

Reconstructing web evolution and spider diversification in the molecular era

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The evolutionary diversification of spiders is attributed to spectacular innovations in silk. Spiders are unique in synthesizing many different kinds of silk, and using silk for a variety of ecological functions throughout their lives, particularly to make prey-catching webs. Here, we construct a broad higher-level phylogeny of spiders combining molecular data with traditional morphological and behavioral characters. We use this phylogeny to test the hypothesis that the spider orb web evolved only once. We then examine spider diversification in relation to different web architectures and silk use. We find strong support for a single origin of orb webs, implying a major shift in the spinning of capture silk and repeated loss or transformation of orb webs. We show that abandonment of costly cribellate capture silk correlates with the 2 major diversification events in spiders (1). Replacement of cribellate silk by aqueous silk glue may explain the greater diversity of modern orb-weaving spiders (Araneoidea) compared with cribellate orb-weaving spiders (Deinopoidea) (2). Within the “RTA clade,” which is the sister group to orb-weaving spiders and contains half of all spider diversity, >90% of species richness is associated with repeated loss of cribellate silk and abandonment of prey capture webs. Accompanying cribellum loss in both groups is a release from substrate-constrained webs, whether by aerially suspended webs, or by abandoning webs altogether. These behavioral shifts in silk and web production by spiders thus likely played a key role in the dramatic evolutionary success and ecological dominance of spiders as predators of insects.

Araneidae | behavioral evolution | cribellate silk | orb web | speciation

Spiders are exceptionally diverse and abundant in terrestrial ecosystems. In contrast to megadiverse orders of insects, evolutionary diversification of spiders is not coupled with major trophic shifts. All spiders are predators of arthropods, and spiders are dominant consumers at intermediate trophic levels (1, 2). Spider diversification is instead linked to key innovations in silk use (3–7). For instance, the araneoid orb web (Fig. 1) with stretchy capture spirals, coated by adhesive viscid silk secretions, provides access to abundant flying insects (3, 8). However, many spiders produce cribellate silk, a radically different dry adhesive that adheres to prey, using van der Waals interactions and hygroscopic forces (9). Some cribellate spiders also construct aerial orb webs, whereas most spin sheet-like webs on the substrate (Fig. S1) or have abandoned capture webs altogether. Furthermore, the most diverse families within “orb-weavers” (Orbiculariae) no longer build orb webs, but instead spin aerial sheet webs (Linyphiidae) or cobwebs (Theridiidae) (Fig. S2). Thus, discovering the pattern of evolution of web spinning behaviors is essential for understanding spider diversification.

Orb webs possessing dry cribellate capture spirals are architecturally similar to those spun from aqueous viscid silk (Fig. 1 *A* and *B*). Cribellate capture silk is produced by spiders first spinning a core axial fiber and then physically combing fine fibrils onto it to make functional capture spiral. This multistep

