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Spiders did not repeatedly gain, but repeatedly lost, foraging webs

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Much genomic-scale, especially transcriptomic, data on spider phylogeny has accumulated in the last few years. These data have recently been used to investigate the diverse architectures and the origin of spider webs, concluding that the ancestral spider spun no foraging web, that spider webs evolved *de novo* 10-14 times, and that the orb web evolved at least three times. In fact, these findings principally result from inappropriate phylogenetic methodology, specifically coding the *absence* of webs as logically equivalent, and homologous to, 10 other observable (i.e. not absent) web architectures. "Absence" of webs is simply inapplicable data. To be analyzed properly by character optimization algorithms, it must be coded as "?" or "-" because these codes, and these alone, are handled differently by such algorithms. Additional problems include critical misspellings of taxon names from one analysis to the next (dropping even one taxon affects taxon sampling and results), and mistakes in spider natural history. In sum, methodological error: 1) causes character optimization algorithms to produce illogical results, and 2) does not distinguish absence from secondary loss. Proper methodology and corrected data instead imply that foraging webs are primitive for spiders and that webs have been lost ~5-7 times, not gained 10-14 times. The orb web, specifically, may be homologous (originated only once) although lost 2-6 times.

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Abstract

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23   the last few years. These data have recently been used to investigate the diverse architectures
24   and the origin of spider webs, concluding that the ancestral spider spun no foraging web, that
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30   these codes, and these alone, are handled differently by such algorithms. Additional problems
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32   taxon affects taxon sampling and results), and mistakes in spider natural history. In sum,
33   methodological error: 1) causes character optimization algorithms to produce illogical results,
34   and 2) does not distinguish absence from secondary loss. Proper methodology and corrected
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36   7 times, not gained 10-14 times. The orb web, specifically, may be homologous (originated only
37   once) although lost 2-6 times.

Introduction

39   "Not all living spiders spin webs, but since 1950 web-building species have been found in
40   almost all the families of spiders once thought of as wandering hunters. It now seems likely that
41   all spiders who actively hunt their prey, or use little or no silk in prey capture, are descendants of
42   web builders." Shear (1994).

43   The evolution of silk use and web architectures, in particular the origin, modification, and/or
44   loss of the orb web is one of the more fundamental questions in spider biology. Although the
45   ancestral spider has always been presumed to employ silk in prey capture, modern spiders do
46   spin two rather different kinds of orb webs whose homology is hotly debated: the Uloboridae
47   and Deinopidae with mechanically adhesive micro-threads produced by the cribellum—a special
48   spinning plate—and the araneoids with viscid glue produced by two pairs of specialized silk
49   spigots. In the decades preceding the 1980's, arachnologists generally hypothesized that the
50   cribellate and viscid silk orb weavers were reciprocally monophyletic and only distantly related;
51   under this scenario the two kinds of orb webs were convergent.
52   Lehtinen (1967) and Forster (1970) most prominently argued that the cribellum was primitive
53   for araneomorph spiders, and that ecribellate lineages, including araneoids, evolved from
54   cribellate ancestors. If true, they jointly refuted the best argument for orb web convergence and
55   orb weaver polyphyly. Orb weavers--the Orbiculariae—were arguably monophyletic, (reviewed
56   in Coddington, 1986b; Coddington & Levi, 1991, Miller et al., 2010). This 'single origin'
57   hypothesis found evidence in silk gland and spigot morphology as well as observations of
58   similar web-building behaviors – often identical stereotypical means of laying down similar
59   threads (Eberhard, 1982; Coddington, 1986a, 1986b, 1986c; reviewed in Eberhard, 1990).
60   Skeptics countered that web architecture was strongly selected, that the orb itself was adaptive
61   and likely convergent, and that morphological and behavioral similarities could be explained
62   away (e.g. Kovoor & Peters, 1988).
63   Although the behavioral and morphological evidence seemed compatible with monophyly,
64   molecular evidence repeatedly questioned orb weaver monophyly. Early targeted gene
65   analyses were largely discounted due to sparse taxon sampling and the perceived inadequacy
66   of the genes sampled (e.g., rRNA and mtDNA genes, Agnarsson, Coddington, Kuntner, 2013).
67   However, Bond et al. (2014) and Fernández et al. (2014) assembled massive phylogenomic
68   datasets that clearly refuted orbicularian monophyly. Both placed the cribellate orb weavers
69   close to the RTA clade, which includes a vast number of cursorial, non-web building taxa, like
70   jumping and wolf spiders.
71   If Orbiculariae was not monophyletic, could the two sorts of orb webs nevertheless be
72   homologous? Phylogenomic data analyzed by Bond et al. (2014) and Garrison et al. (2016)
73   supported homology, but the orb evolved earlier than previously supposed and was lost several
74   times (the ancient origin hypothesis). Comparative and functional morphology (spinneret spigots
75   and silk glands) and behavior (stereotypical motor patterns) analyzed under maximum likelihood
76   support the ancient origin hypothesis. Recent genomic studies suggest that the novel
77   flagelliform and aggregate silk genes found in the viscid orbweavers (Araneoidea) are most
78   closely related to each other (Babb et al. 2017). Their simultaneous origin makes functional
79   sense if the viscid orb web originated from the cribellate silk orb web.
80   Fernández et al. (2018, hereafter F&al) recently analyzed new transcriptomic data to add
81   important taxa to the phylogenomic spider tree (Bond et al. 2014; Fernández, Hormiga, &
82   Giribet, 2014; Garrison et al., 2016). F&al has an odd, but relevant history. First published in
83   April 2018, with data in a repository, the authors in June issued an "erratum" that 1) modified
84   their homology hypothesis on web variation, 2) altered their conclusions on web evolution, 3)
85   changed the original data in the repository, and 4) resulted in a new publication, with little trace
86   of the original publication or data.

