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The phylogenetic placement of Psechridae within Entelegynae and the convergent origin of orb-like spider webs

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Abstract

Evolutionary convergence of phenotypic traits provides evidence for their functional success. The origin of the orb web was a critical event in the diversification of spiders that facilitated a spectacular radiation of approximately 12 000 species and promoted the evolution of novel web types. How the orb web evolved from ancestral web types, and how many times orb-like architectures evolved in spiders, has been debated for a long time. The little known spider genus *Fecenia* (Psechridae) constructs a web that resembles the archetypal orb web, but morphological data suggest that Psechridae (*Psechrus* + *Fecenia*) does not belong in Orbiculariae, the 'true orb weavers', but to the 'retrolateral tibial apophysis (RTA) clade' consisting mostly of wandering spiders, but also including spiders building less regular webs. Yet, the data are sparse and no molecular phylogenetic study has estimated *Fecenia*'s exact position in the tree of life. Adding new data to sequences pulled from GenBank, we reconstruct a phylogeny of Entelegynae and phylogenetically test the monophyly and placement of Psechridae, and in doing so, the alternative hypotheses of monophyletic origin of the orb web and the pseudo-orb versus their independent origins, a potentially spectacular case of behavioural convergence. We also discuss the implications of our results for Entelegynae systematics. Our results firmly place a monophyletic Psechridae within the RTA clade, phylogenetically distant from true orb weavers. The architectural similarities of the orb and the pseudo-orb are therefore clearly convergent, as also suggested by detailed comparisons of these two web types, as well as the spiders' web-building behaviours and ontogenetic development. The convergence of *Fecenia* webs with true orbs provides a remarkable opportunity to investigate how these complex sets of traits may have interacted during the evolution of the orb.

Key words: *Fecenia* – *Psechrus* – orb web – evolution – convergence

Introduction

Spiders are a model system for the phylogenetic study of adaptation; for instance, orb-weaving spiders provide a test case for investigating the importance of homology versus convergence in adaptive evolution (Coddington 1994). They also illustrate how phylogeny elucidates the origins of sexual size dimorphism (Coddington et al. 1997; Hormiga et al. 2000). Finally, silk production and web-spinning behaviours provide a powerful example of the role of key innovations for species diversification (Bond and Opell 1998). In particular, innovations associated with the evolution of the araneoid orb web helped make these spiders dominant predators of insects in most terrestrial ecosystems.

The elegant architecture of the spider orb web (Fig. 1) represents a highly efficient snare for flying insect prey (Eberhard 1986; Blackledge et al. 2011). The orb is a derived web architecture that contrasts with most other types of spider webs in being suspended in the air column by a discrete framework of silk threads. The orb's size and shape are therefore predetermined by this framework, and the web targets a unique set of prey – flying insects – in contrast to ancestral web types (Blackledge et al. 2009). The orb web depends upon two distinct types of silk to capture flying insects – dry stiff dragline silk dissipates prey energy as the insects impact webs while highly extensible adhesive capture silk then retains the insects long enough to be subdued by the spider (Blackledge et al. 2011; Blackledge 2012). The dragline silk produced by orb spiders is notably stronger and tougher than in other taxa (Swanson et al. 2006), while the viscid capture silk is a unique homology in orb spiders and their derived kin (Eberhard 1982; Opell 1997; Blackledge et al. 2011). The evolution of orb webs therefore required significant

innovations in both web-spinning behaviours and the production of silk (Blackledge et al. 2009, 2011; Harmer et al. 2011). In addition to making orb spiders dominant predators of flying insects in many terrestrial ecosystems, the innovations necessary to spin orb webs also facilitated the origin of new types of webs, in particular major radiations of cobweb and sheet web-spinning spiders (Blackledge et al. 2009).

