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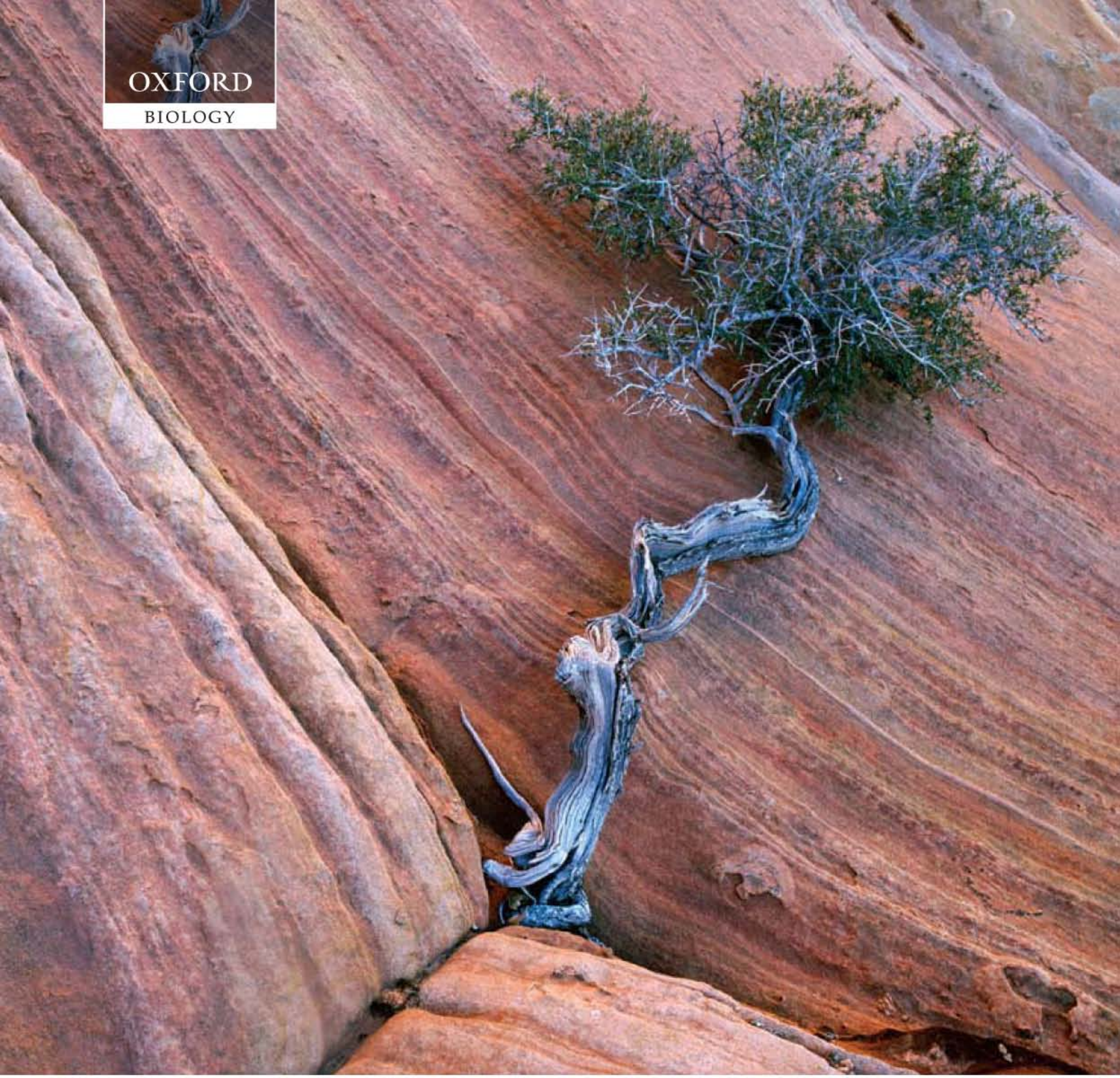

the TIMETREE of LIFE

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Spiders (Araneae)

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Abstract

Spiders (~40,000 sp.), Order Araneae, are members of the Class Arachnida and are defined by numerous shared-derived characters including the ability to synthesize and spin silk. The last few decades have produced a growing understanding of the relationships among spider families based primarily on phylogenetic analysis of morphological characters. Only a few higher-level molecular systematic studies have been conducted and these were limited in their taxonomic sampling. Nevertheless, molecular time estimates indicate that spider diversification is ancient and that many families radiated rapidly in the early Cretaceous (146–100 million years ago, Ma) and before.

