WILEY-BLACKWELL

Cladistics 33 (2017) 574–616

Cladistics

10.1111/cla.12182

The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling

Ward C. Wheeler[a,*], Jonathan A. Coddington[b], Louise M. Crowley[a], Dimitar Dimitrov[c,d], Pablo A. Goloboff[e], Charles E. Griswold[f], Gustavo Hormiga[d], Lorenzo Prendini[a], Martín J. Ramírez[g], Petra Sierwald[h], Lina Almeida-Silva[f,i], Fernando Alvarez-Padilla[f,d,j], Miquel A. Arnedo[k], Ligia R. Benavides Silva[d], Suresh P. Benjamin[d,l], Jason E. Bond[m], Cristian J. Grismado[g], Emile Hasan[d], Marshal Hedin[n], Matías A. Izquierdo[g], Facundo M. Labarque[f,g,i], Joel Ledford[f,o], Lara Lopardo[d], Wayne P. Maddison[p], Jeremy A. Miller[f,q], Luis N. Piacentini[g], Norman I. Platnick[a], Daniele Polotow[f,i], Diana Silva-Dávila[f,r], Nikolaj Scharff[s], Tamás Szűts[f,t], Darrell Ubick[f], Cor J. Vink[n,u], Hannah M. Wood[f,b] and Junxia Zhang[p]

[a]Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA; [b]Smithsonian Institution, National Museum of Natural History, 10th and Constitution, NW Washington, DC 20560-0105, USA; [c]Natural History Museum, University of Oslo, Oslo, Norway; [d]Department of Biological Sciences, The George Washington University, 2029 G St., NW Washington, DC 20052, USA; [e]Unidad Ejecutora Lillo, FML—CONICET, Miguel Lillo 251, 4000, SM. de Tucumán, Argentina; [f]Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, Golden State Park, San Francisco, CA 94118, USA; [g]Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'—CONICET, Av. Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina; [h]The Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA; [i]Laboratório Especial de Coleções Zoológicas, Instituto Butantan, Av. Vital Brasil, 1500, 05503-900, São Paulo, São Paulo, Brazil; [j]Departamento de Biología Comparada, Facultad de Ciencias, Laboratório de Acarología, Universidad Nacional Autónoma de México, Distrito Federal Del. Coyoacán, CP 04510, México; [k]Departamento de Biología Animal, Facultat de Biología, Institut de Recerca de la Bioversitat, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain; [l]National Institute of Fundamental Studies, Hantana Road, Kandy 20000, Sri Lanka; [m]Department of Biological Sciences, Auburn University Museum of Natural History, Auburn University, Rouse Life Sciences Building, Auburn, AL 36849, USA; [n]Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA; [o]Department of Plant Biology, University of California, Davis, CA 95616, USA; [p]Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada; [q]Department of Terrestrial Zoology, Netherlands Centre for Biodiversity Naturalis, Postbus 9517 2300 RA, Leiden, The Netherlands; [r]Departamento de Entomología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Apartado Postal 140434, Lima 14, Peru; [s]Biodiversity Section, Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, Copenhagen, Denmark; [t]Department of Zoology, University of West Hungary, H9700, Szombathely, Hungary; [u]Canterbury Museum, Rolleston Avenue, Christchurch, 8013, New Zealand

Accepted 24 October 2016

Abstract

We present a phylogenetic analysis of spiders using a dataset of 932 spider species, representing 115 families (only the family Synaphridae is unrepresented), 700 known genera, and additional representatives of 26 unidentified or undescribed genera. Eleven genera of the orders Amblypygi, Palpigradi, Schizomida and Uropygi are included as outgroups. The dataset includes six markers from the mitochondrial (12S, 16S, COI) and nuclear (histone H3, 18S, 28S) genomes, and was analysed by multiple methods, including constrained analyses using a highly supported backbone tree from transcriptomic data. We recover most of the higher-level structure of the spider tree with good support, including Mesothelae, Opisthothelae, Mygalomorphae and Araneomorphae. Several of our analyses recover Hypochilidae and Filistatidae as sister groups, as suggested by previous transcriptomic analyses. The Synspermiata are robustly supported, and the families Trogloraptoridae and Caponiidae are found as sister to the Dysderoidea. Our results support the Lost Tracheae clade, including Pholcidae, Tetrablemmidae, Diguetidae,

Plectreuridae and the family Pacullidae (**restored status**) separate from Tetrablemmidae. The Scytodoidea include Ochyroceratidae along with Sicariidae, Scytodidae, Drymusidae and Periegopidae; our results are inconclusive about the separation of these last two families. We did not recover monophyletic Austrochiloidea and Leptonetidae, but our data suggest that both groups are more closely related to the Cylindrical Gland Spigot clade rather than to Synspermiata. Palpimanoidea is not recovered by our analyses, but also not strongly contradicted. We find support for Entelegynae and Oecobioidea (Oecobiidae plus Hersiliidae), and ambiguous placement of cribellate orb-weavers, compatible with their non-monophyly. Nicodamoidea (Nicodamidae plus Megadictynidae) and Araneoidea composition and relationships are consistent with recent analyses. We did not obtain resolution for the titanoecoids (Titanoecidae and Phyxelididae), but the Retrolateral Tibial Apophysis clade is well supported. Penestomidae, and probably Homalonychidae, are part of Zodarioidea, although the latter family was set apart by recent transcriptomic analyses. Our data support a large group that we call the marronoid clade (including the families Amaurobiidae, Desidae, Dictynidae, Hahniidae, Stiphidiidae, Agelenidae and Toxopidae). The circumscription of most marronoid families is redefined here. Amaurobiidae include the Amaurobiinae and provisionally Macrobuninae. We transfer Malenellinae (*Malenella*, from Anyphaenidae), Chummidae (*Chumma*) (**new syn.**) and Tasmarubriinae (*Tasmarubrius*, *Tasmabrochus* and *Teeatta*, from Amphinectidae) to Macrobuninae. Cybaeidae are redefined to include *Calymmaria*, *Cryphoeca*, *Ethobuella* and *Willisius* (transferred from Hahniidae), and *Blabomma* and *Yorima* (transferred from Dictynidae). Cycloctenidae are redefined to include *Orepukia* (transferred from Agelenidae) and *Pakeha* and *Paravoca* (transferred from Amaurobiidae). Desidae are redefined to include five subfamilies: Amphinectinae, with *Amphinecta*, *Mamoea*, *Maniho*, *Paramamoea* and *Rangitata* (transferred from Amphinectidae); Ischaleinae, with *Bakala* and *Manjala* (transferred from Amaurobiidae) and *Ischalea* (transferred from Stiphidiidae); Metaltellinae, with *Austmusia*, *Buyina*, *Calacadia*, *Cunnawarra*, *Jalkaraburra*, *Keera*, *Magua*, *Metaltella*, *Penaoola* and *Quemusia*; Porteriinae (**new rank**), with *Baiami*, *Cambridgea*, *Corasoides* and *Nanocambridgea* (transferred from Stiphidiidae); and Desinae, with *Desis*, and provisionally *Poaka* (transferred from Amaurobiidae) and *Barahna* (transferred from Stiphidiidae). *Argyroneta* is transferred from Cybaeidae to Dictynidae. *Cicurina* is transferred from Dictynidae to Hahniidae. The genera *Neoramia* (from Agelenidae) and *Aorangia*, *Marplesia* and *Neolana* (from Amphinectidae) are transferred to Stiphidiidae. The family Toxopidae (**restored status**) includes two subfamilies: Myroinae, with *Gasparia*, *Gohia*, *Hulua*, *Neomyro*, *Myro*, *Ommatauxesis* and *Otagoa* (transferred from Desidae); and Toxopinae, with *Midgee* and *Jamara*, formerly Midgeeinae, **new syn.** (transferred from Amaurobiidae) and *Hapona*, *Laestrygones*, *Lamina*, *Toxops* and *Toxopsoides* (transferred from Desidae). We obtain a monophyletic Oval Calamistrum clade and Dionycha; Sparassidae, however, are not dionychans, but probably the sister group of those two clades. The composition of the Oval Calamistrum clade is confirmed (including Zoropsidae, Udubidae, Ctenidae, Oxyopidae, Senoculidae, Pisauridae, Trechaleidae, Lycosidae, Psechridae and Thomisidae), affirming previous findings on the uncertain relationships of the "ctenids" *Ancylometes* and *Cupiennius*, although a core group of Ctenidae are well supported. Our data were ambiguous as to the monophyly of Oxyopidae. In Dionycha, we found a first split of core Prodidomidae, excluding the Australian Molycriinae, which fall distantly from core prodidomids, among gnaphosoids. The rest of the dionychans form two main groups, Dionycha part A and part B. The former includes much of the Oblique Median Tapetum clade (Trochanteriidae, Gnaphosidae, Gallieniellidae, Phrurolithidae, Trachelidae, Gnaphosidae, Ammoxenidae, Lamponidae and the Molycriinae), and also Anyphaenidae and Clubionidae. *Orthobula* is transferred from Phrurolithidae to Trachelidae. Our data did not allow for complete resolution for the gnaphosoid families. Dionycha part B includes the families Salticidae, Eutichuridae, Miturgidae, Philodromidae, Viridasiidae, Selenopidae, Corinnidae and Xenoctenidae **(new fam.**, including *Xenoctenus*, *Paravulsor* and *Odo*, transferred from Miturgidae, as well as *Incasoctenus* from Ctenidae). We confirm the inclusion of *Zora* (formerly Zoridae) within Miturgidae.

Introduction

Spiders (Araneae) are a distinctive and megadiverse group of predators, abundant in virtually any terrestrial ecosystem. With over 46 000 described species in ca. 4000 genera (World Spider Catalog—WSC, 2016), all Araneae retain the two synapomorphies of the order: the spinnerets, appendages at the posterior end of the body, used to spin silk through minute hair-like outlets (spigots); and male copulatory organs that have to be charged with sperm prior to copulation. Spinning organs and genital systems represent two of the main sources of characters in spider systematics (e.g. Agnarsson, 2004; Griswold et al., 2005; Álvarez-Padilla and Hormiga, 2011; Ramírez, 2014; Lopardo and Hormiga, 2015, among numerous others).

The silk-producing organs are thought to have played a determinant role in the diversification of spiders, following the diversification of their flying and crawling insect prey, as well as the evolution and increasing complexity of terrestrial habitats (Penney et al., 2003; Dimitrov et al., 2012; Garrison et al., 2016). The diversity of silk structures made by spiders, e.g. lined burrows, trapdoors, aerial webs, cocoons, silken cells and draglines, have an anatomical correlate in their glands and spigots (up to seven types in a given species; e.g. Coddington, 1989; Kovoor and Peters, 1988), combined in a myriad of ways across spider diversity. The resulting wealth of information

*Corresponding author:
E-mail address: wheeler@amnh.org

from spinnerets and web-building behaviour has been at the centre of dispute in spider systematics since the arrival of quantitative phylogenetic methods, underlying the iconic debate on the monophyly of orb-weavers (see Coddington, 1986; Dimitrov et al., 2016; and references therein). While phenotypic data analyses have relied on many characters from spigots and web-building behaviour to obtain orb-weavers as monophyletic (e.g. Coddington, 1990), molecular analyses have had difficulties obtaining supported resolution for the deep, relevant branches of the phylogeny (Blackledge et al., 2009; Dimitrov et al., 2012). The controversy has only lurched to resolution recently through the production of enlarged sequence data sets (Bond et al., 2014; Fernández et al., 2014; Garrison et al., 2016) and extensive taxon sampling for target genes (Dimitrov et al., 2016). Both strategies suggest the non-monophyly of orb-weavers, multiple losses of orb-webs and continuing uncertainty about the placement of important clades despite large quantities of data.

Genital characters are used in spider systematics at every taxonomic level, from species to higher taxa. Some of the largest clades of spiders have been characterized precisely by these characters: the Haplogynae, by a simplified male copulatory bulb with fused sclerites (Platnick et al., 1991); the Entelegynae, by a more complex uni-directional flow of sperm in the female genital system; and within entelegynes, the Retrolateral Tibial Apophysis (RTA) clade, by a process on the male palpal tibia (Griswold et al., 2005). While the more distal groups within these clades are stable across multiple analyses, the basal splits have seen radical rearrangement recently. These changes include the discovery of new taxa and the collection of new data from previously known species. The discovery of Trogloraptoridae, a new spider family allied to haplogynes (Griswold et al., 2012), for example, provided a possible morphological intermediate between dysderoids and other haplogynes. Additionally, a re-examination of *Archoleptoneta*, thought to be a derived haplogyne, revealed a cribellum, a spinning organ that was thought to be long lost in the group (Ledford and Griswold, 2010). Finally, recent analyses of phylogenomic data have revealed that the most basal splits of entelegynes and former haplogynes require profound remodelling (Bond et al., 2014; Garrison et al., 2016; Hormiga et al., 2016). This reconfiguration has had significant impact on evolutionary hypotheses in spiders, such as the origin and transformations of webs mentioned above, the timing and mode of diversification (Garrison et al., 2016), and the paths of simplification of circulatory and respiratory systems (Huckstorf et al., 2015).

A growing number of multi-family target gene phylogenetic analyses are incrementally covering parts of the spider tree of life. These studies have focused on Mesothelae (Xu et al., 2015b), Mygalomorphae (Bond et al., 2012; and references therein), Palpimanoidea (Wood et al., 2012), many on orb-weavers (Blackledge et al., 2009; Dimitrov et al., 2016; and references therein), symphytognathoids (Rix et al., 2008; Lopardo et al., 2011; Lopardo and Hormiga, 2015), entelegynes (J. Miller et al., 2010; Spagna et al., 2010), the Oval Calamistrum (OC) clade (Polotow et al., 2015), psechrids (Agnarsson et al., 2012; Bayer and Schönhofer, 2013), eresids (Miller et al., 2012), pholcids (Dimitrov et al., 2013) and sparassids (Moradmand et al., 2014). These analyses show significant agreement as well as important contradictions. A summary analysis compiling sequences from GenBank (Agnarsson et al., 2013) has shown that new, unexpected results emerge when diverse data are combined with broad taxon sampling. Several of these heretofore unexpected results have been corroborated by recent phylogenomic (Bond et al., 2014; Fernández et al., 2014; Garrison et al., 2016) and high taxon sampling, target gene analyses (Dimitrov et al., 2016).

Spider systematics is advancing along multiple fronts: technological advances are making possible the production of unprecedented quantites of sequence data, repositories of morphology based on digital images are documenting the anatomy of large groups, and advances in computational techniques have allowed the analysis of larger, more complex data sets. In this study, we aim to establish the higher-level features of spider history via unprecedentedly broad sampling of spider diversity for multiple target genes.

Materials and methods

Taxonomic sampling

This dataset represents a nearly comprehensive sampling of the arachnid order Araneae at the family rank. The dataset comprised 932 spider species, representing 115 families (only the family Synaphridae is unrepresented), 700 known genera and additional representatives of 26 unidentified or undescribed genera. Eleven outgroup genera of the orders Amblypygi, Palpigradi, Schizomida and Uropygi were included, thus sampling the three orders of the clade Pedipalpi, which is the well-accepted sister group of spiders (Shultz, 1990, 2007; Regier et al., 2010; Sharma et al., 2015). All trees were rooted on the more distantly related order Palpigradi. Several of the sequences generated for this study have already been incorporated into published works on more restricted taxonomic groups, including zodarioids and other entelegynes (J. Miller et al., 2010), araneoids (Lopardo et al., 2011; Lopardo and Hormiga, 2015), palpimanoids (Wood et al., 2012) and Anyphaenidae (Labarque et al., 2015). We also augmented our taxon

sampling by the incorporation of important representatives from other studies prior to 2014 (Supporting Information, Table S1).

Character sampling

Molecular data. Genes with differing degrees of variability were chosen, and included both mitochondrial and nuclear markers. DNA sequence data from the mitochondrial genome were generated from three regions and included 12S ribosomal RNA (12S), 16S ribosomal RNA (16S) and cytochrome *c* oxidase subunit 1 (COI) genes. Three nuclear genes were targeted for phylogenetic reconstruction and included the protein-coding histone H3 (H3), as well as the small and large subunits of ribosomal RNA genes (18S and 28S, respectively).

The number of sequence data per terminal varied from 752 bp (*Calamoneta* sp. MR661) to 6210 bp (*Antrodiaetus unicolor*), with an average of 4186 bp per taxon (Table S1). The newly generated sequences were deposited in GenBank under accession numbers KY015264–KY018569 (Table S1).

Laboratory protocols

DNA extraction and PCR amplification. Total genomic DNA was extracted from leg tissue. In cases where the specimen was small, the whole specimen was used for DNA extraction. Sources for tissue samples and locality information are provided in Table S1. DNA extraction was achieved with a DNeasy animal tissue extraction kit (Qiagen). DNA amplification was carried out in a 25-μL volume reaction, using Illustra PuReTaq Ready-To-Go PCR beads (GE Healthcare). As a rule, 2 μL of genomic DNA, along with 1 μL of both 10 μM forward and reverse primers were included in each reaction. The primers (and their sources) used in the amplification and sequencing of gene regions in this study are given in Table 1. Molecular-grade distilled water made up the remaining volume. PCRs were executed on an Eppendorf Mastercycler ep gradient thermocycler and subsequently visualized with 1.5% agarose gel electrophoresis.

The amplification profile and annealing temperatures varied for the individual genes and across taxa for the same gene. A number of different PCR profiles were used in this study; initially, all amplifications proceeded with a standard protocol. This PCR profile consisted of an initial denaturing step at 94 °C for 2 min, 30 amplification cycles [94 °C for 30 s, 50 °C or optimal annealing temperature (T_m °C) for 45 s, 72 °C for 45 s], followed by a final extension step at 72 °C for 5 min. The PCR profiles were adjusted for the different primer pair and taxon combinations, until such time that amplification and subsequent sequencing were successful. The annealing temperatures were increased or decreased by 1–2 °C to maximize

Table 1
Primers used for the amplification and sequencing of DNA in this study.

Gene	Primer	Primer sequence (5′ to 3′)	Source
12S	12S-ai	AAACTAGGATTAGATACCCTATTAT	Köcher et al. (1989)
	12S-bi	AAGAGCGACGGGCGATGTGT	Köcher et al. (1989)
16S	16S-A	CGCCTGTTTATCAAAAACAT	Palumbi et al. (1991)
	16S-B	CTCCGGTTTGAACTCAGATCA	Palumbi et al. (1991)
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCOoutout	GTAAATATATGRTGDGCTC	Wheeler laboratory fide Schulmeister et al. (2002)
	ExtA	GAAGTTTATATTTTAATTTTACCTGG	Wheeler laboratory fide Schulmeister et al. (2002)
	ExtB	CCTATTGAWARAACATARTGAAAATG	Wheeler laboratory fide Schulmeister et al. (2002)
H3	aF	ATGGCTCGTACCAAGCAGACVGC	Colgan et al. (1998)
	aR	ATATCCTTRGGCATRATRGTGAC	Colgan et al. (1998)
18S	18S-1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. (1996)
	18S-5R	CTTGGCAAATGCTTTCGC	Giribet et al. (1996)
	18S-3F	GTTCGATTCCGGAGAGGGA	Giribet et al. (1996)
	18S-bi	GAGTCTCGTTCGTTATCGGA	Whiting et al. (1997)
	18S-a2.0	ATGGTTGCAAAGCTGAAA	Whiting et al. (1997)
	18S-9R	GATCCTTCCGCAGGTTCACCTAC	Giribet et al. (1996)
28S	28S-Rd1a	CCCSCGTAAYTTAGGCATAT	Crandall et al. (2000), modification of Van der Auwera et al. (1994): primer 4
	28S-Rd4b	CCTTGGTCCGTGTTTCAAGAC	Crandall et al. (2000), modification of Van der Auwera et al. (1994): primer 10
	28S-Rd3.2a	AGTACGTGAAACCGTTCASGGGT	Wheeler laboratory fide Whiting (2002)
	28S-B	TCGGAAGGAACCAGCTACTA	Whiting et al. (1997)
	28S-A	GACCCGTCTTGAAGCACG	Whiting et al. (1997), modification of Nunn et al. (1996)
	28S-Bout	CCCACAGCGCCAGTTCTGCTTACC	Wheeler laboratory fide Hovmöller et al. (2002)
	28S-Rd4.8a	ACCTATTCTCAAACTTTAAATGG	Wheeler laboratory fide Whiting (2002)
	28S-Rd7b1	GACTTCCCTTACCTACAT	Wheeler laboratory fide Whiting (2002)

specificity. For primer pairs that amplified longer fragments, increasing the denaturation and extension time by 30–60 s often yielded better results. Moreover, increasing the number of amplification cycles to 35–40 often helped achieve the necessary results.

Sequences of 12S, ranging in length from 287 to 356 bp, were successfully obtained using the standard primer combination, 12S-ai and 12S-bi. This region, located in the 3′ end of the gene, corresponds to approximately half of the entire 12S rRNA gene found in this group. Primers developed by Palumbi et al. (1991) were used to amplify approximately half of the complete 16S rRNA gene. This fragment, ranging from 421 to 552 bp, is located in the 3′ region of the gene. Sequences for a large fragment of COI were determined using the primers pairs LCO1490 and HCOoutout, and ExtA and ExtB. These overlapping primers amplified a region approximately 1100 bp in size (the complete gene being ~ 1500 bp in length).

In addition to these mitochondrial genes, a single nuclear protein-coding gene (H3) was also targeted. The standard primer combination of Colgan et al. (1998) successfully amplified a 328-bp fragment of this gene. The complete 18S (approximately 1.7 kb) was amplified in three overlapping fragments, using the primer pairs 18S-1F and 18S-5R, 18S-3F and 18S-bi, and 18S-a2.0 and 18S-9R. Multiple primers were employed in the amplification of a large region of 28S (approximately 2.2 kb). These overlapping primers include the pairs 28S-Rd1a and 28S-Rd4b, 28S-Rd3.2A and 28S-B, 28S-A and 28S-Bout, and 28S-4.8A and 28S-Rd7b1.

PCR clean up and sequencing. PCR products were cleaned by use of a Beckman Coulter Laboratory Automation Workstation using Agencourt magnetic bead technology (AMPure). Double-stranded cycle-sequencing of purified products was achieved using dye-labelled terminators (BigDye Terminator v.3.1 Cycle Sequencing Reaction Kit, Applied Biosystems) in a thermocycler. The cycle-sequencing reactions consisted of 0.5 μL BigDye, 2.0 μL BigDye Extender Buffer, 2.0 μL 3.2 μM primer and 3.5 μL purified PCR product (for a total of 8 μL). In all cases, the same primer used in the amplification process was used for sequencing. The cycle-sequencing programme consisted of 25 amplification cycles (96 °C for 15 s, 50 °C for 15 s and 60 °C for 4 min). Tagged products were subsequently cleaned on the workstation using CleanSEQ (Agencourt). Sequencing of the purified PCR products was conducted by the dideoxy termination method (Sanger et al., 1977) using an automated ABI Prism 3730xl DNA sequencer (Applied Biosystems).

Sequence editing and error checking. Sequence chromatograms were assembled, visualized and edited using Sequencher 4.1 (Gene Codes Corp.). Once assembled, contigs were then queried against the online NCBI BLAST database. The resulting BLAST hits were checked to highlight possible contaminants (from external sources). The sequences were subsequently aligned using the CLUSTALW (Thompson et al., 1994) package (under the default settings), as spawned through BioEdit (Hall, 2007). The alignment was also visualized in BioEdit. While a multiple sequence alignment (MSA) is not necessary for the analysis of sequences with dynamic homology, it is desirable for two reasons. The first relates to quality control—an MSA can highlight problems within a sequence (e.g. extraneous nucleotides disrupting the reading frame in protein coding sequences), as well as highlight aberrant sequences (e.g. sequences that may have been inadvertently reverse complemented during contig assembly are clearly evident in an MSA). The second concerns the partitioning of the sequence data into smaller fragments for analysis under direct optimization and is discussed below.

Phylogenetic analyses

Datasets and analyses. A number of analytical methods of phylogenetic inference were explored in this study and are discussed in turn below. These methods were conducted using the dynamic homology approach (POY analyses) or with the use of static alignments (all other analyses).

Direct optimization (DO). The MSAs generated by CLUSTALW were used to partition the data. The procedure for partitioning the MSA is explained in detail elsewhere (see Wheeler et al., 2014; : chapter 4). The partitioning of sequences of unequal length (due to incomplete sequencing) reduces the amount of ambiguity (IUPAC X or N coding) in these regions. Hence, these regions of the MSA are subsequently treated as missing data in the analysis, and therefore do not influence subsequent phylogenetic analysis. Furthermore, partitioning allows more rapid and efficient optimization of the sequences (see Giribet, 2002). These MSAs in no way constrained the subsequent analysis of the data under DO, given that gaps in the MSA are removed prior to analysis with DO. This procedure is commonly used in the analysis of molecular data under dynamic homology (e.g. Arango and Wheeler, 2007; Lindgren and Daly, 2007; Liu et al., 2009; Padial et al., 2014).

Analysis of these datasets was conducted on two 1024-GB RAM, AMD Opteron 6380 Series 2.5-GHz, parallel 64-core computers at the AMNH using dynamic homology (Wheeler, 2001), with the DO method (Wheeler, 1996), as implemented in a parallel version of POY 5 (Wheeler et al., 2015) version 5.1.1 (source code Wheeler et al., 2014).

Multiple datasets were analysed in this study—each molecular partition, as well as a combined analysis of all the molecular data. The separate analysis of these data partitions facilitated the assessment of the pattern of relationships from each. An exploration of different parameter costs [gap opening, insertion/deletion (indel) and transversion/transition (tv/ts)] was undertaken as a sensitivity analysis (Wheeler, 1995). Three indel cost ratios (1, 2, 4) and three tv/ts cost ratios (1, 2, 4) were employed. Character congruence was measured using the incongruence length difference index (ILD) (Farris, 1973). The parameter set that minimized the incongruence among the partitions was considered optimal.

