



Modular patterns in behavioural evolution: webs derived from orbs

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Abstract

Imperfect knowledge of ancestral behaviour often hampers tracing behavioural evolution. This limitation is reduced in orb weaving spiders, because spider orb web construction behaviour and the cues used by modern orb-weavers are well-studied and highly conserved. Several species in orb-weaving families build non-orb webs that are clearly derived from orbs, allowing transitions from ancestral to modern behaviours to be described with high confidence. Three major patterns of general evolutionary significance were found in 69 phylogenetically independent transitions in 15 groups in 8 families: ancestral traits were often maintained as units; the most frequent of the eight different types of ancestral trait change was transfer of an ancestral behaviour to a new context; and 'new' traits that had no clear homology with ancestral traits were also common. Changes occurred in all major stages of orb construction. This may be the most extensive summary of evolutionary transitions in behaviour yet compiled.

Keywords

behaviour modules, behavioural evolution, orb webs, spiders.

1. Introduction

Orb web construction is a classic example of a complex behaviour performed by a small animal with only modest neural equipment (Quesada et al., 2011), and offers opportunities to document how transitions occur in the evolution of behaviour. The evolution of behavioural traits can be traced by using the phylogenetic relations between different groups of animals, and recent ad-

vances have clarified the probable phylogenies of some (but not all) groups of orb-weavers (Coddington, 1986a; Scharff & Coddington, 1997; Kuntner et al., 2008; Lopardo et al., 2011; Garrison et al., 2016; Fernández et al., 2017, 2018). In addition, a gradual accumulation of evidence has demonstrated striking uniformities in the overall organization and execution of the process of orb construction (e.g., the same sequence of similar stages) by species in diverse groups (e.g., Emerton, 1883; Wiehle, 1931; Fukumoto, 1981; Eberhard, 1982, in press; Shinkai, 1982; Coddington, 1986a; Kuntner et al., 2008; Lopardo et al., 2011; Eberhard & Barrantes, 2015). Several somewhat lower-level aspects of orb construction are also uniform across wide taxonomic spans: the identities of the legs that are used to locate the inner loop during sticky spiral construction; the legs that hold different lines while attachments are being made; whether contact with the temporary spiral lines is maintained during early sticky spiral construction; the order of thread placement during radius construction; whether the centre of the hub is removed; whether the transition between hub and temporary spiral construction is abrupt; and whether the temporary spiral is continuous or broken into circles or is omitted entirely (Eberhard, 1982, in press; Kuntner et al., 2008). These traits show consistent differences among higher taxonomic categories such as families and groups of families (Eberhard, 1982; Shinkai, 1982), and are among the most consistently useful phenotypic characters for characterizing higher-level groups of orb weaving spiders (Ramirez et al., 2004; Kuntner et al., 2008; Blackledge et al., 2011; Eberhard & Barrantes, 2015).

This conservatism in the process of orb construction behaviour can be exploited to solve the common difficulty of determining details of the behaviour of ancestors in evolutionary studies. Orb-weaving spiders have repeatedly evolved modified orbs, whose designs are still similar enough to orb webs that the homologies with the lines and construction behaviour in orbs are clear; the derivations of these species from orb weaving ancestors is unquestioned (e.g., Scharff & Coddington, 1997). This combination of uniformity, confidence in phylogenetic relations, and homology means that the behaviour of the orb-weaving ancestors of modern groups that build moderately modified orbs such as those in Figure 1 ('modified orbs' hereafter) can be deduced with unusually good confidence. It is thus possible to confidently deduce the evolutionary changes in behaviour that occurred in several of these groups of species with modified orbs. In addition, because stimuli

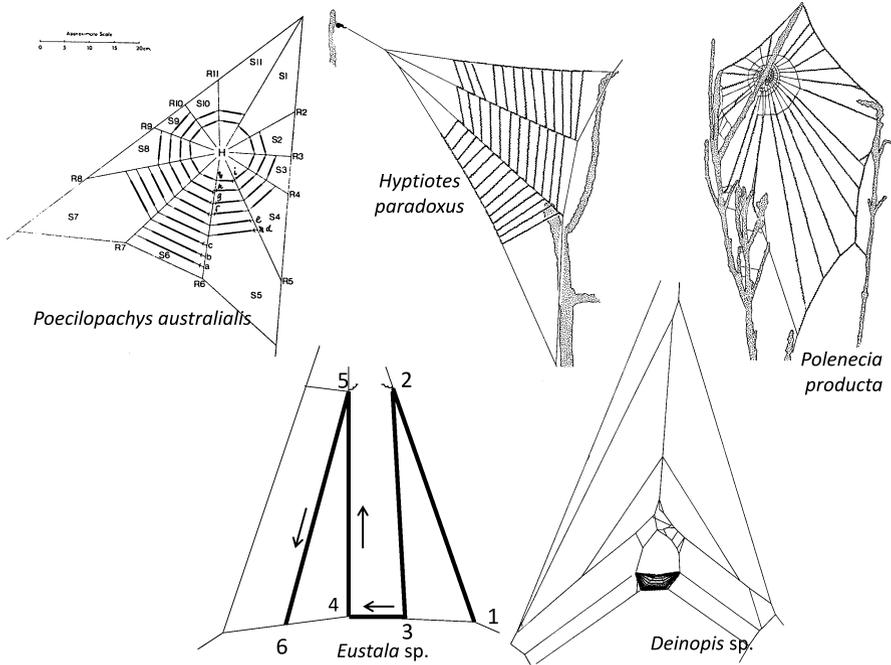


Figure 1. Examples of ‘modified orb’ webs built by adult females of the araneids *Poecilopachys australialis* (from Clyne, 1973), and *Eustala* sp. (from Eberhard, 1985), the uloborids *Hyptiotes paradoxus* (from Marples & Marples, 1937) and *Polonecia producta* (after Peters, 1995), and the deinopid *Deinopis* sp. (from Coddington, 1986b) (scale for *P. australialis*).

from direct contact with lines are used to guide construction (see Eberhard, in press), it is also possible to deduce the probable stimuli that could be available to a spider during certain stages of the construction of modified orbs, using leg lengths and the distances between lines, and to thus deduce some additional evolutionary changes in the stimuli that guide construction behaviour. This paper summarizes published data on the construction of modified orbs in 15 groups in 8 families, and traces the likely changes in a large number of behavioural details and also a few guiding stimuli, thus allowing estimations of the frequencies with which different types of behavioural transitions have occurred in 69 different cases. It may be the most extensive data set on evolutionary behavioural transitions in a single order ever assembled.

2. Material and methods

The species and traits in Table A1 in the Appendix were chosen so that the designs of their webs were sufficiently similar to orbs to allow relatively confident determination of homologies, some of which were mentioned in previous taxonomic works (Eberhard, 1982; Scharff & Coddington, 1997; Griswold et al., 2005; Kuntner et al., 2008). I omitted more substantially modified webs, such as the gumfoot webs of theridiids and nesticids, the hanging curtain webs of *Wendilgarda*, and the single line webs of *Miagrammopes*, that are also derived from orb-weaving ancestors but in which the homologies of web lines and behaviour patterns ('primary' homologies in the terms of Agnarsson & Coddington, 2007) are uncertain. It is possible that, because of this bias, the transitions in my sample are biased in favour of smaller changes that involve recognizable ancestral traits. On the other hand, I see no obvious reason to expect that this bias would favour one type of shuffling of homologous traits over any other.