Spiders (Araneae) constitute one of the most diverse orders of animals with greater than 39,000 described species, which are found worldwide in virtually all terrestrial habitats (*1*). They are members of the Class Arachnida, which also includes orders such as ticks and mites (Acari), scorpions (Scorpiones), and harvestmen or daddy long legs (Opiliones). Arachnid phylogeny is poorly understood, but the current consensus is that the closest relative of spiders is the Pedipalpi, which is a group of arachnids composed of whip-scorpions (Uropygi), tail-less whip-scorpions (Amblypygi), and short-tailed whip-scorpions (Schizomida) (*2, 3*). Monophyly of spiders is strongly supported by a number of shared-derived characters, including cheliceral venom glands, male pedipalpi modified for sperm transfer, lack of a trochanter-femur depressor muscle, and abdominal spinnerets and silk glands (*2, 4*). Spiders are arranged into two suborders: the Mesothelae (one family with 87 species), which retains significant traces of abdominal segmentation, and the Opisthothelae (107 families with 39,638 species), which has lost all traces of abdominal segmentation (*5*). Here, we review relationships and divergence times among families of the highly diverse Opisthothelae.

Most systematic studies of spiders at the family level have relied exclusively on morphological characters (reviewed in *6*). These studies are often hindered by many spider taxa retaining ancestral characters and exhibiting high levels of convergence or parallelism (e.g., *5, 7, 8*). Spiders are thought to have arisen in the Devonian (416–359 Ma) (*9*), and their antiquity contributes to these problems. Fossil representatives of many extant families have been found in the early to mid-Cretaceous, 146–100 Ma (*10*). Despite these issues, phylogenetic analyses over the last 30 years have dramatically improved our understanding of spider relationships.

Within the Opisthothelae, spiders are divided into two major groups (*5*): the tarantulas and their kin (Mygalomorphae; 15 families with 2564 species), and the "true" spiders (Araneomorphae; 92 families with 37,074 species). Mygalomorphs retain numerous primitive characters and are, for the most part, large, stout-bodied, dispersal-limited spiders that occupy similar ecological niches (e.g., Fig. 1). In contrast, araneomorphs display numerous derived traits and a vast array of morphological and behavioral characters, which are reflected in the tremendous species diversity of this clade compared to mygalomorphs. Although there have been several

Fig. 1 A tarantula (*Aphonopelma seemanni*) from Costa Rica. Credit: M. Chappell.

