

## **Phylogeny of the orb-weaving spider family Araneidae (Araneae, Araneoidea).**

### **Authors:**

**Nikolaj Scharff<sup>a,b</sup>, Jonathan A. Coddington<sup>b</sup>, Todd A. Blackledge<sup>c</sup>, Ingi Agnarsson<sup>b,d</sup>, Volker Framenau<sup>e,f,g</sup>, Tamas Szűts<sup>a,h</sup>, Cheryl Y. Hayashi<sup>i</sup> & Dimitar Dimitrov<sup>a,j,k</sup>**

### **Institutions:**

<sup>a</sup> Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark.

<sup>b</sup> Smithsonian Institution, National Museum of Natural History, 10th and Constitution, NW Washington, DC 20560-0105, USA.

<sup>c</sup> Integrated Bioscience Program, Department of Biology, University of Akron, Akron, Ohio, USA.

<sup>d</sup> Department of Biology, University of Vermont, 109 Carrigan Drive, Burlington, VT, 05405-0086, USA.

<sup>e</sup> Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia.

<sup>f</sup> School of Animal Biology, University of Western Australia, Crawley, Western Australia 6009, Australia.

<sup>g</sup> Harry Butler Institute, Murdoch University, 90 South St, Murdoch, Western Australia 6150, Australia

<sup>h</sup> Department of Ecology, University of Veterinary Medicine Budapest, H1077, Budapest, Hungary.

<sup>i</sup> Division of Invertebrate Zoology and Sackler Institute for Comparative Genomics, American Museum of Natural History, New York, New York 10024, USA.

<sup>j</sup> Natural History Museum, University of Oslo, PO Box 1172 Blindern, NO-0318 Oslo, Norway.

<sup>k</sup> Department of Natural History, University Museum of Bergen, University of Bergen, Bergen, Norway.

**Short running title:** Phylogeny of Araneidae

**Corresponding author:** Nikolaj Scharff, nscharff@snm.ku.dk

## **Table of Contents**

**Abstract**

**Introduction**

**Materials and Methods**

**Taxon sampling**

**Sequences and sequencing methods**

**Alignments**

**Phylogenetic analyses**

**Dating and calibration points**

**Comparative analyses**

**Taxonomic results and discussion**

**ARA Clade groups**

**Additional noteworthy results**

**Comparative analyses**

**Evolution of sexual size dimorphism**

**Evolution of web architecture and stabilimentum**

**Discussion**

**Acknowledgements**

**References**

**Legends**

## 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 the authors. 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 analyzed 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, the ingroup comprises three Zygiellinae and four Nephilinae genera, and 85 ARA Clade genera (10 new). Within the ARA Clade, we recognize ten informal groups that contain at least three genera each and are supported under Bayesian posterior probabilities ( $\geq 0.95$ ): “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” (*Colaranaea*, *Cryptaranaea*, *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, behavior, 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*, *Poltya*, *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.

## Introduction

Few spider families have been the object of so much general interest and research as the family 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 (Elgar *et al.*, 1990; Elgar, 1991; Hormiga *et al.*, 2000; Foellmer and Moya-Laraño, 2007; Cheng and Kuntner, 2014), behavior (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 1,000 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 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 three hundred 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 created or synonymized as necessary (we identify 10 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 one hundred years accelerated. The same is true for araneids (Fig. 3C), due principally to the work of H.W. Levi from the 1970's on—however, all such graphs are bedeviled 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 Framenau and Scharff (unpublished data) estimate that approximately 30 new genera will be described.

Since Simon (1893) the family Araneidae has been considered a ‘natural group’, but 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” (Simon, 1895). Since then nobody 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 3,100 species in 174 genera (World Spider Catalog, 2018) 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 redefinitions. 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), 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 20<sup>th</sup> 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 its 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 (Kallal *et al.*, 2018; Kuntner *et al.*, 2013; Dimitrov *et al.*, 2017). Kallal and Hormiga (2018) included the araneid genus *Paraplectanoides* and found strong support for a sistergroup 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 so 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 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 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 - *Poltyis*; 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, behavioral 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 relationship (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 support 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.*, 2016). 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 were 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 morphological 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, 2018), 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 most likely 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 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*

158 taxa were sampled, 133 of which belong to the in-group and represent 83 described araneid genera and, implied by this analysis, 10 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 Gen Bank accession numbers information is available in Table S2.

The choice of out-groups was guided by recent phylogenetic results focused on higher level orb-weavers 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 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 species 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 4,150bp of data per taxon.

50uL PCR reactions were prepared using ~0.5-1uL of genomic DNA, 1 uL dNTP mix, 0.5 uL of each primer, ~0.25uL Invitrogen *Taq* polymerase, 6.5 uL of buffer and 41uL of sdH<sub>2</sub>O. Up to 3 uL of additional MgCl was added to poorly amplifying reactions. Amplifications typically involved 40–50 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 v7 (Kato 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 (Kato 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 1,000 bootstrapping 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 substitutions models and here we used the best-fit models of molecular evolution from the jModelTest analyses. The MB 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).

Parsimony analyses (MP) were carried out in the program TNT v1.1 (Carpenter *et al.*, 1998). 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, Ratchet, 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 1,000 pseudo replicates 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 v2.4.2 (Drummond and Rambaut, 2007) 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 ultrametric starting tree that complies with both the dating and the topological constraints was generated with the program treePL v1.0 (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; Kuntner *et al.*, 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. Araneidae stem minimum age was constrained to 115Ma based on the species *Mesozygiella dunlopi* described from Lower Cretaceous amber from Spain (Penney and Ortuño, 2006). Linyphiidae minimum age was constrained as 125Ma based on a linyphiine species described from Lebanese amber (Penney and Selden, 2002). Another Lebanese amber fossil, *Palaeomicromenueus lebanensis* (Penney, 2003), was used to constrain the minimum age of Deinopidae (125Ma). Finally, the stem age of *Nephila* was constrained to a minimum of 16Ma 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, the 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 lognormal 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 of 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 sexual size dimorphism we used the methodological approaches described in 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 in 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 & Leroy, 1996). Species which do not build webs or for which we lack observations were not scored for stabilimentum. For the analyses of sexual size dimorphism 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 to those scored in 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 analyze quantitatively the internal phylogenetic structure of the family Araneidae. The former study, based on morphology and behavior, 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, and 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 to 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*, *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 resemble the web design of the mygalomorph purse web spider *Sphodros rufipes* (Atypidae)(Eberhard, pers. com.). The second species currently placed in *Paraplectanoides*, *P. kochi*, only known from its type specimen collected in tropical eastern Australia, is likely 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 taxon sample, 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 Catalogue, 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 Catalogue (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). Gregoric *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 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. ~~We prefer to keep zygiellines and nephilines as separate clades (subfamilies) within the broader concept of Araneidae given the placement of *Paraplectanoides* and because numerous Araneid taxa have not been included in the current and/or in other phylogenetic studies and their placements are uncertain.~~

The ARA Clade contains most of araneid diversity with 165 described genera, of which 83 are included here (Fig. 3A, 4A, S1-S4 and supplementary tree files). Of the spiders included in this study, we expect that at least 10 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 no doubt still 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 we predict that when *A.*

*angulatus* is sequenced, it will group with the former four species, and thus anchor phylogenetically the genus name *Araneus*, the family name Araneidae, and the ordinal name Araneae (all Clerck, 1757).