The probable phylogenetic relations between different modified orb groups (Figure 2) were used to decide which changes in Table A1 should be considered as independently derived, and also to determine some homologies (see footnotes in Table A1). Some details of these phylogenies will probably change in the future, because some aspects of spider phylogeny are unsettled (Agnarsson et al., 2013); few of the interpretations in this paper are likely to be affected, however (see Figure 2, footnotes in Table A1).

3. Results

Table A1 lists 69 different behavioural transitions in 19 genera in eight families. Most changes (91%) involved behavioural details; the others (9%) involved changes in the stimuli guiding construction behaviour. Some of my classifications of transitions are open to alternative interpretations (see footnotes in Table A1), and I will include mention alternative, maximum possible numbers for the types of transitions ('maximum' counts) that were open to alternative interpretations.

There are several clear trends. In the first place, changes were not concentrated in any particular stage of orb construction, but occurred in all major stages. In the sample in this study, changes occurred in about half of the behavioural details that characterized each stage of construction (27 in Table A2 in the Appendix).

Secondly, about two thirds of the 63 behavioural transitions involved recognizable ancestral traits that were shuffled one way or another in the derived species. A third pattern was that the modular evolutionary changes were not limited to one or just a few types of transition: there were changes in the contexts in which ancestral behaviours occurred, the order in they were performed, and the frequencies with which they were performed. The most frequent type among these transitions was to transfer an ancestral behaviour more or less intact to a new context (29%; maximum 35%). The next two most common were to reduce the frequency of an ancestral behaviour or lose it altogether (14%), and increase in the frequency of an ancestral behaviour (13%; maximum 16%). Less common transitions included accentuation of ancestral behaviour (5%), and recovery of an ancestral behaviour that had been lost previously (3%; maximum 5%). ‘New’ traits that had no clear homology with ancestral traits were also common (36%, maximum 40%).

Of the 6 evolutionary changes in the stimuli used to guide construction behaviour, 50% involved the loss of an ancestral stimulus (but persistence of a second, alternative cue with the same function), 33% the use of a new stimulus to guide an ancestral response, and 17% the use of an ancestral stimulus to elicit a new response.

4. Discussion

4.1. General patterns

Classifying some transitions in Table A1 was not simple (see footnotes), and the frequencies of different types of transitions represent only approximations rather than precise measurements. Nevertheless, the clear patterns just mentioned remain substantially similar even if alternative classifications are adopted: no single stage was particularly prone to change; about two thirds of the transitions involved recognizable ancestral behaviours; and the contexts of transitions varied widely. These patterns are accord with other data and arguments which suggest that orb construction is largely composed of semi-independent traits (Eberhard, in press).

This modular pattern occurs at multiple levels of analysis. For instance, lower level traits or sub-units were sometimes even shuffled within a single trait when it was transferred to a different context. In *Nephila pilipes* (= *maculata*) and *N. clavipes*, for example, the tangle of lines in the barrier web built adjacent to the orb was transformed into a reduced, orb-like web

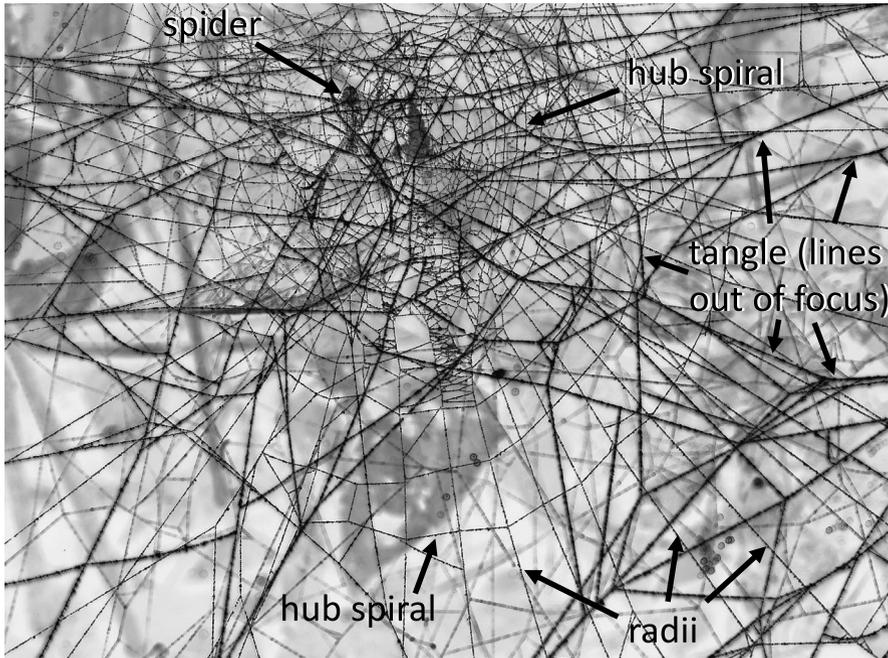


Figure 3. This negative image illustrates the derived ‘resting’ web, a three-dimensional tangle with a more or less vertical planar area in the central portion where the spider rested that was built by an immature *Nephila clavipes* just prior to moulting. Resting webs in this species had several traits transferred from prey-capture orbs, including radial lines converging on a central ‘hub’, a tightly spaced hub spiral, and a short temporary spiral. The attachments of the temporary spiral to the radii differed from those in the typical prey capture orb web of this species, however, in being single rather than double. A double temporary spiral-radius attachment is a derived trait in *Nephila* (Kuntner et al., 2008), so the single attachments in resting webs represent reversion of an ancestral condition.

that consisted of a hub, radii, temporary spiral and frame lines. Some elements of these modified orbs were themselves modified: the attachments of both the ‘radii’ to the ‘frames’ and of the ‘temporary spiral’ to the ‘radii’ in the barrier web reverted to the ancestral single rather than double attachments (Figure 3) (Robinson & Robinson, 1973). Similar shifts of sub-units occurred in the orb-like resting webs built by mature males of *Allocyclosa bifurca* and *Zosis geniculata*, and in the moulting webs of immature *Argiope trifasciata* (Eberhard, 2013, in press). The evolutionary persistence of recognizable ancestral behaviour patterns resembles behavioural evolution in other animals, including both body movements and song components in birds

(Prum, 1990; Price & Lanyon, 2002). The evolution of manakin displays included derived movements within ancestral postures, novel postures within ancestral displays, and initial and terminal additions of novel elements to display sequences (Prum, 1990). These studies treated behavioural characters as present/absent, so it is not possible to compare them with the spiders with respect to possible shifts of the contexts in which units were expressed.

In addition to changes in movements, the cues that were used to direct movements also changed and displayed substantial variation. In some, the ancestor used more than a single cue to orient and guide construction behaviour, and the descendant continued to use only one of these cues, having discarded the other (Nos 9, 24, 49 in Table A1). In others, new stimuli were added to guide ancestral behaviour (Nos 2, 43), and in one an ancestral stimulus came to be used to guide a new response (No. 15).

Of course, evolutionary change classically involves the transformation of ancestral traits into new traits, so finding traces of ancestral behaviour in the derived building behaviour of modern species is not surprising. Nevertheless, the frequently modular or semi-independent nature of these traits is significant, as most of the traits examined were complex and included multiple, lower-level components. It should be noted, however, that the typological process of categorizing behaviour patterns in both ancestral and derived webs may result in some pseudo-modularity.