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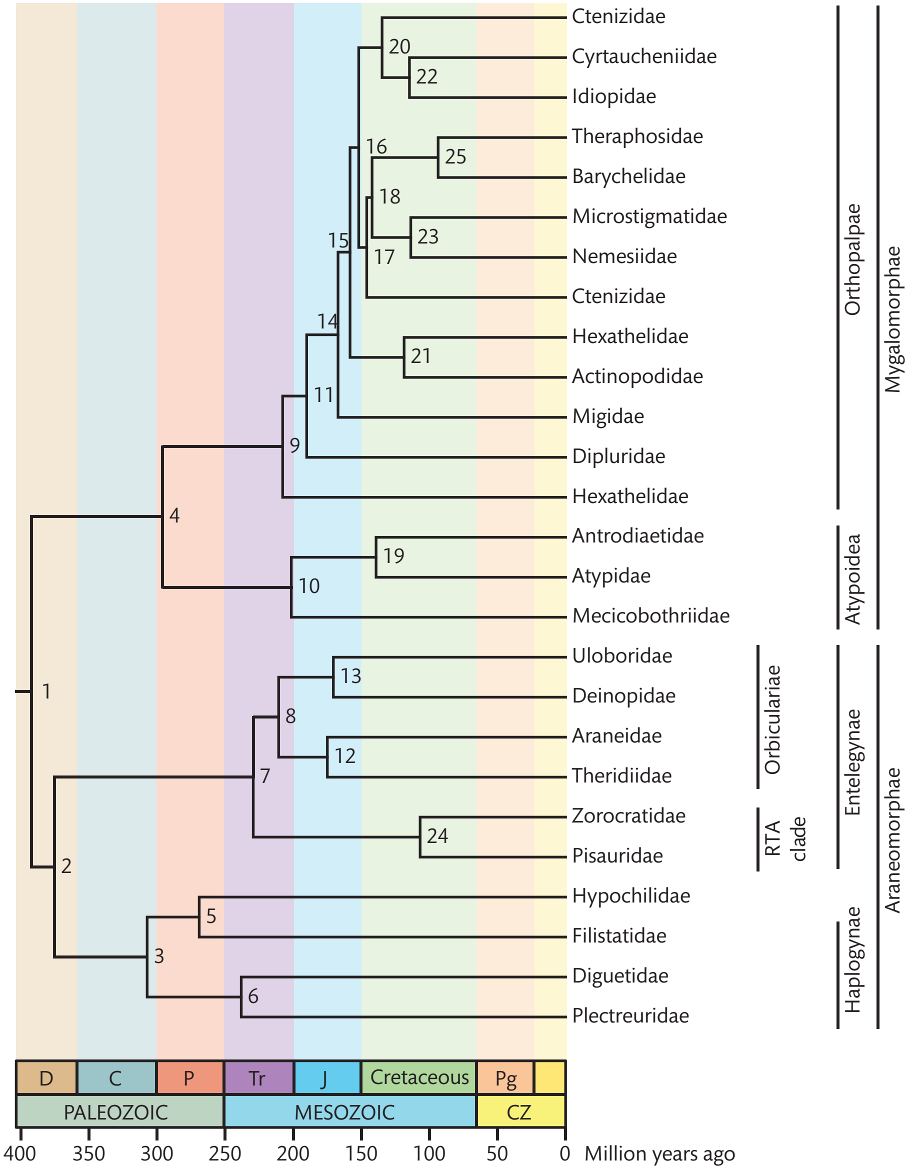

Fig. 2 A timetree of spiders (Araneae). Divergence times are from Table 1. Ctenizidae and Hexathelidae are shown in part; these families are typically found to be paraphyletic or polyphyletic (*7, 25, 26*). *Abbreviations*: C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), P (Permian), Pg (Paleogene), and Tr (Triassic).

phylogenetic studies within and among particular araneomorph families, none has treated all families simultaneously. Instead, relationships have been reconstructed by piecing together evidence from separate analyses to create a consensus phylogeny for araneomorphs (*4, 6*). Thus, many putative clades are uncertain and poorly resolved. The Family Hypochilidae is the presumed closest relative of all other araneomorphs, which includes two commonly recognized clades: Haplogynae (17 families) and Entelegynae (72 families) (*11, 12*). Over half (39) of the families in the Entelegynae are grouped into the "RTA-clade" on the basis of possessing a knob on the male palpi termed the "retrolateral tibial apophysis" (*4, 13, 14*).

Within Entelegynae, the Orbiculariae is a very species-rich and controversial clade (*15*). The Orbiculariae is composed of two superfamilies, the Deinopoidea (Deinopidae and Uloboridae, 320 species) and the Araneoidea (12 families with 11,075 species), both of which include orb-web weavers. Orb webs are wagon-wheel shaped aerial nets built from spoke-like radii

Table 1. Divergence times (Ma) and their 95% confidence/credibility intervals (CI) among spiders (Araneae).

Timetree		Estimates					
Node	Time	Ref. (*26*)(a)		Ref. (*26*)(b)		Ref. (*29*)	
		Time	CI	Time	CI	Time	CI
1	392.0	392	–	392	–	279	307–251
2	375.5	371	381–346	380	385–350	–	–
3	307.0	301	326–282	313	332–293	–	–
4	296.0	290	318–276	302	326–286	–	–
5	269.0	–	–	269	294–246	–	–
6	238.0	230	250–201	246	272–216	–	–
7	229.5	219	242–203	240	261–225	222	231–213
8	210.5	219	242–203	202	223–192	–	–
9	207.5	202	233–186	213	240–198	–	–
10	201.5	198	232–177	205	237–185	–	–
11	190.0	190	215–174	–	–	–	–
12	175.0	200	223–180	150	172–139	–	–
13	170.5	175	203–159	166	187–152	–	–
14	167.0	167	194–157	–	–	–	–
15	158.0	158	182–146	–	–	–	–
16	152.0	152	174–139	–	–	–	–
17	146.0	146	168–133	–	–	–	–
18	142.0	142	161–129	–	–	–	–
19	139.0	142	172–130	136	161–124	–	–
20	134.5	137	158–125	132	146–118	–	–
21	118.5	122	146–110	115	139–103	–	–
22	114.5	120	138–107	109	122–96	–	–
23	113.5	114	136–103	113	130–104	–	–
24	106.9	84.8	104–75	129	153–113	–	–
25	93.5	93.5	111–82	–	–	–	–