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

**ARA Clade groups.** Ten groups within the ARA Clade have either Bayesian (PP) support values  $\geq 0.95$  or maximum likelihood support values (BS)  $\geq 70$  (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 has started to diversify about 121Ma (84–123, Fig. 4B); 94Ma (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 absent in *Caerostris*. Furthermore, the male pedipalp of *Caerostris* does not have a paracymbium and the somatic morphology is unusual for an araneid, like 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 place them 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 the maximum likelihood (BS = 77) support values for the monophyly and interrelationships of this group are high (Fig. 3A). Simon (1895) thought 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 Gasteracanthae) 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 94Ma (80–109, Fig. 4B; 63Ma, 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 have previously been associated with *Micrathena* and there are no known morphological synapomorphies that confirm this group but the Bayesian (PP = 1.00) and the maximum likelihood (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 83Ma old (70–97, Fig. 4B; 46Ma, 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 maximum likelihood 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 (Framenau and 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 maximum likelihood analysis, but without support. The inferred age of this lineage is 77Ma (64–90, Fig. 4B; 41Ma, 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 85Ma 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 (Framenau and Scharff, unpublished data).

The Oriental-Australian *Parawixia dehaani* forms part of the Backbourkiine 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 likely transferred to *Parawixia* due to superficial similarities of the female epigyne to those of Neotropical *Parawixia*. *Parawixia dehaani* likely 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 Backbourkiines requires further investigation. However, other species of the Backbourkiines putatively dispersed into South-East Asia and the Indian subcontinent after Australia collided with the Sunda shelf, for example in the genus *Plebs*, that 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*, *Togocantha* and the New World *Encyosaccus* in his Gasteracanthae. 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 71Ma (59–84, Fig. 4B; 35Ma, 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* and *Cyrtophora*) and Argiopines *sensu stricto* (*Argiope* and *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 83Ma (74–101, Fig. 4B; 53Ma, 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 since they only included *Gasteracantha kuhli* as 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 behavioral characters (Eberhard, 1980; Robinson, 1982; Stowe, 1986) and Scharff and Coddington (1997) also found support for such a sister group relationship when using these behavioral characters in their phylogenetic matrix. The combined clade “cyrtarachnines” + “mastophorines” are 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 latter 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 U.S.A. and have all radiated unusually rapidly (Fig. 4B).

“Cyrtarachines” and “Mastophorines” are sister to each other and have diverged from their most recent common ancestor about 62Ma (71–74, Fig. 4B; 32Ma, 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 9Ma (5–13) (even younger in the UCE estimates ca. 3Ma, Fig. S5) that belongs to otherwise old lineage 46Ma (34–57) (ca. 19Ma under UCE, Fig. S5).

“**Zealaraneines**” includes at least *Colaranaea*, *Cryptaranaea*, *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). *Colaranaea*, *Cryptaranaea*, and *Zealaranea* are monophyletic and endemic to New Zealand. Similar to the “Backobourkiines” (see above), the inferred age of this clade, 61Ma (51–73, Fig. 4B; younger under UCE ca. 33Ma, Fig. S5), suggests that it has likely diversified after Australia and New Zealand have 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 60Ma (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 as 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 maximum likelihood (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, Scharff and Coddington, unpublished data), but such features may be homoplasious. “Nuctenines” are relatively young clade 54Ma (40–68) (Fig. 4B) (or less under UCE clock, ca 33Ma), 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 been for many years 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 3-4) 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, 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 araneids 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), maximum

likelihood (BS = 97) and parsimony (GC = 99) criteria. Quite surprisingly, the otherwise typical North American *Araneus bicentenarios* 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 highly 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 the 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 with maximum likelihood, 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 maximum likelihood 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 even though most of Grasshoff's new genera are considered valid by the WSC, 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 3-4). 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, *Acusilas* placement within "Argiopines" is strongly supported, whereas the placement of *Cyclosa* is uncertain. The monophyly of *Cyclosa* is strongly supported in this study (PP = 1; BS = 99; GC = 100) but the placement of the clade including *Cyclosa* within the ARA-clade is uncertain. Their sistergroup 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*.

**Xylethrae**, **Physioleae** and **Hypognatheae** of Simon (1895) included single genera and since 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* related to *Gasteracantha* but this is not supported here.

**Bertraneae** of Simon 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 sistergroup 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 (MB, ML & MP) and none of the placements are 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 (MB, ML & MP) is not supported.

**Poltyeae** of Simon (1895) included *Poltyis*, *Kaira*, *Pycnacantha*, *Homalopoltyis* (= *Dolichognatha*, Tetragnathidae) and *Cyphalonotus*. We did not include *Cyphalonotus*, but the rest of the genera join different parts of the tree, and therefore suggests polyphyly. However, none of the placements of these three genera are significantly supported on our trees. We included two species of *Poltyis*, including the type species *Poltyis illepidus*, and the support for the monophyly of *Poltyis* is high (PP = 1.0; BS = 100; Fig. 4A). *Poltyis*, *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*, *Poltyis*, *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, we should also notice 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 maximum likelihood and Bayesian inference analyses (Figs S10, S11).

## Comparative analyses

### *Evolution of sexual size dimorphism*

Our results show that all genera that exhibit extreme sexual dimorphism (female  $\geq 2x$  male) do not form a clade (Fig. S6). In most of these cases sexual size dimorphism appears to be driven by 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 decrease of male size does contribute towards the observed sexual size dimorphism (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 174 genera. Here we treat 83 genera (including ~90% of all currently named araneid species) in Araneidae as currently recognized.

What of the 91 omitted genera? Twenty-five of these are known from three or fewer species, all described prior to the 20<sup>th</sup> 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 strongly suggests synonymy of the genus with *Acroaspis*. As another example, *Collina* only includes 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 38 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 behavior, almost uniquely informative in orb-web weaving spiders (Eberhard, in press), correlate 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 (Framenau and 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 biogeographic 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 variety of 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 likely 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 morphology. As molecular data density increases for Araneidae, the density of direct observations of putatively selected traits, such as web architecture or decorations, and sexual size dimorphism, 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.

**Acknowledgments.** JC & NS acknowledges NSF EAR-0228699 (Assembling the Tree of Life: phylogeny of Spiders). TAB & NS acknowledges NSF DEB-0516038 (Collaborative Research: Araneid Phylogeny and Evolution of Spider Silk Phenotypes). DD & NS received support by the Danish National Research Foundation grant DNRF96 to the Center for Macroecology Evolution and Climate. NS acknowledges the Danish Natural Science Research Council Award 21020502. NS & TS acknowledge Marie Curie Intra European Fellowship Award 025850. NS and VWF received support by the Australian Biological Resources Study (ABRS grant no. 205–24). Access to the Abel computing facilities at the University of Oslo was granted through the Norwegian Metacenter for Computational Science (NOTUR; project NN9601K) to DD. We thank Joel Duff for access to his molecular laboratory. We thank Alpana Chaudhuri, Mariam Lekveishvili, and Kimberly Lorentz for assistance with sequencing of many specimens. In addition to specimens collected by ourselves, we thank David Britton, Matthew Bruce, David Court, Paula Cushing, Mike Gray, Charles Griswold, Aaron Harmer, Mark Harvey, Ken Haynes, Marshal Hedin, Marie Herberstein, Miki Kusahara, Laura Leibensperger, Astri and John Leroy, Brent Opell, Phil Sirvid, Helen Smith, Mark Stowe, Akio Tanikawa, Cor Vink and Ken Yeorgan for providing specimens. We thank Miquel Arnedo,

Charles Griswold and Martín Ramírez for their constructive criticism of a previous version of the manuscript. We thank associate editor Lorenzo Prendini for assistance with the manuscript.