87   Their June corrected data and publication confirmed orbicularian polyphyly. Their homology

88   hypothesis for web architectures refuted the single origin hypothesis (Blackledge et al., 2009;

89   Bond et al., 2014; Garrison et al., 2016). They found that orb webs and their associated

90   behaviors and machinery evolved 3-6 times. More surprisingly, prey capture webs evolved

91   approximately 14 times across spiders from a webless ancestor. These are bold claims of

92   convergent evolution—and a stark departure from most other modern studies.

93   When closely examined these inferences of convergence, either of webs in general or orbs,

94   derive more from what we regard as inappropriatein phylogenetic methods than from the data

95   (although we do dispute some facts, see below). All character optimization algorithms assume

96   that the digits representing character states code for observable, real phenomena. The only

97   exception is missing or inapplicable data, both by convention coded as "?". F&al, however,

98   coded absence of webs using digits (states "6" and "8"), and, given the taxon sample, "no

99   foraging web" optimizes as the ancestral spider condition. But "absence" of webs is not the

100   presence of anything. Absence codes in the data matrix could mean missing, if the taxon is

101   thought to possess a character state, or inapplicable if it is known to lack one, as in this case.

102   Optimization algorithms purposely treat "?" as a special case, different from digits. Given how

103   optimization algorithms work, coding web absence as an observed state (a digit) rather than "?"

104   affects the results.

105   To disentangle the effects of this practice, as well as the relevant shifting data, figures, and

106   publications from April until June, we attempt to duplicate their results to investigate the effect of

107   this methodological choice (composite coding, Strong & Lipscomb, 1999) (and a few empirical

108   mistakes), and to reanalyze their emended data (and our emendations to that) to assess

109   whether web building in spiders evolved 10-14 times, and the orb web 3-6 times.

110   The objectives of this paper are threefold. First, we justify in more detail below why coding

111   absence as the presence of something homologous and coordinate to observable web

112   architectures yields illogical results in this case, as well as disputing some empirical details.

113   Second, we reanalyze the F&al June dataset (with their altered data but methodological

114   problems fixed) to show that webs are primitive and homologous for spiders. Finally, we show

115   that the orb web single origin hypothesis is still reasonable and supported by data, and

116   recommend future improvements to homology hypotheses on web evolution.

117   Properly analyzed, the evidence suggests that prey capture webs are an ancient trait of all

118   spiders. They did not independently evolve 10-14 times. Orb webs may be homologous as orb

119   webs.