4.2. Origins of 'new' behaviour

Approximately one-third of the behavioural changes in Table A1 involved novel behaviour patterns. It is possible that many (perhaps all) of the 'new' behaviour patterns would, if examined at lower levels of analysis, be found to include lower-level behavioural traits that were derived from ancestral behaviour. Orb web construction behaviour shows a strong tendency to have large amounts of variation at lower levels of behavioural organization (for example, the details of the movements of different legs), but for adjustments to be made to produce lower variation at higher levels (for example, the sites at which lines are attached) (Eberhard, in press). The lack of variation at higher levels thus often obscures abundant variation at lower levels. Hidden variation of this sort could explain the apparent problem presented by the high frequency of evolutionary transitions in which there were no apparent ancestral precursors.

Take, for example, the 'new' behaviour involved in choosing which radius on which to re-initiate each new segment of sticky spiral in *Poecilopachys*

australasia (Clyne, 1973) (No. 7 in Table A1). Lower level subunits of this ‘new’ behaviour are ancestral, including walking to the attachment site, seizing the radius with legs III and IV, and applying the spinnerets to the radial line between them to initiate a new sticky spiral line by attaching it to the radius. In these respects, this ‘new’ behaviour pattern represents transfers of lower level ancestral traits to a new context. These fine details have almost never been included in published descriptions of web construction (for an exception see Coddington, 1986b), and their variations, which might have given rise to new behaviours, are even less studied.

A example of how quantitative variation in leg movements could affect evolutionary changes in stimuli used to guide behaviour is illustrated by the occasional failures by the araneid *Micrathena duodecimspinosa* to contact the inner loop of sticky line already in place during sticky spiral construction (Eberhard, 2012, in press). Analyses of video recordings showed that spiders usually contacted the inner loop with leg oIV a few tenths of a second prior to the moment at which this leg grasped the radius and the sticky line was attached to it. The details of this oIV leg movement varied, however, and sometimes the leg was not extended all the way to the inner loop, and thus failed to contact this loop before the spider turned to make the attachment. This deprived the spider of one of the two ‘reference point’ cues (distance from the inner loop) that normally guide sticky spiral construction in this species (Eberhard & Hesselberg, 2012; Eberhard, in press). In other words, some small quantitative differences in leg movements had qualitative effects on the stimuli used to guide behaviour. These small variations in leg oIV movements resulted in changes in how sticky spiral construction was guided, as they were associated with changes in where the spiral was attached to the radius: when the point where oIV grasped the radius was farther from the inner loop, the sticky spiral attachment tended to be farther from the inner loop (Eberhard, 2012). Similar variations in making contact with the inner loop during sticky spiral construction occur in other species (Kuntner et al., 2008; Eberhard, in press). More extensive use of video recordings will probably reveal that many of the previous accounts that used behavioural traits as taxonomic characters (e.g., Eberhard, 1982; Kuntner et al., 2008) were overly typological, and that these traits display variations that could sometimes lead to evolutionary change than have been previously recognized.

The origin of a given new behaviour could be of more than one type. Take, for example, the ‘new’ ability of *Poecilopachys australasia* to repeatedly interrupt sticky spiral construction and to initiate successive segments of sticky

spiral line on the same radius (transitions No. 3 and No. 7 in Table A1). The movements of legs, the spinnerets, and probably the muscles associated with silk gland ducts and their valves that are used to initiate each new segment of sticky line were probably simply transferred with little or no modification to this new context. The initiation itself resembled the process when the spider initiated the sticky spiral after terminating the temporary spiral during typical orb construction. In sum, the 'new' behaviour pattern may have resulted from lower-level ancestral components of the new behaviour being transferred to a new context, and may not have been completely new. This is only speculation, however, because the published descriptions do not have enough detail to make direct tests of this hypothesis (or similar hypotheses for other traits in Table A1).

In sum, the evolution of 'new' behaviour may have involved the transfer of pre-existing units of lower-level behaviour to new contexts. The new behaviour could have originated from either shuffling of lower-level traits, or accentuation of variations that already existed. The likelihood of this 'evolve new traits from underlying variation' hypothesis being correct would seem even greater at especially lower levels of analysis, such as muscle contractions.

This explanation hinges on the hypothesis that traits themselves evolve gradually due to changes at lower levels. The possible importance of variation leads to the question of the origins of variations at lower levels. I see three possible extremes. One is the usual, common textbook formulation of evolutionary sequences: the variants on which natural selection acts in the evolution leading to novel traits originally appeared as the results of new mutations. A second possibility is that the variants originally arose due to adaptive flexibility in expression of the phenotypes that was already present in the population, and that the effect of selection favouring such variants was to both alter the frequencies of pre-existing alleles in the population (favouring those better able to produce particular, adaptive flexible responses) and, subsequently, to favour new mutations that further increased this type of variant (West-Eberhard, 2003). This flexibility could result from learning, from cognitive phenomena such as goal directed motivation, or from other processes that trigger behavioural changes in an individual. A third possibility is that the variants arose originally as a result of imprecision in the nervous system (Eberhard, 1990a, 2000). In this case the original variation would be

random with respect to whether or not the differences were adaptive; selection would subsequently favour filters that were imposed on this imprecision that increased the expression of some behavioural variants and the inhibited that of others. I know of no empirical data that link any of these possibilities to the behavioural transitions in Table A1. There is, however, indirect evidence (from web diversity) that imprecision may have been important in the theridiosomatid genus *Wendilgarda* (Eberhard, 2000); similar arguments can be made for the uloborid genus *Miagrammopes* (Eberhard, in press). There are also preliminary indications suggesting the importance of goal-directed motivation in orb weaving spiders. Learning, on the other hand, appears to have little importance in orb construction.

4.3. *Evolutionary recall of lost behavioural traits*

One prediction from the high degree of modularity that characterizes web construction behaviour is that many evolutionary changes will consist of ‘shifting, deletion, and recall of unit traits, like moving furniture’ (West-Eberhard, 2003). As just discussed, the predicted shifting and deletion of behavioural units appear to be widespread in web construction behaviour. There were, however, only four possible reversions (some uncertain) in Table A1 (Nos 47 and 53 in *Hyptiotes*, and Nos 33 and 34 in *Nephila*, and I know of only one other published case of the recovery of an orb web trait that had been lost: the recovery of oval, aerial orb webs in the genus *Nephila* after more basal nephilids lost such webs as they evolved to build vertically elongate orbs against large tree trunks (Kuntner et al., 2008) (Kuntner et al., 2016, subsequently proposed a different sequence, so this interpretation is uncertain). Given the surprising design adjustments that another, distantly related trunk web species, *Telaprocera maudae*, made when spiders were forced to build in an oval space away from a trunk in captivity (Harmer & Herberstein, 2009), the reversion in this case could have resulted at least in part from a change in website choice, rather than from orb construction behaviour per se.

The samples of behavioural traits in the present study were biased against documenting recovery of lost traits, however, as they generally included only one ancestral stage rather than the necessary two ancestral stages, so the rarity of such recovered traits remains uncertain. A recent discovery suggests a much more impressive recovery (of the entire orb itself) in the theridiosomatid *Wendilgarda galapagensis* (D. Cotoras, pers. comm.). This species is

endemic to the humid tropical forests on the depauperate oceanic island Isla del Coco. Other, continental species of *Wendilgarda* are all strictly associated with open water surfaces, to which they attach their sparse, curtain-like webs (Coddington & Valerio, 1980; Coddington, 1986c; Eberhard, 2000); the genus is thought to be descended from an orb-weaving theridiosomatid ancestor (Coddington, 1986c). The Cocos Island species built typical *Wendilgarda* curtain webs over water, but also built at least two and perhaps three other web types unique to this species, and some individuals built two web types on successive days (Eberhard, 1989). A recent discovery indicates that some individuals built orb webs, similar to those of *Theridiosoma* (D. Cotorra, pers. comm. — current studies are checking species identity genetically and morphologically). No other orb weaving spider is known to build such a diversity of web designs (Eberhard, in press).