More than 95% of all extant orb spiders coat their capture threads with viscid glue that consists of adhesive glycoproteins surrounded by an aqueous cocktail of low-molecular weight molecules. However, a few species employ dry cribellate adhesive silk that adheres through van der Waals forces, depending on the thin diameters and high surface areas of the numerous dry fibrils (Blackledge et al. 2011). Orb spiders are therefore categorized as ecribellate if they coat their capture spiral with viscid glue or cribellate if they use dry adhesive silk. Viscid capture silk requires its aqueous coating for adhesion while the cribellate fibrils must remain dry to maintain high surface area, suggesting that the two types of orb webs might have evolved independently of one another. Thus, the origin of the spider orb web, and especially whether the orb web evolved more than once, has been the subject of a long debate (Kaston 1964; Kullmann 1972; Eberhard 1982; Coddington 1986a,b; Garb et al. 2006; Blackledge et al. 2009). However, recent advances in both morphological and molecular phylogenetics more or less settled the issue in favour of Coddington's (1986a) hypothesis of a single origin of the orb web, where cribellate capture threads transitioned to viscid capture threads, followed by various modifications of the orb leading to aerial sheet webs, cobwebs and other architectures (Griswold et al. 1998; Eberhard et al. 2008; Kuntner et al. 2008, 2010; Blackledge et al. 2009). Orbs, therefore, are monophyletic despite substantial diversity in the details of their architectures among various taxa.

Determining how the orb derived from ancestral webs, however, remains a challenging question, as the sister group of Orbiculariae (cribellate + viscid orb weavers) has not been

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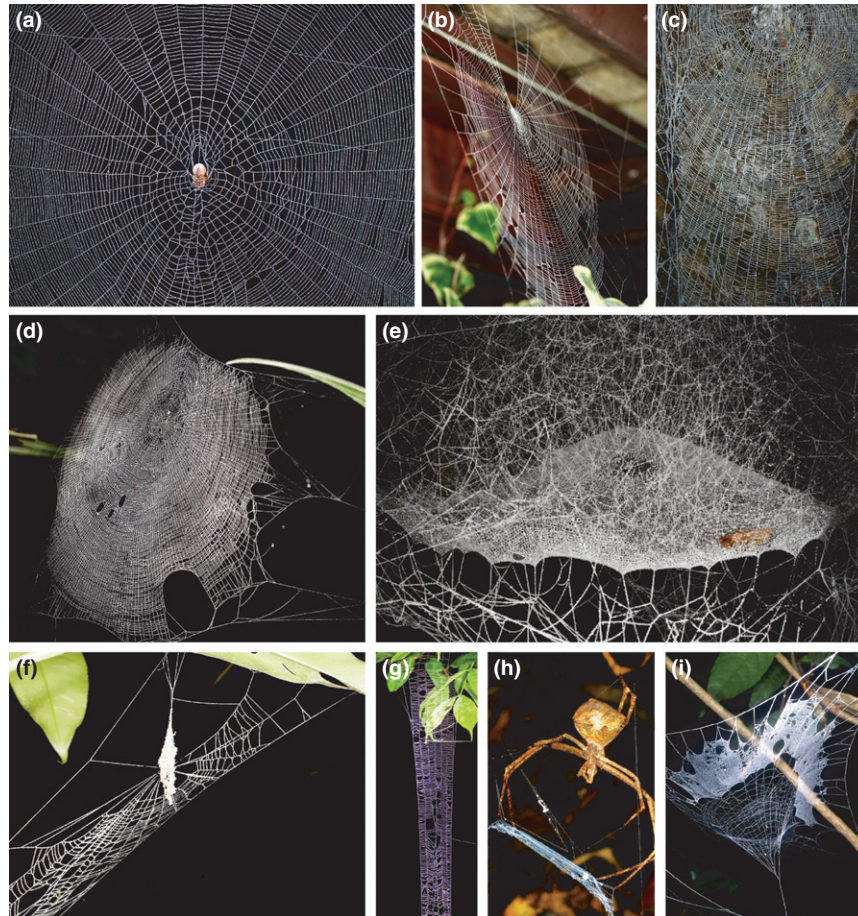


