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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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20 21 Abstract

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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.

38 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. Kooor & 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 inappropriate in 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

121 **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 *Macrothele*, 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

163 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

200 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 conflation,
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&aI 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

296 **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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332

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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