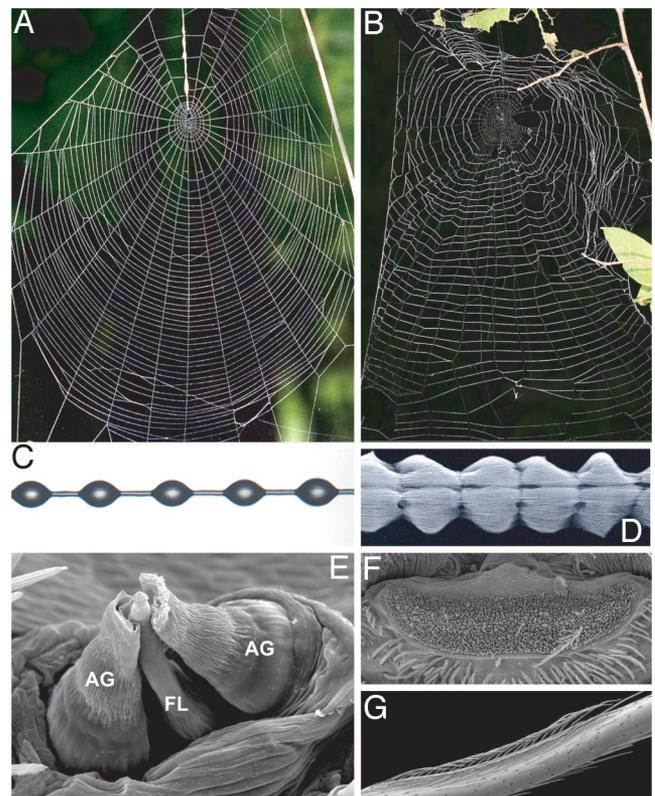


Fig. 1. Comparison of modern gluey orb webs spun by araneoid spiders to cribellate orb webs. (*A* and *B*) The web architectures are strikingly similar. (*C* and *D*) However, they use radically different adhesive silks. (*C*) Capture threads in araneoid orbs are coated by droplets of aqueous glue that are chemically adhesive. (*D*) Cribellate spiders coat capture threads with puffs of tiny, dry silk fibrils. (*E*) Araneoid spiders quickly spin the central capture fiber and its surrounding glue simultaneously, using a triad of silk spigots on their posterior lateral spinnerets (the outer pair of aggregate spigots produces the glue, whereas the central flagelliform spigot produces the core fiber). The droplet morphology arises spontaneously soon after the glue is applied to the silk. (*F*) Cribellate spiders also produce the core fibers of their capture threads from spigots on the posterior lateral spinneret. However, they use hundreds of tiny spigots on the cribellum, anterior of the spinnerets, to produce the adhesive fibrils. (*G*) The puffed morphology results from the spiders behaviorally combing the silk, using a calamistrum located on their hind legs. *D* is courtesy of B. Opell.

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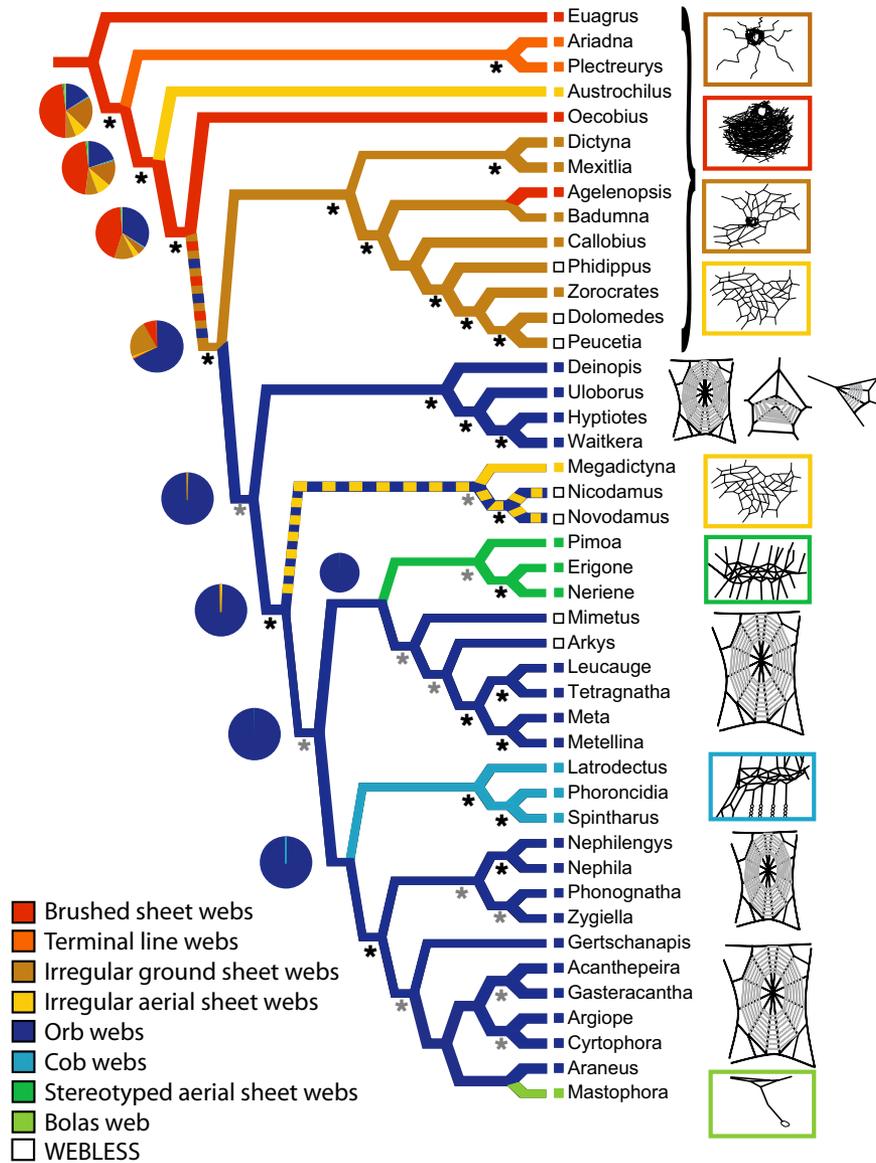


Fig. 2. Optimization of web architecture on the preferred topology. Black stars indicate strong support for a node from both MP (jackknife > 75%) and Bayesian (posterior probabilities > 90%) analyses, and gray stars indicate nodes strongly supported only by one methodology or with jackknife 50–74%. Branch colors represent MP reconstruction of webs, and pie charts represent the relative probabilities from ML reconstructions. Colors of boxes to the left of taxon names represent their webs, and open boxes indicate that taxa do not spin prey capture webs.