Fig. 1. Typical and modified orb webs of orbicularian spiders: (a) *Deliochus* sp. (Australia); (b) *Zyiella x-notata* (Slovenia); (c) *Clitaetra episinoides* (Mayotte); (d) *Nephila pilipes* (Singapore); (e) *Mecynogea* sp. (French Guiana); (f) *Spilasma* sp. (French Guiana); (g) *Scoloderus* sp. (French Guiana); (h) *Menneus capensis* (South Africa); (i) unknown uloborid (Australia)

determined with any certainty. Candidate taxa include the 'retrolateral tibial apophysis (RTA) clade' (Coddington and Levi 1991), *Megadictyna* Dahl 1906 and Nicodamidae Simon 1897 (Griswold et al. 1998, 1999), and all entelegyne families (Griswold et al. 1999; Coddington 2005). Two recent analyses utilizing molecular data find that Nicodamidae including *Megadictyna* is instead a part of Orbiculariae, and suggests the RTA clade, possibly plus Hersiliidae and Oecobiidae, as the sister lineage of orb weavers (Blackledge et al. 2009; Dimitrov et al. 2012). Another difficulty is that the orb web is so derived that identifying architectural homologies in potential sister lineages is challenging. Planar, aerial webs are almost unique to Orbiculariae. Even derived orbicularian sheet and cobwebs bear little resemblance to the ancestral orbs (Barrantes and Eberhard 2010; Blackledge et al. 2011). The web of *Fecenia* Simon 1887 (Psechridae) provides a provocative exception. *Fecenia* builds a web referred to as a 'pseudo-orb' (Robinson and Lubin 1979; Bayer 2011). The pseudo-orb is architecturally similar to the 'true' orbs spun by Orbiculariae (Fig. 2) in consisting of an array of non-sticky radial threads, upon which adhesive capture 'spirals' are laid, resulting in a two-dimensional aerial web that at least superficially includes the defining elements of true orbs (Blackledge et al. 2011). However, structural similarity among orbs and pseudo-orbs has not been investigated in detail (e.g. Robinson and Lubin 1979).

The phylogenetic affinities of Psechridae, especially the 'pseudo-orb'-weaving *Fecenia*, are unclear. A recent taxonomic revision of *Fecenia* (Bayer 2011) did not test its phylogenetic

position, nor that of Psechridae. Only a single phylogenetic study, based on 68 morphological characters, included *Fecenia* (Griswold 1993), but the study ignored web structure. The other psechrid genus, *Psechrus* Thorell 1878, has been included in both morphological (Griswold 1993) and molecular (Fang et al. 2000) studies, but again these analyses used few data and sparse sampling of taxa. The web of *Fecenia* might link it to Orbiculariae, while the presence of the RTA on the male palps instead indicates a placement within the RTA clade, as supported by both prior studies (Griswold 1993; Fang et al. 2000). However, the placement of the RTA clade itself is far from resolved (Blackledge et al. 2009; Dimitrov et al. 2012). Thus, current phylogenetic data present ambiguous results for testing alternative hypotheses about the origin of the pseudo-orb web. Could it be that (1) *Fecenia* branches off early in the evolutionary history of RTA, perhaps implying a common and earlier origin of orb-like webs than previously thought? Or, (2) could the RTA be convergent in *Fecenia* and it be sister to true orb weavers? Or (3) is rather the *Fecenia* 'pseudo-orb' an example of convergence?

Here, we test the phylogenetic placement of *Psechrus* and *Fecenia* by adding the sequences of these genera to data pulled from GenBank, mostly from the studies of Blackledge et al. (2009) and Miller et al. (2010). We test the three alternative hypotheses for the origin of pseudo-orbs and discuss the implications of our findings for Entelegynae phylogenetics. We then discuss the similarities and differences in the biology and web architecture between the orb and the pseudo-orbs in the light of these results.