The analyses were performed in two stages. The initial analyses consisted of random addition sequence Wagner builds, followed by TBR branch swapping. Tree fusing (Goloboff, 1999) followed. Each run held a maximum of eight trees per replicate. A final round of TBR branch swapping was performed, prior to reporting the resulting trees [command line: build(8) swap() fuse(iterations:240) select(best:8) swap() select()]. The first round of analyses was performed for each of the nine parameter combinations under investigation. All subsequent analyses involved combining the trees from the previous analyses and using them as input trees in the next round. The process was repeated until such time that the results of all the parameter combinations were stable (27 rounds). This strategy (Simulated Annealing Tree Fusing, SATF) has proven to be quite effective in identifying stable and heuristically optimal results (D'Haese, 2003; Wheeler et al., 2004; Boyer et al., 2005; Sørensen et al., 2006; Giribet, 2007; Schuh et al., 2009) in other analyses.

Parsimony analysis 'static' (EW, IW). MSAs were carried out with MUSCLE (Edgar, 2004) under default options, and analysed with the parallel version of TNT (Goloboff et al., 2008) running on 32 processors in the cluster of the Fundación Miguel Lillo—CONICET. For the equal weights analysis (EW) each processor produced ten replicates of RAS + TBR, followed by sectorial searches and tree-drifting, and the trees from all processors were combined by tree-fusing. The extended implied weighting analysis (IW; Goloboff, 2014) used the same search, computing average weighting against homoplasy in blocks of 50 sites for the ribosomal markers, and the average of 1st, 2nd and 3rd positions for protein coding genes; in both cases the reference constant of concavity for the weighting function was set to 500. For each group of characters, this reference concavity was decreased based on the proportion of missing entries, so that the weight for the block decreases more rapidly with homoplasy as there are more missing entries, assuming missing entries have 0.75 of the homoplasy in observed entries, and using a concavity ratio within 5 [command line: xpiwe (*0.75 < 5] (see Goloboff, 2014: 264). Bootstrap proportions were calculated with 100 pseudoreplicates, each of five replicates of RAS + TBR, followed by sectorial searches and tree drifting. The resulting trees from the five replicates were subsequently subjected to tree-fusing.

Maximum-likelihood (ML). MSAs were carried out with MAFFT v7.243 (Katoh and Standley, 2013). Alignments of the protein-coding H3 and COI genes were trivial due to the lack of gaps and were produced using the L-INS-i method [command line: mafft—thread 3—threadit 0—reorder—maxiterate 1000—retree 1—localpair]. Due to the highly variable nature of ribosomal genes, the E-INS-i method, which incorporates affine gap costs, was used to generate alignments of 12S, 16S, 28S and 18S [commands line: mafft—thread 3—threadit 0—reorder—maxiterate 1000—retree 1—genafpair]. A concatenated dataset of these alignments was generated. An additional dataset was constructed where ambiguously aligned regions in the ribosomal genes were excluded. To detect and exclude ambiguously aligned regions, alignments of the ribosomal genes were processed with the program trimAl v1.3 (Capella-Gutiérrez et al., 2009) using the heuristic *automated1* method, except for the hypervariable region of 28S. This region of 28S was processed using the *gappyout* method, as the *automated1* failed to provide a plausible solution (i.e. 99% of the characters were removed).

ML analyses of the concatenated dataset were conducted with the program RAxML (Stamatakis, 2014) on the Abel Cluster at the University of Oslo or using the CIPRES Science Gateway (M. Miller et al., 2010). The concatenated gene matrix was partitioned by gene. Bootstrap and optimal trees were computed in the same run using the—*fa* option using 1000 bootstrapping replicates. The GTRCAT model was used for the fast bootstrap replicates and GTRGAMMA for optimal topology searches. The raxmlHPC-HYBRID binaries were employed and the job was run using 12 mpi processors, each with four threads [command line: raxmlHPC-HYBRID -T 4 -n result -s infile.txt -q part.txt -p 12345 -x 12345 -N 1000 -c 25 -f a -m GTRCAT -o Palpigradi sp. JA-2011].

The recent phylogenomic study of Garrison et al. (2016) was used to construct a backbone constraint tree for additional rounds of RAxML analyses. This study, which included 50 spider families, and involved extensive molecular sampling (3398 gene regions and 696 652 amino acid sites), was based on transcriptomic data. Therein, many of the relationships in the resulting trees were well supported, albeit for a restricted sample of families. The topology of the preferred tree of Garrison et al. (2016) was modified, such that terminals not included in our study were pruned from the tree and nodes for the terminals that were not highly supported (e.g. with bootstrap supports below 100)

were collapsed. The positions of all the remaining taxa not included in this constrained topology were unrestricted as to placement. Constrained RAxML analyses were run as described above with the addition of the—*g* flag. In all cases, the bootstrap proportions were calculated with 1000 pseudoreplicates of the rapid bootstrap analysis.

Bayesian inference (BI). Bayesian analyses were carried out in ExaBayes 1.4.1 (Aberer et al., 2014) using the same dataset that was subjected to RAxML analyses. All ExaBayes analyses were run using the Abel cluster at the University of Oslo. Because the current version of ExaBayes does not allow the use of topological constraints, only unconstrained analyses, using the same partitioning scheme and model settings as in the RAxML analyses, were run. Two independent analyses, each with four independent chains and using Metropolis-Coupling (numCoupledChains was set to 2) to speed up convergence, were run. Each run was started using a parsimony starting tree. All model parameters were unlinked among partitions except for branch length. Results were checked for convergence and effective sampling sizes of all parameters using the tools distributed with the ExaBayes package. Support values are expressed as posterior probabilities.

Taxonomic congruence and selection of working tree. Results from the different phylogenetic analyses are summarized in the form of a preferred working tree (Figs 1–8). Selection of this tree, among all the trees produced by the different optimality criteria, was achieved by computing the correspondence of each candidate tree with previously and herein established families and infraorders of spiders (*taxonomic congruence*). The tree with the greatest correspondence with previous taxonomic hypotheses was reasoned to be conservative by definition, and probably more robust, by having a better fit to previous knowledge and independent data, including morphology. We also calculated how many of the groups most stable to all optimality criteria were recovered by each individual criterion. Furthermore, the quantity of shared groups with the transcriptomic study of Garrison et al. (2016) was also measured (*transcriptomic congruence*). For this comparison, only those groups with high support values and consistency across the different analyses (Garrison et al., 2016: fig. 2; see next paragraph for groups and mapping of terminals) were considered. The correspondence with taxonomy was checked using the [command line: taxonomy] command of TNT (Goloboff and Catalano, 2012) and by custom scripts written in TNT macro language. Congruence between the *taxonomic* and skeleton *transcriptomic* trees was assessed by the number of shared groups in a strict consensus, as well as by a symmetric topological similarity coefficient [command line: symcoeff]. To control for possible biases in the taxonomic congruence measures, the taxonomic congruence was calculated twice, for the families as here relimited, or excluding the relimited families (*conservative* taxonomic tree). Graphics of trees were obtained with FigTree v. 1.4.2 (Rambaut, 2014), TNT and POY.

Constrained analyses using a highly supported backbone tree from transcriptomic (TR) data. Results from the Garrison et al. (2016) analysis of transcriptomic data were used as a skeleton tree to produce additional, constrained tree searches. Fifty-eight of the 74 terminals of this phylogenomic study were mapped to our representative taxa (Table S2). Of these mapped individuals, 25 were the same species (thus mapping was unproblematic), 28 were congeneric terminals and the remaining five mapped individuals were representatives of the same subfamily or family (three and two, respectively). The latter five were added to recover the monophyly of additional, important groups. This strategy is justified on the basis that highly supported groups (bootstrap 1) and groups that were robust to all types of analyses in the transcriptomic analysis were likely to remain well supported upon the addition of our six target genes. Having removed all unmatched terminals from the TR tree, nodes that were unstable across analyses or with bootstrap values < 1 were collapsed. The resulting tree (Fig. S1) was then used as a skeleton to constrain the analysis, only affecting the 58 mapped terminals; all the remaining terminals in our dataset were left unconstrained, free to connect anywhere as dictated by our data. To assess whether the six molecular markers included in this study might overturn the highly supported groups of the transcriptomic dataset, an analysis of the smaller dataset of Bond et al. (2014), consisting of 110 808 characters and 43 terminals, combined with our sequence data, was performed. This dataset was too large for full analysis (not shown; 122 001 characters by 1005 terminals, 89% missing entries), but, as expected, superficial parsimony searches of this dataset did not challenge the monophyly of any of the groups that were highly supported in the original transcriptomic analysis.

Results

Phylogenetic analyses

The primary phylogenetic analyses of the concatenated markers are presented as Figs S6–S10. The sensitivity analysis for the DO analysis (Table S3) found minimum character incongruence at an indel cost ratio of 1 and tv/ts cost ratio of 2, and thus we used that tree for subsequent congruence comparisons with other methods.

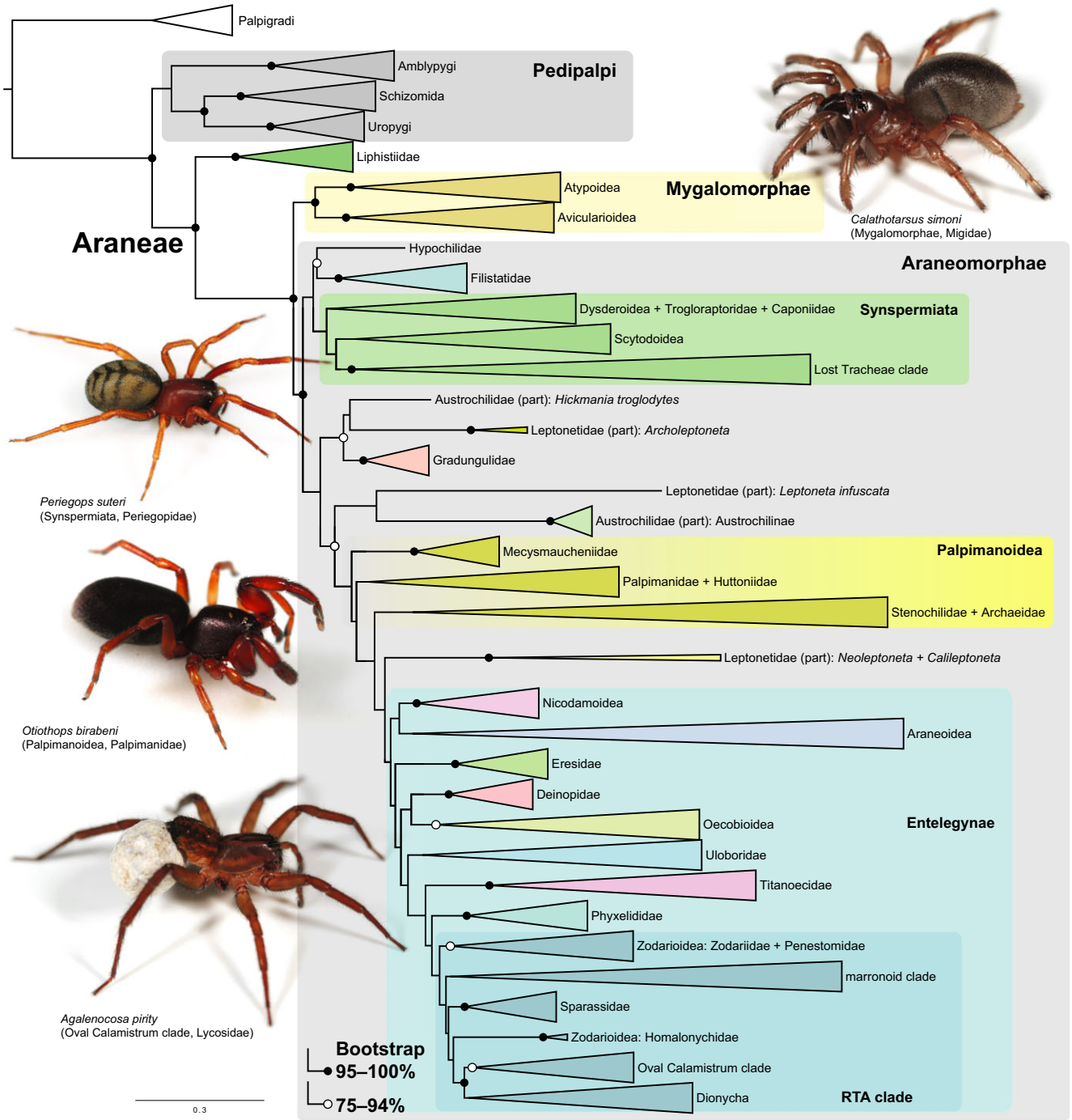

Fig. 1. Summary phylogenetic tree from concatenated analysis of six markers obtained under maximum likelihood, constrained by highly supported groups from transcriptomic analysis, four unstable terminals pruned (C-ML-P analysis).

Congruence with taxonomy (TX) and transcriptomic tree (TR)

A taxonomic classification of our spider terminals is presented in Fig. S2. This reference tree (TX) contains 105 multi-sampled families (103 of spiders, two of outgroups), and four higher groups (the order Araneae, the suborder Opisthothelae, and the infraorders Mygalomorphae and Araneomorphae). This taxonomy is based on the current classification of the WSC (2016), with additional taxonomic changes as introduced by Dimitrov et al. (2016) and herein (see *Taxonomy* section below). A second calculation was made with the groups that are not relimited, or whose rank is not

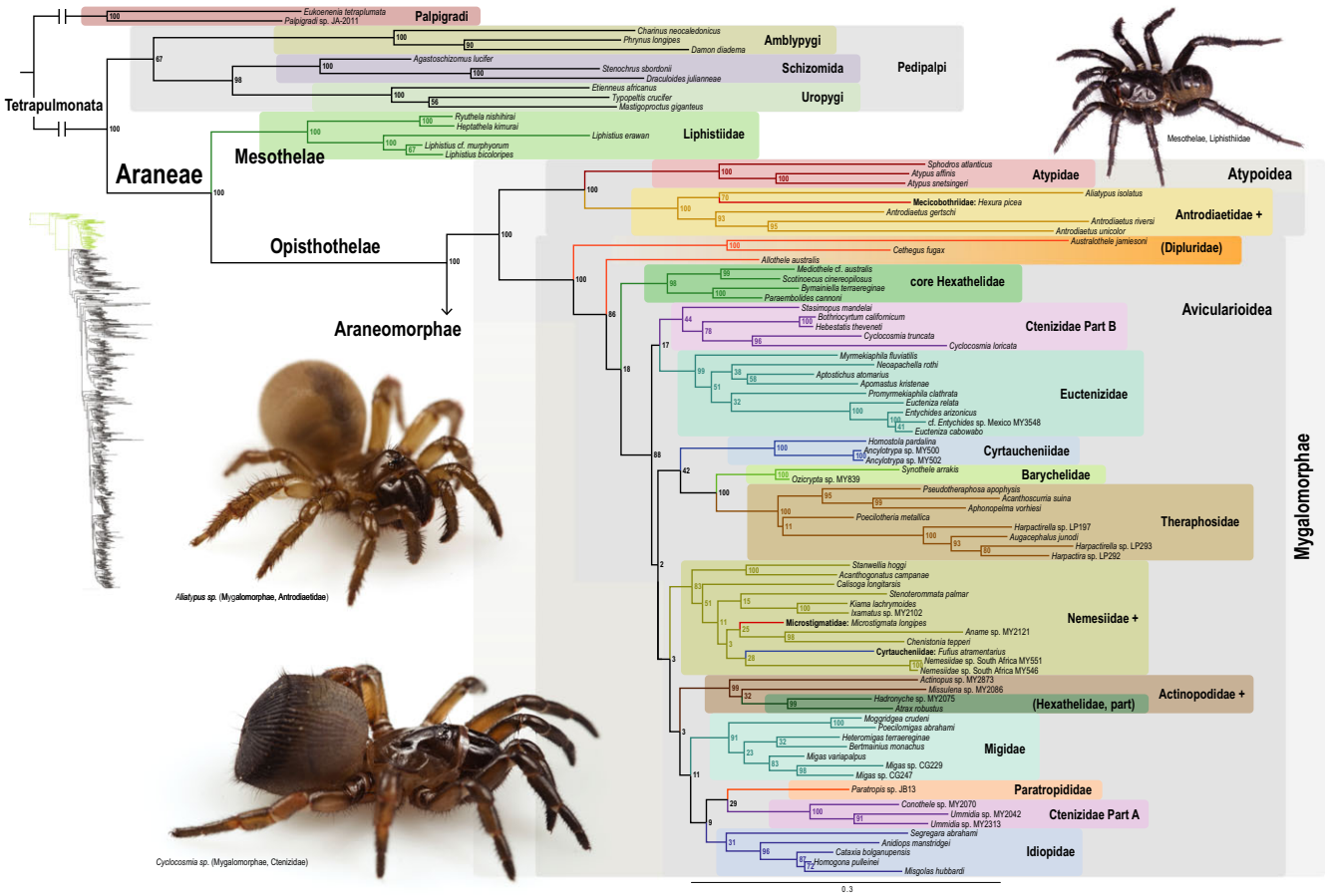

Fig. 2. Outgroups, Liphistiomorphae and Mygalomorphae. C-ML-P tree with bootstrap values on groups. Symbols + and − denote groups that are non-monophyletic by the addition or subtraction of few groups, respectively. Paraphyletic groups are in parentheses.

changed here (see Table S4). This conservative reference tree (TX-C) has only 84 spider families (Fig. S3, Table S4), and produced the same result as the full taxonomic reference, but with slightly more marked differences. This is expected, because the taxonomic changes introduced here are robust to analytical strategies. In the unconstrained analyses, the ML tree (Fig. S6) recovered the most taxonomic groups (74%), followed by BI (68%; Fig. S7), DO (60%; Fig. S8), IW (52%; Fig. S10) and EW (50%; Fig. S9) (Table 2). The second reference is the transcriptomic tree from Garrison et al. (2016); after pruning taxa that did not map to our terminals and collapsing groups not highly supported (bootstrap below 100%, or variable across analytical regimes), this tree has 45 groups (Fig. S1). Of these, 36 of the 45 groups are recovered by the BI tree, 34 by the ML and IW trees, 33 by the DO tree, and 31 by the EW tree. A topological measure (a symmetric distortion coefficient modified after Farris, 1973; implemented in TNT, Goloboff et al., 2008) produced the same preferences for the BI and ML trees when compared with the reference trees. The majority rule consensus tree of the five optimality criteria (EW, IW, DO, BI, ML) has 728 groups shared by at least three criteria, and hence more stable (Fig. S12). We calculated how many of those stable groups were recovered by each criterion: ML and BI recovered the most (90.2 and 89.8%, respectively), followed by IW, DO and EW (85.6, 85.4 and 83.1%, respectively) (Table 2). The ML criterion was subsequently used for the constrained analysis; the BI criterion also performed well in our taxonomic tests, but the current version of ExaBayes does not allow constrained tree searches.

Constrained analysis

The constrained ML tree (C-ML; Fig. S4), obtained after constraining the backbone topology from the transcriptomic analysis, is topologically very similar to the unconstrained ML analysis, sharing 84% of the recovered groups (788 out of 941 groups; see Table 2). Support values are also similar, with slightly lower overall group support (average bootstrap 0.71 in ML vs. 0.69 in C-ML). It shows, however, a few important differences in the resolution of some higher-level

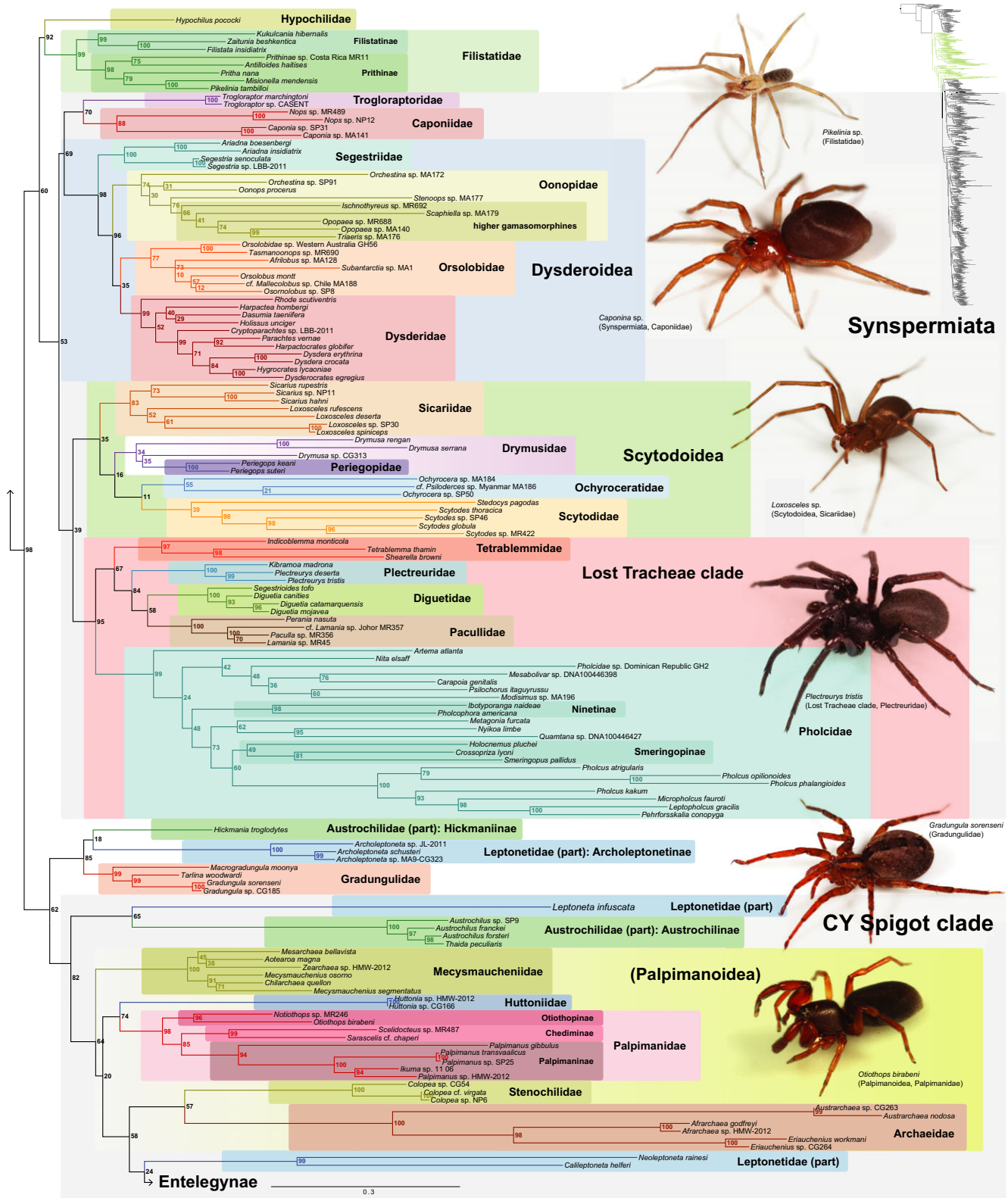

Fig. 3. Non-entelegyne Araneomorphae (same conventions as in Fig. 2).

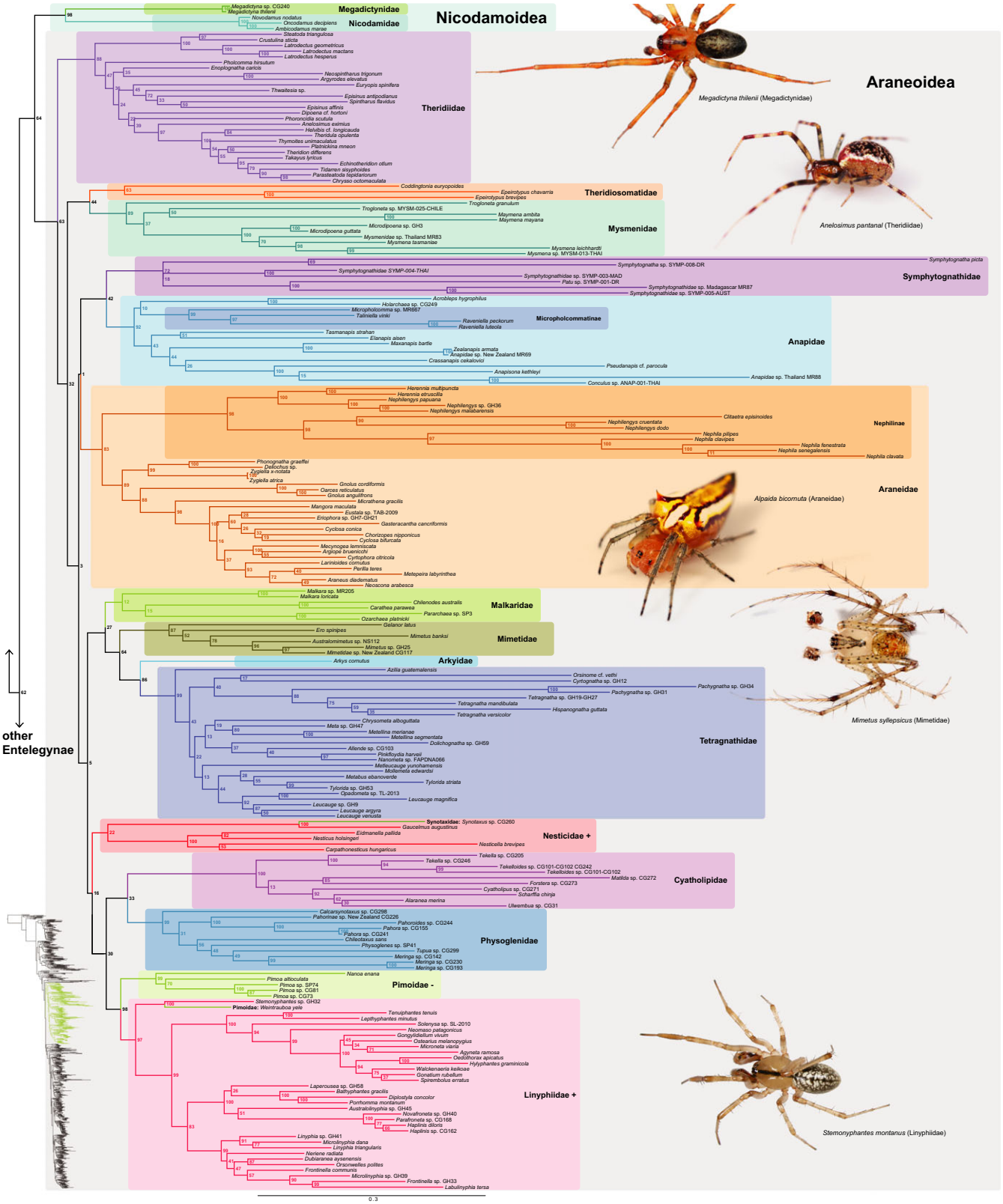

Fig. 4. Nicodamoidea and Araneoidea (same conventions as in Fig. 2).