## References

- Agnarsson, I., Coddington, J.A., Kuntner, M. 2013. Systematics: progress in the study of spider diversity and evolution, in: Penney, D. (Ed.), *Spider Research in the 21st Century*. pp. 58–111.
- Agnarsson, I., Kuntner, M., Blackledge, T.A. 2010. Bioprospecting finds the toughest biological material: Extraordinary silk from a giant riverine orb spider. *PLoS ONE*. 5, e11234. doi:10.1371/journal.pone.0011234
- Agnarsson, I., LeQuier, S.M., Kuntner, M., Cheng, R.-C., Coddington, J.A., Binford, G. 2016. Phylogeography of a good Caribbean disperser: *Argiope argentata* (Araneae, Araneidae) and a new ‘cryptic’ species from Cuba. *ZooKeys*. 625, 25–44.
- Babb, P.L., Lahens, N.F., Correa-Garhwal, S.M., Nicholson, D.N., Kim, E.J., Hogenesch, J.B., Kuntner, M., Higgins, L., Hayashi, C.Y., Agnarsson, I., Voight, B.F. 2017. The *Nephila clavipes* genome highlights the diversity of spider silk genes and their complex expression. *Nature Genetics*. 49, 895–903. doi:10.1038/ng.3852
- Blackledge, T.A. 2012. Spider silk: a brief review and prospectus on research linking biomechanics and ecology in draglines and orb webs. *Journal of Arachnology*. 40, 1–12. doi:10.1636/M11-67.1
- Blackledge, T.A., Scharff, N., Coddington, J.A., Szuts, T., Wenzel, J.W., Hayashi, C.Y., Agnarsson, I. 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Sciences*. 106, 5229–5234. doi:10.1073/pnas.0901377106
- Bond, J.E., Garrison, N.L., Hamilton, C.A., Godwin, R.L., Hedin, M., Agnarsson, I. 2014. Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology*. 24, 1765–1771. doi:10.1016/j.cub.2014.06.034
- Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J. 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*. 10(4):e1003537
- Bradley, R.A. 2012. *Common spiders of North America*. University of California Press, California.

- Bristowe, W.S. 1958. *The World of Spiders*. Collins, London.
- Brunet, B. 1994. *The Silken Web – a natural history of Australian spiders*. Reed New Holland, Sydney, Australia.
- Brunetta, L., Craig, C.L. 2012. *Spider silk: Evolution and 400 Million years of spinning, waiting, snagging, and mating*. Yale University Press.
- Carpenter, J.M., Goloboff, P.A., Farris, J.S. 1998. PTP is meaningless, T-PTP is contradictory: A reply to Trueman. *Cladistics*. 14, 105–116.
- Cheng, R.-C., Kuntner, M. 2014. Phylogeny suggests nondirectional and isometric evolution of sexual size dimorphism in argiopine spiders. *Evolution*. 68, 2861–2872.  
doi:10.1111/evo.12504
- Clerck, C. 1757. Svenska spindlar, uti sina hufvud-slågter indelte samt under några och sextio särskildte arter beskrefne och med illuminerade figurer uplyste. *Stockholmia*, Stockholm.
- Coddington, J.A., Hormiga, G., Scharff, N. 1997. Giant female or dwarf male spiders? *Nature*. 385, 687–688. doi:10.1038/385687a0
- Coddington, J.A., Levi, H.W. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics*. 565–592.
- Cotoras, D.D., Murray, G.G., Kapp, J., Gillespie, R.G., Griswold, C., Simison, W.B., Green, R.E. and Shapiro, B. 2017. Ancient DNA resolves the history of *Tetragnatha* (Araneae, Tetragnathidae) spiders on Rapa Nui. *Genes*. 8(12), p.403.
- Court, D.J., Forster, R.R. 1988. The spiders of New Zealand: Part VI. Araneidae-Araneinae. *Otago Museum Bulletin*. 6, 68–124.
- Dahl, F. 1914. Die Gasteracanthien des Berliner Zoologischen Museums und deren geographische Verbreitung. *Mitteilungen aus dem Zoologischen Museum in Berlin*. 7, 235–301.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*. 9, 772–772. doi:10.1038/nmeth.2109
- Davies, V.T. 1988. An illustrated guide to the genera of orb-weaving spiders in Australia. *Memoirs of the Queensland Museum*. 25, 273–332.
- Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G., Griswold, C.E., Scharff, N., Hormiga, G. 2017. Rounding up the usual suspects: a standard target-gene approach for resolving the interfamilial phylogenetic relationships of ecribellate orb-weaving spiders with a new family-rank classification (Araneae, Araneoidea). *Cladistics*. 33, 221–250.  
doi:10.1111/cla.12165

- Dimitrov, D., Lopardo, L., Giribet, G., Arnedo, M., Alvarez-Padilla, F., Hormiga, G. 2012. Tangled in a sparse spider web: single origin of orb weavers and their spinning work unraveled by denser taxonomic sampling. *Proceedings of the Royal Society B: Biological Sciences*. 279, 1341–1350. doi:10.1098/rspb.2011.2011
- Dippenaar-Schoeman, A.S., Leroy, A. 1996. Notes on the biology of *Pycnacantha tribulus*, *Revue Suisse de Zoologie*, vol. hors serie: 165-171.
- Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology*. 4, e88. doi:10.1371/journal.pbio.0040088
- Dunlop, J.A., Penney, D., Jekel, D. 2018. A summary list of fossil spiders and their relatives [WWW Document]. The world spider catalog, version 19.0. URL <http://wsc.nmbe.ch/resources/fossils/Fossils19.0.pdf> (accessed 13.07.18).
- Eberhard, W.G. 1980. The natural history and behavior of the bolas spider, *Mastophora dizzydeani* sp. n. (Araneae). *Psyche*. 87, 143–170.
- Eberhard, W.G. 1990. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics*. 21, 341–372. doi:10.1146/annurev.es.21.110190.002013
- Eberhard, W. G. In press. Spider webs: function, behavior and evolution. University of Chicago press. Chicago, IL:
- Elgar, M.A. 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). *Evolution*. 45, 444–448. doi:10.1111/j.1558-5646.1991.tb04419.x
- Elgar, M.A., Ghatfar, N., Read, R.F. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology*. 222, 455–470.
- Emerit, M. 1973. Contribution a la connaissance des Araneidae Gasteracanthinae du sud-est africain: les Gasteracantes du Natal Museum. *Annals of the Natal Museum*. 21, 675–695.
- Fachim, H.A., Cunha, A.O.S., Pereira, A.C., Belebani, R.O., Gobbo-Neto, L., Lopes, N.P., Coutinho-Netto, J., dos Santos, W.F. 2011. Neurobiological activity of Parawixin 10, a novel anticonvulsant compound isolated from *Parawixia bistriata* spider venom (Araneidae: Araneae). *Epilepsy & Behavior*. 22, 158–164. doi:10.1016/j.yebeh.2011.05.008
- Farris, J.S. 1997. The future of phylogeny reconstruction. *Zoologica Scripta*. 26, 303–311.
- Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G., Hormiga, G. 2018. Phylogenomics, diversification dynamics, and comparative transcriptomics across the spider Tree of Life. *Current Biology*. 28, 1489-1497.e5. doi:10.1016/j.cub.2018.03.064

