of the tissue used in this study is indexed by GGBN. Recent advances in molecular techniques have shown that older museum

material, not originally collected for molecular analyses, can be used for next-generation museum genomics (Cotoras et al., 2017; Wood et al., 2018).

Morphological taxonomy, however, remains crucial for advancing araneid phylogenetic research. Only the comprehensive and seminal generic revisions by H. W. Levi have allowed the compilation of a representative taxon set for the American fauna for this study and, likewise, the selection of Australian taxa was supported by an exhaustive review of Australian araneid material in local collections that included described and undescribed species (V.W. Framenau and N. Scharff, unpublished data). The morphological diversity of orb-weaving spiders at the genus level will facilitate the future establishment of new genera based on morphological characters alone and will provide testable phylogenetic hypotheses, in particular in poorly studied biogeographical regions. However, it appears clear that discovering interrelationships between these genera will require molecular tools.

Similarly, molecular dating of the deeper nodes in araneids and in spiders in general is not a trivial task due to the scarcity of old fossils, their poor preservation and their questionable identification. Potential effects that methodological approaches may have on the inferred ages should also be considered. Here we have used the two most widely used relaxed clock models, the ULC and UEC. Although for some nodes they result in similar age estimates and overlapping 95% highest posterior densities intervals, they also differ as for example in the estimated age of "Eriophorines". There are several quantitative approaches to choose among different clock models (e.g. by performing path analyses and using Bayes factors). We tried to implement them with our dataset but unfortunately effective sampling sizes remained very low and achieving good statistical results seemed unattainable in a reasonable amount of time. However, recent comparison of different clock models applied to a diverse set of datasets has shown that ULC performs better under various conditions (Lepage et al., 2007). Here we show results from both ULC and UCE that despite differences in their results support our conclusions. However, based on the findings of Lepage et al. (2007) we suggest that ULC estimates are probably a better estimate of araneid lineage divergence times. Despite this caveat, in araneids, molecular dating and observations of recent range expansion of some taxa (e.g. *Argiope*) suggest that many of the araneid lineages are good long-distance dispersers and support previous conclusions on the importance of dispersal in the evolution of araneid taxa (Kuntner et al., 2013; Agnarsson et al., 2016).

Despite the weakness of studies based on few Sanger-sequenced genes, this study is relevant to araneid phylogeny because it includes most of the largest genera, and, by implication, the vast majority of araneid species. It omits many nominally valid araneid genera, but the majority of these contains few species and are poorly studied. Most are hard to collect and have never been revised, so that the strategy employed here seems like a promising first step in applying molecular methods to the third largest spider family. Sanger-sequenced marker studies are fast becoming obsolete, but they frequently provide superior taxon sampling that currently exceeds what phylogenomic studies can provide (e.g. Kallal and Hormiga, 2018). Studies like Wood et al. (2018) show that museum material can generate phylogenomic-scale data, but the methods involved are relatively new, and we are not aware of any organized effort as yet to investigate araneid phylogeny in such a systematic fashion. In the future, assuming that the phylogenomic backbone for Araneidae can be improved adequately, the sequences published here can be combined to place more taxa, relying on marker data for recent nodes, and phylogenomic data for the backbone.

The increasing availability of phylogenomic-scale data for dense taxon samples of large clades is revolutionary. Unfortunately, no such revolution has occurred either for natural history data or for morphology. As molecular data density increases for Araneidae, the density of direct observations of putatively selected traits, such as web architecture or decorations, and SSD, decreases. In this study, the great preponderance of missing data makes conclusions weak, if not suspect. More biological data are urgently needed to make the increase in tree inference truly relevant to testing adaptationist and evolutionary hypotheses.

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Supporting Information

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

Fig. S1. Full tree from the MB analysis.

Fig. S2. Results from the ML analyses.

Fig. S3. Strict consensus of 64 MP trees found under an equal weights search in TNT.

Fig. S4. Maximum-parsimony jackknife supports based on 1000 replicates with character removal probability of 36% under equal weights.

Fig. S5. Results from the BEAST dating analyses under a UCE clock model.

Fig. S6. Female and male body size (adult body length) evolution.

Fig. S7. Sexual size dimorphism (male to female body size ratio) evolution.

Fig. S8. Web evolution in Araneidae.

Fig. S9. Stabilimentum evolution in Araneidae.

Fig. S10. Results from unconstrained MB analysis.

Fig. S11. Results from unconstrained ML analysis.

Table S1. Simon's classification in the Histoire naturelle des Araignées (Simon 1894, 1895).

Table S2. Full list of species included in this study along with locality, specimen depository and GenBank accession numbers.

Table S3. BEAST setting used for the molecular dating analyses.

Table S4. Web characters.