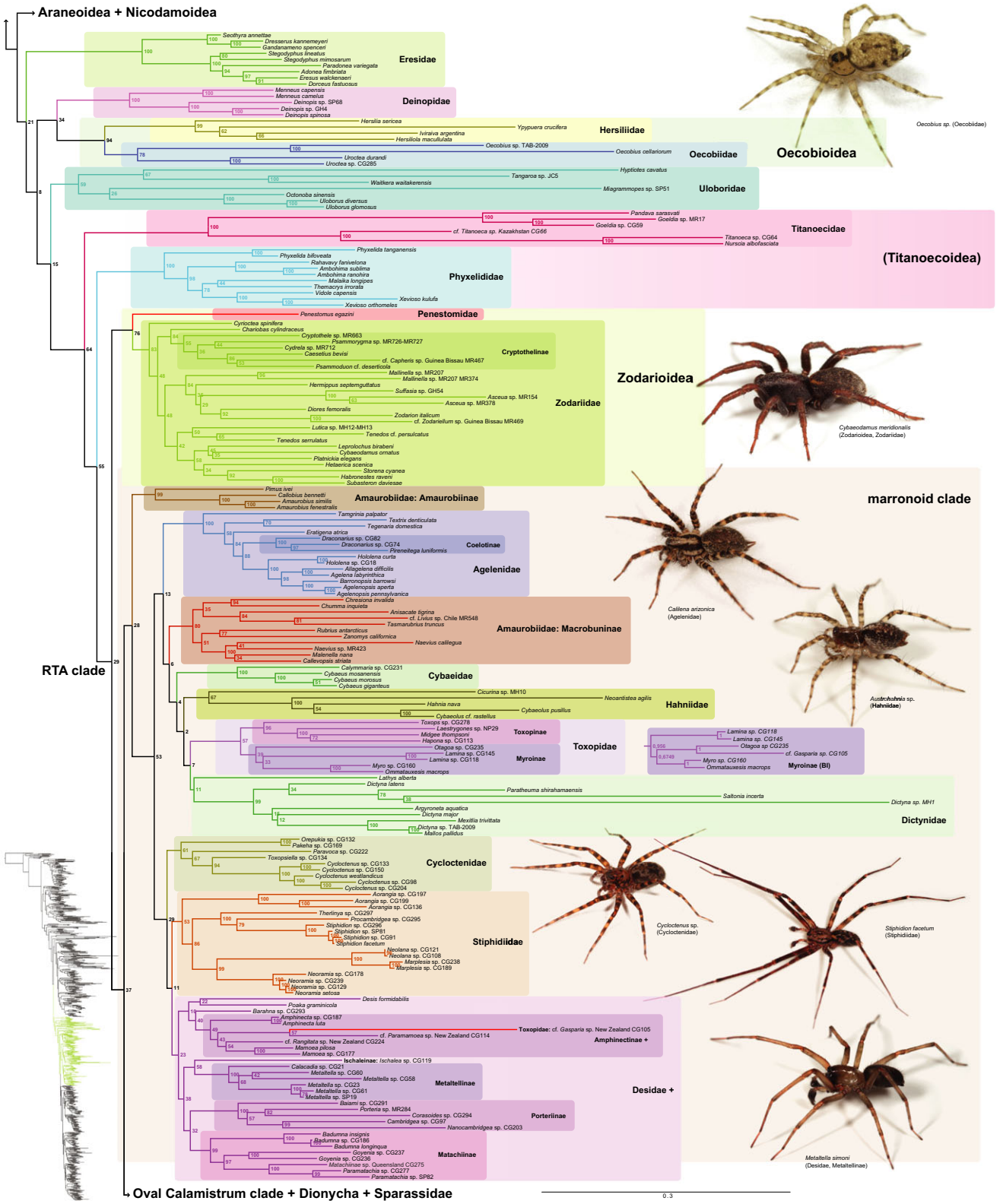

Fig. 5. The marronoid clade and other groups of Entelegynae: Eresidae, Deinopidae, Uloboridae, Oecobioidea, Titanoecoidea and Zodarioidea, with alternative resolution for Myroinae from Bayesian analysis (BI) (same conventions as in Fig. 2).

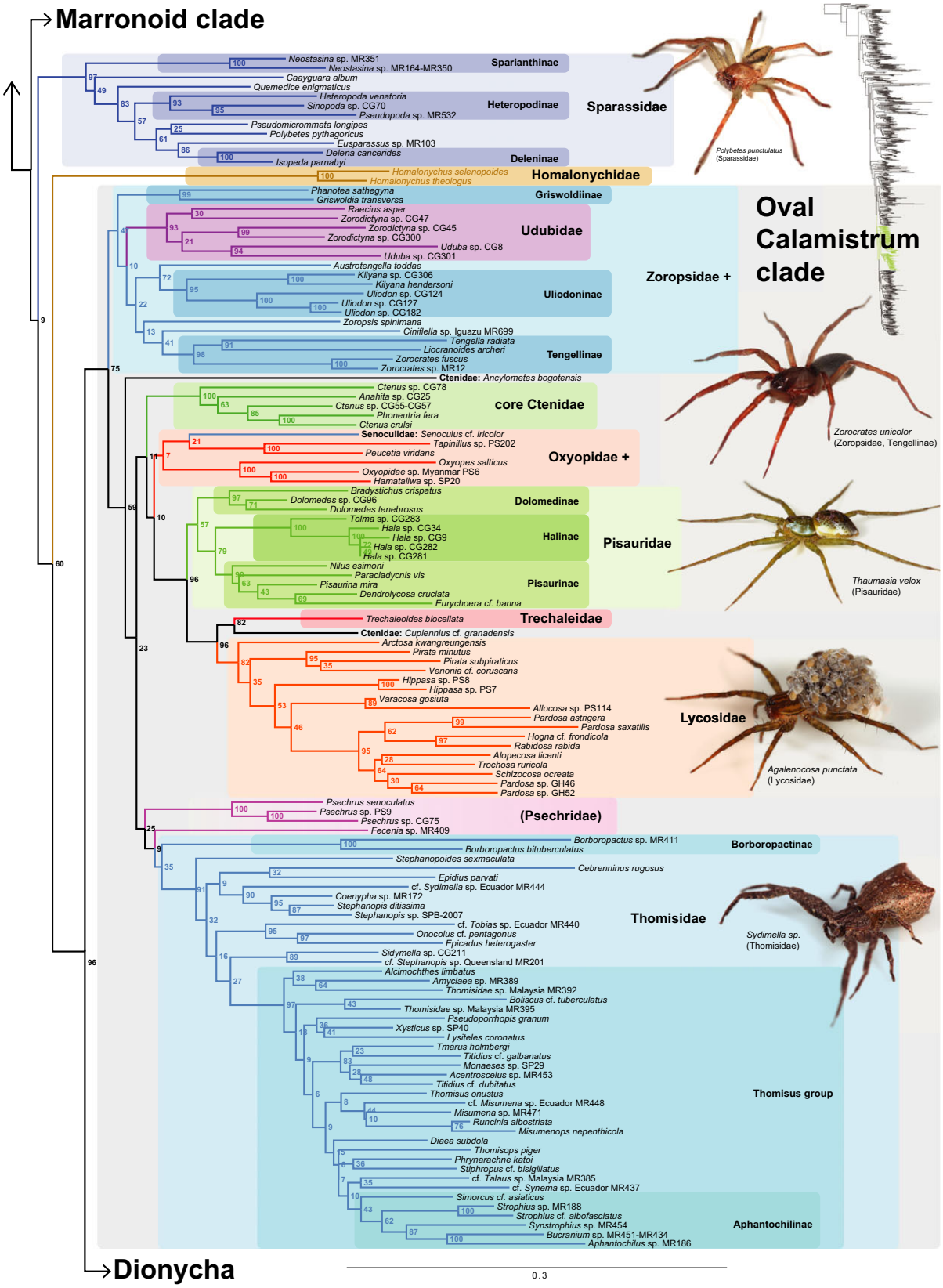

Fig. 6. Sparassidae, Homalonychidae and the Oval Calamistrum clade (same conventions as in Fig. 2).

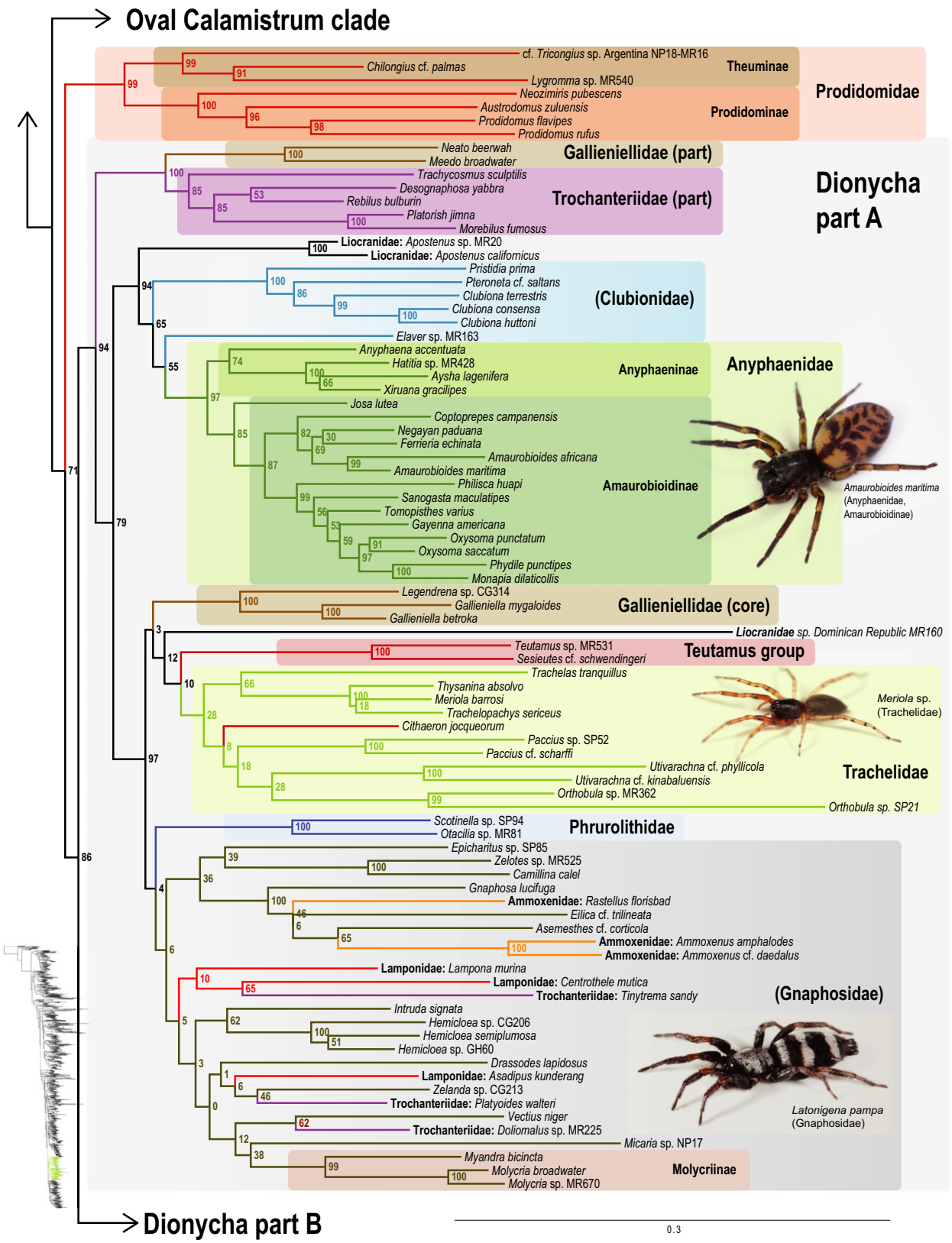

Fig. 7. Prodidomidae and Dionycha part A (same conventions as in Fig. 2).

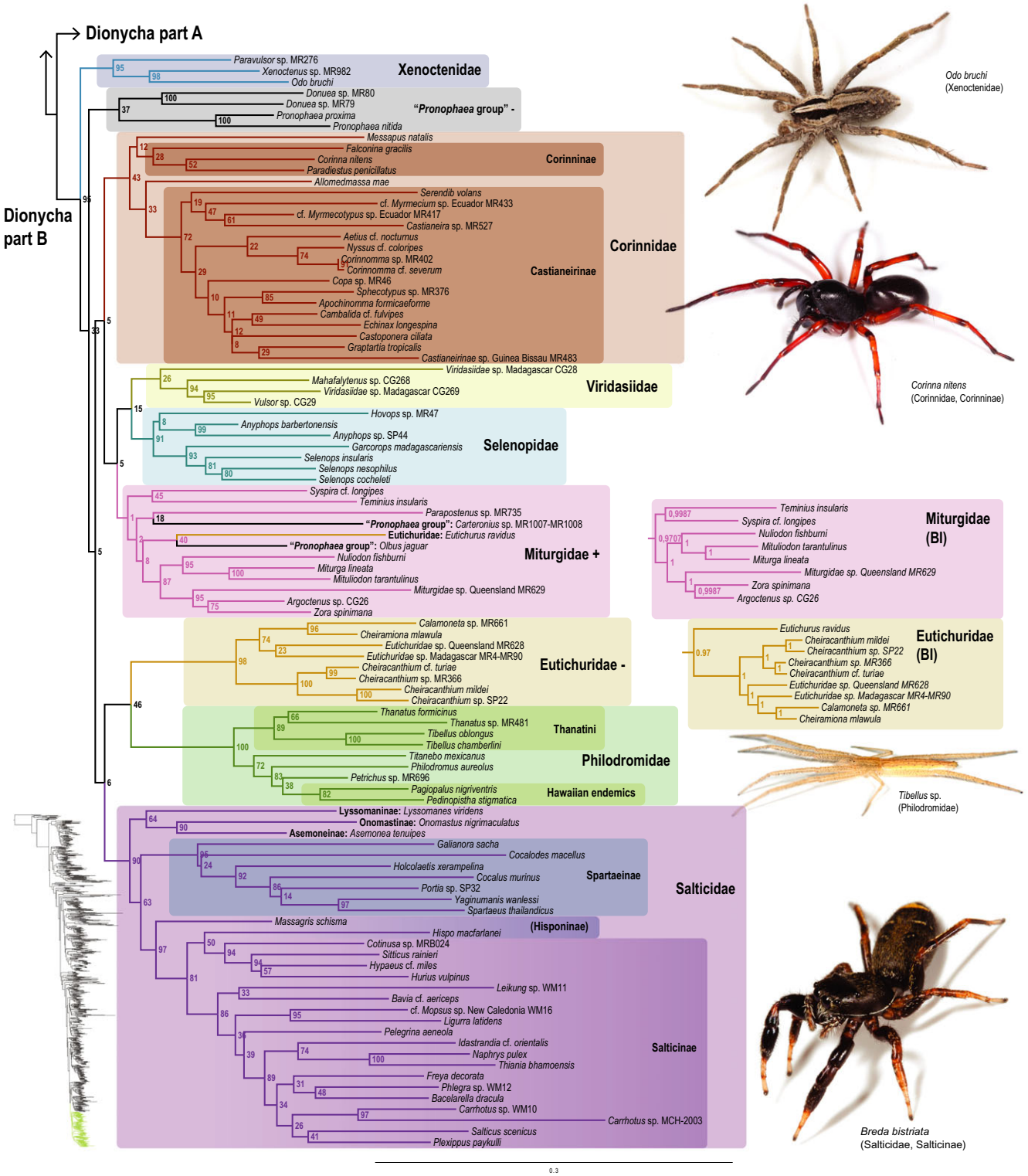

Fig. 8. Dionycha part B, with alternative resolutions from Bayesian analysis (BI) (same conventions as in Fig. 2).

Table 2
Congruence analysis between reference taxonomic (TX, TX-C) or transcriptomic (TR) trees, and the trees obtained in different phylogenetic analyses. Congruence is measured as number and percentage of groups recovered, and as topological similarity coefficients. Groups of the C-ML tree recovered by the different analyses are also reported

Tree	Groups in tree	TR groups recovered		TX groups recovered		TXC groups recovered		Sym. Coeff. vs. TR	Sym. Coeff. vs. TX	Sym. Coeff. vs. TXC	C-ML groups recovered		Stable groups recovered	
(TR) Transcriptomic skeleton	45	45		14		12		1	0.905	0.905				
(TX) Taxonomy reference	109	14		109		94		0.905	1	1				
(TXC) Taxonomy reference, conservative	94	12	27%	94	86%	94	100%	0.913	1	1				
(IW) Parsimony, implied weights	941	34	76%	57	52%	49	52%	0.996	0.722	0.722	542	58%	623	85.6%
(EW) Parsimony, equal weights	907	31	69%	54	50%	45	48%	0.995	0.736	0.736	528	58%	605	83.1%
(DO) Direct optimization	941	33	73%	65	60%	56	60%	0.995	0.753	0.753	566	60%	622	85.4%
(BI) Bayesian inference	940	36	80%	74	68%	62	66%	0.997	0.772	0.772	706	75%	654	89.8%
(ML) Maximum likelihood	941	34	76%	81	74%	70	74%	0.997	0.766	0.766	788	84%	657	90.2%
(C-ML-T) Trimmed alignments, maximum likelihood constrained by skeleton TR tree	941	44	98%	70	64%	61	65%	0.998	0.761	0.761	714	76%	618	84.9%
(C-ML) Maximum likelihood constrained by skeleton TR tree	941	44	98%	76	70%	66	70%	0.999	0.779	0.779	941	100%	623	85.6%

groups in Araneomorphae: the structure within Synspermiata; the clade Hypochilidae + Filistatidae; as well as the relationships of the leptonetid *Calileptoneta* and of Amaurobiidae. Recovery of taxonomic groups by the C-ML tree is slightly lower (by five groups), as compared to the unconstrained ML tree (Table 2). The difference is limited to six families: the unconstrained ML analysis recovers the monophyly of six more families (Actinopodidae, Ctenizidae, Dictynidae, Drymusidae, Sicariidae, Zoropsidae), and the C-ML tree only one more (Idiopidae). All these groups have low support (see *Relationships* below), and the topological changes are still limited to a restricted neighbourhood. We carried out an additional analytical variant, a constrained analysis excluding ambiguously aligned regions (C-ML-T; Fig. S5). This scheme recovered fewer taxonomic or transcriptomic groups than either the BI or the ML analyses (Table 2). As the C-ML tree recovered many of the previously accepted families, and incorporates the recent highly supported groups, this analysis was used to summarize our results and the sensitivity of selected groups to different methodological approaches. Four terminals had very long branches and were very unstable across analyses: *Caerostris sexcuspidata* (Araneidae), *Theotima* sp. MR15 (Ochyroceratidae), *Usofila* sp. MR71 (Telemidae) and *Theridiosoma gemmosum* (Theridiosomatidae). The removal of these four terminals from the dataset and running a new ML analysis (C-ML-P) produced an increment in bootstrap of several branches in the vicinity where these species were formerly connected (increasing average support from 0.69 to 0.71). Hence, we present this analysis of 939 terminals as our working hypothesis (C-ML-P tree, Figs 1–8).

Relationships

The results presented are based on molecular data analysed using a diversity of optimality criteria (Figs 1–8). Morphological characters, where discussed, are used *ad hoc* and were not included in the phylogenetic analyses. To summarize the results and guide the discussion, we use a tree that is based on ML analyses of the concatenated dataset implementing a backbone constraint based on the phylogenomic results from Garrison et al. (2016), removing four unstable terminals, the C-ML-P tree as discussed above. Based on bootstrap support values (Figs 2–8), in the text we refer to clade support as weak (< 50), low (50–65), moderate (66–79), good/well (80–94) or with high/strong (95–100) support. We treat those groups monophyletic in > 70% of the different analyses as robust (Fig. S11). Additional results from analyses under different analytical criteria and data treatments are given in Table S4. Results from several unconstrained

analyses are reported in the supplementary materials and discussed briefly below.

A number of taxonomic changes are suggested based on these analyses, and are in general conservative. In a few cases, we refer to the results of clade-specific total evidence (DNA sequences and morphology) analyses recently performed for Mygalomorphae (Bond et al., 2012; with morphological characters for Euctenizidae), Palpimanoidea (Wood et al., 2012, 2013) and Lycosoidea (Polotow et al., 2015). Although our results here differ in some ways from those studies, we rely on the total evidence results to guide taxonomic suggestions for Mygalomorphae, Palpimanoidea and Lycosoidea.

Outgroups

We recover a strongly supported Tetrapulmonata, consisting of a monophyletic Pedipalpi, sister to Araneae, following Shultz (1990) and others (Fig. 2). Amblypygi is monophyletic, with Charinidae placing basally in the order, following Weygoldt (1996). Pedipalpi comprise the monophyletic Schizomida plus Uropygi, which follows Weygoldt and Paulus (1979), and Amblypigi. Protoschizomidae place basally within Schizomida, following Cokendolpher and Reddell (1992).

Mesothelae versus Opisthothelae

The Mesothelae (family Liphistiidae, Liphistiomorphae) retain external abdominal segmentation; at least vestiges of all four pairs of spinnerets and body segments 12–18 are present, extending behind the spinnerets such that these appear to be beneath the middle of the abdomen, hence "meso-thele". Four book lungs and orthognath fangs are also retained in this group. The Mesothelae sampling herein includes three species of *Liphistius*, and one each of *Ryuthela* and *Heptathela*. We find that *Liphistius*, Liphistiinae, Heptathelinae, Liphistiidae, Mesothelae and Opisthothelae are all monophyletic with strong support (Fig. 2), in agreement with the recent analyses of Xu et al. (2015a,b).

Opisthothelae

This group represents spiders in which the abdominal segments 12–18 are suppressed such that the spinnerets appear to be beneath the apex of the abdomen, hence "opistho-thele". We find a monophyletic Opisthothelae with strong support (Fig. 2).

Mygalomorphae

These taxa retain the primitive four book lungs and orthognath fangs but have reduced spinning organs. None has a homologue of the anterior median spinnerets (AMS), and only a few retain anterior lateral spinneret (ALS) homologues; most have only four posterior spinnerets. A monophyletic Mygalomorphae is recovered and strongly supported. Like previous molecular studies that have included a broad sampling of mygalomorph taxa (Hedin and Bond, 2006; Bond et al., 2012, 2014; Garrison et al., 2016), we recover a basal split between the Atypoidea and the Avicularioidea (Fig. 2). The Atypoidea (Antrodiaetidae, Atypidae and Mecicobothriidae) are a clade of behaviourally disparate mygalomorphs that retain vestiges of segmentation as dorsal abdominal tergites. Holarctic Atypidae are monophyletic, whereas Holarctic Antrodiaetidae are rendered paraphyletic, by the inclusion of Mecicobothriidae. The latter show a bipolar (North and southern South America), disjunct distribution. North America is a centre of diversity and endemism for Atypoidea.

We recover a monophyletic Avicularioidea, comprising all non-atypoidine mygalomorphs, which have lost all vestige of external abdominal segmentation. Resolution with Avicularioidea has similarities and differences with previous molecular studies of Mygalomorphae (Hedin and Bond, 2006; Bond et al., 2012, 2014; Garrison et al., 2016). When we compare our results to the analyses recently performed by Bond et al. (2012) (combining sequence data with morphological characters for Euctenizidae), we notice several differences. Of the groupings found by Bond et al. (2012), we recover Mygalomorphae, Atypoidea and Avicularioidea, although arrangements within differ, Theraphosoidina including Barychelidae and Theraphosidae, and the families Atypidae, Euctenizidae, Migidae and Idiopidae (the latter with weak support). We obtained a monophyletic Actinopodidae in several of our analyses (but not C-ML or BI); our results find a close association of actinopodids with some Hexathelidae, reproducing previous results by Bond et al. (2012) and Opatova and Arnedo (2014). Nemesidae are a large group paraphyletic with respect to Microstigmatidae and at least *Fufius* of Cyrtaucheniidae. Our results differ from those of Bond et al. (2012) in that our data do not recover any of the following taxa as monophyletic: Domiothelina, Crassitarsae, Ctenizoidina, Euctenizoidina, Antrodiaetidae, Dipluridae or Ctenizidae. Since these differences are all weakly supported, we do not draw further conclusions on this basis.

Ctenizidae, represented by eight taxa, are diphyletic. The American *Ummidia* and Eurasian *Conothele* form a strongly supported group (Ctenizidae part A), apart from a weakly supported group of South African (*Stasimopus*) and North American genera (Ctenizidae part B). The three diplurid exemplars in this study are not monophyletic, although the genera *Australothele*

and *Cethegus* are joined with high support. Cyrtaucheniidae, with four exemplars, break into two parts—*Homostola* plus *Ancylotrypa* are strongly related and are supported as related to the Theraphosoidina, a result consistent with Bond et al. (2012), while *Fufius* fell within Nemesiidae. We suspect that the non-monophyly of Ctenizidae and Dipluridae may be due to inadequacies in our data, and we defer to the total evidence results of Bond et al. (2012), and refrain from making any taxonomic changes for these families. Only the unconstrained ML analysis retrieves a monophyletic Ctenizidae, although with weak support.

Araneomorphae

As with some mesotheles, the AMS are present in some araneomorphs, but with many functional spigots. The araneomorph AMS are unrecognizable as spinnerets, as they are modified into a cribellum. The cribellum is a synapomorphy for Araneomorphae, although in a majority of species it is reduced to a non-functional colulus, or lost altogether. Another synapomorphy for Araneomorphae are piriform silk glands, which produce a sticky glue that bonds threads to each other or to the substrate, making possible a much more varied and precise use of silk than in mesotheles and mygalomorphs. The basal branches of Araneomorphae are in a state of flux. The most recent analysis from transcriptomes (Garrison et al., 2016) finds strong support for some basal clades, which we reflect in our backbone constraint. As expected, it is in the deeper nodes of Araneomorphae where the transcriptomic data have a stronger stabilizing effect, even with a limited taxon sampling.