- Foellmer, M.W., Moya-Laraño, J. 2007. Sexual size dimorphism in spiders: patterns and processes, in: Fairbairn, D.J., Blanckenhorn, D.J., Székely, T. (Eds.), *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Dimorphism*. Oxford University Press, Oxford, pp. 71–81.
- Forster, R., Forster, L. 1999. *Spiders of New Zealand and their worldwide kin*. University of Otago Press, Dunedin, New Zealand.
- Framenau, V.W. 2011. *Lariniophora*, a new monotypic orb-weaving spider genus from Australia (Araneae: Araneidae: Araneinae). *Records of the Western Australian Museum*. 26. 191–201.
- Framenau, V.W., Dupérré, N., Blackledge, T.A., Vink, C.J. 2010a. Systematics of the new Australasian orb-weaving spider genus *Backbourkia* (Araneae: Araneidae: Araneinae). *Arthropod Systematics & Phylogeny*. 68, 79–111.
- Framenau, V.W., Scharff, N. 2008. The orb-weaving spider genus *Larinia* in Australia (Araneae: Araneidae). *Arthropod Systematics and Phylogeny*. 66, 227–250.
- Framenau, V.W., Scharff, N., Harvey, M.S. 2010b. Systematics of the Australian orb-weaving spider genus *Demadiana* with comments on the generic classification of the Arkyinae (Araneae : Araneidae). *Invertebrate Systematics*. 24, 139–171. doi:10.1071/IS10005
- Garrison, N.L., Rodriguez, J., Agnarsson, I., Coddington, J.A., Griswold, C.E., Hamilton, C.A., Hedin, M., Kocot, K.M., Ledford, J.M., Bond, J.E. 2016. Spider phylogenomics: untangling the Spider Tree of Life. *PeerJ*. 4, e1719. doi:10.7717/peerj.1719
- Chousou-Polydouri, N., A., Carmichael, T., Szüts, A., Saucedo, R., Gillespie, Griswold, C., Wood, H. (2018) Giant Goblins above the waves at the southern end of the world: The biogeography of the spider family Orsolobidae (Araneae, Dysderoidea). *Journal of Biogeography* 2018;00: 1–11. <https://doi.org/10.1111/jbi.13487>
- GGBN. 2018. The GGBN Data Portal. GGBN Secretariat, NMNH, Washington D.C., USA. Compiled by GGBN Technical Management, BGBM, Berlin, Germany. [WWW Document]. URL <http://data.ggbn.org> (accessed 5.6.18).
- Giribet, G., Boyer, S.L. 2010. ‘Moa’s Ark’ or ‘Goodbye Gondwana’: is the origin of New Zealand’s terrestrial invertebrate fauna ancient, recent, or both? *Invertebrate Systematics*. 24(1), 1–8. doi:10.1071/IS10009
- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*. 15, 415–428.
- Grasshoff, M. 1970. Die Gattung *Kilima* n. gen. (Arachnida: Araneae: Araneidae). *Senckenberg. Biologica*. 51, 119–128.



- Gregorič, M., Agnarsson, I., Blackledge, T.A., Kuntner, M. 2015. Phylogenetic position and composition of Zyiellinae and *Caerostris*, with new insight into orb-web evolution and gigantism. *Zoological Journal of the Linnean Society* 175, 225-243. doi:10.1111/zoj.12281
- Griswold, C.E., Coddington, J.A., Hormiga, G., Scharff, N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society*. 123, 1–99.
- Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids. Symposium, Series*. 41, 95-98.
- Harmer, A.M., Framenau, V.W. 2008. *Telaprocera* (Araneae: Araneidae), a new genus of Australian orb-web spiders with highly elongated webs. *Zootaxa*. 1956, 59–80.
- Harrod, J.C., Levi, H.W., Leibensperger, L.B. 1990. The neotropical orbweavers of the genus *Larinia* (Araneae: Araneidae). *Psyche*. 97, 241–266.
- Harvey, M.S., Rix, M.G., Harms, D., Giribet, G., Vink, C.J., Walter, D.E. 2017. The biogeography of Australasian arachnids, in: Ebach, C.M. (Ed.), *Handbook of Australasian Biogeography*. CRC Press, pp. 267–294.
- Heimer, S. 1984. Remarks on the spider genus *Arcys* Walckenaer, 1837, with description of new species (Araneae, Mimetidae). *Entomologische Abhandlungen Dresden*. 47, 155–178.
- Heimer, S., Nentwig, W. 1983. Thoughts on the phylogeny of the Araneoidea Latreille, 1806 (Arachnida, Araneae). *Journal of Zoological Systematics and Evolutionary Research*. 20, 284–295. doi:10.1111/j.1439-0469.1983.tb00554.x
- Herberstein, M.E., Craig, C.L., Coddington, J.A., Elgar, M.A. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews*. 75, 649–669.
- Hesselberg, T. 2015. Exploration behaviour and behavioural flexibility in orb-web spiders: A review. *Current Zoology*. 61, 313–327.
- Hickman, V.V. 1975. On *Paraplectanoides crassipes* Keyserling Araneae: Araneidae. *Bulletin of the British arachnological Society*. 3, 166–174.
- Hormiga, G., Griswold, C.E. 2014. Systematics, phylogeny, and evolution of orb-weaving spiders. *Annual Review of Entomology*. 59, 487–512. doi:10.1146/annurev-ento-011613-162046
- Hormiga, G., Scharff, N., Coddington, J.A. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology*. 49, 435–462.

- Joseph, M.M., Framenau, V.W. 2012. Systematic review of a new orb-weaving spider genus (Araneae: Araneidae), with special reference to the Australasian-Pacific and South-East Asian fauna. *Zoological Journal of the Linnean Society*. 166, 279–341. doi:10.1111/j.1096-3642.2012.00845.x
- Kallal, R.J., Fernández, R., Giribet, G., Hormiga, G. 2018. A phylotranscriptomic backbone of the orb-weaving spider family Araneidae (Arachnida, Araneae) supported by multiple methodological approaches. *Molecular Phylogenetics and Evolution*. 126, 129–140. doi:10.1016/j.ympev.2018.04.007
- Kallal, R.J., Hormiga, G. 2018. Systematics, phylogeny and biogeography of the Australasian leaf-curling orb-weaving spiders (Araneae: Araneidae: Zygiellinae), with a comparative analysis of retreat evolution. *Zoological Journal of the Linnean Society*. doi:10.1093/zoolinnean/zly014
- Kaston, B.J. 1964. The evolution of spider webs. *American Zoologist*. 4, 191–207.
- Kaston, B.J. 1948. Spiders of Connecticut. *Bulletin of the Connecticut State Geological and Natural History Survey*. 70, 1–874.
- Katoh, K., Standley, D.M. 2013. MAFFT Multiple sequence alignment software Version 7: Improvements in performance and usability. *Molecular Biology and Evolution*. 30, 772–780. doi:10.1093/molbev/mst010
- Katoh, K., Toh, H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*. 9, 286–298. doi:10.1093/bib/bbn013
- Kluge, J.A., Rabotyagova, O., Leisk, G.G., Kaplan, D.L. 2008. Spider silks and their applications. *Trends in Biotechnology*. 26, 244–251. doi:10.1016/j.tibtech.2008.02.006
- Kuntner, M. 2006. Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). *Zoologica Scripta*. 35, 19–62. doi:10.1111/j.1463-6409.2006.00220.x
- Kuntner, M. 2002. The placement of *Perilla* (Araneae, Araneidae) with comments on araneid phylogeny. *Journal of Arachnology*. 30, 281–287.
- Kuntner, M., Agnarsson, I. 2010. Web gigantism in Darwin's bark spider, a new species from Madagascar (Araneidae: *Caerostris*). *Journal of Arachnology*. 38, 346–356. doi:10.1636/B09-113.1