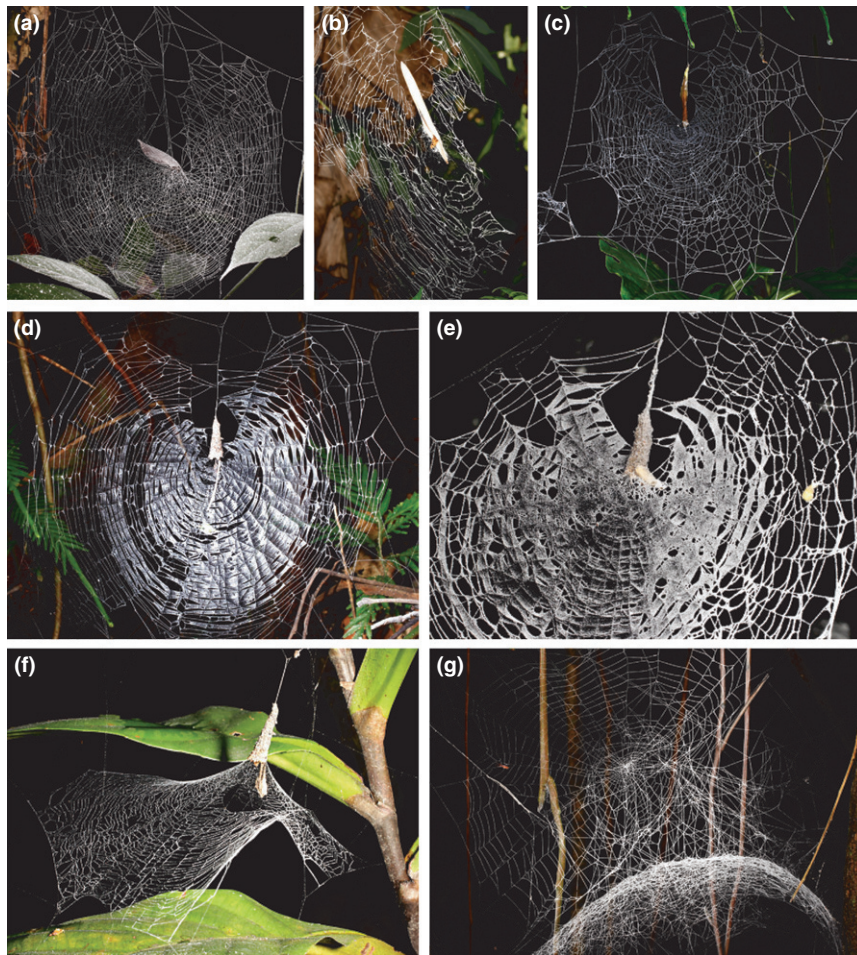


Fig. 2. Orb webs, pseudo-orb webs or proto orbs? Representatives of Psecchidae: (a–e) *Fecenia* spp. (a) Malaysia; (b) Halmahera; (c, d) New Britain; (e) Singapore; (f) *Fecenia* sp. juvenile web architecture with horizontal web (Singapore); (g) *Psecchus* sheet web (below, horizontal) providing substrate for uloborid orb (*Philoponella*, above, vertical)

Methods

A *Fecenia* specimen was collected from MacRitchie Reservoir Park, Singapore, and another in New Britain, Papua New Guinea, and the specimen of *Psecchus* was collected from Pulau Ubin, Singapore. We then used the QIAGEN DNeasy Tissue Kit (Qiagen Inc., Valencia, CA, USA) to extract DNA from one or two legs of each specimen. We amplified partial fragments for two mitochondrial (16S and COI) and four nuclear (18S, 28S, H3 and wingless) loci using primers and amplification protocols as described in Blackledge et al. (2009). Amplified fragments were sequenced in both directions by Macrogen Corporation (GenBank accession numbers KC011009–KC011021). Sequences were assembled with Phred (Green and Ewing 2002) and Phrap (Green 2009) via Mesquite (Maddison and Maddison 2012), using the Chromaseq module (Maddison and Maddison 2011). Sequences were also proofread using Chromaseq in Mesquite. We then created a large data matrix of orb-weaving spiders and their relatives, RTA clade spiders with putative morphological affinity to *Fecenia*, and a variety of potential outgroups. In addition to our sequenced taxa, we pulled taxa and sequences from two published matrices: the ‘orbicularian matrix’ (Blackledge et al. 2009) and the ‘RTA matrix’ [Miller et al. 2010; enlarged from Spagna and Gillespie (2008)], and further added the lycosoids *Sosippus* and *Anoteropsis*, the former of which is web-building. The full dataset is 5723 bp; however, none of the included species have data for all genes, missing data range from 24% to 84%. We aligned the protein coding genes in Clustal W (Thompson et al. 1997), while the ribosomal sequences were aligned using MAFFT through the EMBL-EBI online portal. We used default settings except by increasing the thoroughness of the alignment algorithm by choosing the maximally detailed alignment parameters offered by that service, with

100 tree rebuilding replications and 100 max iterations. For all analyses, gaps were treated as missing data. Our matrix includes taxa that diverged over 100 million years ago. Most gaps occur in regions where alignment appears ambiguous and treating gaps as informative can add unwarranted weight to the most ambiguous regions (e.g. Agnarsson et al. 2007).