120

Materials & Methods

122   To test for the effect of methodological errors on results, we attempted to replicate F&al's

123   results for their transcriptomic data using their corrected web codings. Their original web

124   character was (0) orb; (1) brush sheet; (2) irregular aerial sheet; (3) irregular ground sheet; (4)

125   stereotyped aerial sheet; (5) cobweb; (6) no foraging web; (7) aerial (above ground) silk tube;

126   (8) tubular silk-lined burrows; (9) irregular tangle (not sheet-like). After F&al first published in

127   April, 2018, they published an erratum in June (thanking colleagues for bringing errors to their

128   attention), as well as a new version of the data (supplementary material) and of the publication.

129   The originals are no longer publicly available, although we will provide them upon request. The

130   June version changed 14% (23 of 159 for the transcriptomic matrix) of character states for

131   webs, changed the meaning of state 8 to "no foraging silk-lined burrows," and added a 11th
132   state, (10) terminal line (see Table S1).
133   Our emended data set (Table S1) recodes 58 F&al "no foraging web" terminals as "?". To
134   capture the homology of all spider webs as webs, we include an additional character "webs:
135   present; absent," a method known as reductive coding (Strong & Lipscomb, 1999). We also take
136   issue with an additional 27 codings that we think are factually wrong (Table S1), but generally
137   accepted F&al's re-codings (e.g. adding an 11th state "terminal line" to code *Segestria*) in order
138   to test fairly the effect of reductive versus composite coding (Strong & Lipscomb, 1999). Most of
139   these changes do not affect our two main points (webs are ancestral for spiders and orb webs
140   may be homologous). Examples are that *Hypochilus* spins a "stereotyped aerial sheet," not an
141   "irregular ground sheet," *Scytodes* spins an "irregular aerial sheet," not "no foraging web," and
142   *Cicurina* and *Cepheia* spin 'irregular ground sheet' webs, not 'irregular aerial sheets. Examples
143   that do affect the optimization of webs as ancestral for spiders are *Microhexura, Porrhothele,*
144   *Macro*thele, and *Megahexura* as brushed sheet webs (JE Bond, pers. obs.), rather than
145   "irregular ground sheet." *Promyrmekiaphila,* scored by F&al as having a "brush sheet" builds a
146   trapdoor and burrow (Stockman and Bond 2008; Bond pers. obs.).
147   Because the tree files produced from the F&al study were not freely available, we
148   reanalyzed the F&al preferred matrix (BUSCO_750). Using IQTree version 1.6.4 (Nguyen et al.,
149   2015, Chernomor et al., 2016) we inferred a phylogeny sufficiently similar to that used by F&al
150   to test the effect of alternative web codings. Character optimizations using the *ape* package
151   (Paradis et al. 2004) 'ace' were checked against those reported by F&al to assess repeatability
152   with our tree and their downloaded data matrix (Fig. S1).
153   We prefer to use the R package *corHMM* (Beaulieu et al. 2013) on an ultrametric tree to infer
154   ancestral character states. The 'rayDISC' package specifically accommodates character
155   polymorphisms and missing data. Character optimizations using equal (ER), symmetric (SYM),
156   and all rates different (ARD) models were explored for these data using 'rayDISC' (*corHMM*).
157   The *ape* package 'ace,' on the other hand, does not handle such data natively, but requires
158   modification to the package code itself and in our experience often passed errors for complex
159   character optimizations with many states and missing/inapplicable data (e.g. the ER, SYM, and
160   ARD models failed at times). Because the results differed moderately based on the model used,
161   AICc scores were employed to select a statistically preferred model.
162

Results

164   We were unable to replicate exactly the online corrected results reported by F&al using the
165   'ace' character reconstruction. Although aspects of the ancestral state reconstruction in our
166   analysis match approximately, orbs evolve four, not three times independently (Fig. S1 versus
167   F&al Figure 3A).
168   This disparity apparently arises because their web optimization (F&al Figure 3A) includes
169   only 158 terminals—omitting *Pararchaea* – which is present in F&al Figure 1A (thus 159
170   terminals). F&al misspelled *Pararchaea as "Pararchea."* If taxon tree and matrix labels in 'ace'
171   do not match exactly, the tip is dropped, which of course affects optimizations. F&al scored
172   *Pararchaea* as "no foraging web" and it fell in the clade sister to tetragnathids. Rather than
173   maintaining a larger probability of an orb web weaving ancestor (with subsequent loss further up
174   the tree) the webless *Pararchaea* shifts the ancestral reconstruction for tetragnathids more