One possible reversion is the inner loop localization behaviour of the triangle web uloborid *Hyptiotes* (Figure 1; No. 53 in Table A1). Instead of tapping laterally with leg oI as she sidled laterally along the radius, as do all other uloborid orb weavers that have been observed (trait A2 of Eberhard, 1982), the spider faced outward as she moved out the radius to touch the inner loop of the sticky spiral with one leg I. This behaviour was similar to or possibly identical with trait A1, which occurs in several araneoid families (Tetragnathidae, Theridiosomatidae, Anapidae) (leg iI contacts inner loop in A1; this detail was not noted in *Hyptiotes*). Nevertheless, the most likely ancestral state for all orb weavers is A2 (Kuntner et al., 2008), implying that A1 may not have occurred previously in the *Hyptiotes* lineage.

In sum, evolutionary recovery of web construction traits occurs as expected for modular traits, but may be rare. Perhaps evolutionary recovery of web construction traits is more likely across shorter taxonomic distances, and the lack of the necessary phylogenetic detail at lower taxonomic levels in orb weavers has biased observations against documenting recoveries. Other possible reasons why evolutionary recoveries may be less common than losses include the following: a smaller amount of information is needed to produce the loss as opposed to the gain of a trait, so losses may arise more frequently; and the cost of retaining neural structures that are not currently useful for small animals such as orb-weavers may be relatively great (Eberhard & Wcislo, 2011).

4.4. Generalizing to other spiders?

In contrast to the conservatism of web construction behaviour in orb weavers, the web designs in the related ‘tangle web’ family, Theridiidae show rampant homoplasy (Eberhard et al., 2008). This difference with orb weavers may be due, at least in part, to different levels of analysis. The theridiid data concerned higher-level traits in finished webs rather than lower-level behavioural details. Orb weavers show similarly elevated levels of homoplasy in relatively higher level web characters such as stabilimenta, open hubs, the degree of vertical symmetry, and the relative densities of radii and sticky spiral lines (Herberstein et al., 2000; Eberhard, in press). Orb web construction may also be more highly conserved because successful construction of an orb makes high demands on the spider’s abilities to orient precisely and consistently without errors, thus imposing stronger selection favouring stricter controls on some types of variation (Eberhard, 1990a, 2000), or because some aspects of orbs depend more on each other mechanically. Whatever the explanation, it is not possible to trace transitions as confidently in theridiids as in orbs due to the difficulties in deducing ancestral behaviour. The question of whether the patterns found in the transitions of orb weavers can be generalized to other spider groups is thus not yet resolved.

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References

- Agnarsson, I. & Coddington, J.A. (2007). Quantitative test of primary homology. — *Cladistics* 23: 1-11.
- Agnarsson, I., Coddington, J.A. & Kuntner, M. (2013). Systematics: progress in the study of spider diversity and evolution. — In: *Spider research in the 21st century: trends and perspectives*. Siri Scientific Press, Manchester, p. 58-111.
- Blackledge, T.A., Kuntner, M. & Agnarsson, I. (2011). The form and function of spider orb webs: evolution from silk to ecosystems. — *Adv. Ins. Physiol.* 40: 175-262.
- Clyne, D. (1973). Notes on the web of *Poecilopachys australasia* (Griffith & Pidgeon, 1833) (Araneidae, Argiopidae). — *Austr. Entomol. Mag.* 1: 2-29.

- Coddington, J.A. (1986a). The monophyletic origin of the orb web. — In: Spiders: webs, behavior and evolution (Shear, W.A., ed.). Stanford University Press, Stanford, CA, p. 319-363.
- Coddington, J.A. (1986b). Orb webs in “non-orb weaving” ocre-faced spiders (Araneae: Deinopidae): a question of genealogy. — *Cladistics* 2: 53-67.
- Coddington, J.A. (1986c). The genera of the spider family Theridiosomatidae. — *Smithson. Contrib. Zool.* 422: 1-96.
- Coddington, J.A. & Sobrevila, C. (1987). Web manipulation and two stereotyped attack behaviors in the ocre-faced spider *Deinopis spinosus* Marx (Araneae, Deinopidae). — *J. Arachnol.* 15: 213-225.
- Coddington, J.A. & Valerio, C.E. (1980). Observations on the web and behavior of *Wendilgarda* spiders (Araneae: Theridiosomatidae). — *Psyche* 87: 93-106.
- Dimitrov, D., Benavides, L.R., Arnedo, M.A., Giribet, G., Griswold, C.E., Scharff, N. & Hormiga, G. (2017). Rounding up the usual suspects: a standard target-gene approach for resolving the interfamilial phylogenetic relationships of cribellate orb-weaving spiders with a new family-rank classification (Araneae, Araneoidea). — *Cladistics* 33: 221-250.
- Eberhard, W.G. (1972). The web of *Uloborus diversus* (Araneae: Uloboridae). — *J. Zool., Lond.* 166: 417-465.
- Eberhard, W.G. (1975). The “inverted ladder” orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. Araneae: Araneidae. — *J. Nat. Hist.* 9: 93-106.
- Eberhard, W.G. (1982). Behavioral characters for the higher classification of orb-weaving spiders. — *Evolution* 36: 1067-1095.
- Eberhard, W.G. (1985). The “sawtoothed” orb web of *Eustala* sp. (Araneae, Araneidae), with a discussion of ontogenetic changes in spiders’ web-building behavior. — *Psyche* 92: 105-118.
- Eberhard, W.G. (1987). Web-building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). — *J. Arachnol.* 14: 339-356.
- Eberhard, W.G. (1989). Niche expansion in the spider *Wendilgarda galapagensis* (Araneae, Theridiosomatidae) on Cocos Island. — *Rev. Biol. Trop.* 37: 163-168.
- Eberhard, W.G. (1990a). Imprecision in the behavior of *Leptomorphus* sp. (Diptera, Mycetophilidae) and the evolutionary origin of new behavior patterns. — *J. Insect Behav.* 3: 327-357.
- Eberhard, W.G. (1990b). Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. — *J. Arachnol.* 18: 205-234.
- Eberhard, W.G. (2000). Breaking the mold: behavioral variation and evolutionary innovation in *Wendilgarda* spiders (Araneae Theridiosomatidae). — *Ethol. Ecol. Evol.* 12: 223-235.
- Eberhard, W.G. (2012). Correlations between leg positions and spaces between sticky lines in the orbs of *Micrathena duodecimsinosa* (Araneae: Araneidae). — *Bull. Br. Arachnol. Soc.* 15: 235-240.
- Eberhard, W.G. (2013). The polysphinctine wasps *Acrotaphus tibialis*, *Eruga* ca. *gutfreundi*, and *Hymenoepimecis tedfordi* (Hymenoptera, Ichneumonidae, Pimplinae) induce their host spiders to build modified webs. — *Ann. Entomol. Soc. Am.* 106: 652-660.