The matrix was assembled and curated in Mesquite (Maddison and Maddison 2012), and data partitions were exported from Mesquite for model choice. Phylogenetic figures were also made in Mesquite and later exported to Adobe Illustrator CS6 for final editing.

MODELTEST v0.1.1 (Guindon and Gascuel 2003; Posada 2008) estimated the best model of nucleotide substitution for each gene, and for each codon position in the case of the protein coding genes COI and H3. We analysed the data matrices using Bayesian inference and maximum likelihood (ML). We partitioned each gene and codon position (COI and H3) for a total of 10 partitions. For each partition, we employed the corresponding model of evolution during the Bayesian analyses: GTR + Γ + I for COI^{1st}, COI^{2nd}, 16S, 18S, 28S, H3^{3rd}, GTR + Γ for H3^{1st} and Wingless; HYK + Γ + I for COI^{3rd}, and JC for H3^{2nd}.

We ran the MC³ (Metropolis coupled Markov chain Monte Carlo) chain in MRBAYES V3.1.2 (Huelsenbeck and Ronquist 2001) for 10 000 000 generations, sampling every 1000 generations. Chain stationarity and appropriate burnin were verified using TRACER 1.5 (Drummond and Rambaut 2007), and the first 10% of the trees were discarded as burnin.

Maximum likelihood analyses were performed in GARLI 2.0 (Zwickl 2006), with the same data partitioning and models as in MRBAYES. ML searches were repeated 100 times, and the tree maximizing likelihood of the data was preferred.

Results

The phylogenetic analysis recovers a monophyletic RTA clade with a monophyletic Psecridae nested deep within it, among the lycosoids. Psecridae (*Fecenia* + *Psechrus*) is sister to Oxyopidae Thorell 1870 and these in turn sister to a clade containing Pisauridae Simon 1890 and Lycosidae Sundevall 1933. Some of the close relatives of Psecridae are thus also web builders, but none build webs resembling orbs. The phylogenetic results, thus, refute the homology of the orb and pseudo-orb webs, but rather point towards their convergence.

In the Bayesian analysis, the root of Entelegynae (Orbiculariae + Eresidae + Oecobiidae + RTA) is placed in between Deinopoidea and the remaining members of the clade, thus Orbiculariae is not monophyletic. Rather, it forms a grade with Deinopoidea sister to a monophyletic Araneoidea, plus the clades Eresidae, Oecobiidae plus Hersiliidae and the RTA clade. The phylogenetic network (Fig. 3) is consistent with monophyly of each of these groups, however, and in the likelihood analysis, the root placement is instead between Orbiculariae and the remaining Entelegynae (Fig. 3). The instability of root placement may relate to long branches linking the outgroups to the Deinopoidea (Fig. 3); recent studies of these clades (Blackledge et al. 2009; Miller et al. 2010; Dimitrov et al. 2012) have differed primarily in taxon sampling and in the placement of the root, suggesting more extensive outgroup data are necessary to robustly place the root. Depending on root placement, our results are consistent with Eresidae (Miller et al. 2010), or the entire remaining Entelegynae as sister group of Orbiculariae. Other than root placement, the Bayesian and ML analyses resulted in nearly identical trees; results of the ML analysis are available from the authors.

The 'canoe tapetum' clade, RTA plus Orbiculariae (Griswold et al. 1999, 2005), however, is not recovered regardless of root placement. Araneoidea here includes the nicodamids *Nicodamus*, *Novodamus* and *Oncodamus* (see also Blackledge et al. 2009; Dimitrov et al. 2012), but not *Megadictyna*. While all families within Orbiculariae are recovered as monophyletic (if accepting the recently proposed Zygiellidae), many of the families and superfamilies within the RTA clade are rejected.