175   towards a webless ancestor. As such misspellings are easy to miss in such a large tree, it is
176   possible that more of the orb web optimizations reported by F&al may be short by one additional
177   origin (F&al Table 1). F&al's corrected figures and data still contain spelling errors (e.g.
178   "*Euryops*" instead of *Euryopis*); other results may need to be checked. Taxon sampling strongly
179   affects inferred ancestral states.
180   Optimizing web presence/absence on these data (Fig. 1A and S2) shows that webs are
181   ancestral with ~6 subsequent losses (ARD AICc = 135.7375). This optimization contradicts
182   F&al, whose results inferred no foraging web as the ancestral spider condition. Irregular aerial
183   sheet webs derived independently three times from "no foraging web," and brushed sheets
184   twice. Cob webs and stereotypical aerial sheets are the only architectures clearly derived from a
185   web building ancestor in F&al's optimization.
186   "Non-foraging silk-lined burrows" is a webless condition and consequently mygalomorphs
187   coded as such should have been scored as "no foraging web" under F&al's corrected character
188   state scheme. If the F&al scoring is modified to reflect that change (all taxa with state '8' receive
189   the webless score '6') spiders optimize as having no foraging web plesiomorphically (i.e., spider
190   are unequivocally primitively webless; Fig. S3, based on an ER model (AICc = 375.491).
191   Using our corrected character matrix (Table S1), orbs (Figs. 1B, S4 ER model, AICc =
192   222.8629, the ancient origin hypothesis) may have evolved once. The ancestral spider spun a
193   web, although which architecture remains ambiguous. In general, optimized ancestral states at
194   deep nodes are also ambiguous. The RTA clade, for example, exhibits a number of web
195   architectures, with some probability of an orb weaving ancestor. An analysis of F&al's matrix
196   that includes *Pararchaea* that is only further modified by changing "no foraging web" to
197   missing/inapplicable optimizes irregular ground and aerial sheets as the ancestral web
198   architectures with four independent origins of the orb web (Fig. S5).
199

Discussion

201   The most common current use of morphological characters is to map them on molecular trees
202   rather combining them with molecules to infer phylogeny. Mapping legacy homology hypotheses
203   on new trees risks uncritical acceptance of those hypotheses, whereas new phylogenetic
204   topologies can require revisions of homology hypotheses (Grande & Bemis, 1998; Poe & Wiens,
205   2000; Rieppel & Kearney, 2002; Jenner, 2002).
206   Hypotheses of homology start with observations of similarity. These are the primary
207   homology hypotheses (de Pinna 1991) to be tested by congruence. For a meaningful
208   phylogenetic test, a precise circumscription of a character and each of its states is needed
209   (Hawkins et al., 1997; Freudenstein, 2005). Primary homology hypothesizes that two traits are
210   the same by descent.
211   Secondary loss is a classic and pervasive problem in comparative biology (Strong &
212   Lipscomb, 1999). Phylogeneticists therefore approach it with theoretical and methodological
213   attention. The biggest pitfall is to code "absence" or "not X" as coordinate, equivalent, and
214   homologous to a series of real, observable, alternative states, that are, among themselves,
215   putatively homologous (Hennig, 1966; Wagner & Gauthier, 1999; Brower & de Pinna, 2014).
216   When background evidence suggests that all absences represent losses, not primitive
217   absences, this approach tests the homology of secondary losses (e.g. Blackledge et al., 2009).
218   When 'absence' conflates primitive absence and secondary loss, as F&al did (e.g., "no foraging