- Kuntner, M., Arnedo, M.A., Trontelj, P., Lokovšek, T., Agnarsson, I. 2013. A molecular phylogeny of nephilid spiders: evolutionary history of a model lineage. *Molecular Phylogenetics and Evolution*. 69, 961–979. doi:10.1016/j.ympev.2013.06.008
- Kuntner, M., Coddington, J.A. 2009. Discovery of the largest orbweaving spider species: the evolution of gigantism in *Nephila*. *PLoS One*. 4, e7516.
- Kuntner, M., Cheng, R-C. 2016. Evolutionary Pathways Maintaining Extreme Female-Biased Sexual Size Dimorphism: Convergent Spider Cases Defy Common Patterns. In: Pontarotti P. (eds) *Evolutionary Biology*. Springer, Cham.
- Kuntner, M., Elgar, M. 2014. Evolution and maintenance of sexual size dimorphism: aligning phylogenetic and experimental evidence. *Frontiers in Ecology and Evolution*. 2, 26pp. doi:10.3389/fevo.2014.00026
- Kuntner, M., Hormiga, G. 2002. The African spider genus *Singafrotypa* (Araneae, Araneidae). *Journal of Arachnology*. 30, 129–139. doi:10.1636/0161-8202(2002)030[0129:TASGSA]2.0.CO;2
- Kuntner, M., Hamilton, C.A., Cheng, R-C., Gregorič, N., Lupše, N., Lokovšek, T., Lemmon, E., Lemmon, A., Agnarsson, I., Coddington, J.A., Bond, J.E. 2018. Golden orbweavers ignore biological rules: phylogenomic and comparative analyses unravel a complex evolution of sexual size dimorphism. *Systematic Biology*.
- Lehtinen, P.T. 1978. Definition and limitations of supraspecific taxa in spiders. *Symposia of the Zoological Society of London*. 42, 255–271.
- Leibensperger, L.B. 2016. Herbert Walter Levi (1921–2014) and Lorna Levi (1928–2014). *Breviora*. 551, 1–37. doi:10.3099/MCZ28.1
- Lepage, T., Bryant, D., Philippe, H., Lartillot, N. 2007. A general comparison of relaxed molecular clock models. *Molecular Biology and Evolution*, 24(12), 2669–2680.
- Levi, H.W. 2005. The spider genera *Heterognatha*, *Testudinaria* and *Ursa* in South America (Araneae: Araneoidea). *Bulletin British arachnological Society* 13, 185.
- Levi, H.W. 2003. The bolas spiders of the genus *Mastophora* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology*. 157, 309–382.
- Levi, H.W. 1997. The American orb weavers of the genera *Mecynogea*, *Manogea*, *Kapogea* and *Cyrtophora* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology*. 155, 215-255.

- Levi, H.W. 1996. The American orb weavers *Hypognatha*, *Encyosaccus*, *Xylethrus*, *Gasteracantha*, and *Enacrosoma* (Araneae, Araneidae). *Bulletin of the Museum of Comparative Zoology*. 155, 89–157.
- Levi, H.W. 1992. Spiders of the orb-weaver genus *Parawixia* in America (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology*. 153, 1–46.
- Levi, H.W. 1986. The Neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). *Bulletin of the Museum of Comparative Zoology*. 151, 91–215.
- Levi, H.W. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology*. 150, 429–618.
- Levi, H.W. 1978. Orb-webs and phylogeny of orb-weavers. *Symposia of the Zoological Society of London*. 42, 1–15.
- Levi, H.W. 1976. The orb-weaver genera *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Scoloderus* and *Alpaida* north of Mexico. *Bulletin of the Museum of Comparative Zoology*. 147, 351–391.
- Levi, H.W. 1975. The American orb-weaver genera *Larinia*, *Cercidia* and *Mangora* north of Mexico (Araneae, Araneidae). *Bulletin of the Museum of Comparative Zoology*. 147, 101–135.
- Levi, H.W., Coddington, J.A. 1983. Progress report on the phylogeny of the orb-weaving family Araneidae and the superfamily Araneoidea (Arachnida, Araneae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*. 26, 151–154.
- Liberato, J.L., Cunha, A.O.S., Mortari, M.R., Gelfuso, É.A., de Oliveira Belebony, R., Coutinho-Netto, J., dos Santos, W.F. 2006. Anticonvulsant and anxiolytic activity of FrPbAII, a novel GABA uptake inhibitor isolated from the venom of the social spider *Parawixia bistriata* (Araneidae: Araneae). *Brain Research*. 1124, 19–27. doi:10.1016/j.brainres.2006.09.052
- Magalhães, I.L.F., Santos, A.J. 2012. Phylogenetic analysis of *Micrathena* and *Chaetacis* spiders (Araneae: Araneidae) reveals multiple origins of extreme sexual size dimorphism and long abdominal spines. *Zoological Journal of the Linnean Society*. 166, 14–53. doi:10.1111/j.1096-3642.2012.00831.x
- McCook, H.C. 1889. *American spiders and their spinningwork*. Philadelphia.
- McGlone, M.S. 2005. Goodbye Gondwana. *Journal of Biogeography*. 32, 739–740. doi:10.1111/j.1365-2699.2005.01278.x
- Nielsen, E. 1932. *Biology of spiders*. Levin & Munksgaard, Copenhagen.