Discussion

The pseudo-orb versus the true orb

We provide the first robust phylogenetic test of the origin of the pseudo-orb webs spun by *Fecenia*, testing their possible monophyly with the true orb-weaving Orbiculariae.

The results from our analysis clearly refute the hypotheses that suggest an evolutionary link between the orbicularian orb and the *Fecenia* pseudo-orb. The similarities between the *Fecenia* pseudo-orb and the true orb, especially the highly regular radial threads and capture spiral, are instead clearly convergent. Webs of other non-Orbiculariae entelegyne spider vary enormously in architecture (see figures in Griswold et al. 2005). Few, however, bear any resemblance to orb webs, though a few, like *Badumna* and *Matachia* (see Griswold et al. 2005, fig. 205) make somewhat regular webs. Other similarities these webs share with orb weavers, however, are more widespread and found in various other RTA clade spiders. *Fecenia* places a curled leaf retreat in the centre of its web as seen in many araneoids (Robinson and Lubin 1979; Kuntner et al. 2008). If disturbed when hiding in the retreat, *Fecenia* drops off web, secured on a dragline (Robinson and Lubin 1979), as typical in many orb weavers. The evolution of these traits remains to be tested through ancestral character reconstruction of leaf use and drop-off escape mechanisms.

The convergence hypothesis is further supported by differences in the structural details of the webs, such that the

resemblance of pseudo-orbs to true orbs is limited mostly to the general architectural theme of adhesive lines laid down more or less regularly over supporting radial spokes (Robinson and Lubin 1979, fig. 1). Like true orb spiders, *Fecenia* first builds non-adhesive supporting threads radiating from a central retreat (or hub in the case of true orbs), and later adds adhesive capture silk on top (Robinson and Lubin 1979). However, the radiating threads are not as regularly spaced as in true orbs (Robinson and Lubin 1979). The capture silk in true orb webs is produced as a single continuous spiral, consisting of two closely appressed fibres and, in the case of primitive orb weavers, adhesive cribellate silk fibrils (Vollrath and Edmonds 1989; Foelix 2010). *Fecenia*, in contrast, never spins a complete spiral, instead spinning discrete bands of silk that often zigzag back and forth across the web surface (Robinson and Lubin 1979). A somewhat similar pattern is seen in some other RTA clade members, such as *Badumna* (see Griswold et al. 2005, fig. 205 B) that builds a two-dimensional web using tangentially parallel instead of radiating non-sticky threads, covered with a zigzag of cribellate adhesive threads (see also Marples 1959; Simo et al. 2011). The two core fibres of the capture silk of *Fecenia* are also often broadly separated from one another, in contrast to true orbs, particularly at the junctions with radial threads. Unlike true orbs, the web in *Fecenia* changes ontogenetically from a conical, tented web with a debris retreat in juveniles to a pseudo-orb with a curled leaf retreat in subadults and adults. *Fecenia* also builds long-lasting webs, persisting for up to several weeks (Robinson and Lubin 1979) as do some cribellate orb weavers. Ecribellate orb weavers, however, typically renew their webs daily (Carico 1986; Foelix 2010). *Fecenia* combs out adhesive cribellate silk with legs IV, as do other cribellate spiders, and attaches it with dabs of abdomen (Robinson and Lubin 1979, fig. 3). Other detailed web-building behaviours are not reported in the literature; thus, a direct comparison with orbicularian stereotypical movements during web-building (e.g. Eberhard 1982) is impossible. Cribellate true orb weavers (Uloboridae) use fourth leg movements as in *Fecenia* when laying the cribellate spirals, which differs from the behaviours of derived ecribellate orb weavers (e.g. Araneoidae, Tetragnathidae and Nephilidae), who use legs only to locate the attachment points, then lay down the sticky spiral directly with their spinnerets (Eberhard 1982).