219   web," "non foraging silk lined burrow," and "no web," all "not" hypotheses), such conflations,
220   viewed as hypotheses of descent or homology, are illogical (de Pinna, 1991; Hawkins et al.,
221   1997; Rieppel & Kearney, 2002). Jenner (2002: 75) identified the problem: "Since most
222   unspecified "absence" states are optimized as plesiomorphies, the reconstructed ground
223   patterns of stem species (nodes) on a cladogram are for many characters entirely ambiguous."
224   More seriously, coding unspecified absence states as homologous to observable states claims
225   homology before it has been tested by congruence, rendering the test tautological at best.
226   Coding variation in spider webs is complicated. Difficult questions include defining webs as
227   such, and, as putative adaptations, what they function to do. Common sense says that webs
228   slow down prey until the predator can attack. Webs can also promote spider speed, enabling
229   prey contact faster than otherwise. The common metric is time: slower prey and faster
230   predators. This more expansive view of the use of silk by spiders to forage expands the
231   discussion from debates about the homology of common or rare architectures, towards when,
232   and how, spiders use, or do not use, silk to improve foraging success. This more inclusive
233   theoretical context is more likely to capture the extensive variation of the use of silk by spiders in
234   foraging, and thus may provide a more stable context for future theoretical and empirical work.
235   Pre-cladistic attempts at coding web architectures suggested implicitly homologous
236   categories such as burrow, tube, sheet, cob, and orb webs, and a smattering of odd
237   architectures that did not fit into any other category (Comstock, 1912; Kaston, 1964; Kullmann,
238   1972; reviewed in Vollrath & Selden, 2007). Informed by phylogenetic theory, arachnologists
239   atomized behavior and morphology into multiple homology hypotheses (e.g. Blackledge et al.
240   (2009) coded 47 characters pertinent to spinnerets, webs, and behaviors). Usable observations
241   were overwhelmingly limited to orb weavers and their relatives because their behavior and
242   morphology was patterned and lent itself to phylogenetic analysis.
243   Blackledge et al. (2009) (and Garrison et al., 2016) attempted to leapfrog ignorance about
244   non-orbweavers by using a phylogenetic perspective to update the earlier theory that whole web
245   architectures could be homologized. They proposed nine states, one of which was, indeed,
246   webless. Although technically the same methodological error as attributed to F&al, whether that
247   error actually results in any particular analysis in illogical findings depends on the taxon sample
248   and the distribution of states. Insofar as two Blackledge et al. (2009) co-authors (Coddington,
249   Agnarsson) are also coauthors here, we can affirm that coding absence of webs as a coordinate
250   state to other architectures was carefully checked, and found to be innocuous, as all absences
251   were secondary losses—very different from the current example.
252   Nevertheless, in retrospect Blackledge and co-authors should have used the more rigorous
253   reductive coding. Coding absences as coordinate to other, real phenomena is probably never
254   the best idea, and possibly always bad. We should have, as we do here, coded the presence or
255   absence of webs as a controlling variable, with variation in web architecture coded only for taxa
256   with webs, and webless taxa scored as inapplicable. Although the absence of this good idea did
257   not affect the results of Blackledge et al. (2009), it strongly affects the results of F&al.
258   F&al emphasize that the orb web evolved three times. We show above that their own
259   character hypothesis, properly analyzed (and assuming the inclusion of *Pararchaea*), implies
260   four origins (taxon sampling matters!). Both the three or four origin results depend on coding "no
261   foraging web" as a real, observable state ("6") rather than as inapplicable data ("?"). When "no
262   foraging web" is coded as inapplicable data (Fig. 1B), the ancient origin hypothesis is sustained.