- Paradis, E. 2012. Analysis of phylogenetics and evolution with R, second edition. Springer, New York.
- Penney, D. 2003. A new deinopoid spider from Cretaceous Lebanese amber. *Acta Palaeontologica Polonica*. 48(4), 569–574.
- Penney, D., Ortuño, V.M. 2006. Oldest true orb-weaving spider (Araneae: Araneidae). *Biology Letters*. 2, 447–450.
- Penney, D., Selden, P.A. 2002. The oldest linyphiid spider in Lower Cretaceous Lebanese amber (Araneae, Linyphiidae, Linyphiinae). *The Journal of Arachnology*. 30, 487–493.
- Pickard-Cambridge, O. 1887. On some new genera and species of Araneidea. *Annals and Magazine of Natural History Series 4*. 19, 26–39.
- Pineda, S.S., Chaumeil, P.-A., Kunert, A., Kaas, Q., Thang, M.W.C., Li, L., Nuhn, M., Herzig, V., Saez, N.J., Cristofori-Armstrong, B., Anangi, R., Senff, S., Gorse, D., King, G.F. 2017. ArachnoServer 3.0: an online resource for automated discovery, analysis and annotation of spider toxins. *Bioinformatics*. doi:10.1093/bioinformatics/btx661
- Rambaut, A., Drummond, A.J. 2007. Tracer v1.4, Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Rash, L.D., Hodgson, W.C. 2002. Pharmacology and biochemistry of spider venoms. *Toxicon*. 40, 225–254.
- Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*. 3, 217–223. doi:10.1111/j.2041-210X.2011.00169.x
- Robinson, M.H. 1982. Courtship and mating behavior in spiders. *Annual Review of Entomology*. 27, 1–20.
- Roewer, C.F. 1942. *Katalog der Araneae von 1758 bis 1940*. Bremen.
- Ronquist, F., Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*. 19, 1572.
- Scharff, N., Coddington, J.A. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society*. 120, 355–434.
- Scharff, N., Hormiga, G. 2012. First evidence of aggressive chemical mimicry in the Malagasy orb weaving spider *Exechocentrus lancearius* Simon, 1889 (Arachnida: Araneae: Araneidae) and description of a second species in the genus. *Arthropod Systematics & Phylogeny*. 70, 107–118.

- Schmidt, J.B., Scharff, N. 2008. A taxonomic revision of the orb-weaving spider genus *Acusilas* Simon, 1895 (Araneae, Araneidae). *Insect Systematics and Evolution*. 39, 1–38.  
doi:10.1163/187631208788784147
- Shear, W.A. 1994. Untangling the evolution of the web. *American Scientist*. 82, 256–266.
- Simon, E. 1864 *Histoire naturelle des araignées (aranéides)*. Paris.
- Simon, E. 1889. *Etudes arachnologiques*. 21e Mémoire. XXXII. Descriptions d'espèces et the genres nouveaux de Nouvelle Calédonie. *Annales de la Société Entomologique de France* (6) 8, 237-247.
- Simon, E. 1890. *Etudes arachnologiques*. 22e Mémoire. XXXIV. Etude sur les arachnides de l'Yemen. *Annales de la Société Entomologique de France* (6) 10, 77-124. Simon, E. 1892. *Histoire naturelle des araignées*. Librairie Encyclopédique, Paris.
- Simon, E. 1893. *Histoire naturelle des araignées*. Librairie Encyclopédique, Paris.
- Simon, E. 1895. *Histoire naturelle des araignées*. Librairie Encyclopédique, Paris.
- Smith, H.M. 2006. A revision of the genus *Poltys* in Australasia (Araneae: Araneidae). *Records of the Australian Museum*. 58, 43–96.
- Smith, S.A., O'Meara, B.C. 2012. Divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics*. 28 (20), 2689-2690.
- Song, D.X., Zhu, M.S., Chen, J. 1999. *The spiders of China*. Hebei Science and Technology Publishing House. Shijiazhuang 640pp.
- Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)*. 30, 1312–1313.  
doi:10.1093/bioinformatics/btu033
- Stowe, M.K. 1986. Prey specialization in the Araneidae, in: Shear, W.A. (Ed.), *Spiders: Webs, behavior, and evolution*. Stanford, California, pp. 101–103.
- Tanikawa, A. 2000. Japanese Spiders of the Genus *Eriophora* (Araneae: Araneidae). *Acta Arachnologica*. 49, 17–28. doi:10.2476/asjaa.49.17
- Tanikawa, A., Shinkai, A., Miyashita, T. 2014. Molecular phylogeny of moth-specialized spider sub-family Cyrtarachninae, which includes bolas spiders. *Zoological science*. 31, 716–720.
- Turnbull, A.L. 1973. Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology*. 18, 305–348. doi:10.1146/annurev.en.18.010173.001513
- Urquhart, A.T. 1891. On new species of Araneae. *Transactions and Proceedings of the New Zealand Institute*. 23, 128–189.

- Walckenaer, C.A. 1837. Histoire naturelle des Insectes: aptères: ouvrage accompagné de planches. Roret.
- Waters, J.M., Craw, D. 2006. Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology*. 55, 351– 356.
- Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramírez, M.J., Sierwald, P., Almeida-Silva, L., Alvarez-Padilla, F., Arnedo, M.A., Benavides Silva, L.R., Benjamin, S.P., Bond, J.E., Grismado, C.J., Hasan, E., Hedin, M., Izquierdo, M.A., Labarque, F.M., Ledford, J., Lopardo, L., Maddison, W.P., Miller, J.A., Piacentini, L.N., Platnick, N.I., Polotow, D., Silva-Dávila, D., Scharff, N., Szűts, T., Ubick, D., Vink, C.J., Wood, H.M., Zhang, J. 2017. The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* 33, 574-616. doi:10.1111/cla.12182
- Wood, H, Gonzalez, V, Lloyd, M, Coddington, J.A. and Scharff, N. 2018. Next-generation museum genomics: Phylogenetic relationships among palpimonooid spiders using sequence capture techniques (Araneae; Palpimanoidea). *Molecular Phylogenetic and Evolution*. 127(18), 907-918.
- World Spider Catalog. 2018. World Spider Catalog. Version 19.0. [WWW Document]. URL <http://wsc.nmbe.ch> (accessed 11.6.18).
- Wunderlich, J. 1986. Spinnenfauna gestern und heute. Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten. Erich Bauer Verlag bei Quelle und Meyer, Wiesbaden, 283 pp.
- Xavier, G.M., Moura, R.R., de Oliveira Gonzaga, M. 2017. Orb web architecture of *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae: Araneidae): intra-orb variation of web components. *Journal of Arachnology*. 45, 160–165. doi:10.1636/JoA-S-17-001.1
- Yin, C.M., Wang, J.F., Zhu, M.S., Xie, L.P., Peng, X.J., Bao, Y.H. 1997. Fauna Sinica: Arachnida: Araneae: Araneidae. Science Press, Beijing.

## Figure legends:

**Figure 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*. H – *Larinioides* sp. Photos: J.A. Coddington (A); T. Szuts (H); N. Scharff (B-G).

**Figure 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).

**Figure 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 Figures 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), darker color corresponds to higher species number. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure 4.** A – Results from the MB analyses (continues from Figure 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 Figure S8.