Discussion

Monophyletic Origin of the Orb Web. The monophyletic origin of orb webs is strongly supported, despite conspicuous differences in the silk used to spin different types of orbs (Fig. 1). This has important implications for understanding both web evolution and spider diversification. Instead of cribellate and ecribellate orb webs evolving in parallel, orb monophyly explicitly implies that dry cribellate capture spirals were replaced by ecribellate gluey spirals. This involves 2 major changes. First, a shift in the silk used to produce the core fibers of capture threads, resulting in novel tensile properties. The core fibers of modern (ecribellate) orb weavers are composed of flagelliform silk, which is much more elastic than the pseudoflagelliform silk core fibers of cribellate spiders (48). Mechanically, flagelliform silk functions like rubber, relying on entropy to resist motion of silk molecules and absorb kinetic energy during prey capture, allowing the

capture spiral to expand and contract repeatedly (49). In contrast, cribellate silk relies on permanent rupturing of molecular bonds to absorb kinetic energy and deforms irreversibly during prey capture (48). The second major shift involves the mechanism of adhesion, from dry cribellate fibrils that adhere through van der Waals forces and hygroscopic interactions to chemically adhesive viscid glue in ecribellate spiders. This results in webs with greater adhesion per surface area (50) and may have facilitated the transition from horizontal to vertical web orientation in modern orb spiders, which is associated with increased prey interception rates (51).

An evolutionary shift in capture silk has been considered improbable because it necessitates the origin of both novel silk production apparatuses (e.g., glands and spigots) and spinning behaviors (refs. 13, 14, and 52; see summary in ref. 53). Modification in production of axial core fibers is relatively easy to

pendently transformed the orb into different aerial sheets. In both cases, these webs are distinguished from ancestral sheets not only in being aerial but also in the overall stereotypy of their architectures, a characteristic inherited from orb weaving ancestors. This suggests that it was not the spinning of webs with sheet-like architectures per se that limited diversification of basal spiders, but rather constraints imposed from having web shape defined by microhabitat location and the costliness of producing the cribellate silk.

We speculate that the success, both in terms of species richness and abundance, of linyphiid and theridiid spiders may be due in part to further reductions in the cost of web spinning from sparse use of glue. Linyphiid webs contain few glue droplets and often lack sticky silk altogether whereas theridiid cobwebs restrict glue to the termini of sticky gumfooted threads. This continues the trend in economization of glue production during the transition from cribellate to ecribellate orb-weavers. Interestingly, ecribellate orb spiders are the only taxa known to regularly recycle webs (58, 60, 61). Sheet and cobweb weavers do not consume their own webs, whereas spider kleptoparasites (Argyrodoxinae) consume silk from their host orb webs, suggesting it is a valuable resource. Although often interpreted as a mechanism to economize on the protein in silk (58, 61), we suggest that web recycling may have to do with recovery of materials in the viscid glue itself (see also ref. 60), explaining why derived orbicularian taxa lost this behavior.

We suspect that other factors also played important roles in diversification of derived orb-weaving spiders. Many theridiids specialize on ants, an ecologically dominant resource avoided by other spiders. Moreover, both theridiids and linyphiids spin highly 3-dimensional webs that allow escape from common predators of orb spiders, especially parasitic wasps (4). Finally, although the evolution of extreme stereotypy in spinning behaviors appears to have been a crucial prerequisite for the transition from substrate defined sheet webs to architecturally defined aerial orbs, subsequent loss of that stereotypy may then allow continued diversification of web shape and thus occupation of novel niches (62, 63). In other words, like the orb architecture itself, stereotypy of spinning behaviors is not an evolutionary end point but rather a stepping stone that allows for new web architectures to evolve.

Summary. Silk use is central to spider ecologies and our analyses reveal how evolutionary shifts in web production likely relate to the diversification of major spider radiations. Both molecular and morphological data support single origins for both orb and RTA clade spiders. We argue that the evolution of aerial orb webs and the evolution of webless hunting strategies were crucial for these 2 groups to escape the constraints of ancestral, substrate-defined cribellate prey capture webs. In the case of the orb, its symmetrical design is distinguished from ancestral webs by an overall architecture defined by the spinning behaviors of the spider, rather than the shape of its microhabitat location. However, the orb is certainly not the final apex of web design. Our analyses also demonstrate subsequent rampant transformation of the orb into other architectures, suggesting that the origin of stereotypical orb webs provides a critical gateway for the evolution of novel web types and the diversification associated with them.