Hypochilidae and Filistatidae

This clade is one of the most exciting findings of the recent transcriptomic analyses of Bond et al. (2014) and Garrison et al. (2016). It not only refutes important higher level groups (Paleo- and Neocribellatae, Araneoclada, Haplogynae; see *Taxonomy* below), but it begs for a substantial re-interpretation of the evolution of important characters, such as respiratory and circulatory systems (see Huckstorf et al., 2015). This clade is well supported after the addition of the TR backbone tree, which contains *Hypochilus* and *Filistata* (Fig. 3). We recover a monophyletic Filistatidae for our eight exemplars. The unconstrained BI and IW analyses also recover the group Hypochilidae + Filistatidae (although in IW a representative of Filistatidae, Prithinae sp. Costa Rica MR11, goes to an odd place, in Dysderidae, seemingly due to a misalignment problem in the parsimony analyses).

Synspermiata

This group was recently named by Michalik and Ramírez (2014) for all the ecribellate "haplogynes", after the unique fusion of several spermatids into one synsperm (Alberti and Weinmann, 1985). Synspermiata includes the superfamilies Dysderoidea, Scytodoidea and the Lost Tracheae Clade. Synspermiata is recovered with low support, but is obtained in all analyses except for two unstable terminals (the telemid *Usofila* and the filistatid Prithinae sp. Costa Rica MR11 mentioned above) (Fig. 3).

Dysderoidea

The four dysderoid families (Dysderidae, Segestriidae, Oonopidae and Orsolobidae) are recovered as monophyletic in all analyses (Fig. 3), except for a few unstable representatives that may go, or come from, elsewhere (the oonopid *Stenoonops* and the telemid *Usofila*). The relationships among the families are homogeneous across analyses, including a new sister group relationship between Orsolobidae and Dysderidae, although weakly supported. This latter result agrees well with the partly fused testes in dysderids, as an intermediate step towards total fusion that is distinctive of oonopids (Burger and Michalik, 2010; Michalik and Ramírez, 2014). Within Oonopidae, the C-ML tree is consistent with the progressive hardening of the body from lower to higher gamasomorphines proposed by Grismado et al. (2014: 7) (see also de Busschere et al., 2014: 186), although not solving the orchestinines and soft-bodied clades, which are undersampled in our study. In Orsolobidae, we obtain a monophyletic group of South American genera, represented by *Orsolobus*, *Osornolobus* and cf. *Mallecolobus* sp. Chile MA188.

Trogloraptoridae and Caponiidae

Trogloraptoridae are the only entirely new spider family described during this century. This taxon, known only from *Trogloraptor marchingtoni*, was discovered in caves and old growth forest in the Klamath-Siskiyou region of Oregon and California. Their morphology suggests a kinship with the Dysderoidea and Caponiidae (Griswold et al., 2012). Most analyses obtain Trogloraptoridae and Caponiidae as sister groups (Fig. 3); C-ML and BI bring the unstable telemid *Usofila* in between, but the removal of *Usofila* increases the support of the group to moderate. This latter clade is the sister group of Dysderoidea after the TR backbone is enforced, and in the BI unconstrained tree; in general, this is in good agreement with the morphology, except that it implies homoplasy in the posterior respiratory system of caponiids, remarkably similar to that of dysderoids (Ramírez, 2000).

Scytodoidea

The scytodoids are a group of Synspermiata with six eyes grouped in three pairs. They include, among others, the brown recluses (*Loxosceles*, Sicariidae) and spitting spiders (Scytodidae). Scytodoids are recovered in the BI tree, and their monophly is only weakly supported by the transcriptomic constraint, although only *Loxosceles* and *Scytodes* are included in the skeleton tree. According to this result, and also supported by all the analyses, the tropical Ochyroceratidae are a member of Scytodoidea (Fig. 3). This relationship had previously been suggested by Lehtinen (1986), and we have confirmed the presence of bipectinate proclaws and a distal dorsal hood covering the claw bases in *Ochyrocera* and *Theotima* (A. Pérez-González and M. Ramírez, unpublished data); both are synapomorphies of Scytodoidea (see Labarque and Ramírez, 2012). Although Drymusidae are monophyletic in several of our analyses (C-ML-T, ML, BI, DO), our results are overall inconclusive about the separation or inclusion of Periegopidae in Drymusidae.

Lost Tracheae Clade

This clade is a group of families of Synspermiata that have lost their posterior respiratory system (Ramírez, 2000). This clade is strongly supported after the stabilization of the skeleton TR tree (which includes *Pholcus* and *Diguetia* as the only representatives of the clade) (Fig. 3), and also in the BI unconstrained tree. The resolution is novel, and implies the separation of the armoured spiders Tetrablemminae from Pacullidae, currently grouped in Tetrablemmidae, but previously considered separate families (see *Taxonomy* below). Pholcidae are strongly supported, but only the subfamilies Ninetinae and Smeringopinae are recovered in our analysis; we refer to the densely sampled analysis of Dimitrov et al. (2013) for intra-familial relationships.

Austrochiloidea and Leptonetidae

These two groups of spiders seem to be an endless source of surprises. Austrochiloids comprise two austral families, Gradungulidae and Austrochilidae, which include some of the largest araneomorphs (Forster et al., 1987). Since Platnick (1977), these families have been placed as an early branching lineage of the higher spiders, as suggested by the retention of the primitive arrangement of four book lungs. Within the last decade, field observations and careful scanning electron microscopy examinations have revealed derived characters in common with higher spiders, thereby challenging their grouping near the araneomorph base. At least some austrochilids have cylindrical gland spigots and card their cribellate silk in a supposedly derived manner, using one leg IV braced against the other, mobile leg IV (Lopardo et al., 2004; Griswold et al., 2005). Leptonetids, tiny fragile spiders of caves and other dark places, were traditionally placed within the simple-genitalia haplogyne spiders. Again, detailed scanning electron microscopy studies have changed things: by discovering, first, a class of spigots that are probably cylindrical gland spigots (Platnick et al., 1991) and, second, a cribellum in *Archoleptoneta* (Ledford and Griswold, 2010). Morphology has suggested a leptonetid affinity to entelegynes (Ledford and Griswold, 2010) and phylogenomics added further support (Garrison et al., 2016). Previous molecular studies have suggested an *Archoleptoneta*–austrochiloid affinity (Agnarsson et al., 2013). Herein, we continue to expand novel interpretations of austrochiloid and leptonetid placement (Fig. 3), underscoring the pivotal importance of these obscure animals.

Gradungulidae

This bizarre family, known only from Australia and New Zealand, is characterized by grotesquely asymmetric tarsal claws and includes cribellate and ecribellate, four-lunged spiders. Gradungulidae are well represented in our study, including the huge Australian cribellate *Macrogradungula moonya* and the ecribellates *Gradungula sorenseni* from New Zealand and *Tarlina woodwardi* from Australia. Gradungulids unite with high support, and appear related to the cribellate, four-lunged sheet-web builder from Tasmania, *Hickmania troglodytes* (Austrochilidae). Gradungulids and *Hickmania* appear also related to the cribellate leptonetids *Archoleptoneta* in a clade of moderate support, although the precise relationships among them are uncertain (Fig. 3).

Leptonetidae

The family Leptonetidae, exclusively Holarctic, had long been placed among the haplogynes. The discovery of a cribellum in *Archoleptoneta*, a relict leptonetid from California (Ledford and Griswold, 2010), changed this scenario. Leptonetids had already been recognized for having a category of spigots with sexual dimorphism like cylindrical gland spigots, and Brignoli (1979) had already remarked on the similarities to Entelegynes. Ledford and Griswold (2010) suggested that *Archoleptoneta* might be a proto-entelegyne, and that the whole family might be misplaced in Synspermiata. Wunderlich (2015: 287) placed leptonetids as part of his LAE clade (Leptonetoids, Archaeoids and Entelegynes), based on cylindrical gland spigots, loss of the posterior lungs and absence of eye triads. Molecular data supported placement of Leptonetidae

outside of the Haplogynae (Agnarsson et al., 2013), as did phylogenomic data (Garrison et al., 2016), probably as sister to Entelegynae, although the latter study lacked some other strong candidates for leptonetid relatives, e.g. austrochiloids and palpimanoids (see below). Our study corroborates the placement of leptonetids outside the Synspermiata and nearer the Entelegynae; in addition, our data challenge leptonetid monophyly (Fig. 3). In our study, the cribellate *Archoleptoneta*, with a simple eye pattern, are separate from the ecribellates, with posterior median eyes displaced behind the lateral eyes. The ecribellate leptonetids of our sample group are, however, diphyletic in the optimal trees, and thus we prefer to defer taxonomic changes in Leptonetidae (see comments below).

The CY Spigot clade, and the austrochiloids

Cylindrical gland spigots (CY), also known as "tubuliform", characterize a large clade of spiders comprising all Araneomorphae except Hypochilidae, Filistatidae and Synspermiata. These spigots appear only in mature females and presumably take part in making the eggsac, but the exact role is still unknown. The aforementioned Leptonetidae join the austral family Austrochilidae in having a category of spigots with the same sexual dimorphism as CY. This last family was long placed in Austrochiloidea near the base of the Araneomorphae, because several (the austrochilid *Hickmania*, together with Gradungulidae) retain four book lungs. Our results place the two-lunged Austrochilidae *Austrochilus* and *Thaida* as a monophyletic group with high support, and ally these with the ecribellate type genus of Leptonetidae, *Leptoneta*, but with low support (Fig. 3). Austrochilids could be giant austral counterparts of leptonetids; at least the peculiar patella/tibia autospasy characteristic of leptonetids and austrochilines supports this hypothesis. Leptonetidae are not without problems though, in that the ecribellate leptonetines *Neoleptoneta* and *Calileptoneta* fall far from *Leptoneta*, forming a group near the Entelegynae, and the cribellate *Archoleptoneta* joins with Gradungulidae (see above). We suspect that this result, especially the diphyletic Leptonetidae, is artefactual, as there are numerous morphological synapomorphies uniting the Leptonetinae, and the results are unstable across analyses. Our data suggest, although with moderate to low support, that the austrochiloids and leptonetids are more closely related to palpimanoids and entelegynes than to Synspermiata (Fig. 3).

Palpimanoidea

Assassin spiders are restricted to five living families, Archaeidae, Huttoniidae, Mecysmaucheniidae, Palpimanidae and Stenochilidae. Palpimanoids were once more widespread, with fossils dating back to the Jurassic in Northern Hemisphere deposits (Selden et al., 2008; Wood et al., 2013). The fossil family Lagonomegopidae was widespread in the Mesozoic world, and 12 fossil genera of Northern Hemisphere Archaeidae contrast to the only four known today from Africa, Australia and Madagascar.

Wood et al. (2012, 2013), in total-evidence analyses including fossil taxa, established the monophyly of a Palpimanoidea comprising the above five families, which we accept as the most robust solution. Molecular data alone repeatedly fail to recover Palpimanoidea. Each of the five palpimanoid families is represented here by multiple exemplars and all of them are recovered with strong support (Fig. 3). Huttoniidae and Palpimanidae unite with moderate support, but the rest of the families, especially Archaeidae, are unstable across analyses, clustering to other long-branched regions of the tree; this situation improves after the removal of *Theridiosoma gemmosum* and in the BI tree. This instability might be the effect of long-branch attraction or indicative of undetected paralogy in some of the nuclear ribosomal genes (see comments in Dimitrov et al., 2016). We prefer to retain the classification of Wood et al. (2012, 2013) and accept a monophyletic Palpimanoidea; among other morphological characters, they have peg teeth on the promargin of the chelicerae and a cheliceral gland mound.

All palpimanoids appear to be prey specialists often feeding on other spiders, hence the broadly applied term "assassin spiders". Araneophagic palpimanids enter the retreats of other spiders, seize them with scopulate anterior legs and prey on them, at least pelican spiders (Archaeidae) attack Araneoidea in the host's webs, and captive stenochilids and huttoniids seem to prefer spider prey (see Wood et al., 2012). Huttoniidae, Palpimanidae and Stenochilidae have extensive, lateral scopulae on their forelegs, which enable them to seize and manipulate prey, and even the web-invading archaeids retain a vestige of these scopulae. Mecysmaucheniidae have a remarkable trap-jaw mechanism (Wood et al., 2012, 2016). They hold the chelicerae widely open and locked before a strike; when prey contacts one of the long, forwardly directed setae (possibly triggers), the chelicerae snap closed at remarkable speed, enabling them to capture such speedy prey as springtails (Collembola). Prey preferences of extinct Palpimanoidea are unknown, but archaeids from amber have the same prey-specialized morphologies as living forms. Within Palpimanidae, our data support the monophyly of the subfamilies Otiothopinae (represented by *Notiothops* and *Otiothops*), Chediminae (by *Scelidocteus* and *Sarascelis*) and Palpimaninae (with *Palpimanus* and *Ikuma*); our *Ikuma* representative is nested in an African group of *Palpimanus* species, suggesting that the generic limits should be re-examined.

Entelegynae

This large clade of spiders is characterized by a "flow-thru" female genital system with separate ducts for copulation and fertilization. Entelegyne monophyly is supported, but with weak support (Figs 4–8). The entelegyne condition and the sclerotized genital plate near the copulatory openings (the epigynum) have long been recognized as a synapomorphy for this clade, with three reversals to a haplogyne organization in tetragnathines, in the uloborids *Waitkera* and *Tangaroa* and in the anapid *Comaroma*. A close examination of the genital system of anapids revealed fertilization ducts in all except *Comaroma* (Lopardo and Hormiga, 2015).

Nicodamoidea and Araneoidea

Araneoidea are a rich, successful clade characterized by a triplet of one flagelliform gland and two aggregate gland spigots on the posterior lateral spinnerets (PLS; variations occur): the flagelliform glands each produce an axial line and the aggregates coat these with viscid glue. The superfamily Araneoidea is a clade and its sister group is the superfamily Nicodamoidea, but, unlike the results in Dimitrov et al. (2016), here the Araneoidea and sister group association of Nicodamoidea and Araneoidea have only low support (Fig. 4). Each included nicodamoid family, represented by two terminals of the same cribellate species (Megadictynidae, New Zealand) and three ecribellate Nicodamidae (Australia and New Guinea), and the superfamily Nicodamoidea, are all strongly supported.

The Araneidae have received much attention in phylogenetic studies and have a checkered history (e.g. Hormiga et al., 1995; Scharff and Coddington, 1997; Kuntner, 2006; Kuntner et al., 2008, 2013; Álvarez-Padilla et al., 2009; Dimitrov and Hormiga, 2009, 2011; Gregorič et al., 2015). Our coverage of these taxa is good, with 13 nephilines and 24 non-nephiline Araneidae including the contentious oarcines (*Gnolus* and *Oarces*), *Caerostris*, *Zygiella* and *Phonognatha*, plus *Arkys*, formerly an araneid but placed in its own family, sister to the tetragnathids by Dimitrov et al. (2016). We obtained good support for Araneidae (excluding *Arkys*), with a strongly supported Nephilinae sister to the rest of the family, as in Dimitrov et al. (2016; but that study included many more terminals). *Caerostris sexcuspidata*, one of the species that we pruned from the analysis, fluctuated across several clades and erased their support (compare Figs 2 and S4).

A poorly supported but robust arrangement emerging from our study and mirroring Dimitrov et al. (2016) is the relationship among Tetragnathidae, Arkyidae and Mimetidae. Our Tetragnathidae comprise 27 exemplars, whose monophyly is strongly supported. These are in turn sister group to the Australian Arkyidae (*Arkys*), with good support. Finally, our six exemplars of the worldwide pirate spiders (Mimetidae) comprise a well-supported family.

The peculiar, poorly known Austral spiders formerly placed in Holarchaeidae and Pararchaeidae long posed classification mysteries, and were alternatively classified with orb builders (Araneoidea) and assassin spiders (Palpimanoidea). *Holarchaea* is strongly allied to the anapid *Acrobleps* and our two pararchaeid exemplars fit within the Malkaridae, compatible with the synonymies proposed by Dimitrov et al. (2016), but with weak support and unstable across analyses. We include Australian and Chilean malkarid exemplars, but none of the undescribed taxa from New Zealand used in that study.

Of the families formerly placed in the symphytognathoids (Griswold et al., 1998) or symphytognathidans (Rix and Harvey, 2010), we only recover a weakly supported group of Anapidae and Symphytognathidae, but the families themselves are in general well supported. Anapidae, comprising 16 exemplars including *Holarchaea* and a variety of micropholcommatines, are well supported, as are Mysmenidae (ten exemplars). Symphytognathidae (six exemplars) have moderate support. We obtained low support for Theridiosomatidae, even after pruning *Theridiosoma gemmosum* due to its unstable placement near Titanoecidae and Archaeidae (e.g. in ML), in a group seemingly characterized only by long branches, suggesting either an analytical artefact or a sequencing problem.

Synotaxus, the sole remaining genus in Synotaxidae, allies strongly to the nesticid *Gaucelmus*. Diphyly of the old Synotaxidae is well justified on molecular, morphological and behavioural grounds: the Neotropical *Synotaxus* builds a unique, "chicken-wire" web with modules of glue-sticky silk (Eberhard, 1995), whereas the southern South American, Australian and New Zealand physoglenids make ordinary sheet or dome webs (Dimitrov et al., 2016; and references therein). We obtain a strongly supported core Nesticidae of four genera (*Nesticus*, *Nesticodes*, *Eidmannella* and *Carpathonesticus*) but *Gaucelmus* fluctuates among analyses, always together with *Synotaxus*. Separation of the cob-web building Nesticidae (five exemplars) and Theridiidae (27 exemplars) is found here, as it has been in previous molecular studies (e.g. Dimitrov et al., 2012, 2016; Agnarsson et al., 2013; Bond et al., 2014; Garrison et al., 2016). The sticky-silk apparatus of these two families is strikingly similar (Coddington, 1989), with enlarged aggregate gland spigots on the PLS (also present in Arkyidae and *Synotaxus*) and a ventral comb on the fourth tarsus for throwing silk blobs (hence, "comb foot spiders"), but nesticid and theridiid genitalia are very different (Agnarsson, 2004). Males of the former have

a typical araneoid paracymbium (a process on the cymbium of the palp), whereas theridiid males have a distal locking mechanism within the alveolus. Theridiidae are well supported but only allied with low support to the remaining Araneoidea. The propinquity between Theridiidae and some Mysmenidae and Anapidae, as found in Dimitrov et al. (2016), is excluded by the backbone constraint, but a liaison with Mysmenidae is obtained in some of the unconstrained analyses (ML, BI).

We recover strongly supported groups for the 11 Physoglenidae exemplars, ten Cyatholipidae and a clade of 39 exemplars comprising Linyphiidae plus Pimoidae (the pimoid *Weintrauboa* clusters with the linyphiid *Stemonyphantes*, otherwise these two families are reciprocally monophyletic; see Dimitrov et al., 2016 for a more detailed discussion).

Eresidae

Velvet spiders comprise an almost exclusively Old World taxon (one species, possibly introduced, is reported from Brazil) that has many species and genera in the arid parts of Africa. Subsociality has evolved at least three times within *Stegodyphus*, once in south Asia (*S. sarasinorum*) and twice in Africa (*S. dumicola* and *S. mimosarum*) (Johannesen et al., 2007). The phylogeny of velvet spiders has recently been studied in detail (Miller et al., 2012). Our nine eresid exemplars form a robust monophyletic group arising near the base of the Entelegynae, but more detailed placement is impossible, as support for relations to other entelegynes is essentially non-existent (Fig. 5). The concept of Eresoidea (Eresidae plus Oecobiidae) was established based on morphological data (Platnick et al., 1991; Griswold et al., 1999, 2005) but molecular data have challenged this (J. Miller et al., 2010) and the Eresoidea hypothesis now seems definitively refuted. The transcriptomic studies are indecisive on the relationships of Eresoidea (only two species of the three putative eresoid families have been included), and hence we did not constrain their placement.

Oecobioidea

These two families, Hersiliidae and Oecobiidae, have modified, elongated PLS that spin sheets or curtains of silk to tie down their prey, which is applied while the spider whirls rapidly in circles around the prey. Tiny, cribellate *Oecobius* include cosmopolitan and pantropical species that are common in houses; ecribellate hersiliids have a worldwide distribution. We include four exemplars of each family; Hersiliidae are strongly supported and the cribellate *Oecobius* and ecribellate *Uroctea* form a moderately supported Oecobiidae (Fig. 5). Grouping of Hersiliidae and Oecobiidae as superfamily Oecobioidea is also well supported in the ML and C-ML trees, while the remaining methods did not recover *Oecobius* and *Uroctea* together.

Orb-web weaving spiders

Perhaps the most dramatic change in spider phylogeny in the last decade is the realization that the complex suite of stereotypical behaviours used to construct an orb-web do not define the corresponding clade "Orbiculariae", formerly comprising all cribellate and ecribellate orb-building spiders (Bond et al., 2014; Fernández et al., 2014; Hormiga and Griswold, 2014; Dimitrov et al., 2016; Garrison et al., 2016). Instead, these studies suggest that the orb-webs are most likely an ancient development of a more inclusive group, probably of all entelegynes, and that the orb-web was subsequently modified or lost in several lineages.

Cribellate orb-weavers

The monophyly of Deinopoidea (Uloboridae and Deinopidae) is disputed by molecular data, as revealed in the molecules-only partitions of Blackledge et al. (2009), as clearly shown by Dimitrov et al. (2012, 2016) and Agnarsson et al. (2013), and now solidly refuted by transcriptomic analyses (Bond et al., 2014; Fernández et al., 2014; Garrison et al., 2016) and herein (Fig. 5).

Not surprisingly, the monophyly of Deinopidae, represented by five exemplars (two *Menneus* and three *Deinopis*), is strongly supported by sequence data. The Uloboridae representatives, seven exemplars, group together with low support. Both families vary their placement across analyses; other than the well-established non-monophyly of Orbiculariae and Deinopoidea, a clear understanding of the placement of cribellate orb-weavers remains a future goal. Although "Orbiculariae" now appears to be an artificial taxonomic concept, recent analyses of character evolution still show some support for a single origin of the orb web, but with multiple losses (e.g. Dimitrov et al., 2016; Garrison et al., 2016), either by modifying the web into architectures no longer recognizable as orbs (e.g. in Cyatholipidae) or by dispensing altogether with foraging webs (e.g. the pirate spiders, Mimetidae).

Ecribellate orb-weavers

The phylogeny of Araneoidea has received extensive recent attention (e.g. Blackledge et al., 2009; Schütt, 2009; Lopardo et al., 2011; Dimitrov et al., 2012, 2016; Agnarsson et al., 2013; Hormiga and Griswold, 2014). The study of Dimitrov et al. (2016) includes representatives of all valid araneoid families, including Synaphridae, which are unrepresented in the present

study. Common results from this study and that of Dimitrov et al. (2016) are the sister group relationship of Nicodamoidea and Araneoidea, of Nephilinae and the rest of Araneidae, close association among Mimetidae, Arkyidae and Tetragnathidae, the inclusion of former Pararchaeidae within Malkaridae, of Holarchaeidae and Micropholcommatidae within Anapidae, isolation of *Synotaxus* from other former Synotaxidae and the remarkable diphyly of the comb-footed "theridioids" (Theridiidae and Nesticidae). Several of those findings are strongly supported in our study as well. Another similarity is the generally low support for interfamilial relations. Disappointingly, the evolution and diversification of ecribellate orb-builders and their kin as yet cannot be understood. Compared to the results of Dimitrov et al. (2016), we do find similarities and differences in family placement, which are detailed in the previous section, Nicodamoidea and Araneoidea.

Spiders with male palpal tibial apophyses

A process or set of processes on the male palpal tibia occurs widely within the Entelegynae. Occurrence of as many as four lateral processes, e.g. in Amaurobiidae, suggests that there may be up to four homologies (Griswold et al., 2005). The retrolateral tibial apophysis (RTA) characterizes a large clade of spiders (see below). The dorsal tibial apophysis (DTA) of Nicodamoidea and some Linyphiidae, Titanoecidae and Phyxelididae is not homologous to the RTA; some phyxelidids (*Vytfutia*) and phrurolithids (*Phonotimpus*) and most Amaurobiidae have both RTA and DTA.

Titanoecidae

Titanoecids lack tarsal trichobothria, a primitive condition, and have a complex DTA but lack an RTA on the male palp. In our dataset, Titanoecidae are well represented by six exemplars and form a robust, strongly supported monophyletic family (Fig. 5).

Phyxelididae

These spiders occur in Africa, Madagascar and Asia, and have been suggested as the sister group of Titanoecidae (Griswold et al., 1999, 2005). We include ten representatives including African Vidoliini and also Phyxelidini from both Africa and Madagascar, but unfortunately the enigmatic Asian Vytfutiini are absent from our analysis. Phyxelididae are strongly supported and robustly allied to the RTA clade, although with low support (Fig. 5). Phyxelididae and Titanoecidae fall apart, provisionally refuting the clade Titanoecoidea (Griswold et al., 1999). A broader representation of phyxelidids, including Vytfutiini, plus enhanced molecular, as well as morphological data, will be necessary to better test the monophyly and the limits of Titanoecoidea.

The RTA clade

These taxa have an RTA on the male palp and also one to many trichobothria on the tarsi and metatarsi, representing advances in mating stabilization and vibration sensitivity, respectively. Spiders with dorsal but not retrolateral male palpal tibial apophyses, i.e. Nicodamoidea, Phyxelididae and Titanoecidae, are historically excluded from the RTA clade (Griswold et al., 1999, 2005). Herein, we recover the RTA clade, albeit with low support (Fig. 5).

Zodarioidea

A gestalt of morphological data long associated the Zodariidae and Homalonychidae, to which the peculiar African Penestomidae were added by J. Miller et al. (2010) based on molecular evidence. One morphological synapomorphy for these three families is that the ALS have the major ampullate gland spigots placed deep within the piriform spinning field (J. Miller et al., 2010; Ramírez et al., 2014), thus providing independent corroboration of the molecular results. We find a robust and well-supported Zodariidae comprising 27 exemplars (Fig. 5). Zodariids are easily distinguished by a combination of characters (see Jocqué, 1991) —an unambiguous synapomorphy for the family was recently discovered by Jocqué and Henrard (2015)—the distal dorsal rim of the leg tibia has a ball-shaped projection, fitting in a cavity of the metatarsus. Within zodariids, we corroborate the kinship of *Cryptothele* with former cydrelines, and thus Cryptothelinae, as indicated by morphological data (Ramírez et al., 2014). Our only representative of Lachesaninae (*Lutica*) is deeply nested among zodariines, although most internal nodes have weak support. Penestomidae (*Penestomus*) are moderately supported as the sister group of Zodariidae. Homalonychidae are placed with zodarioids in our DO, BI and ML analyses, with weak support, but are driven elsewhere in the tree by the backbone constraint of Garrison et al. (2016), close to the OC Clade and Dionycha, but with weak support. Considering the congruence in morphology and the molecular data found here, we suspect that the breakup of Zodarioidea forced by the transcriptomic analysis backbone tree may be artefactual.