**Figure S1.** Full tree from the MB analysis. Values at nodes represent posterior probabilities, only values >0.95 are shown. C – constrained node. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S2.** Results from the ML analyses. Values at nodes represent bootstrap supports based on 1000 fast bootstrap replicates in RAXML, bootstrap values below 50 are not shown. C – constrained node. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S3.** Strict consensus of 64 MP trees found under equal weights search in TNT. C – constrained node. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S4.** Maximum parsimony Jackknife supports based on 1000 replicates with character removal probability 36% under equal weights. Only jackknife values above 50 are shown. C – constrained node. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S5.** Results from the BEAST dating analyses under an UCE clock model. Numbers at node show inferred mean ages and bars depict the 95% highest posterior density interval (HPD) for the



nodes height estimates. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S6.** Female and male body size (adult body length) evolution. A - based on the ultrametric tree from the molecular dating under UCL clock model, B - based on the tree resulting from the implementation of UCE clock model. Warmer colors correspond to smaller body sizes. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S7.** Sexual size dimorphism (male to female body size ratio) evolution. Colder colors (i.e., blues) show higher levels of sexual size dimorphism. A - based on the ultrametric tree from the molecular dating under UCL clock model, B - based on the tree resulting from the implementation of UCE clock model. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S8.** Web evolution in Araneidae. Summary of 1000 SIMMAP characters maps using the UCL dated tree and equal rates of transition between states model (ER). Colors represent different web types and sectors of pies at nodes are proportional to the probabilities of each state at that node. Result using the UCE tree are the same and are not shown. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S9.** Stabilimentum evolution in Araneidae. Summary of 1000 SIMMAP characters maps using the UCL dated tree and equal rates of transition between states model (ER). Sectors of pies at nodes are proportional to the probabilities of each state at that node. Result using the UCE tree are the same and are not shown. Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Figure S10.** Results from unconstrained MB analysis. Values at nodes represent posterior probabilities (only values above 0.95 are shown). Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

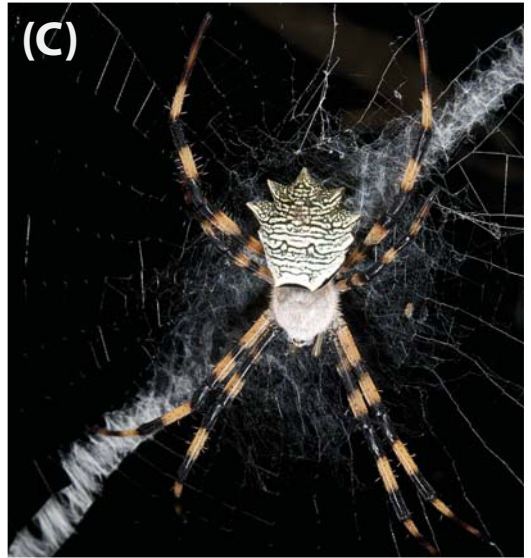
**Figure S11.** Results from unconstrained ML analysis. Values at nodes represent bootstrap supports based on 1000 bootstrap replicates (only values above 50 are shown). Note: Kuntner et al. (2018) transferred all *Nephila* species figured here to *Trichonephila*.

**Table S1.** Simon's classification in the Histoire naturelle des Araignées (Simon 1894, 1895). ~ in Simon 1929 it is in *Zygielleae*; \*as *Araneus*; \*\*as *Gasteracantha*; \*\*\* as *Caira*; § as *Glyptocranium*; # for *A. bicentenarius*.

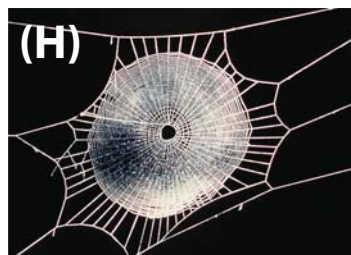
**Table S2.** Full list of species included in this study along with locality, specimen depository and Gen Bank accession numbers. Note: Kuntner et al. (2018) transferred all *Nephila* species mentioned here to *Trichonephila*.

**Table S3.** BEAST setting used for the molecular dating analyses. S – stem calibration.

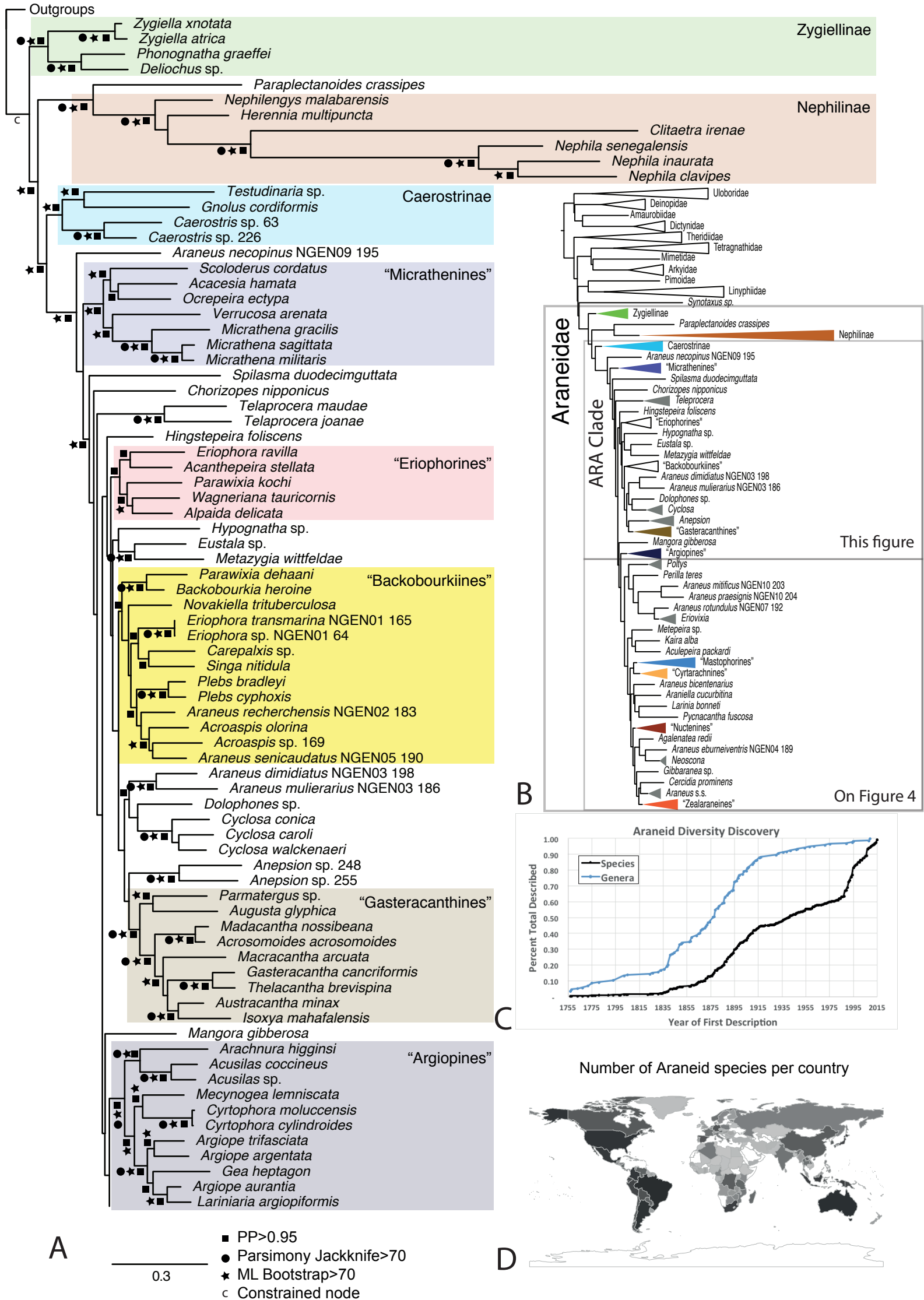
**Table S4.** Web characters. Character states for web type: 0. Vertical orb; 1. Horizontal orb; 2. Bolas; 3. Foraging web lost; 4. Irregular ground sheet; 5. Stereotyped aerial sheet; 6. Irregular aerial sheet; 7. Cobweb; 8. Spanning-thread; 9. *Paraplectanoides*; 10. Trapeze. Character states for Stabilimentum: 0. No; 1. Yes.