Methods

Taxon, Gene, and Morphology Sampling. We selected 44 species from 24 families (Table S1) to broadly represent modern orb spiders, hypothesized outgroups, and distantly related spiders. To test monophyly of orbicularian spiders we included 4 genera from 2 families of cribellate orb weavers, 14

genera from 4 families of ecribellate orb weavers, and 9 genera from 5 families that morphological evidence place as descendants of orb-weaving ancestors but who now spin nonorb architectures or no prey-catching webs at all. We sampled 17 genera from 13 families as potential outgroups, including the nicodamids *Megadictyna*, *Nicodamus* and *Novodamus*, several representatives of the diverse RTA clade, Oecobiidae, and Austrochilidae, and the more distantly related Haplogynae and Mygalomorphae.

We used routine DNA extraction, amplification, and sequencing methods for partial fragments of 2 mitochondrial (16S rRNA) and 4 nuclear (18S rRNA, 28S rRNA, H3, *wingless*) loci, providing ≈4,600 bp of data (Table S2). Five loci were used in previous studies of spider phylogeny (29, 64, 65). However, our study includes a new marker for spider systematics, *wingless* gene (*wnt1*), that we obtained by modifying lepidopteran primers (66) to match spider cDNA sequences (*Cupiennius* (67) and *Achaearanea* GenBank accession no. AB167808).

We assembled a morphological matrix from the literature (8, 19, 42, 62, 68–74), extracting 143 characters (SI Appendix, section 5). Ten genera lacked morphological data, which led to the construction of 2 matrices: The full 44 taxon dataset missing some morphological/ethological data, and a reduced dataset of 34 taxa for which both molecular and morphological/ethological data were available for all taxa. In 5 cases, we used morphological data from closely related genera to complete the 34 taxon matrix [*Thaïda* for *Austrochilus* (Austrochilidae), *Tricholathys* for *Mexitlia* (Dictynidae), *Steatoda* for *Latrodectus* (Theridiidae), *Linyphia* for *Neriene* (Linyphiidae) and *Neoramia* for *Agelenopsis* (Agelenidae)]. Missing data were scored as question marks.

Phylogenetic Analysis. We conducted 64 different analyses, using 4 phylogenetic approaches—a model-based approach (Bayesian), equal weights MP, implied weights MP, all for 2 different alignments of ribosomal data, and an implied alignment approach (POY). We analyzed molecular data in isolation and combined with morphological data for both the full and reduced datasets. Finally, we analyzed the morphological data alone as a 65th analysis. Details are in SI Appendix.

Ancestral Character Reconstruction. We reconstructed ancestral characters in Mesquite 2.5 (75) to examine trait evolution and test the single origin of the orb web, using both equal-weights MP and ML [one parameter MK1 model (76)].

Web Homology. The extreme regularity of orbs makes their coding straightforward. Indeed, similarity in architecture and spinning behaviors leads to the a priori hypothesis of orb homology that we test herein. Most other webs appear, at least superficially, less regular such that recognizing potential homologies among distantly related taxa is difficult.

We delimit diagnostic characteristics (see SI Appendix) to differentiate potentially homologous categories of sheet webs. Eight major web categories emerge: simple terminal line webs (*Ariadna*, *Plectreurus*); brushed sheet webs (*Euagrus*, *Oecobius*, and, secondarily, *Agelenopsis*); irregular ground sheet webs (*Callobius*, *Megadictyna*, *Dictyna*, *Mexitlia*, *Badumna*); irregular aerial sheet webs (*Austrochilus*, *Megadictyna*); stereotyped aerial sheet webs (*Erigone*, *Linyphia*, *Pimoida*); cobwebs, or sticky gumfooted thread webs (*Steatoda*, *Spintharus*, *Phoroncidia*); bolas webs (*Mastophora*) and orb webs (*Acanthepeira*, *Araneus*, *Argiope*, *Cyrtophora*, *Gasteracantha*, *Gertschanapis*, *Leucauge*, *Meta*, *Metellina*, *Nephila*, *Nephilengys*, *Phonognatha*, *Tetragnatha*, *Zygiella*, *Deinopsis*, *Hyptiotes*, *Uloborus*, *Waitkera*). This categorization ignores the type of sticky silk in webs because it seems to be far less conservative evolutionarily than web architecture. For instance, cribellate silk is often lost in derived lineages (37).

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