The marronoid families

Our informal name marronoid (*marrón*, brown in Spanish) comes from grouping together several spider families lacking striking characters and formerly classified together in such "tailor's drawer" families as

Agelenidae, Desidae, Dictynidae and Amaurobiidae. Most are brown, grey or mottled but also have complex, distinctive genitalia with an elaborate RTA and several bulbal sclerites, all retain three claws, and most families have both cribellate and ecribellate species. The globally representative taxon sample in Griswold et al. (1999, 2005) suggested a dichotomy roughly between the spiders placed in Amaurobioidea and Dictynoidea, but not equivalent to the tracheae-based groups Amaurobioidea and Dictynoidea as defined by Forster and Wilton (1973). Instead, their results hinted at a basic dichotomy between Holarctic (Amaurobiidae, Dictynidae) and Austral (Desidae, Stiphidiidae) spiders, the latter informally referred to as the "Fused Paracribellar clade" (FPC) after a peculiarity of their spinning organs. A series of molecular phylogenetic studies beginning with Spagna and Gillespie (2008) and continued through J. Miller et al. (2010), Spagna et al. (2010), Agnarsson et al. (2013) down to the current study have divided and reassembled these taxonomic concepts, hence requiring the reclassification of Forster and Wilton's concepts of Amaurobioidea and Dictynoidea. Our study comprises by far the densest and broadest taxon sampling for target genes. This convinces us to formalize the taxonomic reorganization presaged by the works cited above and corroborated and extended here. The families Agelenidae, Amaurobiidae, Amphinectidae, Cybaeidae, Desidae, Dictynidae, Hahniidae, Neolanidae and Stiphidiidae all require radical reclassification due to our analysis, and below we provide the transfers and in some cases new synonymies necessary for a phylogenetically robust classification. The "marronoid" group is recovered by all our analyses albeit with weak support, only differing in the inclusion of Sparassidae as a member in the unconstrained analyses (sister to Amaurobiidae, with weak support), or exclusion after the constraint skeleton from Garrison et al. (2016), which did not have sparassids in their sample (Fig. 5).

Amaurobiidae

This family is strongly supported only if drastically redelimited (Fig. 5). Of the 15 taxa in our dataset formerly classified as amaurobiids, only four species in three genera, *Amaurobius* (two species), *Callobius* and *Pimus*, remain to comprise the core of Amaurobiidae, i.e. subfamily Amaurobiinae. Others are distributed to Agelenidae (*Paracoelotes*), Cycloctenidae (*Pakeha* and *Paravoca*) and Toxopidae (*Midgee*). This classical family has been picked apart so that of the nine subfamilies recognized by Lehtinen (1967), only the Holarctic Amaurobiinae, the principly austral Macrobuninae and the mysterious Neotropical Altellopsinae remain. The subfamily Macrobuninae was proposed by Lehtinen (1967) within Amaurobiidae, but clear synapomorphies were discovered in recent years, in the male palps: a peculiar gland discharging in the retrolateral tibial apophysis (Compagnucci and Ramírez, 2000), and a stridulatory area on the cymbium (Griswold et al., 2005). The molecular study of J. Miller et al. (2010) indicated that the African and North American macrobunines *Chresiona* and *Zanomys* allied with the monogeneric South African Chummidae, falling far from the core Amaurobiidae. We link here these taxa with the core South American macrobunines, confirming that they are not amaurobiids, although their nomenclatorial status is still unsolved (under study by Almeida-Silva, pers. comm., Almeida-Silva, 2013; unpublished thesis). Macrobunines generally occur in temperate and subantarctic habitats in Africa, Australia and South America, where they predominate in collections of undetermined "amaurobiids". This group received good support in our analysis. Our constellation of Macrobuninae includes genera listed in Amaurobiidae (*Anisacate*, *Callevopsis*, *Chresiona*, *Livius*, *Naevius*, *Rubrius* and *Zanomys*), Chummidae (*Chumma*), Amphinectidae (*Tasmarubrius*) and most surprisingly, Anyphaenidae (*Malenella*). *Malenella nana* exhibits one of the many striking convergences into a dionychan-like morphology. This Chilean species has the extensive tracheal system and expanded claw tuft setae typical of Anyphaenidae, where it was originally described (Ramírez, 1995). The morphological analysis of Ramírez (2014) obtained *Malenella* in the vicinity of anyphaenids, but still uncovered several convergences in tracheal systems and claw tuft setae strikingly similar to those of anyphaenids (e.g. in some Eutichuridae and in *Hortipes*). The present analysis strongly supports the placement of *Malenella* among macrobunines, independently supported by each molecular marker; we sequenced several specimens with identical results, so the possibility of contamination is discounted.

Agelenidae

This is a large Holarctic family, only native to Africa, south of the Equator. This family received high support in our analysis. As noted above, austral "agelenids", e.g. *Neoramia*, were misclassified and belong elsewhere. Invasive *Tegenaria* occurs in South America, New Zealand and Australia; otherwise agelenids comprise numerous genera and myriad species in North America and temperate Eurasia, extending to South Africa. There is a single cribellate agelenid genus, *Tamgrinia* (J. Miller et al., 2010), a little known taxon from central Asia. Most are ecribellate funnel or sheet web builders with lengthened PLS and a characteristic divided colulus; in tropical Africa there are even subsocial species. Of our agelenid representatives, two genera are moved to other families: *Orepukia*, from New Zealand, allies with Cycloctenidae and *Neoramia* is placed in Stiphidiidae. Among the Agelenidae, Coelotinae and a core

Ageleninae are each robust and strongly supported, but we obtain *Textrix* and *Tegenaria* outside these subfamilies, grouped with moderate support; the cribellate *Tamgrinia* is sister to the rest of the family (Fig. 5). All these results were first suggested by J. Miller et al. (2010). Bolzern et al. (2013) obtained a different composition for agelenines, including *Textrix* and *Tegenaria*.

The "Dictynidae", a polyphyletic group

The current catalogue of spiders lists 52 genera and 578 species in the family Dictynidae, and includes cribellate and ecribellate spiders (WSC, 2016). Whereas morphological data are adequate to group the cribellates together (Griswold et al., 2005), the family falls apart in molecular analyses that include cribellate and ecribellate members (Spagna and Gillespie, 2008; J. Miller et al., 2010; Spagna et al., 2010). Dictynidae are clearly in need of a major overhaul, which was begun by Spagna et al. (2010) and Zamani et al. (2016). In our analysis, former dictynids are scattered among at least three clades, including the newly circumscribed families Cybaeidae, Hahniidae and Dictynidae (Fig. 5).

Cybaeidae

In our analysis, Cybaeidae receive strong support (Fig. 5), but differ from tradition by including *Calymmaria* (formerly Hahniidae) but excluding *Argyroneta* (moved to Dictynidae, see below). The genus *Cybaeus* was subject to a revision (Bennett, 1991; unpublished thesis), revealing several new genera and many new species. *Calymmaria* has been revised (Heiss and Draney, 2004). Like *Calymmaria*, little-known genera with patella/tibia autospasy probably belong here as well. The ecribellate *Cryphoeca*, *Blabomma, Willisus* and *Yorima* have been associated with *Cybaeus* and *Calymmaria* by Roth and Brame (1972) and Spagna et al. (2010) and we follow the latter study in classifying these ecribellate genera in our redefined Cybaeidae.

Hahniidae

This family contains the clearly monophyletic Hahniinae with a strongly modified arrangement of spinnerets in a single transverse row, here represented by *Hahnia* and *Neoantistea* (Fig. 5). These group with the austral Cybaeolinae (*Cybaeolus*), forming a strongly supported core Hahniidae. In our analysis, the monophyly of the Holarctic *Cicurina* group with our core Hahniidae is only moderately supported.

Dictynidae

This group represents a dumping ground for a diverse array of cribellate and ecribellate three-clawed Entelegynae. Of the several genera representing Dictynidae in our analysis, *Cicurina* departs to Hahniidae, leaving *Dictyna*, *Mallos*, *Mexitlia* and *Saltonia* in Dictynidae (Fig. 5). We add to these the ecribellate *Argyroneta* (formerly Cybaeidae). Corroborating Zamani et al. (2016), the intertidal genus *Paratheuma* also falls here. All these together form a strongly supported Dictynidae. The cribellate residue of Dictynidae contains *Dictyna*, of course, and similar genera such as *Mexitlia*, and *Mallos*, but the cribellate *Lathys* is not clearly placed in any of the above families (Spagna et al., 2010), but is provisionally kept in Dictynidae.

Toxopidae

We resurrect the family Toxopidae to accommodate an array of small spiders, typically with strongly curved eye rows, from Australia and New Zealand. In addition to the Tasmanian *Toxops*, a small, flattened spider with large eyes, typically found running on forest vegetation, Toxopidae include the genera *Hapona* and *Laestrygones* from New Zealand, which are similar in morphology and lifestyle. Also circumscribed in this family is the tropical Australian genus *Midgee*, formerly Amaurobiidae; these together as the subfamily Toxopinae are strongly supported. A second group of toxopids comprises *Lamina*, *Ommatauxesis*, *Otagoa* and *Myro*. The first three are restricted to Australia and New Zealand but *Myro* is scattered across sub-Antarctic islands south of New Zealand and in the southern Indian Ocean (e.g. Kerguelen, Marion and the Crozets). Toxopidae might be an austral analogue of the Dictynidae. Like dictynids, toxopines, e.g. *Toxops*, *Hapona* and *Midgee*, are small hunters on foliage or in soil, whereas myroines, e.g. *Otagoa*, *Myro* and *Ommatauxesis*, are largely intertidal. Myroines are monophyletic in several of our analyses, only varying in the placement of cf. *Gasparia* sp. New Zealand CG105 (occasionally with Desidae, Amphinectinae).

Relationships among the above six families generally receive extremely weak support and are unstable across analyses, as is typical in target gene analyses. A relationship of at least Hahniidae plus Cybaeidae receives support from phylogenomics; Garrison et al. (2016) associate *Cicurina* and *Calymmaria*, and were placed by them in Dictynidae and Hahniidae, respectively. In the context of our revised classification, this is equivalent to uniting Hahniidae and Cybaeidae.

"Austral Cribellates" or the "Fused Paracribellar clade"

Many species of this group are characterized by unusual arrangements of the paracribellar spigots within the posterior median spinneret (PMS) spinning field, typically with two to many shafts arising from common bases—the function of these multi-shaft spigot

arrangements, as opposed to the more widely encountered single shaft spigot, is unknown. The "Fused Paracribellar Clade" was named by Griswold et al. (1999) and corroborated by Spagna and Gillespie (2008) ("Austral Cribellates"); this is now known to be one of the dominant spider clades in the southern hemisphere, but is represented by only a few invasives in North America. Of the families previously associated with the FPC, Agelenidae are here excluded: cribellate agelenids, e.g. *Neoramia*, are not related to true Agelenidae and phylogenies relying on *Neoramia* for agelenid placement (e.g. Griswold et al., 2005; Blackledge et al., 2009) are erroneous. We find a weakly supported group fairly coincident with the FPC clade (Desidae, Stiphidiidae, newly joined by Cycloctenidae), although the composition of these families will differ radically from former classifications (see *Taxonomy*) (Fig. 5).

Cycloctenidae

In our dataset, the genera *Cycloctenus* and *Toxopsiella*, traditionally placed in Cycloctenidae, group with high support (Fig. 5). The family may be expanded to a group with lower support to include *Paravoca* (formerly Amaurobiidae) and *Orepukia* (formerly Agelenidae) plus *Pakeha* (formerly Amaurobiidae), which we circumscribe as Cycloctenidae *sensu lato*. The New Zealand genera *Pakeha* and *Orepukia* are closely related, and all the cycloctenids in our analysis are restricted to Australia and New Zealand.

Stiphidiidae

Twelve taxa in our dataset formerly assigned to Stiphidiidae are distributed among a few families, rejecting the monophyly of traditional Stiphidiidae. The newly circumscribed Stiphidiidae recover a well-supported core Stiphidiidae, comprising the type genus *Stiphidion*, together with *Therlyna* and *Procambridgea*. The former Neolanidae *Marplesia* and *Neolana* (incorrectly synonymized with Amphinectidae; Jocqué and Dippenaar-Schoeman, 2006) group with the former agelenid *Neoramia*; these also refer to the core Stiphidiidae (Neolanidae = Stiphidiidae, new synonymy). *Aorangia*, a New Zealand genus formerly attributed to Amphinectidae, is related to core Stiphidiidae with moderate support (Fig. 5).

Desidae

We recognize a broadly circumscribed Desidae with weak support (Fig. 5). Classification of the "Austral Cribellates" or "FPC" remains one of the largest unsolved family-level problems in spiders, in spite of 30 years of effort, and we leave most uncertainty within our broad Desidae.

Desis is quite distinct from other genera placed in this family, and other genera unstably associated near *Desis*, i.e. *Poaka* and *Barahna*, do so with weak support. Forster and Wilton (1973) assigned many pre-existing and new genera to families first recognized from the northern hemisphere, e.g. Agelenidae or Amaurobiidae, but the presence of any true Agelenidae or Amaurobiidae native to the Australia–New Zealand region is doubtful. Davies took the most careful approach to classifying her new Australian genera, placing them with quantitative analyses (Davies, 1990, 1997, 1998), but the shortage of outgroups in most of her analyses renders the conclusions uncertain. We are also unable to test another of her discoveries, e.g. the Kababinae, for which no material was available. Within our loosely conceived Desidae, we identify at least five subgroups with stronger support. One could recognize as families the taxon clusters around *Desis*, *Amphinecta*, *Porteria*, *Metaltella* and *Paramatachia*, but this risks stranding many genera, particularly those not treated in our phylogeny, without family assignment. Instead, we retain the broad Desidae and treat subgroups as subfamilies.

Subfamily Amphinectinae

We have six exemplars representing four genera, including *Amphinecta*, which cluster within Desidae as Amphinectinae with weak support. All of our exemplars, *Amphinecta*, *Mamoea*, *Paramamoea* and *Rangitata*, are from New Zealand. We obtained the species cf. *Gasparia* sp. New Zealand CG105 within Amphinectinae in the preferred tree, but it falls among myroines (where *Gasparia* is currently listed) in the EW, IW, BI and DO analyses.

Subfamily Metaltellinae

The South American and Australian metaltellines, formerly attributed to Amphinectidae, but distant from amphinectines here, are easily recognized by a unique male palpal conformation. *Calacadia* and *Metaltella* group with high support. The enigmatic former stiphidiid *Ischalea* from New Zealand groups near these, representing Davies' (1990) Ischaleinae.

Subfamily Matachiinae

Matachia and *Paramatachia* (our exemplar) are elongate spiders with large chelicerae sometimes likened to cribellate *Desis*. Their genitalia and spinning organs differ greatly from *Desis*, however. *Badumna* exhibit genitalia strikingly similar to *Paramatachia*, and the other genera that fall here are also similar. Matachiinae as a whole and all subgroups are strongly supported.

Subfamily Porteriinae

Five genera include some striking genital, somatic and behavioural similarities, regardless of their disparate distribution among families. *Porteria* (South America) runs atop its sheet web and the abdomen is boldly marked with guanine; *Corasoides* (Australia) could be a giant version of *Porteria*, with which they group with good support. *Cambridgea* and *Nanocambridgea* are closely allied, long-legged spiders from New Zealand that hang beneath their sheet webs. All four genera mentioned above have a unique configuration of the piriform gland spigot field on the anterior lateral spigots. *Baiami* (Australia) also hangs beneath sheet webs, and shares genital similarities with the above. The Porteriinae have strong support; *Porteria* remains in the Desidae; the other four genera are transferred here from Stiphidiidae.

Evidence for combining the subfamilies and main groups of Desidae is weak and unstable across analyses. Scores of genera attributed to Desidae and Amphinectidae are not included in our dataset, so it would be premature to suggest finer familial subdivisions. In the *Taxonomy* section below, we reclassify several genera, but others we leave where they are because knowledge of their characters and phylogenetic placement remains poor.

Sparassidae

Huntsman spiders are difficult to place even though they have many synapomorphies (e.g. the fleshy, trilobate metatarsal dorsal tip) and are indisputably monophyletic (Moradmand et al., 2014); except for the sparianthines (first split in the family), all the rest have a unique tapetum for acute night vision, as a shiny, regularly perforated plate (Nørgaard et al., 2008). Phylogeny within the family has been investigated using DNA sequences (Agnarsson and Rayor, 2013; Moradmand et al., 2014) and morphology (Rheims, 2007; unpublished thesis); although our sample of 12 representatives is not very extensive, we recover the Heteropodinae and Deleninae with strong support (Fig. 6). Morphology places Sparassidae among the Dionycha (Ramírez, 2014) but molecular data are ambiguous and to date there is no clear association with other families, Dionycha or not; Moradmand et al. (2014) found sparassids near the base of the RTA clade, far from other Dionycha, a result mirrored by Agnarsson et al. (2013). Sparassidae, comprising 12 exemplars in our analysis, are recovered with high support. Unconstrained versions of our analyses occasionally grouped Sparassidae with Amaurobiinae (Amaurobiidae), but with weak support. In our constrained analysis, Sparassidae are possibly related to the combined OC clade and Dionycha, although this has very weak support as well. Sparassid placement remains a goal for future studies.

Oval Calamistrum clade and Dionycha

Molecular, morphological and total evidence analyses agree on associating the venerable Dionycha, or two-clawed spiders, with a more recently discovered clade (Griswold, 1993) characterized by a calamistrum with several rows of setae, typically forming a patch, hence the Oval Calamistrum clade. These spiders have numerous tarsal and metatarsal trichobothria, sharpening their vibration detection, most have extensive scopulae at least on the forelegs and usually claw tufts for feet adherence; and several clades have remarkable specializations of the eyes as befits fast moving, visually aware predators. Each clade has good support, i.e. the OC Clade and the Dionycha, and their sister group status is strongly supported (Fig. 6); these higher groups are also obtained in the transcriptomic analysis of Garrison et al. (2016), but we obtain higher support values with our target genes without applying a constrained skeleton tree (see Figs S6 and S7). This may be related to the position of Homalonychidae, which we believe is an artefact of the TR analysis (see above).

The OC clade

Phylogenetic studies (e.g. Griswold, 1993) have associated two remarkable morphologies: a cribellum comprising several lines or a patch of modified setae and an autospasy joint through the bases of the tibia of males ("male tibial crack"). A series of studies based on morphology grouped the Lycosoidea, including Lycosidae, Pisauridae, Oxyopidae and Ctenidae, with the less known Trechaleidae, Senoculidae and even the cribellate Psechridae, Tengellidae, Zorocratidae and Zoropsidae (see Raven and Stumkat, 2005; Piacentini et al., 2013). A recent total evidence phylogeny (Polotow et al., 2015) differs in some details from our tree: the findings of Polotow et al. (2015) are used as the basis for our classification here.

The Udubidae are well supported (Fig. 6); our exemplars comprise *Raecius* from Africa and two species of *Uduba* and three of *Zorodictyna*, all from Madagascar. For the Zoropsidae, we found good support for several of the subfamilies as found in Polotow et al. (2015), but the family as a whole fluctuates across analyses (Fig. 6). The ecribellate Griswoldiinae, *Griswoldia* and *Phanotea*, from South Africa ally with strong support. *Tengella*, *Zorocrates* and *Liocranoides* unite as Tengellinae with strong support; *Kilyana* and *Uliodon* unite as Uliodoninae, again with high support, to which are allied *Austrotengella*, forming a moderately supported Australia and New Zealand clade. The

analyses are unstable for the relationships among these three subfamilies, the South American *Ciniflella* and *Zoropsis*, and in some of them Ududidae are nested within Zoropsidae, although with negligible support. This extends to all the branches near the base of the OC clade.

Ctenidae are a large, mainly tropical family that has been persistently hard to circumscribe. Griswold (1993) made the first quantitative attempt using a few exemplars, and the first extensive phylogeny was produced by Silva-Dávila (2003). Polotow et al. (2015) provided the first analysis including sequence data and morphology. We find a core Ctenidae of *Anahita*, *Ctenus* and *Phoneutria* grouped with high support (Fig. 6). Ctenidae continues to be a problematic taxon. Polotow et al. (2015) solved some problems by revealing that *Vulsor*, *Viridasius* and some other genera from Madagascar are not ctenids at all but belong among the Dionycha as family Viridasiidae, a result corroborated here (see below). Other genera traditionally placed in Ctenidae also fall outside this family. The model genus *Cupiennius* here allies with Trechaleidae with good support, and these together ally with the Lycosidae, again with strong support. This is similar to the result from Polotow et al. (2015), with *Cupiennius* allied to Lycosidae and a paraphyletic Pisauridae. *Ancyclometes bogotensis* sits alone as sister to the higher Lycosoidea, but with low support; *Ancylometes* placement is unsolved here, except as Lycosoidea, and its affinities remain another goal for future studies.

The wolf spiders (Lycosidae), fishing and nursery web spiders (Pisauridae) and lynx spiders (Oxyopidae) are well known Lycosoidea. Most are cursorial hunters relying on their excellent eyesight to find prey, but at least some members of each family construct sheet webs, which may have evolved in parallel (e.g. Murphy et al., 2006). Lycosidae, represented by 17 exemplars, are recovered with good support and in turn are related with the clade *Trechaleoides* (Trechaleidae) plus *Cupiennius* ("Ctenidae") (Fig. 6). Sister group to this clade, with high support, we have Pisauridae, with low support, which may be divided into three subfamilies, each with high to good support: Halinae, comprising *Hala* and *Tolma*; Dolomedinae, comprising *Bradystichus* and *Dolomedes*; and Pisaurinae, represented here by *Dendrolycosa*, *Eurychora*, *Paracladycnis*, *Pisaura* and *Nilus*.

The East Asian Psechridae are monophyletic only in some of our analyses, although with weak support, and usually ally with Thomisidae (Fig. 6). A grate-shaped tapetum and oval calamistrum place them in the OC Clade (Homann, 1971; Griswold, 1993; Griswold et al., 1999, 2005; Agnarsson et al., 2012), but psechrids possess a bizarre combination of characters: true claw tufts in addition to a third tarsal claw at all life stages. All psechrids hang from cribellate sheet webs (Robinson and Lubin, 1979; Griswold et al., 2005: fig. 208A, B, D, E). Psechridae monophyly and placement deserve further study. Male genitalia and adult web types differ greatly. Psechrid placement was also dubious for Polotow et al. (2015), with their exemplar *Psechrus* placed within a paraphyletic Ctenidae, far from the Thomisidae. The more detailed analysis of Bayer and Schönhofer (2013) also obtained low support, if any, for the monophyly of psechrids.

Crab spiders (Thomisidae) are well represented in our analysis with 44 terminals (Fig. 6). All thomisids, except *Borboropactus*, group with good support; our two *Borboropactus* join these with weaker support, and then only in the BI, ML and C-ML analyses, resembling the results of Benjamin et al. (2008). We prefer to keep the more traditional Thomisidae *sensu lato* with weak support, but our results are also compatible with the split of a robust Thomisidae *sensu stricto* and a separate Borboropactidae as proposed by Wunderlich (2004). We also obtain a strongly supported and robust *Thomisus* group, including all genera with few or no cheliceral teeth, also including the bird-dropping genus *Phrynarachne* and the ant-specialists Aphantochilinae as obtained by Benjamin (2011). Our resolution inside Aphantochilinae is slightly different from the one obtained by Teixeira et al. (2013) using morphological data, but the conflicting clades are not strongly supported in either analysis. Of the thomisids retaining several cheliceral teeth ("stephanopines"), we obtain a lengthy multinode grade separated by branches with weak support. Homann (1971) suggested thomisid affinity to Lycosoidea based on their eye structure (a grate-shaped tapetum as in lycosoids), but Griswold (1993) discounted Homann's opinion. Sequence data settled the placement of crab spiders among lycosoids (Bayer and Schönhofer, 2013; Polotow et al., 2015), while the morphological data were slightly in favour of dionychans (Ramírez, 2014). Here, our data place Thomisidae firmly among the Lycosoidea.

In addition to the above stated problems with ctenid circumscription, the families Senoculidae and Oxyopidae are also problematic (Fig. 6). Polotow et al. (2015) found a monophyletic Oxyopidae, not surprising given the distinctive eye pattern and spinose legs of the lynx spiders. Senoculidae (the sole genus *Senoculus*) emerged from a long branch within Zoropsidae in Polotow et al. (2015), a dubious result and one different from our current analysis. Here, *Senoculus* is allied to some Oxyopidae, a result that harkens back at least to Griswold (1993). Several of our analyses find Oxyopidae diphyletic. Each clade (*Tapinillus* plus *Peucetia* and *Oxyopes* plus *Hamataliwa*) is recovered with high support, but these and *Senoculus* combine in different ways and with other lycosoid branches, always with weak support. It is possible that the long branch of

Senoculus is responsible for instability in the higher lycosoids.

Dionycha

We obtained a relatively robust Dionycha with moderate support, without the use of the backbone constraint (Figs 7 and 8). Some of the larger clades within dionychans are quite unexpected, and we are cautious in their interpretation. Three main clades compose dionychans in our tree: (A) Prodidomidae *sensu stricto* (see below) (Fig. 7); (B) a well-supported clade of Gnaphosoidea *sensu lato* (herein referred to as Dionycha part A), for lack of a better name, roughly equivalent to the morphology-based groupings of gnaphosoids delineated by Platnick (2002) or the Claw-Tuft Clasper and the Oblique Median Tapetum clades (proposed by Ramírez, 2014) (Fig. 7); and (C) a strongly supported large clade (herein referred to as Dionycha part B) that includes corinnids, jumping spiders and miturgids, among others (Fig. 8). The latter two clades are united with good support.