Note: Node times in the timetree are based on the MP topology (a) for mygalomorphs and the ML topology (b) for araneomorphs (*26*). Node times are averaged across estimates from the two topologies.

overlaid with sticky capture spirals. Both deinopoid and araneoid orb weavers spin architecturally similar webs but differ in the type of silk they use to construct the sticky capture spiral. This difference is part of the evidence for the traditional interpretation of the orb web as a spectacular example of convergent evolution (see *16, 17*). However, phylogenetic analysis of morphological and behavioral characters associated with orb-web construction supports monophyly of Orbiculariae (e.g., *15, 18*). In addition, Deinopoidea and Araneoidea share silk protein-coding genes not found in other groups of spiders, corroborating monophyly of Orbiculariae and the single origin of the orb web (*19*).

The Mygalomorphae has received considerably less phylogenetic attention than the Araneomorphae. However, Raven (*20*) performed a comprehensive taxonomic overview that laid the groundwork for mygalomorph systematics by defining 15 families and proposed a hypothesis of their relationships. A later phylogenetic analysis by Goloboff (*7*) of a subset of mygalomorph genera assessed monophyly of the families defined by Raven (*20*) and provided a revised hypothesis of mygalomorph relationships. The phylogenetic analysis indicated that a number of the families described in the taxonomic overview were paraphyletic (species sharing ancestral characteristics but not forming a single evolutionary group), including Ctenizidae, Dipluridae, Cyrtaucheniidae, Nemesiidae, and Barychelidae. In addition, the two hypotheses of higher-level relationships differed considerably, although both recognized a few common clades: (1) a close relationship between Antrodiaetidae and Atypidae, (2) the Rastelloidina (Migidae, Actinopodidae, Ctenizidae, Idiopidae, Cyrtaucheniidae), and (3) the Theraphosoidina (Theraphosidae, Barychelidae, and Paratropididae). Traditional taxonomists grouped Mecicobothriidae with Antrodiaetidae and Atypidae into the Atypoidea, which was thought to be closest to the remaining mygalomorphs (*21–23*). Both Raven's (*20*) taxonomic overview and Goloboff's (*7*) phylogenetic analysis removed mecicobothriids from this clade, but the latter study recovered the grouping of Antrodiaetidae and Atypidae as the closest relative of all other mygalomorphs. Mecicobothriidae was found to be closest to a clade of the remaining families, which was referred to as the Orthopalpae. Hexathelids and diplurids were considered to form a paraphyletic grade at the base of Orthopalpae (*7*).

Molecular studies of family-level relationships among spiders are sparse. A ribosomal RNA gene (*28S rRNA*) was used to reconstruct relationships of eight araneomorph families (*24*). These *28S* data weakly supported the monophyly of two haplogyne families but strongly supported monophyly of six entelegyne families, two RTA-clade families, and three araneoid families. In contrast to morphological results, the araneoids were closest to the RTA-clade representatives, rather than the deinopoid exemplar, but this relationship was not well supported. Another investigation used *18S* and *28S rRNA* genes from representatives of each mygalomorph family (80 genera sampled, *25*). This study found support for monophyly of the traditional Atypoidea as well as monophyly of the remaining mygalomorphs, the Orthopalpae. Additionally, the rRNA genes positioned diplurids and hexathelids as a paraphyletic grade at the base of Orthopalpae and rejected monophyly of many of the same families that cladistic analysis of morphological characters had recovered as paraphyletic (*7*). The rRNA data found barychelids and theraphosids to be each other's closest relatives, but did not support monophyly of Theraphosoidina or Rastelloidina.