263 The webs of all extant orb weavers may be homologous as orbs. So much for orbs evolving 3-6
264 times.
265   Their more startling result is that ancestral spiders spun no webs and used no silk to
266 improve foraging success. Although their June Fig. 3A shows some probability of "non-foraging
267 silk lined burrow," (modified from "no foraging web" in April) and "irregular ground sheet," the
268 former is the same, scarcely disguised, methodological choice, and the latter includes factual
269 errors.
270   F&al apply "non-foraging silk lined burrow" exclusively to liphistiomorphs and
271 mygalomorphs. What does this mean? Both "no foraging web" and "non-foraging silk lined
272 burrow," share the notion of "non-foraging," presumably intentionally. If, therefore, all are coded
273 as "no foraging web," it persists as the ancestral spider condition, as in their April publication
274 (see Fig. S3, ER model, AICc = 375.491).
275   However, we argue that mygalomorph spiders do use silk in prey capture. Most
276 mygalomorphs build foraging webs; that is, the majority of species employ silk either in a sheet
277 web or at a burrow entrance to detect, localize, and manipulate (see above) prey. Although the
278 connection with prey capture is most obvious for mygalomorph sheet webs (Coyle, 1986, Coyle
279 and Dellinger, 1992, Bond and Coyle, 1995), trapdoor spiders employ silk at their burrow
280 entrance and in the door that is used directly in prey detection. Moreover, many trapdoor spider
281 species add silk lines, plant material, and tabs to their burrow entrance to detect prey (e.g.,
282 some nemesiids, actinopodids, cyrtaucheniids, antrodiaetids, and barychelids). Trapdoor
283 covered burrows may not entangle or impede prey, but aspects of the burrow do clearly serve to
284 enhance the sensory capacity of, and speed up the predator. Multiple mygalomorph taxa are
285 attracted to the burrow entrance by vibrations (JE Bond pers. obs.), demonstrating the role of
286 silk in prey detection for these taxa.
287   Ancient uraraneid fossils, and close relatives like *Chimerarachne* (Wang et al., 2018; Eskov
288 & Selden, 2005) may have constructed sheet webs. Recent advances in mygalomorph
289 systematics (Hedin and Bond, 2006; Bond et al. 2012; Hedin et al., 2018) place diplurid and
290 hexathelid (all sheet web weavers) as the sister group to all other non-atypoid mygalomorphs.
291 The uraraneid sister taxon to all spiders, coupled with extensive mygalomorph sampling, could
292 resolve the ancestral spider web condition as a simple sheet web. Reductive coding of presence
293 absence scoring optimizes foraging webs as the ancestral spider condition with secondary web
294 loss.
295

Conclusions

297   Reconstructing the evolution of spider webs remains an exciting yet unstable field of study:
298 not only the origin and evolution of webs, as such, but the origin of the iconic orb web. Given the
299 sensitivity of optimization algorithms to adjacent nodes, taxon sampling will always bedevil
300 conclusions. Other factors include the optimization algorithm used (especially the proper
301 handling of inapplicable/missing data), maximum likelihood rates of change among states, and
302 subjective disagreements about which conceptual state to apply to which observed web
303 architecture. That said, the notion that the single ancient origin hypothesis "crumbles under the
304 weight of additional transcriptomic data coupled with a significantly increased taxon sampling" is
305 premature, especially if based on a publication with as many irregularities as Fernández et al.
306 (2018).

307   Spider genomics and NGS sequencing technologies may presage stable phylogenetic trees
308   for spiders, but they are just beginning to influence fundamental questions about web
309   construction, its underlying genetics, and the emergent phenotype of web architecture. Rather
310   than homologizing whole web architectures, we recommend a more reductionist approach more
311   likely to accommodate new taxa and data. For example: 1) silk use in prey capture; presence or
312   absence of 2) ampullate, 3) piriform, 4) aggregate, 5) flagelliform and 6) cribellate silks; 7) web
313   location and attachment points; 8) prey locomotion (such as web 'designs' focused towards
314   aerial vs pedestrian prey); 9) refugium location; 10) architectural elements (such as disordered
315   vs patterned, ordered or stereotypical); 11) pattern type (for example 2D vs 3D), and more. This
316   approach avoids arbitrary coding of whole webs as loosely defined conglomerate homology
317   hypotheses, and could allow hypotheses of web architectures to emerge from nuclei of
318   concordant, more objective homology hypotheses.
319   Regardless, our best efforts to reanalyze data on web architecture variation in spiders,
320   including careful attention to the treatment of "absence" or inapplicable/missing data, suggests
321   that the ancient single origin of the orb web is feasible. Orb did not originate 3-6 times, and
322   spider webs did not originate 14 times. Their ancestor spun a web. These results, after all, just
323   reinforce prevailing views regarding the evolutionary history of spider webs. They do illustrate
324   the pitfalls of disregarding long accepted rules for coding homology and mis-coding of "absence"
325   characters, in particular. While we do not make the claim that a multiple origin hypothesis is
326   false, we strongly disagree with assertion that a single origin hypothesis has been falsified, let
327   alone that it has 'crumbled' under the force of evidence.
328

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Figure 1(on next page)

Ancestral state reconstruction of foraging webs

Ancestral state reconstruction of foraging webs. A. Ancestral state reconstruction of web presence/absence using the 'rayDISC' function within *corHMM*, with an all rates different model (ARD) model (AICc = 135.7375; note that ER and SYM recover nearly identical optimizations with only minor differences). This hypothesis implies six independent losses of web foraging. B. Preferred ancestral state reconstruction of web types using a corrected character coding scheme (Table S1, modified from Blackledge et al. 2009), the ER model in *corHMM*, and with webless taxa treated as inapplicable (-); tree modified as ultrametric; AICc = 222.8629. This hypothesis implies a single ancient origin of the orb web; spiders primitively use webs for foraging.