Prodidomidae

The first and surprising split of dionychans is the Prodidomidae *sensu stricto*, containing three genera of Prodidominae (*Prodidomus, Austrodomus* and *Neozimiris*) and three of Theuminae (cf. *Tricongius* sp. Argentina NP18-MR16, *Lygromma* and *Chilongius*), all with high support. The bizarre Australian Molycriinae, here represented by three species of *Molycria* and *Myandra*, fall distantly from other prodidomids, among other gnaphosoid-like taxa separated from Prodidomidae *sensu stricto* by several branches with high support; molycriines have extremely long ALS placed anteriorly, far removed from the other spinnerets (Platnick, 1990; Platnick and Baehr, 2006) (Fig. 7). We defer taxonomic action until other prodidomids are more adequately studied, especially *Zimiris*, which has an intermediate morphology between prodidomines and molycriines (Platnick and Penney, 2004), and is also bearer of a family-level group name.

Dionycha part A

This large clade includes the gnaphosoids, Trachelidae, Phrurolithidae, members of the poorly defined "Liocranidae" and, most surprisingly, Anyphaenidae plus Clubionidae (Fig. 7). The linking of these last two families in a group confirms Platnick's (1990) suspicions due to their common absence of cylindrical gland spigots, but their inclusion among "gnaphosoids" is unexpected. The North American liocranid *Apostenus* serves as a link between these two families and the rest, in a well-supported clade.

Clubionidae

We obtain a strongly supported core Clubionidae except for the American *Elaver*, which group with Anyphaeninae with low support (Fig. 7); we believe that this is an artefactual result, as the DO analysis obtains a monophyletic Clubionidae, and *Elaver* have many morphological characters in common with clubionines (Ramírez, 2014), but a basal placement in the family seems plausible, as it is the only genus of clubionids that retains a median apophysis on the male palp (Saturnino and Bonaldo, 2015).

Anyphaenidae

We obtain the family as strongly supported mirroring the results of Labarque et al. (2015), with a well-supported Anyphaeninae and Amaurobioidinae, and *Josa* as a basal split in Amaurobioidinae (Fig. 7). Our larger sample of outgroups allowed the detection of a remarkable morphological convergence in the Chilean *Malenella nana*, the sole representative of Malenellinae, hereby transferred to Macrobuninae (Amaurobiidae).

Trachelidae

We obtain trachelids together but with weak support, probably due to two terminals floating nearby through the different analyses; one of them is *Cithaeron*, the only representative of Cithaeronidae, and the other is an unidentified Liocranidae from the Dominican Republic (Fig. 7). We obtain the minute soil dweller *Orthobula* deep inside Trachelidae, a possibility considered by Ramírez (2014) as suboptimal but still plausible; a re-examination of the foot morphology of *Orthobula calceata* revealed that they have the claw lever file projections interlocking with the claw tuft bases, uniquely found in some trachelids (Ramírez, 2014: character 171 and fig. 76D). With this evidence, we thus transfer the genus *Orthobula* from Phrurolithidae to Trachelidae.

Phrurolithidae

We obtained strong support for the family after the removal of *Orthobula* to Trachelidae, although our sampling is limited to two genera from North America and South East Asia (*Scotinella* and *Otacilia*, respectively). We confirm also that the *Teutamus* group, here represented by *Teutamus* and *Sesieutes* and joined with high support, are not phrurolithids, although its family association remains to be solved with a better sampling (Fig. 7).

Liocranidae

We were unable to get suitable samples of the South European *Liocranum*. Of our five representatives, one

is very unstable (Liocranidae sp. Dominican Republic MR160), two are species of the North American *Apostenus*, linked with good support to Anyphaenidae plus Clubionidae, and two are species of the Malagasy *Donuea*, which remain mysterious and only loosely associated to a few rogue terminals in Dionycha part B. Liocranids are poorly defined and are a target for future research (Fig. 7).

Gallieniellidae, Trochanteriidae and Lamponidae

We obtain a core group of the Malagasy *Gallieniella* and *Legendrena* with strong support (Fig. 7), but the Australian gallieniellids *Neato* and *Meedo* are grouped, also with high support, with five Australian trochanteriids (*Trachycosmus*, *Desognaphosa*, *Rebilus*, *Platorish* and *Morebilus*). These trochanteriids are in turn isolated from other Australian (*Tinytrema*), American (*Doliomalus*) and South African (*Platyoides*) genera placed in Trochanteriidae. Most trochanteriids are extremely flat bark-dwellers, but this is a syndrome that has occurred many times in spider phylogeny producing remarkable convergences, including the gnaphosid *Hemicloea* (see below). Ramírez (2014) already detected at least two unrelated groups of "trochanteriids" using morphological data. Our results are in partial agreement with this, in having the Australian trochanteriids in a basal split, and the African and South American genera more closely associated to Gnaphosidae, but otherwise gnaphosoids are quite mixed up. This is another target of future research, especially after the name-bearer genus *Trochanteria* is better studied. Our three lamponid representatives (*Lampona*, *Centrothele* and *Asadipus*) fall nearby but not together.

Ammoxenidae

We did not retrieve the South African ammoxenids *Rastellus* and *Ammoxenus* in a monophyletic group [Ramírez (2014) did not find morphological support for ammoxenid monophyly either], but obtain them nested within gnaphosids, together with *Eilica* and *Asemesthes* although with weak support (Fig. 7). This is biologically interesting; *Asemesthes* are sand-dwelling spiders, as are *Rastellus* and *Ammoxenus*, and *Eilica* are specialized feeders on ants, while *Rastellus* and *Ammoxenus* specialize on termites.

Gnaphosidae

We included 14 genera placed in Gnaphosidae, with a wide geographical and morphological breadth (Fig. 7). Our results are daunting, as they are all involved in weakly supported, unstable groups, mixed with other gnaphosoid families. The three *Hemicloea* species, all flat bark dwellers from Australia, are joined with moderate support with *Intruda*, a typical gnaphosid from Australasia, thus confirming the placement suggested by their gland spigot morphology (Platnick, 1990). It seems that Gnaphosidae will have to be profoundly reorganized, but this will have to wait for a better taxon and character sampling. A comprehensive morphological phylogenetic assessment of gnaphosids and their kin is underway (G. Azevedo, pers. comm.).

Dionycha part B

This clade includes the Salticidae, Philodromidae, Eutichuridae, Miturgidae, Corinnidae, Selenopidae, Viridasiidae and the new family Xenoctenidae. The group is strongly supported and robust, even if not constrained by the transcriptomic backbone (only represented by the salticid *Habronattus* in the study of Garrison et al., 2016). The internal relationships among families have, however, weak support and are unstable (Fig. 8).

Salticidae

Jumping spiders are well supported and robust (Fig. 8). Our results agree in general with those of Maddison and collaborators for the family (see Maddison et al., 2014, 2016; Maddison, 2015), using a larger taxon sampling and more markers. The three subfamilies Lyssomaninae, Onomastinae and Asemoninae are joined in an unstable group with low support. The Spartaeinae and a clade of Hisponinae plus Salticinae are strongly supported, although we did not recover the Hisponinae, probably because of shallow taxon sampling (*Hispo* joins the *Salticinae*, leaving *Massagris* behind). The sister group to salticids is, unfortunately, not solved by our analyses and will remain a subject of future studies.

Philodromidae

The family is strongly supported and robust (Fig. 8). We recover the tribe Thanatini with good support, represented by *Tibellus* and *Thanatus*, sister to a group of all other philodromids with moderate support, but this is unstable and does not agree well with the morphological analysis of Muster (2009). The two Hawaiian endemics *Pedinopistha* and *Pagiopalpus* are together with good support, thus suggesting a single colonization event to the islands.

Eutichuridae

A core Eutichuridae is retrieved with strong support and robustness; the entire family including *Eutichurus*,

however, is only retrieved in the BI analysis and the MUSCLE alignments (EW, IW), with very low support; in DO and ML *Eutichurus* floats around a few rogue terminals of unclear affiliation (see the *Pronophaea* group). Four species of *Cheiracanthium* group with strong support (Fig. 8).

Xenoctenidae

We reproduce previous morphological results of Silva-Dávila (2003) and Ramírez (2014) by obtaining a strongly supported clade of three lycosoid-looking genera with a distal division in the tegulum of the male copulatory bulb (*Xenoctenus*, *Odo*, *Paravulsor*). These were previously assigned to Zoridae and Miturgidae for lack of a better affiliation (see the *Xenoctenus* group in Ramírez, 2014). This analysis has a wide taxonomic coverage allowing us to formalize the new family here (Fig. 8).

Viridasiidae

A core Viridasiidae is obtained with strong support, and resting among the Dionycha, confirming the results of Polotow et al. (2015) for this recently established Malagasy family (Fig. 8). We included an undescribed genus from Madagascar (Viridasiidae sp. Madagascar CG28) that is probably allied to the family as well.

Selenopidae

The flatties, or Selenopidae, are well supported, with two to three successive basal splits from Africa and Madagascar (*Anyphops*, *Hovops*, *Garcorops*); the remaining terminals in our analysis are three American *Selenops* species (Fig. 8). This is in agreement with the much more detailed findings of Crews and Gillespie (2010).

Miturgidae

The family is retrieved with weak support, probably because of several rogue terminals of unclear association (see below). Two genera of former zorids (*Zora*, *Argoctenus*) plus a zorid-like undescribed genus (Miturgidae sp. Queensland MR629) are grouped as sister to three Australian miturgines (*Miturga*, *Mituliodon*, *Nuliodon*). The American miturgines *Teminius* and *Syspira* are on a basal split. According to our results, the enigmatic African genus *Parapostenus* could be a miturgid or a viridasiid (ML and BI analyses, respectively) (Fig. 8).

Corinnidae

We included a good breadth of Corinnidae (21 representatives of 20 genera), and recovered the family as a group, confirming its separation from the Trachelidae and Phrurolithidae as proposed by Ramírez (2014). Corinnidae are obtained with weak support; the subfamily Castianeirinae, well known from the many ant-mimicking genera, is moderately supported, and the recently described genus *Allomedmassa* is suggested as its sister group. Although the details differ, we confirm the findings of Haddad (2013) that the non-ant-mimicking castianeirines (*Copa* sp. MR46 and *Echinax*, in our dataset) have derived from an ant-mimicking ancestor through loss of myrmecomorphy (Fig. 8).

The "Pronophaea" group

A few corinnid-looking genera retaining a median apophysis on the male copulatory bulb were loosely grouped in the *Pronophaea* group by Ramírez (2014), although it is not clear that they are all closely related to each other. In that study, it was rejected that they were basal corinnids, as proposed before by Bonaldo (1997) and Ramírez et al. (2001). We include here two species of *Pronophaea*, two of *Donuea*, and one each of *Olbus* and *Carteronius*. The congeners grouped with high support, but besides a weak but consistent grouping of *Donuea* with *Pronophaea* (all analyses except EW) and sometimes also *Olbus* (BI), our study only indicates that they belong to the Dionycha part B (Fig. 8); solving their affiliation remains a future goal.

Taxonomy

Family Agelenidae C. L. Koch, 1837

Type genus *Agelena* Walckenaer, 1805 (type species *Araneus labyrinthicus* Clerck 1757).

Diagnosis. RTA clade spiders with a divided colulus, i.e. with two separate patches of hairs, and, in most species, PLS with the apical segment pointed and greater than or equal to the length of the basal; the cribellate genus *Tamgrinia* may be recognized by details of the genitalia, as presented by Wang (2000).

Composition. The WSC (2016) lists 73 genera and 1195 species in this family. As discussed below, it is unlikely that 13 genera and nearly 100 species endemic to Australia and New Zealand truly belong here, but even discounting these, the more than 1000 species distributed across Africa and the Holarctic region make this one of the largest families of spiders.

Remarks. Lehtinen (1967) noted that the presence of a divided colulus, i.e. with two separate patches of hairs, allows recognition of the family. This bifid

colulus serves as an agelenid synapomorphy (Lehtinen, 1967; Spagna and Gillespie, 2008; J. Miller et al., 2010) for the taxa represented in this study and include Ageleninae, Textricinae, Tegenariinae and Coelotinae. As pointed out by J. Miller et al. (2010) and in this study, at least the New Zealand *Neoramia*, a cribellate "agelenid" exemplar (Griswold et al., 2005; Blackledge et al., 2009), is not an agelenid; other austral agelenid genera may also be misplaced. At least 13 genera, most described by Forster and Wilton (1973), are recorded as endemic to New Zealand (WSC, 2016). These authors note that "the ecribellates ... do not possess a divided colulus. The colulus is then a more or less triangular structure, and the hairs are not separated into two bunches" (Forster and Wilton, 1973: 11). Absence of the agelenid synapomorphy, plus placement elsewhere by our study for some of the New Zealand genera, e.g. *Neoramia* to Stiphidiidae, *Orepukia* to Cycloctenidae, suggests that none of the New Zealand genera may belong in true Agelenidae. We defer transfer of these genera to other families until they can be studied in more detail, and preferably with molecular data.

Family Amaurobiidae Thorell, 1870 (**new circumscription**)

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

Diagnosis. This diverse and probably non-monophyletic taxon is difficult to diagnose. All are entelegyne Araneomorphae in the RTA clade, and most have male palpal tibial processes in addition to the RTA (Griswold et al., 2005). Amaurobiinae have a "pseudocalamistrum", a row of prominent setae adjacent and parallel to the calamistrum (Lehtinen, 1967; Jocqué and Dippenaar-Schoeman, 2006: fig. 8f). Macrobuninae have several teeth on the retromargin of the cheliceral fang furrow, reduced anterior median eyes in most species, and many have enlarged male palpal tibiae, some with an internal gland and/or a tibia/cymbium stridulation mechanism. The monotypic subfamilies Arctobiinae and Ovtchinnikoviinae may be diagnosed by characters of the included genus of each. Altellopsinae might be recognized by characters of the female genitalia (Lehtinen, 1967: 334), although this group remains poorly known.

Composition. Five subfamilies remain in Amaurobiidae: Altellopsinae (South America), Amaurobiinae (Holarctic), Arctobiinae (Holarctic), Macrobuninae (Africa, Australia, South America and Western North America) and Ovtchinnikoviinae (western Palearctic).

Remarks. Amaurobiidae remain problematic in spite of continuing phylogenetic and taxonomic progress. Of the nine subfamilies (Altellopsinae, Amaurobiinae, Desinae, Macrobuninae, Matachiinae, Metaltellinae, Phyxelidinae, Rhoicininae and Stiphidiinae) listed by Lehtinen (1967: 321), only three remain: Altellopsinae, Amaurobiinae and Macrobuninae. To these have subsequently been added Arctobiinae, Midgeeinae and Ovtchinnikoviinae. The enigmatic Altellopsinae Lehtinen, 1967 is too poorly known to diagnose or even confirm as an amaurobiid, whereas affinities of the Arctobiinae and Ovtchinnikoviinae remain to be tested: we provisionally leave them here for lack of a better alternative. The Macrobuninae are discussed in detail below. Our results suggest that some of Forster and Wilton's (1973) austral amaurobiid genera are misplaced: we move *Pakeha* and *Paravoca* to Cycloctenidae and *Poaka* to the Desidae. *Ischalea* (from Stiphidiidae) is transferred to Desidae Ischaleinae: our phylogeny places *Ischalea* within Desidae near Metaltellinae. Davies (1990: 102) suggested that *Ischalea*, *Bakala* and *Manjala* form the Ischaleinae. Although the latter genera are listed in Amaurobiidae (WSC, 2016) we transfer all to Desidae Ischaleinae. *Midgee* and *Jamara* [placed in Amaurobiidae, Midgeeinae by Davies (1995: 93)] are here transferred to Toxopidae Toxopinae. Pending resolution of the taxonomic situation for Macrobuninae, there may be no true amaurobiids native to the southern hemisphere. See below for a discussion of Macrobuninae, including the new synonyms Tasmarubriinae (Amphinectidae), Malenellidae (Anyphaenidae) and Chummidae.

Subfamily Macrobuninae Lehtinen, 1967

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

Malenellinae Ramírez, 1995. Type genus *Malenella* Ramírez, 1995 (Type species *Malenella nana* Ramírez, 1995). **New synonymy.**

Chummidae Jocqué, 2001. Type genus *Chumma* Jocqué, 2001 (type species *Chumma inquieta* Jocqué, 2001). **New synonymy.**

Tasmarubriinae Davies, 2002. Type genus *Tasmarubrius* Davies, 1998 (type species *Rubrius milvinus* Simon, 1903). **New synonymy.**

Diagnosis. Entelegyne RTA clade spiders with a single row of tarsal trichobothria distinguished by the presence of denticles on the cheliceral retromargin (Almeida-Silva et al., 2015: fig. 2E), an oblique cheliceral groove (e.g. Griswold et al., 2005: 231; fig. 130G, I) and reduced anterior median eyes (Almeida-Silva et al., 2015: figs 1A, 2A–B).

Composition. Macrobuninae comprise taxa from Australia, western North America, South Africa and South America. Currently included are *Anisacate*, *Auximella*, *Callevopsis*, *Cavernocymbium*, *Chresiona*, *Chumma*, *Emmenomma*, *Hicanodon*, *Livius*, *Macrobunus*, *Malenella*, *Naevius*, *Neoporteria*, *Obatala*, *Parazanomys*, *Pseudauximus*, *Retiro*, *Rubrius*, *Tasmarubrius*, *Tasmabrochus*, *Teeatta*, *Urepus*, *Yupanquia* and *Zanomys*.

Remarks. Lehtinen (1967: 333) recognized the distinctness of a group of genera related to *Macrobunus*. Compagnuci and Ramírez (2000) discovered a gland in the male palpal tibia of *Anisacate*, *Emmenomma* and *Naevius*, and Griswold et al. (2005) noted a stridulatory area on the retrobasal area of the cymbium of *Anisacate*, *Emmenomma*, *Macrobunus* and *Rubrius*, comprising characters that may be useful in outlining the phylogeny of the group. J. Miller et al. (2010) treated the macrobunine *Chresiona* in a molecular phylogeny and found *Chresiona* to fall far from the core amaurobiids, represented by *Amaurobius*, *Callobius* and *Pimus*, and also found the South African *Chumma* and North American *Cavernocymbium* and *Zanomys* closely allied to *Chresiona*. Although noting the distinctness from the core Amaurobiidae, no taxonomic changes were made. *Malenella*, formerly Anyphaenidae, and *Tasmarubrius*, formerly Amphinectidae, are newly transferred here. Macrobunine placement and taxonomy are currently under study by Almeida-Silva (pers. comm.), who has provided diagnostic characters and putative synapomorphies (Almeida-Silva, 2013; unpublished thesis; Almeida-Silva et al., 2014, 2015). Macrobuninae is provisionally kept in Amaurobiidae.

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

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

Cryphoecinae Lehtinen, 1967. Type genus *Cryphoeca* Thorell, 1870 (type species *Tegenaria silvicola* C. L. Koch, 1834). **New synonymy.**

Diagnosis. Araneomorphs with three claws and branched tracheae; most have an apophysis on the male palpal patella in addition to the RTA.

Composition. This family comprises several genera from the Holarctic, and especially genera endemic to North America. The family Cybaeidae has been revised in North America (Bennett, 1991; unpublished thesis; Bennett et al., 2016).

Remarks. Our exemplars include *Cybaeus* and *Calymmaria*, the latter transferred here from Hahniidae. Closely related to *Cybaeus* are *Cybaeina*, *Cybaeota* and *Cybaeozyga* (Lehtinen, 1967; Bennett, 1991; unpublished thesis). *Calymmaria* has a peculiar form of autospasy, with a break through the leg patellae: this was recognized by Roth and Brame (1972), who considered this a synapomorphy for a group of several poorly known genera. Following their suggestion, we include other genera with patellar autospasy: *Cryphoeca*, *Ethobuella* and *Willisius* (from Hahniidae) and *Blabomma* and *Yorima* (from Dictynidae) are here transferred to Cybaeidae. Based on our results and those of J. Miller et al. (2010) and Spagna et al. (2010), we transfer *Argyroneta* from Cybaeidae to Dictynidae.

*Family Cycloctenidae Simon, 1898 (***new circumscription**)

Type genus *Cycloctenus* L. Koch, 1878 (type species *Cycloctenus flaviceps* L. Koch, 1878).

Diagnosis. Araneomorphae with three claws, simple posterior tracheae, a complex RTA and a hyaline conductor on the male palp. At least *Cycloctenus* and *Toxopsiella* have a strongly recurved anterior eye row, and *Cycloctenus* a laterigrade habitus, resembling Ctenidae.

Composition. All the classic and newly assigned genera occur in New Zealand and Australia.

Remarks. Our exemplars comprise the classic (Lehtinen, 1967; Forster and Wilton, 1973) cycloctends *Cycloctenus* and *Toxopsiella*. To these we add *Orepukia* (from Agelenidae) and *Pakeha* and *Paravoca* (from Amaurobiidae). There may be other taxa currently placed in Agelenidae and Amaurobiidae that more appropriately conform to Cycloctenidae.

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

Type genus *Desis* Walckenaer, 1837 (type species *Aranea maxillosa* Fabricius 1793).

Amphinectidae Forster and Wilton, 1973. Type genus *Amphinecta* Simon, 1898 (type species *Amphinecta decemmaculata* Simon, 1898). **New synonymy.**

Diagnosis. Araneomorphae with three claws, tarsal trichobothria, cribellate or ecribellate. Our phylogenetic concept brings together a diverse set of spiders, including some with simple and some with complex, branched posterior tracheae. The male palpal tibia of most included taxa has a complex RTA, with several separate processes (Matachiinae) or separate distal and proximal processes (Metaltellinae and many Amphinectinae). The included subfamilies have strong diagnostic characters, e.g. the peculiar palpal bulbs of

metaltellinaes and matachiines and narrowed piriform gland spigot field on the ALS of Porteriinae.

Composition. In addition to *Desis*, which occur worldwide on tropical seacoasts, our Desidae occur in Australia and New Zealand and nearby parts of Asia and in southern South America. We recognize *Desis* and the subfamilies Metaltellinae, Matachiinae, Amphinectinae, Ischaleinae and Porteriinae (**new rank**).

Remarks. Our dataset includes numerous exemplars that we group together in our enlarged Desidae. In addition, we follow the suggestions of authors to include presumed close relatives of our exemplars. *Desis*, which branches basally in our enlarged Desidae, is the most divergent genus: we could establish it as a monotypic family and retain (Amphinectidae) or establish family rank for the several related subfamilies, e.g. "Metaltellidae" and "Porteriidae", but the low support values for the basal branches and numerous additional taxa not treated give us pause, and we feel the most cautious and conservative approach is to recognize a large, polythetic Desidae. On our tree, *Desis* is close to *Poaka*, which is transferred from Amaurobiidae to Desidae. Our exemplars include the former amphinectids *Amphinecta*, *Mamoea*, *Maniho*, *Paramamoea* and *Rangitata*; along with *Maniho*, as suggested by Forster and Wilton (1973), these are placed in Desidae Amphinectinae. Our phylogeny also places *Barahna* in Desidae Amphinectinae, transferred from Stiphidiidae. Our exemplars of Amphinectidae Metaltellinae (*Calacadia* and *Metaltella*) form a group transferred to Desidae Metaltellinae; to these we add *Austmusia*, *Buyina*, *Cunnawarra*, *Jalkaraburra*, *Keera*, *Magua*, *Penaoola* and *Quemusia*, following the classification of Davies (1998). *Ischalea* falls near the metaltellines: we transfer this genus from Stiphidiidae, along with *Bakala* and *Manjala* from Amaurobiidae, to comprise Desidae Ischaleinae (Davies, 1990: 102). Our exemplars *Goyenia*, *Badumna*, Matachiinae sp. Queensland CG275 and *Paramatachia* form a group; to these we add *Matachia*, *Notomatachia* and *Nuisiana*, following Forster (1970) and Griswold et al. (1999, 2005), to comprise the Desidae Matachiinae. Finally, to the Chilean desid genus *Porteria*, we add *Baiami*, *Cambridgea*, *Corasoides* and *Nanocambridgea* from Stiphidiidae to comprise Desidae Porteriinae, a group first recognized by Lehtinen (1967, as Porteriini) and that is currently under study (Morrill, 2014; unpublished thesis).

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

Type genus *Dictyna* Sundevall, 1833 (type species *Aranea arundinacea* Linnaeus 1758).

Diagnosis. Araneomorphae with three claws and branched median tracheae; cribellate or ecribellate. All have a characteristic male palpus: the conductor is fleshy, and embraces the embolus, and the conductor apex extends proximally along the retrolateral side of the cymbium.

Composition. A worldwide taxon of cribellate web builders; ecribellates appear to be associated with water or former wet places, i.e. *Argyroneta*, *Saltonia* and *Paratheuma*.

Remarks. The family Dictynidae has long been a receptacle for a miscellany of cribellate and ecribellate RTA clade spiders. Cribellate Dictynidae are easy to recognize and seem to be a natural group: all have the characteristic male palp, and many males have chelicerae that are concave medially. With our transfer of many ecribellates to other families, e.g. of *Blabomma* and *Yorima* to Cybaeidae, Dictynidae become more consistent and the remaining ecribellate genera also have the characteristic male palp. Spagna and Gillespie (2008), J. Miller et al. (2010) and Spagna et al. (2010) have explored the molecular phylogenetics of the RTA clade and our results corroborate many of theirs. We find support for inclusion of *Saltonia* and *Paratheuma*, and based on our results and those of J. Miller et al. (2010) and Spagna et al. (2010), *Argyroneta* is transferred from Cybaeidae to Dictynidae. The cribellates *Mexitlia*, *Dictyna* and *Mallos* fall in the Dictynidae; *Lathys* also groups here but with little support.

Family Hahniidae Bertkau, 1878 (**new circumscription**)

Hahniidae Bertkau, 1878. Type genus *Hahnia* C. L. Koch, 1841 (type species *Hahnia pusilla* C. L. Koch, 1841).

Diagnosis. Araneomorphae with three claws, an RTA and in many species a process on the patella as well; typical Hahniinae have the spinnerets in one transverse row.

Composition. Hahniinae are worldwide; Cybaeolinae (*Cybaeolus*) are endemic to southern South America; *Cicurina* is Holarctic.

Remarks. Our dataset includes the hahniid exemplars *Hahnia* and *Neoantistea* (Hahniinae), *Cybaeolus* (Cybaeolinae) and *Calymmaria* (Cryphoecinae). We find that the Hahniinae and Cybaeolinae are valid members of Hahniidae, but that *Calymmaria*, along with *Cryphoeca*, *Ethobuella* and *Willisius*, must be transferred to Cybaeidae (see

above and J. Miller et al., 2010). *Cicurina*, also in our dataset, is transferred from Dictynidae to Hahniidae.