One molecular study sampled multiple representatives of both araneomorph and mygalomorph taxa (*26*). These authors used a nuclear protein-coding gene, elongation factor-1 gamma (*EF-1γ*), to reconstruct relationships among 14 mygalomorph families and 10 araneomorph families (Fig. 2). The *EF-1γ* study grouped Hypochilidae with the three families in the Haploygnae, instead of closest to all araneomorphs, perhaps as a result of long-branch attraction at the base of the araneomorph clade (*26*). The six entelegyne families clustered with strong support. Orbiculariae was found to be monophyletic in one analysis of the *EF-1γ* data, but in another, the RTA-clade respresentatives were intermingled with the sampled araneoids (Araneidae and Theridiidae). Relationships among mygalomorph families based on *EF-1γ* were largely consistent with those based on rRNA (*25*). For instance, monophyly of both Atypoidea and Orthopalpae were well supported, and nemesiids, ctenizids, and hexathelids were paraphyletic. Unexpectedly, one of the hexathelid genera was placed with an actinopodid, a previously unproposed relationship. Sampling of other families was insufficient to assess their monophyly. Rastelloid monophyly was not supported, but could not be rejected by the *EF-1γ* data. Analyses of *EF-1γ* further found barychelids to be the closest relatives of theraphosids. While relationships within the Orthopalpae differed according to optimality criterion, the parsimony analysis placed hexathelids and diplurids at the base of the Orthopalpae in agreement with phylogenetic analysis of morphological (*7*) and rRNA (*25*) characters.

The most comprehensive study to estimate divergence times among spider families used *EF-1γ* sequences, five fossil calibration points, and a nonparametric rate smoothing method (NPRS, *27*) to account for rate heterogeneity (*26*). Due to discrepancies in some of the phylogenetic results, this study calculated estimates using both the maximum parsimony (MP) and the maximum likelihood (ML) trees (Fig. 2, Table 1). Divergence time estimates show that spider lineages are ancient. The split of araneomorphs from mygalomorphs was estimated at 392 Ma, the maximum constraint for this node based on the oldest known spider fossil (*9*). However, when the common ancestor of living mygalomorphs was fixed to the age of the oldest mygalomorph fossil (240 Ma, *28*), the divergence of mygalomorphs from araneomorphs was estimated at 340 Ma. The other age estimate for this node is based on hemocyanin protein sequences assuming a strict molecular clock and using a fossil calibration point for the divergence of Xiphosura (horseshoe crabs) from Arachnida (*29*). This estimate of 279 (±28) Ma, which is much younger than that determined from the *EF-1γ* data and spider fossil constraints, is likely biased by the sparse taxon sampling (three spider families) and the use of a single non-spider calibration point.

Within Mygalomorphae, the primary split between atypoids and orthopalps was estimated to have occurred 326–276 Ma, in the late Carboniferous or early Permian. While the exact timing of divergences within Orthopalpae is unclear, most family-level diversification appears to have occurred between the late Jurassic and early Cretaceous, 170–100 Ma. Many mygalomorph families, such as Migidae and Idiopidae, have classic Gondwanan distributions (*30*). The *EF-1γ* divergence times are consistent with migids (194–157 Ma) predating the initial breakup of Gondwanaland 165–150 Ma, and the divergence of African and Australian idiopids (130–90 Ma, *26*) with the opening of the southern South Atlantic Ocean approximately 135 Ma (*31*).

Despite the antiquity of mygalomorph families, perhaps even more striking is that mygalomorph diversification is recent when compared to araneomorph diversification. The estimated appearance of Haplogynae 332–282 Ma is much older than the age suggested by the fossil record (~94 Ma, *32*). Even the divergence 272–201 Ma of Diguetidae and Plectreuridae, which are thought to be each other's closest relatives (*33*), dates to the Triassic. The entelegyne node (261–203 Ma) also dates to the Triassic. The estimate from the *EF-1γ* data for this node overlaps with the estimate from hemocyanins of 231–213 Ma (*29*). The orbicularian superfamilies diverged in the late Triassic or early Jurassic, which implies that the orb-web architecture minimally dates to this period and has subsequently been modified, and even lost, in some araneoids and deinopoids (*15, 18*).

As predicted from the fossil record (*10*), diversification of extant spider families is ancient, dating to well before or during the Cretaceous. Ancient rapid radiations, no doubt, contribute to the difficulties in reconstructing relationships among spider families. More studies with denser taxonomic sampling that are based on a broader range of independent loci and fossil calibrations than are currently available are needed to accurately reconstruct the time line of spider evolution.

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