- Eberhard, W.G. (in press). Spider webs: behavior, function and evolution. — University of Chicago Press, Chicago, IL.
- Eberhard, W.G. & Barrantes, G. (2015). Cues guiding uloborid construction behavior support orb web monophyly. — J. Arachnol. 43: 371-387.
- Eberhard, W.G. & Hesselberg, T. (2012). Cues that spiders (Araneae: Araneidae, Tetragnathidae) use to build orbs: lapses in attention to one set of cues because of dissonance with others? — Ethology 118: 610-620.
- Eberhard, W.G. & Wcislo, W.T. (2011). Grade changes in brain-body allometry: morphological and behavioural correlates of brain size in miniature spiders, insects, and other invertebrates. — Adv. Insect Physiol. 60: 155-214.
- Eberhard, W.G., Agnarsson, I. & Levi, H.W. (2008). Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order. — Syst. Biodiv. 6: 415-475.
- Emerton, J.H. (1883). The cobwebs of *Uloborus*. — Am. J. Sci. 3(25): 203-205.
- Fernández, R., Sharma, P.P., Tourinho, A.L. & Giribet, G. (2017). The Opiliones tree of life: shedding light on harvestmen relationships through transcriptomics. — Proc. Roy. Soc. Lond. B: Biol. Sci. 284: 20162340.
- Fernández, R., Kallal, R.J., Dimitrov, D., Ballesteros, J.A., Arnedo, M.A., Giribet, G. & Hormiga, G. (2018). Phylogenomics, diversification dynamics, and comparative transcriptomics across the spider tree of life. — Curr. Biol. 28: 1489-1497.
- Fukumoto, N. (1981). Notes on the web-weaving activity. — Atypus 78: 17-20.
- Garrison, N.L., Rodriguez, J., Agnarsson, I., Coddington, J.A., Griswold, C.E., Hamilton, C.A., Hedin, M., Kocot, K.M., Ledford, J.M. & Bond, J.E. (2016). Spider phylogenomics: untangling the Spider Tree of Life. — PeerJ 4: e1719.
- Griswold, C.E., Ramirez, M.J., Coddington, J.A. & Platnick, N.I. (2005). Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. — Proc. Calif. Acad. Sci. 56(Suppl. II): 1-324.
- Harmer, A.M.T. & Herberstein, M.E. (2009). Taking it to extremes: what drives extreme web elongation in Australian ladder web spiders (Araneidae: *Telaprocera maudae*)? — Anim. Behav. 78: 499-504.
- Herberstein, M.E., Craig, C.L., Coddington, J.A. & Elgar, M.A. (2000). The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. — Biol. Rev. 75: 649-669.
- Hingston, R.W.G. (1920). A naturalist in Himalaya. — H. F. and G. Witherby, London.
- Hingston, R.W.G. (1922a). The snare of the giant wood spider (*Nephila maculata*). Part I. — J. Bombay Nat. Hist. Soc. 28: 642-649.
- Hingston, R.W.G. (1922b). The snare of the giant wood spider (*Nephila maculata*). Part II. — J. Bombay Nat. Hist. Soc. 28: 911-917.
- Hingston, R.W.G. (1922c). Part III. Further lessons of the *Nephila*. — J. Bombay Nat. Hist. Soc. 28: 917-923.
- Hiramatsu, T. & Shinkai, A. (1993). Web structure and web-building behaviour of *Patu* sp. (Araneae: Symphytognatidae). — Acta Arachnol. 42: 181-185.

- Kuntner, M., Coddington, J.A. & Hormiga, G. (2008). Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. — *Cladistics* 24: 147-217.
- Kuntner, M., Gregorič, M., Cheng, R.-C. & Li, D. (2016). Leaf masquerade in an orb web spider. — *J. Arachnol.* 44: 397-400.
- Lopardo, L., Giribet, G. & Hormiga, G. (2011). Morphology to the rescue: molecular data and the signal of morphological characters in combined phylogenetic analyses — a case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. — *Cladistics* 27: 278-330.
- Lubin, Y.D. (1986). Web building and prey capture in the Uloboridae. — In: *Spiders: webs, behavior, and evolution* (Shear, W.A., ed.). Stanford University Press, Stanford, CA, p. 132-171.
- Lubin, Y.D., Opell, B.D., Eberhard, W.G. & Levi, H.W. (1982). Orb plus cone-webs in Uloboridae (Araneae), with a description of a new genus and four new species. — *Psyche* 89: 29-64.
- Marples, M.J. & Marples, B.J. (1937). Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica*. — *Proc. Zool. Soc. Lond. A* 107: 213-221.
- Opell, B.D. (1979). Revision of the genera and tropical American species of the spider family Uloboridae. — *Bull. Mus. Comp. Zool.* 148: 443-549.
- Opell, B.D. (1982). Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae, Uloboridae). — *J. Arachnol.* 10: 185-191.
- Peters, H.M. (1937). Studien am netz der kreuzspinne (*Aranea diadema* L.). II. Über die herstellung des rahmens, der radialfäden und der hilfsspirale. — *Zeitschr. Morphol. Ökol. Tiere* 33: 128-150.
- Peters, H.M. (1995). *Polenecia producta* and its web: structure and evolution (Araneae, Uloboridae). — *Zoomorphology* 115: 1-9.
- Price, J.J. & Lanyon, S.M. (2002). Reconstructing the evolution of complex bird song in the oropendolas. — *Evolution* 56: 1514-1529.
- Prum, R.O. (1990). Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves: Pipridae). — *Ethology* 84: 202-231.
- Quesada, R., Triana, E., Vargas, G., Seid, M., Niven, J., Douglass, J., Eberhard, W.G. & Wcislo, W.T. (2011). Disproportionately large brains extend into the legs of miniaturized spiders. — *Arthrop. Struct. Dev.* 40: 521-529.
- Ramirez, M.J., Lopardo, L. & Platnick, N.I. (2004). Notes on Chilean anapids and their webs. — *Am. Mus. Novitat.* 3428: 1-13.
- Robinson, M.H. & Robinson, B. (1973). Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. — *Smithson. Contrib. Zool.* 149: 1-76.
- Robinson, M.H. & Robinson, B. (1975). Evolution beyond the orb web: the web of the araneid spider *Pasilobus* sp., its structure, operation and construction. — *Zool. J. Linn. Soc.* 56: 301-313.
- Santos, A.J. & Gonzaga, M.O. (2017). Systematics and natural history of *Uaitemuri*, a new genus of the orb-weaving spider family Uloboridae (Araneae: Deinopoidea) from south-eastern Brazil. — *Zool. J. Linn. Soc.* 180: 155-174.

- Scharff, N. & Coddington, J.A. (1997). A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). — Zool. J. Linn. Soc. 120: 355-434.
- Shinkai, A. (1982). Web structure and construction behaviour of *Cyrtarachne yunoharuensis* strand: is *Cyrtarachne* web an ordinary web? — Atypus 100: 4-12.
- Shinkai, A. & Shinkai, E. (1988). Web structure of *Conoculus lyugadinus* Komatsu (Araneae: Anapidae). — Acta Arachnol. 37: 1-12.
- Stowe, M. (1986). Prey specialization in the Araneidae. — In: Spiders: webs, behavior, and evolution (Shear, W.A., ed.). Stanford University Press, Stanford, CA, p. 101-131.
- Townley, M.A. & Tillinghast, E.K. (2013). Aggregate silk gland secretions of araneoid spiders. — In: Spider ecophysiology (Nentwig, W., ed.). Springer, Heidelberg, p. 283-302.
- Vollrath, F. (1992). Analysis and interpretation of orb spider exploration and web-building behavior. — Adv. Stud. Behav. 21: 147-199.
- West-Eberhard, M.J. (2003). Developmental plasticity and evolution. — Oxford University Press, New York, NY.
- Wiehle, H. (1931). Neue beiträge zur kenntnis des Fanggewebes der Spinnen aus den familien Argiopidae, Uloboridae und Theridiidae. — Zoomorphology 22: 349-400.
- Witt, P.N., Reed, C.F. & Peakall, D.B. (1968). A spider's web: problems in regulatory biology. — Springer, New York, NY.