Family Pacullidae Simon, 1893 (**restored status**)

Type genus *Paculla* Simon, 1887 (type species *Phaedima granulosa* Thorell, 1881).

Pacullinae, Lehtinen, 1981.

Diagnosis. Ecribellate, three-clawed Synspermiata with six eyes, similar to Tetrablemmidae by the abdomen with dorsal and ventral scuta and laterally with thin, sclerotized strips or lines of platelets, distinguished from those by the much larger size (greater than 5 mm length), heavily rugose cuticle and by lacking a pair of large membranous receptacles in the female genitalia (Shear, 1978; Lehtinen, 1981).

Composition. Four genera, all from Southeast Asia: *Paculla*, *Perania*, *Lamania* and *Sabahya* (Lehtinen, 1981; WSC, 2016).

Remarks. Our matrix includes the paculline exemplars *Paculla* sp., *Lamania* sp. and *Perania nasuta*, which form a family group distinct from the tetrablemmines and sister to the Diguetidae within the "lost tracheae clade" (Diguetidae, Pacullidae, Plectreuridae and Tetrablemmidae).

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

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

Neolanidae Forster and Wilton, 1973. Type genus *Neolana* Forster and Wilton, 1973 (type species *Ixeuticus dalmasi* Marples, 1959). **New synonymy.**

Diagnosis. Three-clawed RTA clade araneomorphs with a simple posterior respiratory system of four tubes that may be cribellate or ecribellate; cribellates have PMS paracribellars with multiple shafts arising from single, enlarged bases. A comprehensive diagnosis is not yet possible, but potential diagnoses are made in the original descriptions of the subfamilies Borralinae, Kababinae and Neolaninae and by the characters of included genera.

Composition. Stiphidiidae *incertae sedis* comprise *Aorangia*, *Neoramia*, *Procambridgea* and *Stiphidion*; Neolaninae comprise *Marplesia* and *Neolana*; Borralinae comprise *Borrala*, *Couranga*, *Elleguna*, *Jamberoo*, *Karriella*, *Pillara* and *Therlinya*; Kababinae comprise *Carbinea*, *Kababina*, *Malarina* and *Wabua*.

Remarks. Lehtinen (1967: 331) placed the group as a subfamily of Amaurobiidae; Forster and Wilton (1973: 128) raised them to family. Our phylogeny suggests several changes in stiphidiid composition: *Neoramia* (from Agelenidae) and *Aorangia*, *Marplesia* and *Neolana* (from Amphinectidae) transferred to Stiphidiidae; *Baiami*, *Cambridgea*, *Corasoides* and *Nanocambridgea* transferred to Desidae Porteriinae, where they are closely related to *Porteria* (Morrill, 2014; unpublished thesis); *Ischalea* is transferred to Desidae Ischaleinae. Our matrix includes the *incertae sedis* genera *Aorangia*, *Neoramia*, *Procambridgea*, *Stiphidion*; *Marplesia* and *Neolana* from the Neolaninae; and *Therlinya* from the Borralinae. We use the discussion of Gray and Smith (2008) to place the other borraline genera, and also to associate Kababinae with Borralinae.

Family Tetrablemmidae O. Pickard-Cambridge, 1873 (**new circumscription**)

Type genus *Tetrablemma* O. Pickard-Cambridge, 1873 (type species *Tetrablemma medioculatum* O. Pickard-Cambridge, 1873).

Diagnosis. Ecribellate, three-clawed Synspermiata with six to no eyes, similar to Pacullidae by the abdomen with dorsal and ventral scuta and laterally with thin, sclerotized strips or lines of platelets, distinguished from those by the much smaller size (less than 3 mm length), smooth cuticle and by having a pair of large membranous receptacles in the female genitalia (Shear, 1978; Lehtinen, 1981).

Composition. Twenty-seven genera scattered across the tropical parts of the world: *Ablemma*, *Afroblemma*, *Anansia*, *Bacillemma*, *Borneomma*, *Brignoliella*, *Caraimatta*, *Choiroblemma*, *Cuangoblemma*, *Fallablemma*, *Gunasekara*, *Hexablemma*, *Indicoblemma*, *Lehtinenia*, *Maijana*, *Mariblemma*, *Matta*, *Micromatta*, *Monoblemma*, *Pahanga*, *Rhinoblemma*, *Shearella*, *Sinamma*, *Singalangia*, *Singaporemma*, *Sulaimania*, *Tetrablemma* (Lehtinen, 1981; WSC, 2016).

Remarks. Our matrix includes the tetrablemmine exemplars *Indicoblemma monticola*, *Tetrablemma thamin* and *Shearella browni*, which form a family group distinct from the pacullines and sister to the remaining families of the "lost tracheae clade" (Plectreuridae, Diguetidae and Pacullidae).

Family Toxopidae Hickman, 1940 (**restored status**)

Type genus *Toxops* Hickman, 1940 (type species *Toxops montanus* Hickman, 1940).

Toxopidae Hickman, 1940 (included in Desidae by Forster and Wilton, 1973).

Midgeeinae Davies, 1995 (included in Amaurobioidea). Type genus *Midgee* Davies, 1995 (type species *Midgee binnaburra* Davies, 1995). **New synonymy.**

Diagnosis. Three-clawed RTA clade cribellate (*Jamara*) or ecribellate Araneomorphae with highly branched posterior median tracheae. Toxopines are small spiders, many laterigrade, that have a T-shaped conductor on the male palp. Many have strongly recurved or procurved eye rows; at least *Midgee*, *Jamara* and *Laestrygones* have a stout seta on the anterior face of the paturon; *Laestrygones* and *Toxops* have a patch of scales anterior to the posterior tracheal spiracle. Myroines may have strongly procurved eye rows (*Myro* and *Ommatauxesis*); all have vulvae with slender, convoluted copulatory ducts.

Composition. Two subfamilies, Toxopinae (*Hapona*, *Jamara*, *Laestrygones*, *Lamina*, *Midgee*, *Toxops* and *Toxopsoides*) and Myroinae (*Gasparia*, *Gohia*, *Hulua*, *Neomyro*, *Myro*, *Ommatauxesis* and *Otagoa*), occur in Australia and New Zealand. *Myro* also occurs on subantarctic islands around the Southern Ocean.

Remarks. *Myro*, *Ommatauxesis* and *Otagoa* (all from Desidae) group together in our phylogeny, far from the taxa that we place in Desidae. *Gasparia* groups among the Desidae in the ML trees, but with myroines in most other analyses. Forster (1970) associated *Gasparia* with *Myro*, and we follow his suggestion. Forster (1970) also placed *Gohia*, *Hulua* and *Neomyro* near *Myro* (in Myroninae, sic.). *Gasparia*, *Gohia*, *Hulua*, *Neomyro*, *Myro*, *Ommatauxesis* and *Otagoa* (all from Desidae) are transferred to Toxopidae Myroinae. Our exemplars include *Toxops*, *Hapona*, *Laestrygones* and *Lamina*, which fall together in a group with the Australian amaurobiid *Midgee*. We transfer Midgeeinae (*Midgee* plus *Jamara*) from Amaurobiidae and *Hapona*, *Laestrygones*, *Lamina*, *Toxops* and *Toxopsoides*, all from Desidae, to Toxopidae Toxopinae.

Family Trachelidae Simon, 1897 (**new circumscription**)

Diagnosis. Trachelids are similar to prurolithids in having claw tufts arising from a non-articulated area of the distal tarsi, made of heavily folded setae, tarsal claws with a claw tuft clasper and reduced leg spination especially on posterior legs and dorsally on all femora, and lacking a median apophysis on the male copulatory bulb. Most trachelids (except *Orthobula*) can be distinguished by lacking a ventral distal hook on the male palpal femur. Most trachelids have also uniquely shaped bases of the claw tuft setae, in the form of rectangular blocks, and frequently the claw lever file projections interlock with the claw tuft bases. With a few exceptions such as *Orthobula* and *Spinotrachelas*, most of the trachelid species lack macrosetae altogether, and the males have leg cusples.

Composition. *Afroceto*, *Cetonana*, *Fuchiba*, *Fuchibotulus*, *Meriola*, *Metatrachelas*, *Orthobula*, *Paccius*, *Paratrachelas*, *Patelloceto*, *Planochelas*, *Poachelas*, *Spinotrachelas*, *Thysanina*, *Trachelas*, *Trachelopachys* and *Utivarachna*.

Remarks. *Orthobula* is transferred from Phrurolithidae to Trachelidae.

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

Diagnosis. Phrurolithids are similar to trachelids in having claw tufts arising from a non-articulated area of the distal tarsi, made of heavily folded setae, tarsal claws with a claw tuft clasper and reduced leg spination especially on posterior legs and dorsally on all femora, and lacking a median apophysis on the male copulatory bulb. They can be distinguished by having ventral modifications on the male palpal femur, especially a ventral median apophysis and usually a ventral apical hook. Phrurolithids (except *Drasinella*) have a globose, often flexible receptacle on the female internal genitalia, in addition to the primary and secondary spermathecae (this receptacle is also present in the trachelid *Orthobula*). Phrurolithids differ from most trachelids by having several pairs of ventral macrosetae on the anterior tibiae, and by lacking characters unique to trachelids (projections of the claw lever file interlocking with claw tuft bases, expanded bases of the claw tuft setae).

Composition. *Abdosetae*, *Dorymetaecus*, *Drassinella*, *Liophrurillus*, *Otacilia*, *Phonotimpus*, *Phrurolinillus*, *Phrurolithus*, *Phruronellus*, *Phrurotimpus*, *Piabuna*, *Plynnon* and *Scotinella*.

Remarks. *Orthobula* is transferred from Phrurolithidae to Trachelidae.

Family Xenoctenidae Ramírez and Silva-Dávila, new family

Type genus *Xenoctenus* Mello-Leitão, 1938 (type species *Xenoctenus unguiculatus* Mello-Leitão, 1938) by present designation.

Xenoctenus group, Ramírez, 2014.

Diagnosis. Xenoctenids are similar to viridasiids and some miturgids by having the eyes in two recurved rows and with grate-shaped tapetum in the indirect eyes, two claws and well-developed scopulae and

sometimes claw tufts, but can be distinguished by having a distal division in the tegulum of the male copulatory bulb, in the region where the embolus arises.

Composition. *Xenoctenus*, *Odo*, *Paravulsor* and *Incasoctenus*, all South and Central American.

Remarks. The group was already distinguished as deserving family-level status by Silva-Dávila (2003), and later confirmed by Ramírez (2014) as the '*Xenoctenus* group'; both authors identified the tegular distal division at the embolar base as a synapomorphy (see Ramírez, 2014: character 343). This analysis confirmed with high support that Xenoctenidae are members of Dionycha. The closer relatives to xenoctenids are, however, uncertain in this and previous analyses, but their monophyly is well supported by all these analyses.

Summary

The present paper is the culmination of years of intensive research on spider systematics and, although mainly based on the findings of the spider AToL project, also summarizes relevant findings from the last decade of systematic studies of that group. Our results reach far into the spider evolutionary tree and many branches are reorganized or newly discovered. We hope that these new insights on spider relationships will stimulate a plethora of follow-up studies on spider evolution and systematics, especially for the areas of the spider tree where we still have too little information to gain insight on taxonomic relationships. We also show the relevance of target gene approaches in the phylogenomics era and how both can be used to build on each other's findings. In our study, the unprecedented taxon sampling would have been very challenging in a phylogenomic framework whilst recent phylogenomic studies have been invaluable assets in improving our results.

Acknowledgements

This work was primarily supported by a grant from the United States National Science Foundation (NSF) (EAR-0228699—'Assembling the Tree of Life: Phylogeny of Spiders') awarded to W. C. Wheeler (P.I.) and J. Coddington (JC), G. Hormiga (GH), L. Prendini (LP) and P. Sierwald (PS) (co-P.I.s). JC acknowledges support from the NMNH Neotropical Lowlands Program, Small Grants Program and Biodiversity of the Guyanas Program, as well as the NSF grants DEB-9712353 (GH, P.I.; JC, co-P.I.) and DBI-0956426 (N. Davies, P.I.; G. Roderick, C. Meyer, JC and T. Orrell, co-P.I.s). Various aspects of this research in the GH Lab at GWU were supported by NSF awards DEB-0328644, DEB-1144492 and DEB-1457300 (to GH and Gonzalo Giribet), by NSF award DEB-0613928 (to N. I. Platnick (P.I.), R. Gillespie, CEG, GH, and PS (co-P.I.s)) and by three NSF REU supplementary grants. GH's stay at the Scharff's lab in the Zoological Museum (University of Copenhagen) was supported by a Villum Kann Rasmussen Fund, VELUX Visiting Professorship. Further support to GH for this project was provided by several awards from GWU. LL acknowledges the Cosmos Club Foundation Program of Grants-in-Aid to Young Scholars and a Weintraub Fellowship from The George Washington University. The participation in this project of F. Álvarez-Padilla, L. Benavides, S. Benjamin, D. Dimitrov and E. Hasan was made possible in part by support of The George Washington University and the aforementioned NSF awards to GH. F. Álvarez-Padilla acknowledges support from a scholarship from the Consejo Nacional de Ciencia y Tecnología of Mexico (CONACYT).

Aspects of this research conducted in the LP lab at the AMNH, including field collections that contributed material to the project, were supported by NSF awards DEB-0413453 (to LP and W. D. Sissom) and DEB-0640219 (to LP and P. E. Cushing), by a grant from the Richard Lounsbery Foundation (to R. DeSalle, LP and M. E. Siddall), and a Constantine Niarchos Expedition Grant (to LP). PS's fieldwork in South Africa and Myanmar was supported by Field Museum's Marshal Field Fund.

C. E. Griswold (CEG) and the CAS Arachnology Lab (L. Almeida-Silva, F. Álvarez-Padilla, J. Ledford, D. Silva-Davila, D. Polotow, F. Labarque, D. Ubick and H. Wood) acknowledge financial support from the CAS Exline-Frizzell Fund for Arachnological Research and CAS Lindsay Expedition Fund and by The Schlinger Foundation; D. Polotow is grateful for CNPq, Conselho Nacional de Desenvolvimento Científico e Tecnológico (PDE programme), D. Polotow and L. Almeida-Silva both acknowledge Bill and Maria Peck Fellowships (CAS); and J. Ledford, D. Silva-Davila, F. Álvarez-Padilla, F. Labarque and L. Almeida-Silva acknowledge Schlinger Chair of Arachnology Postdoctoral Fellowships from CAS. T. Szűts' participation was funded by a Marie Curie Intra European Fellowships (Life Sciences Panel, No. 025850) and he acknowledges support from the OTKA/NKFI 106241. Aspects of this research were supported by NSF grants: DEB-0072713 (to CEG and B. Fisher), DEB-9296271 (to CEG), DEB-0613775 (to NIP, CEG, GH, MJR) and BSI-0103795 (to Jablonski and Fritsch, P.I.s). Participation by undergraduate students (Robin Carlson, Joel Ledford, Hillary Guttman, Nibia Soto-Rolón, Christopher Vo, Vanessa Knutson, Jasper

Bash, Erika Garcia and Rachel Gibbs) in the CAS Arachnology lab was made possible by NSF BIR-9531307 (to R. Mooi, T. Gosliner and D. Kavanaugh, P.I.s). CEG also thanks Sarah Weigold and Meghan Culpepper for documenting morphology of selected taxa. M. J. Ramírez (MJR) and the MACN lab (C. Grismado, M. Izquierdo, F. Labarque, L. Piacentini) acknowledge financial support from CONICET and grants from FONCyT PICT 2011-1007, PICT-2007-01393, PICT 2003-14092, CONICET PIP 6502, PIP 2008-03209 and PEI 6558.

Aspects of this research in the Scharff lab (NS) at the Zoological Museum, University of Copenhagen, were supported by a grant from the Danish National Science Research Council (SNF21-02-0502). NS acknowledges travel grants for fieldwork in Thailand from DANIDA (Danish development cooperation), as well as from the Carlsberg Foundation (grant no. 0537/60) for fieldwork in Australia. Participation by undergraduate student Jesper Birkedal Schmidt in the NS lab was made possible by the above-mentioned grants.

Fieldwork was made possible thanks to the support of Andrés A. Ojanguren-Affilastro, Luis Compagnucci, Gonzalo Rubio and Ana Quaglino (Argentina); Barbara Baehr, Lisa Boutin, Mark S. Harvey, Robert Raven and Michael Rix (Australia); Valerio Vignoli (Benin); Joseph Koh and Natalia Chousou-Polydouri (Brunei Darussalem); Elizabeth Arias, Juan Enrique Barriga Tuñón, Camilo I. Mattoni, Peter Michalik and Jose A. Ochoa (Chile); Brian D. Farrell, Kelvin Guerrero, Jeremy Huff and Erich S. Volschenk (Dominican Republic); Jeremy Huff (French Guiana); Jeremy Huff and Valerio Vignoli (Guinea Bissau and Senegal); Alexander Gromov, Alex and Elena Kreuzberg (Kazakhstan and Uzbekistan); Oscar Francke, Andrew Gluesenkamp, Edmundo González-Santillán, Randy Mercurio, Hector Montaño, Ricardo Paredes, Javier Ponce-Saavedra, Charles Savvas and Peter Sprouse (Mexico); Da Aye Aye Cho, Dong Lin, U Kin Mawng Zaw, U Tin Mya Soe and Joe Slowinski (Myanmar); Tharina and Chris Bird, Quinton and Nicole Martins and Elizabeth Scott (Namibia); Ray Forster, Lyn Forster and Steven King (New Zealand); Pedro Cardoso (Portugal); Lauren Esposito (Puerto Rico); Ansie Dippeaar-Schoeman, Ian Engelbrecht, Charles Haddad, Norman Larsen, Robin Lyle, Randy Mercurio, Audrey Ndaba, Elizabeth Scott and Esther van der Westhuizen (South Africa); and Weerachai Nanakorn, Suyanee Vessabutr and Chaweewan Hutacharern (Thailand).

Specimens for this project were provided by Andrés A. Ojanguren-Affilastro, Ingi Agnarsson, Elizabeth Arias, Barbara Baehr, Domir De Bakker, Jorge Barneche, Jesper Birkedal Schmidt, Marius Burger, Tomás Cekalovic, Fred Coyle, Sara Crews, Michael Driessen, Ian Engelbrecht, Mike Fitzgerald, Charles Haddad, Mark S. Harvey, Bernhard Huber, Jeremy Huff, Joseph Joh, Matzaj Kuntner, James Lazell, Steven Lew, Camilo Mattoni, José Ochoa, Vladimir Ovtsharenko, Pierre Paquin, Robert Raven, Carles Ribera, Michael Rix, Sergio Rodríguez Gil, Cristina Scioscia, Carlos Viquez and Peter Weygoldt.

DNA sequence data were generated at the AMNH by Rebecca B. Dikow, Torsten Dikow, Jeni Kuszak, Diana Pietri and Dana Price. We thank Bryce McQuillan for providing a photograph of *Megadictyna thilenii*.

Author contributions

Led the project: WCW. Directed the study: WCW, JAC, GH, LP, PS. Directed a lab/group: WCW, JAC, CEG, GH, LP, MJR, PS, JEB, MH, WPM, NS. Participated in taxon selection, collected, identified specimens, processed samples: JAC, CEG, GH, LP, MJR, PS, LAS, FAP, MA, LBS, SB, JEB, CJG, EH, MH, MAI, FML, JL, LL, WPM, JM, LNP, NIP, DP, DSD, NS, TS, DU, CV, HMW, JZ. Managed tissue sample and voucher flow among project participants and AMNH: LP. Directed molecular lab: WCW. Edited sequences and generated data files: LMC. Provided additional sequences: DD, CEG, GH, LP, MJR, PS, JEB, MH, FML, JL, LL, WPM, JM, DP, NS, HMW, JZ. Curated and maintained tissue samples and voucher the data: LMC, LP.

Examined preliminary analyses, detected contaminations: LMC, DD, CEG, GH, MJR. Performed phylogenetic analyses: WCW (direct optimization), DD (maximum-likelihood and Bayesian), PAG (parsimony). Performed congruence analyses: MJR.

Drafted manuscript sections: LMC (Methods); MJR (Results); CEG, MJR (Relationships, Taxonomy). Made illustrations: MJR. Made tables: LMC, MJR.

Submitted sequences to GenBank: LMC. All authors approved the final text.

References

Aberer, A.J., Kobert, K., Stamatakis, A., 2014. ExaBayes: massively parallel Bayesian tree inference for the whole-genome era. Mol. Biol. Evol. 31, 2553–2556.

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

Agnarsson, I., Rayor, L.S., 2013. A molecular phylogeny of the Australian huntsman spiders (Sparassidae, Deleninae): implications for taxonomy and social behaviour. Mol. Phylogenet. Evol. 69, 895–905.

Agnarsson, I., Gregoric, M., Blackledge, T.A., Kuntner, M., 2012. The phylogenetic placement of Psechridae within Entelegynae and the convergent origin of orb-like spider webs. J. Zool. Syst. Evol. Res. 51, 100–106.

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: Trends and Perspectives. Siri Scientific Press, Rochdale, UK, pp. 58–111.

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

Almeida-Silva, L., 2013. Análise cladística de Macrobunidae Petrunkevitch 1928 stat. nov. e revisão de Macrobuninae (Araneae). Cladistic analysis of Macrobunidae Petrunkevitch, 1928 new rank and revision of Macrobuninae (Araneae). Universidade de São Paulo 2013, unpublished thesis.

Almeida-Silva, L., Griswold, C., Brescovit, A., 2014. Análise cladística de Macrobunidae Petrunkevitch 1928 stat. nov. e revisão de Macrobuninae (Arachnida: Araneae). 2014. IV Congreso Latinamericano de Aracnología, Morelia, Mexico.

Almeida-Silva, L., Griswold, C.E., Brescovit, A.D., 2015. Revision of *Emmenomma* Simon, (Amaurobiidae, Macrobuninae). Zootaxa 3931, 387–400.

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

Álvarez-Padilla, F., Dimitrov, D., Giribet, G., Hormiga, G., 2009. Phylogenetic relationships of the spider family Tetragnathidae (Araneae, Araneoidea) based on morphological and DNA sequence data. Cladistics 25, 109–146.

Arango, C.P., Wheeler, W.C., 2007. Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based on direct optimization of six loci and morphology. Cladistics 23, 255–293.

Bayer, S., Schönhofer, A.L., 2013. Phylogenetic relationships of the spider family Psechridae inferred from molecular data, with comments on the Lycosoidea (Arachnida: Araneae). Invertebr. Syst. 27, 53–80.

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

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

Bennett, R., 1991. The systematics of the North American cybaeid spiders (Araneoidea, Dictynoidea, Cybaeidae). University of Guelph, unpublished thesis.

Bennett, R., Copley, C., Copley, C., 2016. *Cybaeus* (Araneae: Cybaeidae): the Nearctic species of the Holarctic clade. Zootaxa 4164, 1–67.

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

Bolzern, A., Burckhardt, D., Hänggi, A., 2013. Phylogeny and taxonomy of European funnel-web spiders of the *Tegenaria-Malthonica* complex (Araneae: Agelenidae) based upon morphological and molecular data. Zool. J. Linn. Soc. 168, 723–848.

Bonaldo, A.B., 1997. On the new Neotropical spider genus *Ianduba* (Araneae, Corinnidae). Iheringia Sér. Zool. 83, 165–180.

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

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

Boyer, S.L., Karaman, I., Giribet, G., 2005. The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. Mol. Phylogenet. Evol. 36, 554–567.

Brignoli, P.M., 1979. The morphology and relationships of the Leptonetidae (Arachnida, Araneae). J. Arachnol. 7, 231–236.

Burger, M., Michalik, P., 2010. The male genital system of goblin spiders: evidence for the monophyly of Oonopidae (Arachnida: Araneae). Am. Mus. Novit. 3675, 1–13.

de Busschere, C., Fannes, W., Henrard, A., Gaublomme, E., Jocqué, R., Baert, L., 2014. Unravelling the goblin spiders puzzle: rDNA phylogeny of the family Oonopidae (Araneae). Arthropod Syst. Phyl. 72, 177–192.

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

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

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

Coddington, J.A., 1990. Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae). Acta Zool. Fenn. 190, 75–87.

Cokendolpher, J.C., Reddell, J.R., 1992. Revision of the Protoschizomidae (Arachnida: Schizomida) with notes on the phylogeny of the order. Texas Mem. Mus., Speleol. Monogr. 3, 31–74.

Colgan, D.J., McLauchlan, A., Wilson, G.D.F., Livingston, S.P., Edgecombe, G.D., Macaranas, J., Cassis, G., Gray, M.R., 1998. Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Aust. J. Zool. 46, 419–437.

Compagnucci, L.A., Ramírez, M.J., 2000. A new species of the spider genus *Naevius* Roth (Araneae, Amaurobiidae, Macrobuninae). Stud. Neotrop. Fauna Environ. 35, 203–207.

Crandall, K.A., Harris, D.J., Fetzner Jr., J.W., 2000. The monophyletic origin of freshwater crayfish estimated from nuclear and mitochondrial DNA sequences. Proc. R. Soc. Lond. B 267, 1679–1686.

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

Davies, V.T., 1990. Two new spider genera (Araneae: Amaurobiidae) from rainforests of Australia. Acta Zool. Fenn. 190, 95–102.

Davies, V.T., 1995. A tiny cribellate spider, *Jamara* gen. nov. (Araneae: Amaurobioidea: Midgeeinae) from northern Queensland. Mem. Queensl. Mus. 38, 93–96.

Davies, V.T., 1997. A redescription and renaming of the Tasmanian spider *Amphinecta milvina* (Simon, 1903) with descriptions of four new species (Araneae: Amaurobioidea: Amaurobiidae). In: Shelden, P.A. (Ed.), Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, pp. 67–82.

Davies, V.T., 1998. A revision of the Australian metaltellines (Araneae: Amaurobioidea: Amphinectidae: Metaltellinae). Invertebr. Taxon. 12, 211–243.

D'Haese, C.A., 2003. Sensitivity analysis and tree-fusing: faster, better. Cladistics 19, 150–151.

Dimitrov, D., Hormiga, G., 2009. Revision and cladistic analysis of the orbweaving spider genus *Cyrtognatha* Keyserling, 1881 (Araneae, Tetragnathidae). Bull. Am. Mus. Nat. Hist. 317, 1–140.