The web of *Fecenia* captures both flying and jumping prey. The cribellate capture silk has anecdotally high adhesiveness, and in contrast to most orb weavers, *Fecenia* webs hold lepidopterans extremely well (Robinson and Lubin 1979). *Fecenia* sometimes starts its approach towards prey in an inaccurate direction, only later correcting its heading. This suggests that these webs transmit information about the location of prey less efficiently than true orb webs (Robinson and Lubin 1979). Prey can escape quickly from orb webs so that fast response times are important (Blackledge and Zevenbergen 2006; Nakata and Zschokke 2010). In orb webs, spiders usually orient quickly towards prey by following strongly directional vibrations transmitted by the radii (Masters 1984). *Fecenia* attack behaviours also differ markedly in several respects from orb weavers (Robinson and Lubin 1979). *Fecenia* bite the prey first, then subsequently attach silk on several spots (Robinson and Lubin 1979), but do not fully wrap prey as is typical of most araneoids (Eberhard 1982; but, see Kuntner et al. 2008 for exceptions).

The monophyly and placement of Psecridae and Entelegynae systematics

Within the RTA clade, Levi (1982) proposed three characters that might help place Psecridae: cribellum, grate-shaped tapetum

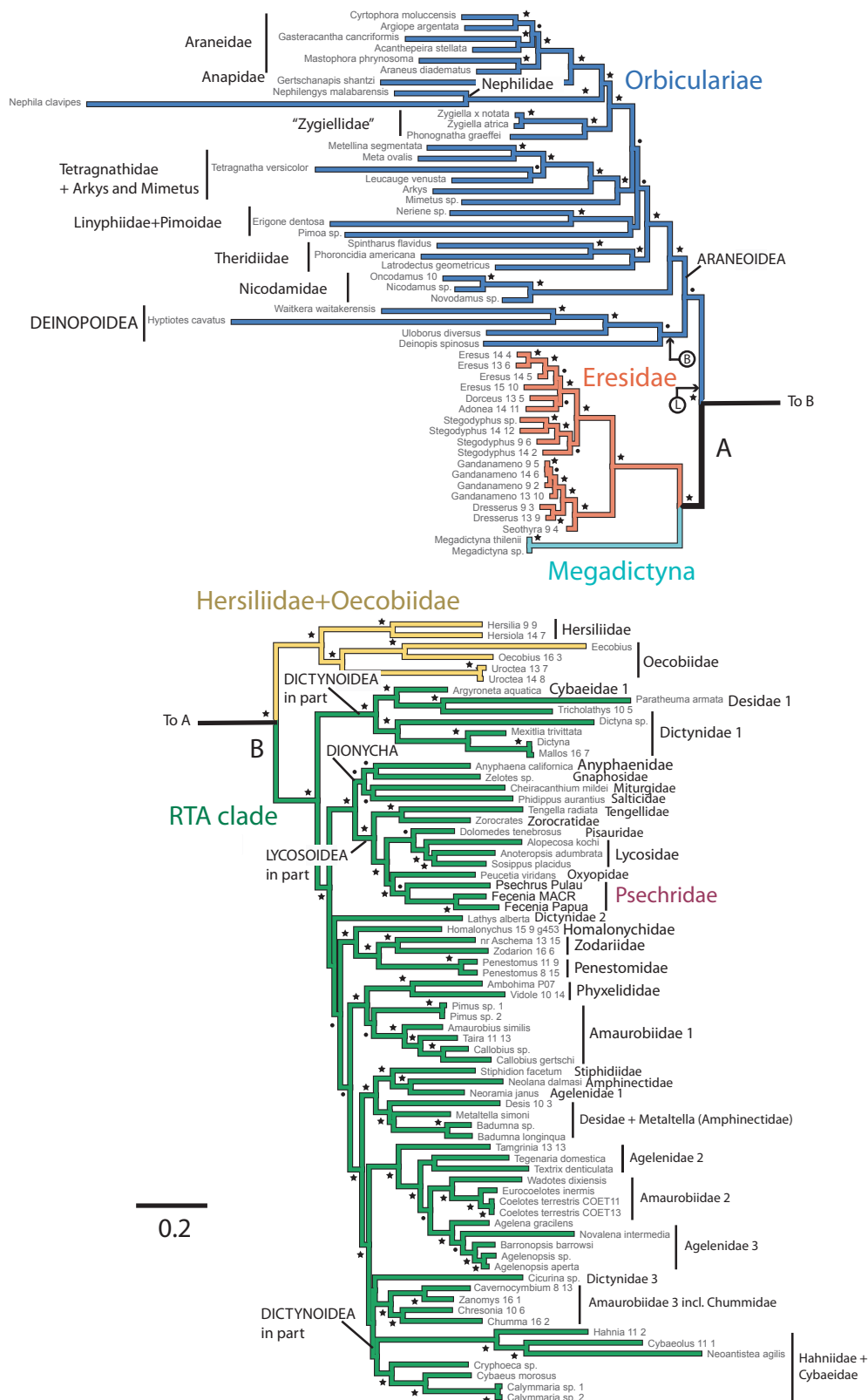


Fig. 3. Results of the Bayesian analysis of Entelegynae spiders, depicted as an unrooted network. A, depicts the part of the network comprising Orbiculariae, Eresidae and *Megadictyna*, while B, shows the retrolateral tibial apophysis (RTA) clade plus Hersiliidae and Oecobiidae. The Psecridae are distant from the true orb weavers, Orbiculariae and nested deep within the RTA clade. The family is surrounded by spiders either building irregular webs, or not building webs at all. Thus, these results support the convergent origin of orb-like webs in *Fecenia*. The phylogeny is congruent with taxonomy, except in the RTA clade where many family level taxa are not recovered as monophyletic. The different root placement suggested by the Bayesian (B) and Likelihood (L) analyses is indicated by a \uparrow symbol. Stars indicate posterior probability support of 100%, circles support of 75–99%; the few nodes with lower support lack a symbol

and female carrying egg sacs in the chelicerae. The grate-shaped tapetum is present in some members of Lycosoidea, such as Lycosidae Sundevall 1833, Pisauridae and Ctenidae Keyserling 1877. Pisaurids and ctenids furthermore carry their egg sacs in the chelicerae. All these lycosoids lack a cribellum; however, the cribellum is a primitive trait that is lost repeatedly (Spagna and Gillespie 2008; Miller et al. 2010) and