Appendix

Table A1.

Changes in behavioural details of web construction in the evolution of modified webs derived from orb weaving ancestors. Legs are designated as outer (o) or inner (i) (e.g., leg oI) as the spider moved on the web. Probable derivations shared with other species in the table are indicated in parentheses around the number in the first column. Traits that were used in four previous publications (Eberhard, 1982; Scharff & Coddington, 1997; Griswold et al., 2005; Kuntner et al., 2008) are also indicated in parentheses in the first column; they give, in order, the labels used for these traits in the other publications. Parentheses around the types of change in the third column indicate derived traits that are shared with other closely related species in the table, and were probably derived only once. The references for the species are as follows: Araneidae: *Poecilopachys australasia* (Clyne, 1973), other cyrtarachnines from Stowe (1986), *Eustala* sp. (No. 2045) (Eberhard, 1985) and *Scoloderus* spp. (Eberhard, 1975; Stowe, 1986); Nephilidae: *Nephila clavipes* and *N. maculata* (Hingston, 1922a,b,c; Eberhard, 1982); Mysmenidae: *Mysmena* sp. (Eberhard, 1987); Anapidae: *Conoculus lyugadinus* (Shinkai & Shinkai, 1988); Symphytognathidae: *Patu* sp. (Eberhard, 1987); Theridiosomatidae: *Theridiosoma* (Coddington, 1986c; Eberhard, in press); Uloboridae: *Uloborus conus* and *U. trilineatus* (Lubin et al., 1982), *Polonecia producta* (Peters, 1995) and *Hyptiotes paradoxus* (Marples & Marples, 1937), *H. cavatus* (Eberhard, in press); Deinopidae: *Deinopus* sp. (Coddington, 1986b). Characterization of presumably ancestral behaviour, as suggested by comparisons with the behaviour of typical araneoid and uloborid orb weavers, was based largely on descriptions in the following references: Hingston (1920), Witt et al. (1968), Eberhard (1982), Vollrath (1992) and Eberhard & Barrantes (2015) for araneoids; Eberhard (1972, 1990b), Lubin (1986) and Eberhard & Barrantes (2015) for deinopoids (see Table A2).

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
Araneoidea		
Araneidae		
<i>Poecilopachys australasia</i>		
1. No temporary spiral was built (H, #77, #148, -)	The temporary spiral was laid from the hub outward	Ancestral behaviour was omitted
2. The attachment point for the first loop of sticky line on a radius was influenced by the distance from the hub ¹	The attachment point was influenced by the distance moved from the outer loop of temporary spiral	Ancestral response using a new point of reference
3. The spider repeatedly interrupted sticky line production, and interruptions occurred at consistent sites ²	The sticky spiral was continuous; it was interrupted only very rarely, without any clear pattern in where interruptions occurred	New behaviour ³

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
4. During the repeated interruptions of sticky line construction, the spider moved across the web without producing any new line	The spider never moved on the web without producing a new line, sticky or non-sticky, except during the transition between temporary and sticky spiral	Ancestral behaviour was expressed in a new context ⁴
5. The coat of glue on the sticky line was missing at the beginning and the end of each segment of sticky line	There were only very small interruptions in the glue at the point of attachment to the radius	Ancestral trait was accentuated
6. The spider pulled out sticky line many times with legs IV before reaching the hub after making the previous attachment, rather than before reaching the radius to which the next attachment would be made (probably similar to #81 of Scharff and Coddington (1997), who may have misunderstood Clyne's term 'spanning line')	The spider pulls out line with one or a few movements of legs IV; these usually occur after reaching the radius where the line will be attached	Ancestral trait was accentuated; and Ancestral behaviour was performed in a new context
7. The radius on which to initiate each new loop of sticky spiral was either the same radius as the one chosen for the previous loop, or the next radius above it	No homologous choices were made ⁵	New behaviour
8. The spider consistently alternated directions when initiating sequential sticky lines in the inner portion of the web	No homologous alternations in directions occur	New behaviour

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
9. During sticky spiral construction, the spider did not touch the inner loop of sticky line already built, presumably used the distance moved from the hub as a cue for where to attach (A, No. 78, No. 151, 219) ⁶	Spiders consistently touched the inner loop of sticky line, and used it (in combination with the distance moved along the radius) as a reference to guide placement of current loop	Ancestral responsiveness to one stimulus was lost, but continued to the other
10. Droplets of glue were laid densely on the highly elastic axial line, and sometimes coalesced (–, No. 80, –, –)	Droplets of glue were laid less densely, and did not normally coalesce on the less elastic axial line ⁷	Ancestral trait was accentuated
11. The second attachment of each segment of sticky line to a radius broke easily ('low shear attachments') (–, No. 79, –, –)	All attachments of sticky lines to radii were similar, and were stronger (did not break free easily)	New behaviour ⁸
12. Sticky lines never extended past the retreat radius, and formed (at most) half circles ⁹	Sticky spiral construction was not interrupted on the retreat radius	New behaviour
<i>Paraplectana tsushimensis</i> (3.) The sticky line was interrupted repeatedly ²	The sticky spiral was continuous	(New behaviour ³)
<i>Cyrtarachne bufo</i> (3.) The sticky line was interrupted repeatedly ² <i>Eustala</i> sp. (No. 2345)	The sticky spiral was continuous	(New behaviour ³)
13. The spider attached the sticky line repeatedly to the same radius while moving along the radius toward the hub ¹⁰	The spider attached the sticky line only once at the start of the trip toward the hub (the sticky line crossed radius rather than running along it) ¹¹	Ancestral behaviour (attach line) was repeated

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
14. The spider consistently alternated the direction of circling: in one direction (along the temporary spiral), and then the opposite direction (along the frame) before attaching the sticky line	The spider circled in a single direction (except after turning back)	New behaviour ¹²
15. Contact with a previously laid sticky line induced termination of the sticky spiral line	Contact with a previously laid sticky line was used as a guide to determine where to attach the next loop of sticky line on the radius No clear homology	Ancestral stimulus released new response
16. The spider doubled the sticky line that was laid along a radius when returning toward the hub on radii that were attached to the substrate rather than to a frame line	The spider attached the sticky line to radii only	New behaviour
17. The spider attached the sticky line to frame lines as well as to radii <i>Scoloderus</i> spp.	The temporary spiral was left intact (convergence with Nos 26–24) (H, No. 77, –, No. 216)	Ancestral behaviour was performed in a new context
Anapidae <i>Conoculus lyugadinus</i>	The spider attached sticky spiral lines only to radii	Ancestral behaviour was performed in a new context; also
19. The spider attached some sticky spiral lines to the surface of the water directly below the orb ¹³	The spider walked only along non-sticky lines during sticky spiral construction	New behaviour ¹⁴ New behaviour ¹⁵
20. The spider climbed the sticky line after attaching it to the water		