Dimitrov, D., Hormiga, G., 2011. An extraordinary new genus of spiders from Western Australia with an expanded hypothesis on the phylogeny of Tetragnathidae (Araneae). Zool. J. Linn. Soc. 161, 735–768.

Dimitrov, D., Lopardo, L., Giribet, G., Arnedo, M.A., Álvarez-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. Proc. R. Soc. Lond. B 279, 1341–1350.

Dimitrov, D., Astrin, J.J., Huber, B.A., 2013. Pholcid spider molecular systematics revisited, with new insights into the biogeography and the evolution of the group. Cladistics 29, 132–146.

Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G., Griswold, C.E., Scharff, N., Hormiga, G., 2016. 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 1–30. doi: 10.1111/cla.12165.

Eberhard, W.G., 1995. The web and building behavior of *Synotaxus ecuadorensis* (Araneae, Synotaxidae). J. Arachnol. 23, 25–30.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32, 1792–1797.

Farris, J.S., 1973. On comparing the shapes of taxonomic trees. Syst. Zool. 22, 50–54.

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

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotech. 3, 294–299.

Forster, R.R., 1970. The spiders of New Zealand. Part III. Otago Mus. Bull. 3, 1–184.

Forster, R.R., Wilton, C.L., 1973. The spiders of New Zealand. Part IV. Otago Mus. Bull. 4, 1–309.

Forster, R.R., Platnick, N.I., Gray, M.R., 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). Bull. Am. Mus. Nat. Hist. 185, 1–116.

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.

Giribet, G., 2002. Relationships among metazoan phyla as inferred from 18S rRNA sequence data: a methodological approach. In: DeSalle, R., Giribet, G., Wheeler, W.C. (Eds.), Molecular Systematics and Evolution: Theory and Practice. Birkhauser Verlag, Basel, pp. 85–101.

Giribet, G., 2007. Efficient tree searches with available algorithms. Evol. Bioinform. Online 3, 341–356.

Giribet, G., Carranza, S., Baguña, J., Riutort, M., Ribera, C., 1996. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Mol. Biol. Evol. 13, 76–84.

Goloboff, P.A., 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15, 415–428.

Goloboff, P.A., 2014. Extended implied weighting. Cladistics 30, 260–272.

Goloboff, P.A., Catalano, S., 2012. GB-to-TNT: facilitating creation of matrices from GenBank and diagnosis of results in TNT. Cladistics 28, 503–513.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

Gray, M.R., Smith, H.M., 2008. A new subfamily of spiders with grate-shaped tapeta from Australia and Papua New Guinea (Araneae: Stiphidiidae: Borralinae). Rec. Aust. Mus. 60, 13–44.

Gregorič, M., Agnarsson, I., Blackledge, T.A., Kuntner, M., 2015. Phylogenetic position and composition of Zygiellinae and *Caerostris*, with new insight into orb-web evolution and gigantism. Zool. J. Linn. Soc. 175, 225–243.

Grismado, C.J., Deeleman, C., Piacentini, L.N., Izquierdo, M.A., Ramírez, M.J., 2014. Taxonomic review of the goblin spiders of the genus *Dysderoides* Fage and their Himalayan relatives of the genera *Trilacuna* Tong and Li and *Himalayana*, new genus (Araneae: Oonopidae). Bull. Am. Mus. Nat. Hist. 387, 1–108.

Griswold, C.E., 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithson. Contrib. Zool. 539, 1–39.

Griswold, C.E., Coddington, J.A., Hormiga, G., Scharff, N., 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zool. J. Linn. Soc. 123, 1–99.

Griswold, C.E., Coddington, J.A., Platnick, N.I., Forster, R.R., 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). J. Arachnol. 27, 53–63.

Griswold, C.E., Ramírez, M.J., Coddington, J.A., Platnick, N.I., 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. Proc. Calif. Acad. Sci. 56, 1–324.

Griswold, C.E., Audisio, T., Ledford, J.M., 2012. An extraordinary new family of spiders from caves in the Pacific Northwest (Araneae, Trogloraptoridae, new family). ZooKeys 215, 77–102.

Haddad, C.R., 2013. Taxonomic notes on the spider genus *Messapus* Simon, 1898 (Araneae, Corinnidae), with the description of the new genera *Copuetta* and *Wasaka* and the first cladistic analysis of Afrotropical Castianeirinae. Zootaxa 3688, 1–79.

Hall, T.A., 2007. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41, 95–98.

Hedin, M., Bond, J.E., 2006. Molecular phylogenetics of the spider infraorder Mygalomorphae using nuclear rRNA genes (18S and 28S): conflict and agreement with the current system of classification. Mol. Phylogenet. Evol. 41, 454–471.

Heiss, J.S., Draney, M.L., 2004. Revision of the Nearctic spider genus *Calymmaria* (Araneae, Hahniidae). J. Arachnol. 32, 457–525.

Homann, H., 1971. Die Augen der Araneae: Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). Z. Morphol. Tiere 69, 201–272.

Hormiga, G., Griswold, C.E., 2014. Systematics, phylogeny and evolution of orb weaving spiders. Ann. Rev. Entomol. 59, 487–512.

Hormiga, G., Eberhard, W.G., Coddington, J.A., 1995. Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae, Tetragnathidae). Aust. J. Zool. 43, 313–364.

Hormiga, G., Fernández, R., Kallal, R., Ballesteros, J.A., Arnedo, M., Dimitrov, D., Giribet, G., 2016. A phylogenomic approach to resolve the relationships among the main lineages of araneoid spiders. Denver Mus. Nat. Sci. Rep. 3, 109–110.

Hovmöller, R., Pape, T., Källersjö, M., 2002. The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. Cladistics 18, 313–323.

Huckstorf, K., Michalik, P., Ramírez, M., Wirkner, C.S., 2015. Evolutionary morphology of the hemolymph vascular system of basal araneomorph spiders (Araneae: Araneomorphae). Arthropod Struct. Dev. 44, 609–621.

Jocqué, R., 1991. A generic revision of the spider family Zodariidae (Araneae). Bull. Am. Mus. Nat. Hist., 201, 1–160.

Jocqué, R., Dippenaar-Schoeman, A.S., 2006. Spider Families of the World. Musée Royal de l'Afrique Central, Tervuren, Belgium.

Jocqué, R., Henrard, A., 2015. The new spider genus *Palindroma*, featuring a novel synapomorphy for the Zodariidae (Araneae). Eur. J. Taxon. 152, 1–33.

Johannesen, J., Lubin, Y., Smith, D.R., Bilde, T., Schneider, J.M., 2007. The age and evolution of sociality in *Stegodyphus* spiders: a molecular phylogenetic perspective. Proc. R. Soc. Lond. B 274, 231–237.

Katoh, K., Standley, D.M., 2013. MAFFT. Multiple sequence alignment software version 7: improvements in performance and usability. Mol. Phylogenet. Evol. 30, 772–780.

Köcher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl Acad. Sci. USA 86, 6196–6200.

Kovoor, J., Peters, H.M., 1988. The spinning apparatus of *Polenecia producta* (Araneae, Uloboridae): structure and histochemistry. Zoomorphology 108, 47–59.

Kuntner, M., 2006. Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). Zool. Scripta 35, 19–62.

Kuntner, M., Coddington, J.A., Hormiga, G., 2008. Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae):

testing morphological and ethological homologies. Cladistics 24, 147–217.
Kuntner, M., Arnedo, M.A., Trontelj, P., Lokovšek, T., Agnarsson, I., 2013. A molecular phylogeny of nephilid spiders: evolutionary history of a model lineage. Mol. Phylogenet. Evol. 69, 961–979.
Labarque, F.M., Ramírez, M.J., 2012. The placement of the spider genus *Periegops* and the phylogeny of Scytodoidea (Araneae: Araneomorphae). Zootaxa 3312, 1–44.
Labarque, F.M., Soto, E.M., Ramírez, M.J., Arnedo, M.A., 2015. Chasing ghosts: the phylogeny of Amaurobioidinae ghost spiders (Araneae, Anyphaenidae). Zool. Scripta 44, 550–561.
Ledford, J.M., Griswold, C.E., 2010. A study of the subfamily Archoleptonetinae (Araneae, Leptonetidae) with a review of the morphology and relationships for the Leptonetidae. Zootaxa 2391, 1–32.
Lehtinen, P.T., 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool. Fenn. 4, 199–468.
Lehtinen, P.T., 1981. Spiders of the Oriental-Australian region. III. Tetrablemmidae, with a world revision. Acta Zool. Fenn. 162, 1–151.
Lehtinen, P.T., 1986. Evolution of the Scytodoidea. Proceedings of the Ninth International Congress of Arachnology, Panama 1983. University of Panama, Smithsonian Tropical Research Institute, and Centre International de Documentation Arachnologique Panama City, Panama, 1–8 August 1983. Smithsonian Institution Press, Washington, D.C., pp. 149–157.
Lindgren, A.R., Daly, M., 2007. The impact of length-variable data and alignment criterion on the phylogeny of Decapodiformes (Mollusca: Cephalopoda). Cladistics 23, 464–476.
Liu, K., Nelesen, S., Raghavan, S., Linder, C.R., Warnow, T., 2009. Barking up the wrong treelength: the impact of gap penalty on alignment and tree accuracy. IEEE/ACM Trans. Comput. Biol. Bioinf. 6, 7–21.
Lopardo, L., Hormiga, G., 2015. Out of the twilight zone: phylogeny and evolutionary morphology of the orb-weaving spider family Mysmenidae, with a focus on spinneret spigot morphology in symphytognathoids (Araneae, Araneoidea). Zool. J. Linn. Soc. 173, 527–786.
Lopardo, L., Ramírez, M.J., Grismado, C., Compagnucci, L.A., 2004. Web building behavior and the phylogeny of austrochiline spiders. J. Arachnol. 32, 42–54.
Lopardo, L., Giribet, G., Hormiga, G., 2011. Morphology to the rescue: molecular data and the signal of morphological characters in combined phylogenetic analyses—a case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. Cladistics 27, 278–330.
Maddison, W.P., 2015. A phylogenetic classification of jumping spiders (Araneae: Salticidae). J. Arachnol. 43, 231–292.
Maddison, W.P., Li, D., Bodner, M., Zhang, J., Xu, X., Liu, Q., Liu, F., 2014. The deep phylogeny of jumping spiders (Araneae, Salticidae). ZooKeys 440, 1–57.
Maddison, W.P., Maddison, D.R., Zhang, J., Szuts, T., 2016. Phylogenetic placement of the unusual jumping spider *Depreissia* Lessert, and a new synapomorphy uniting Hisponinae and Salticinae (Araneae, Salticidae). ZooKeys 549, 1–12.
Michalik, P., Ramírez, M.J., 2014. Evolutionary morphology of the male reproductive system, spermatozoa and seminal fluid of spiders (Araneae, Arachnida) – Current knowledge and future directions. Arthropod Struct. Dev. 43, 291–322.
Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Workshop (GCE), 14 November 2010, New Orleans, LA, pp. 1–8.
Miller, J.A., Carmichael, A., Ramírez, M.J., Spagna, J.C., Haddad, C.R., Rezac, M., Johannesen, J., Kral, J., Wang, X., Griswold, C.E., 2010. Phylogeny of entelegyne spiders: affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). Mol. Phylogenet. Evol. 55, 786–804.
Miller, J.A., Griswold, C.E., Scharff, N., Rezac, M., Szuts, T., Marharbai, M., 2012. The velvet spiders: an atlas of the Eresidae (Arachnida, Araneae). ZooKeys 195, 1–144.
Moradmand, M., Schönhofer, A.L., Jäger, P., 2014. Molecular phylogeny of the spider family Sparassidae with focus on the genus *Eusparassus* and notes on the RTA-clade and 'Laterigradae'. Mol. Phylogenet. Evol. 74, 48–65.
Morrill, L., 2014. Revision and phylogenetic analysis of the spider genus *Porteria* (Araneae, Desidae). San Francisco State University, unpublished thesis.
Murphy, N.P., Framenau, V.W., Donnellan, S.C., Harvey, M.S., Park, Y.-C., Austin, A.D., 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA, and NADH1 genes: implications for classification, biogeography, and the evolution of web building behavior. Mol. Phylogenet. Evol. 38, 583–602.
Muster, C., 2009. Phylogenetic relationships within Philodromidae, with a taxonomic revision of *Philodromus* subgenus *Artanes* in the western Palearctic (Arachnida: Araneae). Invertebr. Syst. 23, 135–169.
Nørgaard, T., Nilsson, D.E., Henschel, J.R., Garm, A., Wehner, R., 2008. Vision in the nocturnal wandering spider *Leucorchestris arenicola* (Araneae: Sparassidae). J. Exp. Biol. 211, 816–823.
Nunn, G.B., Theisen, B.F., Christensen, B., Arctander, P., 1996. Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. J. Mol. Evol. 42, 211–223.
Opatova, V., Arnedo, M.A., 2014. From Gondwana to Europe: inferring the origins of Mediterranean *Macrothele* spiders (Araneae: Hexathelidae) and the limits of the family Hexathelidae. Invertebr. Syst. 28, 361–374.
Padial, J.M., Grant, T., Frost, D.R., 2014. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. Zootaxa 3825, 001–132.
Palumbi, S.R., Martin, A., Romano, S., McMillan, W.O., Stice, L., Grabowski, G., 1991. The simple fool's guide to PCR, Version 2.0. University of Hawaii, Honolulu. Privately published, compiled by S. Palumbi.
Penney, D., Wheater, C.P., Selden, P.A., 2003. Resistance of spiders to Cretaceous-Tertiary extinction events. Evolution 57, 2599–2607.
Piacentini, L.N., Ramírez, M.J., Silva-Dávila, D., 2013. Systematics of *Cauquenia* (Araneae: Zoropsidae), with comments on the patterns of evolution of cribellum and male tibial crack on Lycosoidea. Invertebr. Syst. 27, 567–577.
Platnick, N.I., 1977. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). Am. Mus. Novit. 2627, 1–23.
Platnick, N.I., 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosoidea). Am. Mus. Novit. 2978, 42 pp.
Platnick, N.I., 2002. A revision of the Australasian ground spiders of the families Ammoxenidae, Cithaeronidae, Gallieniellidae, and Trochanteriidae (Araneae: Gnaphosoidea). Bull. Am. Mus. Nat. Hist. 271, 1–244.
Platnick, N.I., Baehr, B., 2006. A revision of the Australasian ground spiders of the family Prodidomidae (Araneae: Gnaphosoidea). Bull. Am. Mus. Nat. Hist. 298, 1–287.
Platnick, N.I., Penney, D., 2004. A revision of the widespread spider genus *Zimiris* (Araneae, Prodidomidae). Am. Mus. Novit. 3450, 1–12.
Platnick, N.I., Coddington, J.A., Forster, R.F., Griswold, C.E., 1991. Spinneret morphology and the higher classification of the haplogyne spiders (Araneae, Araneomorphae). Am. Mus. Novit. 3016, 1–73.
Polotow, D., Carmichael, A., Griswold, C.E., 2015. Total evidence analysis of the phylogenetic relationships of Lycosoidea spiders (Araneae, Entelegynae). Invertebr. Syst. 29, 124–163.
Rambaut, A., 2014. FigTree, tree figure drawing tool. v. 1.4.2. Institute of Evolutionary Biology, University of Edinburgh,

Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/ [accessed 5 June 2016].
Ramírez, M.J., 1995. A phylogenetic analysis of the subfamilies of Anyphaenidae (Arachnida, Araneae). Entomol. Scand. 26, 361–384.
Ramírez, M.J., 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). J. Arachnol. 28, 149–157.
Ramírez, M.J., 2014. The morphology and phylogeny of dionychan spiders (Araneae: Araneomorphae). Bull. Am. Mus. Nat. Hist. 390, 1–374.
Ramírez, M.J., Lopardo, L., Bonaldo, A.B., 2001. A review of the Chilean spider genus *Olbus*, with notes on the relationships of the Corinnidae (Arachnida, Araneae). Insect. Syst. Evol. 31, 441–462.
Ramírez, M.J., Grismado, C.J., Labarque, F.M., Izquierdo, M.A., Ledford, J.M., Miller, J.A., Haddad, C.R., Griswold, C.E., 2014. The morphology and relationships of the walking mud spiders of the genus *Cryptothele* (Araneae: Zodariidae). Zool. Anz. 253, 382–393.
Raven, R.J., Stumkat, K.S., 2005. Revisions of Australian ground-hunting spiders: II. Zoropsidae (Lycosoidea: Araneae). Mem. Queensl. Mus. 50, 347–423.
Regier, J.C., Shultz, J.W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J.W., Cunningham, C.W., 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463, 1079–1083.
Rheims, C.A., 2007. Análise cladística dos gêneros de Sparassidae Bertkau (Arachnida, Araneae). Instituto de Biociências da Universidade de São Paulo, unpublished PhD thesis.
Rix, M.G., Harvey, M.S., 2010. The spider family Micropholcommatidae (Arachnida: Araneae: Araneoidea): a relimitation and revision at the generic level. ZooKeys 36, 1–321.
Rix, M.G., Harvey, M., Roberts, J., 2008. Molecular phylogenetics of the spider family Micropholcommatidae (Araneae: Araneae) using nuclear rRNA genes (18S and 28S). Mol. Phylogenet. Evol. 46, 1031–1048.
Robinson, M.H., Lubin, Y.D., 1979. Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea. II. *Psechrus argentatus* and *Fecenia* sp. (Araneae: Psechridae). Pac. Insects 21, 133–164.
Roth, V.D., Brame, P.L., 1972. Nearctic genera of the spider family Agelenidae (Arachnida, Araneida). Am. Mus. Novit. 2505, 1–52.
Sanger, F., Nicklen, S., Chase, A.R., 1977. Sequencing with chain terminating inhibitors. Proc. Natl Acad. Sci. USA 74, 5463–5468.
Saturnino, R., Bonaldo, A.B., 2015. Taxonomic review of the New World spider genus *Elaver* O. Pickard-Cambridge, 1898 (Araneae, Clubionidae). Zootaxa 4045, 1–119.
Scharff, N., Coddington, J.A., 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zool. J. Linn. Soc. 120, 355–434.
Schuh, R.T., Weirauch, C., Wheeler, W.C., 2009. Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total-evidence analysis. Syst. Entomol. 34, 15–48.
Schulmeister, S., Wheeler, W.C., Carpenter, J.M., 2002. Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. Cladistics 18, 455–484.
Schütt, K., 2009. The limits of the Araneoidea (Arachnida: Araneae). Aust. J. Zool. 48, 135–153.
Selden, P.A., Huang, D.Y., Ren, D., 2008. Palpimanoid spiders from the Jurassic of China. J. Arachnol. 36, 306–321.
Sharma, P.P., Fernández, R., Esposito, L.A., González-Santillán, E., Monod, L., 2015. Phylogenomic resolution of scorpions reveals multilevel discordance with morphological phylogenetic signal. Proc. R. Soc. Lond. B 282, 20142953.
Shear, W.A., 1978. Taxonomic notes on the armored spiders of the families Tetrablemmidae and Pacullidae. Am. Mus. Novit. 2650, 1–46.
Shultz, J.W., 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6, 1–38.
Shultz, J.W., 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zool. J. Linn. Soc. 150, 221–265.
Silva-Dávila, D., 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). Bull. Am. Mus. Nat. Hist. 274, 1–86.
Sørensen, M.V., Sterrer, W., Giribet, G., 2006. Gnathostomulid phylogeny inferred from a combined approach of four molecular loci and morphology. Cladistics 22, 32–58.
Spagna, J.C., Gillespie, R.G., 2008. More data, fewer shifts: molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. Mol. Phylogenet. Evol. 46, 347–368.
Spagna, J.C., Crews, S.C., Gillespie, R.G., 2010. Patterns of habitat affinity and Austral/Holarctic parallelism in dictynoid spiders (Araneae: Entelegynae). Invertebr. Syst. 24, 238–257.
Stamatakis, A., 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313.
Teixeira, R.A., Campos, L.A., Lise, A.A., 2013. Phylogeny of Aphantochilinae and Strophiinae sensu Simon (Araneae; Thomisidae). Zool. Scripta 43, 65–78.
Thompson, J.D., Higgins, D.G., Gibson, T.J., 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matric choice. Nucleic Acids Res. 22, 4673–4680.
Van der Auwera, G., Chapelle, S., De Wachter, R., 1994. Structure of the large ribosomal subunit RNA of *Phytophthora megasperma*, and phylogeny of the oomycetes. FEBS Lett. 338, 133–136.
Wang, X.P., 2000. A revision of the genus *Tamgrinia* (Araneae: Amaurobiidae), with notes on amaurobiid spinnerets, tracheae and trichobothria. Invertebr. Taxon. 14, 449–464.
Weygoldt, P., 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). J. Zool. Syst. Evol. Res. 34, 185–202.
Weygoldt, P., Paulus, H.F., 1979. Untersuchungen zur morphologie, taxonomie und phylogenie der Chelicerata. II. Cladogramme und die entfaltung der Chelicerata. J. Zool. Syst. Evol. Res. 17, 177–200.
Wheeler, W.C., 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. Syst. Biol. 44, 321–331.
Wheeler, W.C., 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12, 1–9.
Wheeler, W.C., 2001. Homology and the optimization of DNA sequence data. Cladistics 17, S3–S11.
Wheeler, W.C., Giribet, G., Edgecombe, G.D., 2004. Arthropod systematics: the comparative study of genomic, anatomical, and paleontological information. In: Cracraft, J., Donoghue, M.J. (Eds), Assembling the Tree of Life. Oxford University Press, Oxford, pp. 281–295.
Wheeler, W.C., Lucaroni, N., Hong, L., Crowley, L.M., Varón, A., 2014. POY 5.1.1. American Museum of Natural History. http://research.amnh.org/scicomp/projects/poy.php
Wheeler, W.C., Lucaroni, N., Hong, L., Crowley, L.M., Varón, A., 2015. POY version 5: phylogenetic analysis using dynamic homologies under multiple optimality criteria. Cladistics 31, 189–196.
Whiting, M.F., 2002. Phylogeny of the holometabolous insect orders: molecular evidence. Zool. Scripta 31, 3–15.
Whiting, M.F., Carpenter, J.C., Wheeler, Q.D., Wheeler, W.C., 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Syst. Biol. 46, 1–68.
Wood, H.M., Griswold, C.E., Gillespie, R., 2012. Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into evolution of the "neck" and predatory behaviors of the superfamily Palpimanoidea. Cladistics 28, 598–626.
Wood, H.M., Matzke, N., Gillespie, R., Griswold, C.E., 2013. Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. Syst. Biol. 62, 264–284.

Wood, H.M., Parkinson, D.Y., Griswold, C.E., Gillespie, R.G., Elias, D.O., 2016. Repeated evolution of power-amplified predatory strikes in trap-jaw spiders (Araneae, Mecysmaucheniidae). Curr. Biol. 26, 1057–1061.
World Spider Catalog, 2016. Natural History Museum Bern. http://wsc.nmbe.ch, version 17.0 [accessed 24 May 2016].
Wunderlich, J., 2004. The new spider (Araneae) family Borboropactidae from the tropics and fossil in Baltic amber. Beitr. Araneol. 3, 1737–1746.
Wunderlich, J., 2015. Mesozoic spiders and other fossil arachnids. Beitr. Araneol. 9, 1–512.
Xu, X., Liu, F., Chen, J., Ono, H., Li, D., Kuntner, M., 2015a. A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae). ZooKeys 488, 1–121.
Xu, X., Liu, F., Cheng, R.C., Chen, J., Xu, X., Zhang, Z., Ono, H., Pham, D.S., Norma-Rashid, Y., Arnedo, M.A., Kuntner, M., Li, D., 2015b. Extant primitively segmented spiders have recently diversified from an ancient lineage. Proc. R. Soc. Lond. B 282, 2014–2486.
Zamani, A., Marusik, M., James, W.B., 2016. A new species of *Paratheuma* (Araneae: Dictynidae) from Southwestern Asia and transfer of the genus. Zool. Middle East 62, 177–183.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Transcriptomic skeleton tree (TR). Skeleton tree obtained from the transcriptomic analysis of Garrison et al. (2016), with terminals mapped to our dataset. All clades have bootstrap values of 100% and are robust to analytical methods.

Fig. S2. Taxonomic reference tree (TX). Includes multi-sampled families of spiders and outgroups.

Fig. S3. Taxonomic reference tree, conservative (TX-C). Same as TX, but excluding the families that are relimited here.

Fig. S4. Maximum-likelihood tree constrained by TR skeleton tree (C-ML). With bootstrap values.

Fig. S5. Maximum-likelihood tree constrained by TR skeleton tree based on the dataset excluding areas of ambiguously aligned position in non-coding genes (C-ML-T). With bootstrap values.

Fig. S6. Unconstrained maximum-likelihood tree (ML). With bootstrap values.

Fig. S7. Unconstrained Bayesian inference tree (BI). With posterior probabilities.

Fig. S8. Direct optimization tree (DO). Tree obtained for InDel cost ratio of 1 and tv/ts cost ratio of 2.

Fig. S9. Parsimony equal weights tree (EW). With bootstrap values.

Fig. S10. Parsimony extended weighting tree (IW). With bootstrap values.

Fig. S11. ree with robust groups. Majority rule consensus tree from all analyses in Figs S4–S10.

Fig. S12. Tree with groups stable to optimality criteria. Majority rule consensus tree from the five optimality criteria (EW, IW, DO, BI, ML), complete alignments without constraints.

Table S1. Voucher and DNA locus information. Specimen and locus information is provided below. The identification code (Voucher Codes) of the tissue or DNA sample from which newly generated sequences were obtained is given. Institution codes (Museum Voucher Code) are also provided. Locality data are also supplied, with localities for conspecific tissues separated by a semicolon. All newly generated sequences, as well as those attributable to the NSF grant EAR-0228699, are highlighted in bold type; all others refer to sequences that were previously deposited in GenBank by other authors.

Table S2. Mapping of our terminals to those of Garrison et al.'s (2016) analysis of transcriptomic data.

Table S3. Combined and partial tree costs and incongruence length difference (ILD) for different schemas of InDel and tv/ts cost ratios.

Table S4. Monophyly of selected taxonomic groups and multi-sampled families as found in the different analyses, and list of taxa used for the taxonomic congruence analyses.