A
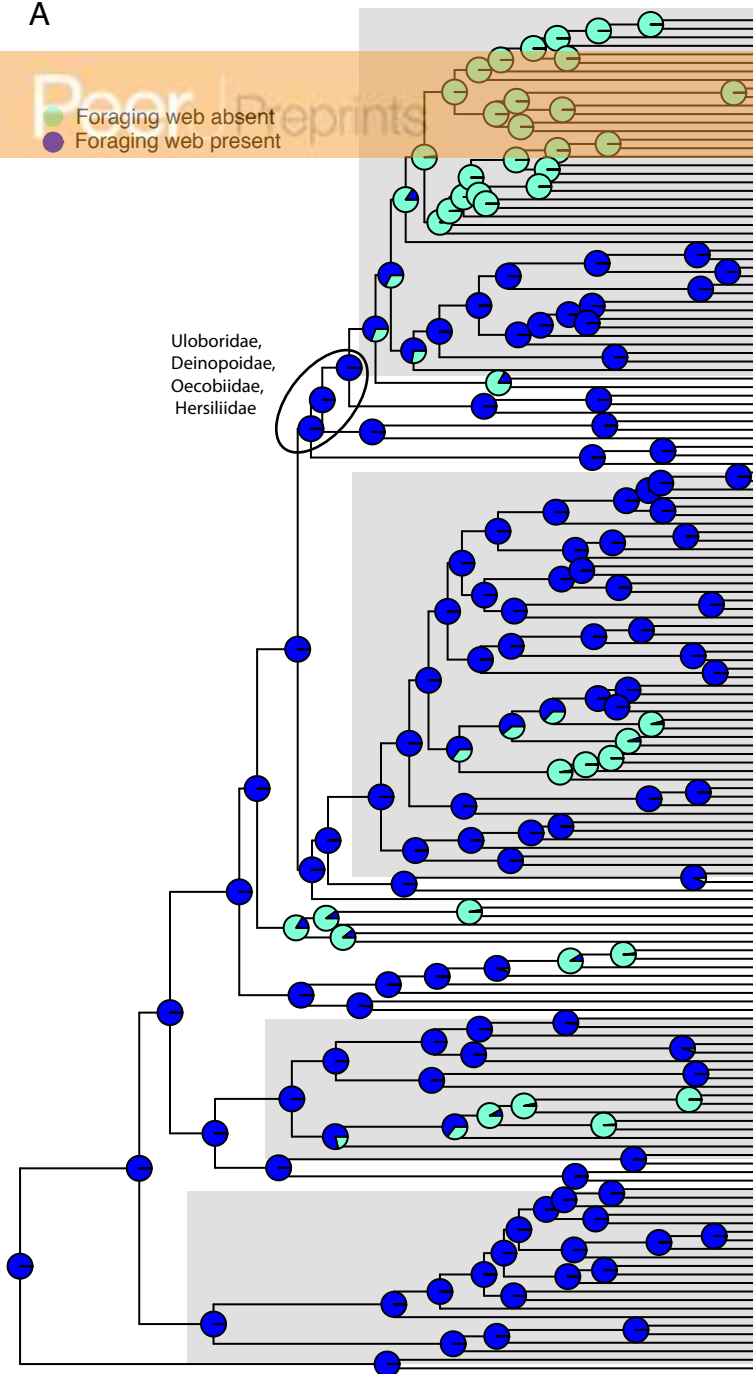
B

Orb web
Sheet web
Irregular aerial sheet web
Irregular ground sheet web
Stereotypical aerial sheet web
Cob web
aerial (above ground) silk tube
Silk lined burrow/trapdoor
Terminal line

RTA

Uloboridae,
Deinopoidae,
Oecobiidae,
Hersiliidae

Uloboridae,
Deinopoidae,
Oecobiidae,
Hersiliidae

Araneoidea

Synspermiata

Mygalomorphae