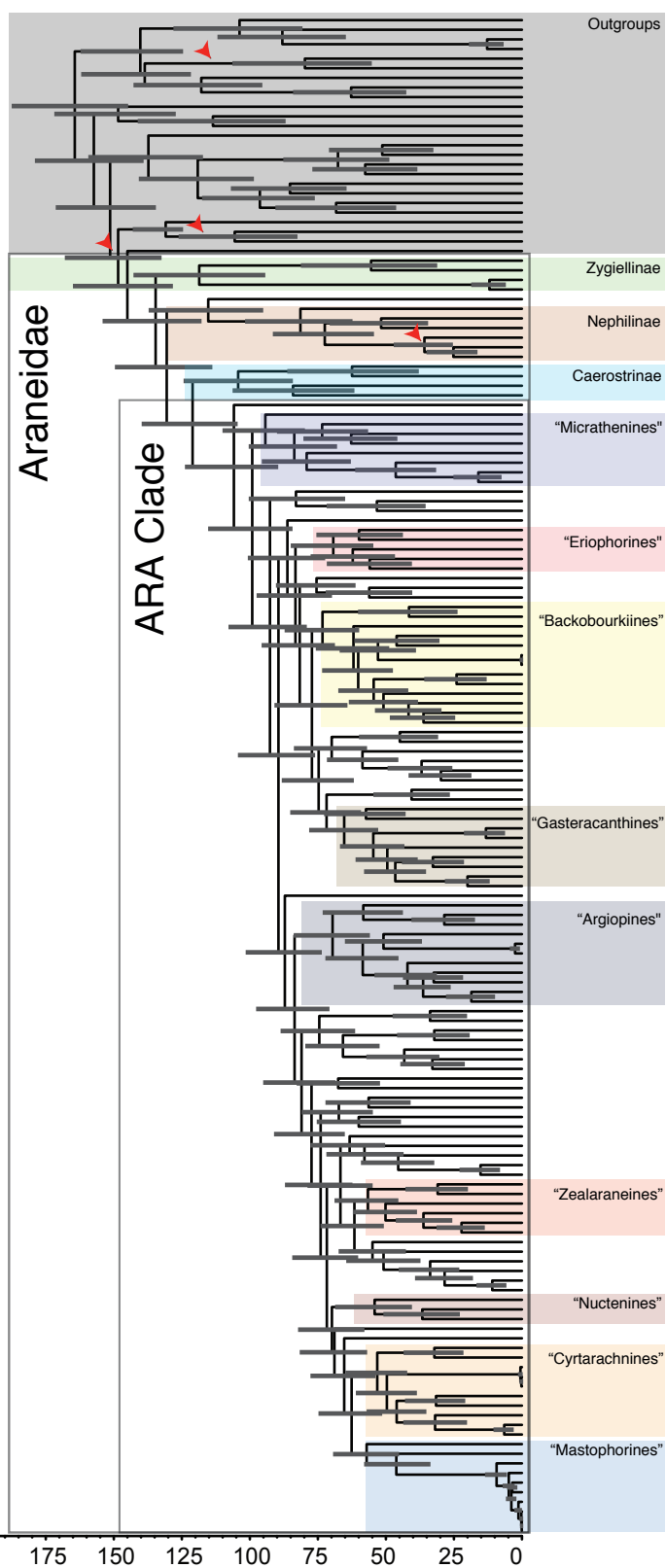
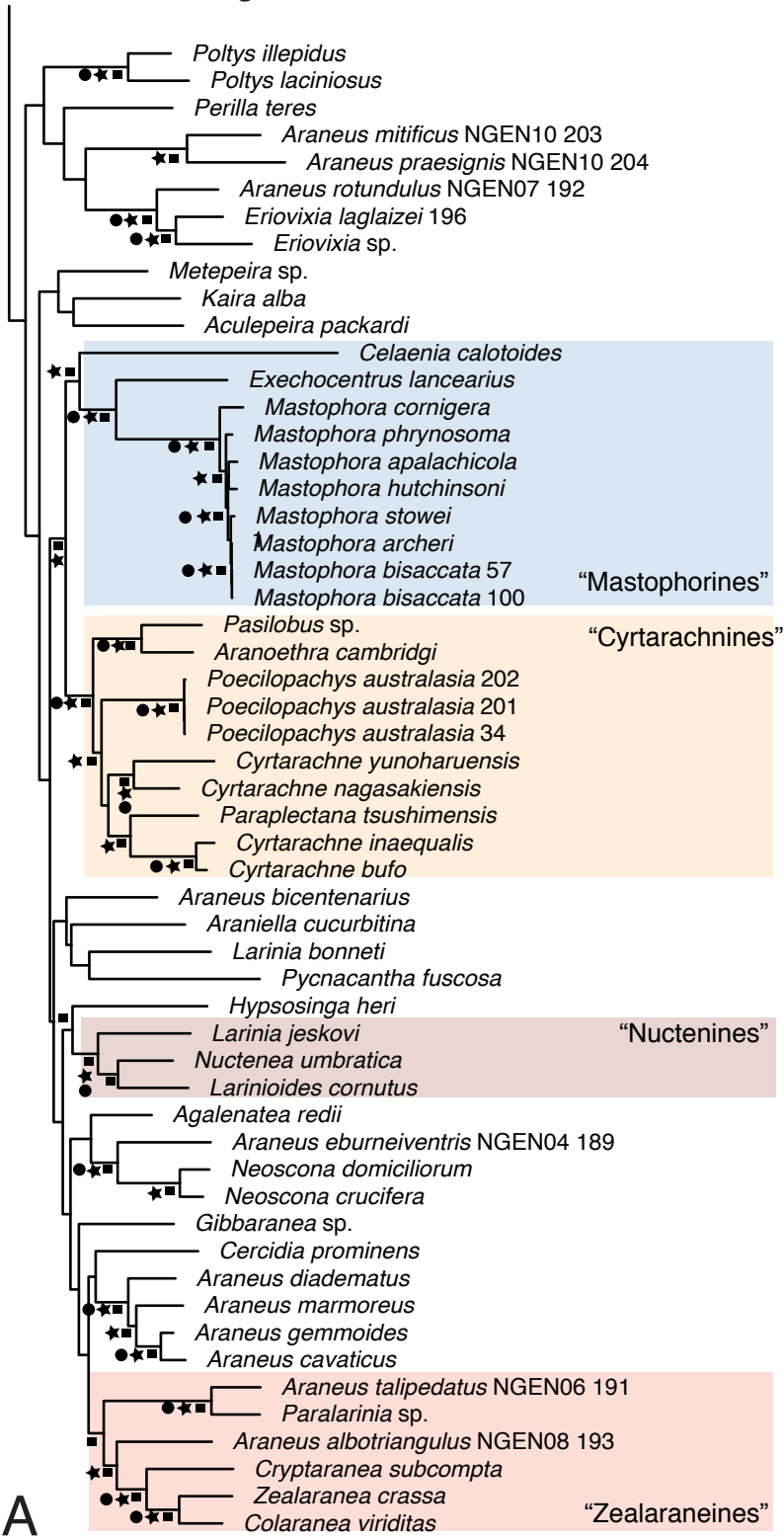








continues from Figure 3



A

B