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
21. The spider lengthened radii by moving a short distance from the hub and breaking the radius, turning 180° and attaching a drag line to the broken end, releasing additional drag line to lengthen the radius while returning to the hub, and then attaching the lengthened radius there ¹⁶	Radius lengths were modified early during exploration using similar behaviour, but were never modified after the radius was built	Ancestral behaviour was performed in a new context ¹⁷
22. The spider removed the first hub (built just following radius construction) entirely after finishing the sticky spiral, and then rebuilt it, lengthening the radii and sometimes circling outward in the process ¹⁸	The spider left the hub built during and immediately following radius construction intact, except (in some species) for removing central portion	Ancestral behaviour (hub construction) was performed in a new context
23. The spider omitted the temporary spiral (convergence with No. 1)	The spider built a temporary spiral	Ancestral behaviour was omitted ¹⁹
<i>Anapisona</i> spp. (21.) The spider lengthened the radii by moving a short distance from the hub and breaking the radius, turning 180° and attaching a drag line to the broken end, releasing additional drag line to lengthen the radius while returning to the hub, and then attaching the lengthened radius there ¹⁶	Radius lengths were modified early during exploration with similar behaviour, but were never modified after they were built	(Ancestral behaviour was performed in a new context ¹⁷)

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
(22.) The spider removed the first hub (built following radius construction) entirely after finishing the sticky spiral, and then rebuild it, lengthening the radii and sometimes circling outward in the process ¹⁸	The spider built the hub during and immediately following radius construction, left it intact except (in some species) for removing central portion	(New behaviour)
(23.) The spider omitted the temporary spiral (convergence with No. 1)	The spider built a temporary spiral	(Ancestral behaviour was omitted ¹⁹)
24. During sticky spiral construction, the spider did not touch the inner loop of sticky line already built, presumably using instead the distance moved from the hub as a cue (convergence with No. 9)	The spider consistently touched the inner loop of sticky line, and used it as a reference point to guide placement of current loop	Ancestral responsiveness to one stimulus was lost, but continued with respect to the other ²⁰
Mysmenidae <i>Mysmena</i> sp.		
(24.) During sticky spiral construction, the spider did not touch the inner loop of sticky line already built, presumably using instead as a cue the distance moved from the hub (convergence with No. 9)	The spider consistently touched the inner loop of sticky line, and used it as a reference point to guide placement of current loop	(Ancestral responsiveness to one stimulus was lost, but continued with respect to the other ²⁰)
25. There was no perceptible pattern in the sequence of radii to which the sticky spiral was attached	Most sticky spiral attachments were to adjacent radii in the same approximately horizontal plane; a few were to the radii above the hub that, judging by lines in finished webs, were usually not adjacent ²¹	Ancestral behaviour was omitted

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
<i>Symphytognathidae</i>		
<i>Patu</i> sp.		
26. Spider added supplementary radii after sticky spiral construction was finished	No radii were added following sticky spiral construction	Ancestral behaviour was expressed in a new context
27. Supplementary radii were doubled, forming a 'V' at the frame (F, No. 76, No. 146 and No. 211) ²²	No 'V' was formed, as the provisional radial line built during secondary radius construction was cut and reeled up as the spider moved back to hub	New behaviour
(21.) The spider lengthened the radii by moving a short distance from the hub and breaking the radius, turning 180° and attaching a dragline to the broken end, and then releasing additional dragline to lengthen the radius while returning to the hub and attaching the lengthened radius there ¹⁶	Radius lengths were modified early during exploration with similar behaviour, but were never once they were built	(Ancestral behaviour was expressed in a new context ¹⁷)
<i>Theridiosomatidae</i>		
<i>Naatlo splendida</i> , <i>Theridiosoma</i> spp., <i>Ogulnius</i> sp.		
(24.) During sticky spiral construction, the spider did not touch the inner loop of sticky line already built, presumably instead using as a cue the distance moved from the hub (convergence with No. 9)	Spiders consistently touched the inner loop of sticky line to use it as a reference point to guide placement of current loop	(Ancestral responsiveness to one stimulus was lost, but continued with respect to the other ²⁰)
<i>Epeirotypus</i> spp., <i>Theridiosoma gemmosum</i> , <i>Epilineutes globosus</i>		

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
28. The temporary ‘spiral’ was circular, forming one or two circles Nephilidae <i>Nephila</i> spp	The temporary spiral was approximately a spiral	New behaviour ²³
29. The spider used leg IV to locate inner loop of sticky spiral, and used its location as a reference point to guide sticky spiral construction	The spider used leg I for this task	New behaviour ²⁴
30. The spider left the temporary spiral intact (convergence with #18)	The spider removed the temporary spiral during sticky spiral construction	Ancestral behaviour was omitted
31. The temporary spiral in the orb was attached twice to each radius it crossed	The temporary spiral was attached only once to each radius it crossed	Ancestral behaviour was repeated
32. A ‘barrier web’ tangle, at least some of which was ‘orb-like’ in organization, was built beside the approximately vertical orb	No barrier web was built	Ancestral behaviour was expressed in a new context
33. Each radial line in the barrier web ‘orb’ was attached to the frame line with a single attachment	Each radial line in the orb was attached twice to the frame	A lost ancestral behaviour was recovered ²⁵
34. The temporary spiral in the barrier web ‘orb’ was attached only once to each radius it crossed (reverse change in No. 31)	The temporary spiral in the orb was attached twice to each radius it crossed	A lost ancestral behaviour was recovered ²⁵
Deinopoidea Uloboridae <i>Uloborus conus</i>	No homologous behaviour at this level of analysis	New behaviour ²⁷
35. The spider built an approximately vertical guy line whose upper end was first attached at its upper end to a frame line, and then moved to attach at the hub ²⁶		

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
36. The spider built the cone spiral without contacting the inner loop of sticky spiral that was already in place	Contact with the previous loop of sticky spiral was used to guide placement of new sticky spiral line	New ability or (more likely) an ancestral ability was expressed in a new context ²⁸
37. The spider broke each radius (or often several radii together) at the edge of the hub, increased its length (and thus decreased its tension), and then reconnected it to the hub preparatory to converting the inner portion of the planar orb to a cone	Spiders broke lines (but only one at a time), just before beginning secondary radius construction ²⁹	Ancestral behaviour was expressed in a new context
38. The spider broke each radius in the cone near its the upper attachment and then moved it outward (toward the frame) to attach it near the innermost loop of sticky spiral	No homologous behaviour ³⁰	New behaviour
39. The spider built a new, inner orb web, attaching its radii to the cone radii in the rim	When repairing and replacing a sector of an orb, the spider attached new radii to old radii	Ancestral behaviour (largely unaltered except that sticky spiral construction was omitted) was expressed in a new context
40. The spider built a cone associated with the prey capture orb <i>Polonecia producta</i>	Cones were only associated with moulting webs (as in <i>U. trilineatus</i>) ³¹	Ancestral behaviour was expressed in a new context ³¹
41. The sticky line construction was interrupted repeatedly (convergence with #3)	The sticky spiral was continuous	New behaviour ³
42. The spider attached the sticky line repeatedly to each radius while moving toward hub (convergence with #16)	The spider attached the sticky line only once to each radius, when the trip toward the hub began	Ancestral behaviour was repeated