several RTA lineages contain both cribellate and ecribellate taxa. Our results, therefore, support Levi's suggestion regarding Psechridae's affinity to pisaurids, though here they group sister to Oxyopidae. Further testing of the exact placement of the family is needed as our matrix includes only a relatively small sample of RTA taxa. Nevertheless, Fang et al. (2000) also supported affinity of psechrids, oxyopids and pisaurids, and Miller et al. (2010) found that the lycosoids grouped with Dionycha, the latter a group that also contains Salticidae. The clade Lycosoidea plus Dionycha is also supported here, although with a modified Lycosoidea, and Psechridae clearly belongs to this clade.

As in the analysis of Miller et al. (2010), our results are consistent with Eresidae as the sister group of Orbiculariae, depending on root placement of Entelegynae. Blackledge et al. (2009) did not include Eresidae, so it is difficult to discuss the different affinities of Orbiculariae between these studies. The study of Dimitrov et al. (2012) is the only one to date to simultaneously include a large sample of eresids, orbicularians and members of the RTA clade. That analysis united the taxon sampling of diverse studies and proposed the sister taxon of Orbiculariae as the remaining Entelegynae (RTA clade plus Oecobiidae + Hersiliidae). The different answers obtained from each of these analyses revolve primarily around different taxon sampling and different root placement, and highlight the need to include more nuclear markers for a greater number of taxa to robustly resolve Entelegynae phylogenetics and positively identify the sister group of Orbiculariae.

Conclusion

In conclusion, the *Fecenia* web bears a striking similarity in overall architecture to the true orb webs spun by Orbiculariae. However, our phylogenetic results leave little doubt that this similarity is convergent. The evolution of the spider orb web was a singular event that helped spiders to gain access to novel resources and facilitated their diversification. The success of orb webs as insect traps depends on much more than simply their general shape – the material properties of silks (Opell and Bond 2001; Swanson et al. 2006), the stickiness of the capture spiral (Opell 1997; Agnarsson and Blackledge 2009; Sahni et al. 2011) and the mechanical dissipation of energy (Cranford et al. 2012; Sensenig et al. 2012) are all critical determinants of prey capture. The convergence of *Fecenia* webs with true orbs therefore provides a remarkable opportunity to begin to investigate how these complex sets of traits may have interacted during the evolution of the orb.

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