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
43. The spider terminated the temporary spiral far from the edge of the web (and sometimes omitted it entirely)	The temporary spiral was consistently present, and terminated in the outer portion of the orb	Ancestral behaviour was triggered by a new cue
44. The spider laid the first loop of sticky line exclusively along frame lines, attaching it at each point where the frame line changed direction or where another (radius or anchor) line was attached	The spider often attached the outer loop of sticky spiral to the frame occasionally, but seldom followed the frame for more than a short distance; it was only occasionally attached to the frame at points where the frame line changed direction	Ancestral behaviour was expressed more frequently ³²
<i>Hyptiotes paradoxus</i> and <i>H. cavatus</i> ³³		
45. The spider built the frame line without adding a radius, starting from a point in the middle of a radius, and then using this point to gain access to the adjacent radius ³⁴	The spider added a radius in the process of building each new frame, starting all frame line construction at the hub, and using the hub to gain access to the second radius	New behaviour ³⁵
46. The hub (intersection of radii) was not formed until after the first frame line was built	The hub was formed before the first frame lines were built	New behaviour ³⁶
47. The spider built no hub lines during secondary radius construction ³⁶	The spider always built hub lines as an integral part of secondary radius construction	Ancestral behaviour was omitted ³⁷
48. The temporary spiral was interrupted repeatedly, with the spider returning to the hub after each loop was built	The temporary spiral was a single, continuous line	New behaviour

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
49. The spider probably used kinesthetic cues to choose attachment sites for the temporary spiral, because it lost contact with previous lines such as the hub or the previous loop of temporary spiral during temporary spiral construction ³⁸	Spiders probably used both the site of previous loop of temporary spiral (they maintained contact with previous loop) as well as kinesthetic cues to choose attachment sites	Ancestral responsiveness was lost for one guiding stimulus, but continued with respect to the other ³⁹
50. The horizontal radius was reinforced very early in web construction ³⁸	Spiders did not reinforce radii (but did reinforce frame lines)	Ancestral behaviour was expressed in a new context
51. The spider consistently interrupted sticky spiral construction repeatedly in a particular context (convergence with #3), and returned to the hub	The sticky spiral was continuous; it was interrupted only rarely, and without any clear pattern in where interruptions occurred	New behaviour ³
52. The spider attached each sticky spiral loop twice to each radius (with the first attachment nearer the frame), producing a zig-zag pattern	Similar zig-zag patterns were less common, and usually occurred only in the outermost loops	Ancestral behaviour was expressed more often
53. The spider tapped anteriorly with leg <i>ii</i> or <i>oI</i> to touch the inner loop of sticky spiral while facing outward while the longitudinal axis of its body was parallel to the radius ⁴⁰	The spider tapped laterally with <i>oI</i> , with its longitudinal axis perpendicular to the radius	New behaviour (or, less likely, a lost ancestral behaviour was recovered) ⁴¹
54. During interruptions in the sticky spiral, the spider repeatedly walked across the web without producing any new line (convergence with #6)	The spider never moved on the web without producing a new line (sticky or non-sticky), except during the transition between temporary and sticky spiral	Ancestral behaviour was expressed in a new context ⁴
Deinopidae <i>Deinopus</i> sp.		

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
55. The spider reinforced an early radius (midline) by adding lines to its central portion ⁴²	The spider never reinforced radii this way, but did reinforce frame lines this way	Ancestral behaviour was expressed in a new context
56. The spider added only two secondary radii (one to each lateral frame)	The spider added many secondary radii	Ancestral trait was repeated less often
57. The spider cut and discarded the midline radius below the hub before initiating temporary spiral	The spider never discarded radii before initiating the temporary spiral, but did cut radii during the exploration stage	Ancestral behaviour was expressed in a new context
58. The spider built only half of one loop of the temporary spiral ⁴³	The spider built several loops of temporary spiral	Ancestral trait was repeated less often
59. The spider cut and discarded the midline radius above the hub after finishing the sticky spiral	The spider never discarded radii after building the sticky spiral, but cut and discarded lines during exploration	Ancestral behaviour was expressed in a new context
60. The spider replaced both radial lines that were laid during the process of primary frame construction (Figure 5A, B in Coddington (1986)) ⁴⁴	The spider very seldom replaced radii (see footnote 12)	Ancestral trait that occurred only occasionally became ‘fixed’; and Ancestral behaviour (reeling up the line) was omitted
61. The web was initiated with a vertical line (‘midline’)	The orb was initiated with an approximately horizontal, ‘bridge’ line	New behaviour
62. The spider walked along the substrate to establish the two lower anchor sites, after construction per se had already begun	At least the major anchor attachments were established during exploration, prior to the initiation of construction per se; only occasionally did the spider establish additional attachment sites by walking along the substrate	Ancestral trait that occurred only occasionally became ‘fixed’

Table A1.
(Continued.)

Taxonomic group and derived behaviour	Behaviour of putative ancestor (typical araneoid or uloborid orb weavers)	Type of change in derived webs
63. The spider pulled out additional line when finishing each new radius, just before attaching it to the midline	The spider occasionally pulled out additional dragline just before attaching the new radius to the hub? ⁴⁵	Ancestral trait that occurred only occasionally became 'fixed' (or, more likely, new behaviour) ⁴⁵
64. The spider consistently made double attachments to the substrate	Only occasionally did the spider make double attachments to the substrate	Ancestral trait that occurred only occasionally became 'fixed'
65. The spider located the inner loop of sticky spiral using leg oIV	The spider probably located the inner loop of sticky spiral with leg I	New behaviour ⁴⁶
66. The spider broke the inner ends of lower and middle radii during sticky spiral construction	The spider never broke radii during sticky spiral construction, but broke the temporary spiral during this stage	Ancestral behaviour was expressed in a new context

¹Use of this cue was deduced from the web structure and the spider's size; no experiments have been performed to test this hypothesis.

²This behaviour probably evolved only once in the closely related genera *Cyrtarachne*, *Poecilopachys* and *Paraplectana*, and was counted as a single derivation.

³Occasionally typical orb weavers interrupted and then resumed sticky spiral construction, especially when the spider was disturbed; the derived aspect of the construction behaviour for the modified web is the apparently spontaneous, consistent, and repeated nature of the interruptions.

⁴Alternatively, this trait could be combined with #3 as a single, compound trait.

⁵Initiation of sticky spiral might be said to be homologous. But initiation in a typical orb occurs near the point of termination of the temporary spiral, not at the hub as in *P. australasia*. Probably *P. australasia* often (though not always) chooses the radius that is oriented most nearly directly downward in the web (suggested by Figure 1 of Clyne (1973)). An ability to orient with respect to gravity is manifested at other stages of typical orb construction, such as determination of the longest axis of the web (Peters, 1937; Eberhard, in press). In this sense, this transition also involves an ancestral cue being used in a new context.

⁶Clyne did not mention contact (or lack of it) with the inner loop. The length of the spider is approximately 8 mm, and its legs are stubby, while the distance between loops is about 20 mm; assuming that the spider does not move 'backward' toward the hub after contacting the inner loop (a behaviour never seen in any orb weaver, to my knowledge), it is thus almost certain that the spider did not touch the inner loop.

⁷The extensibility of the base line may be affected by behaviour, because it is thought to be increased when the line is covered with adhesive (Townley & Tillinghast, 2013).

Table A1.
(Continued.)

⁸Low shear attachments also occur in the closely related *Pasilobus* sp., which builds a somewhat similar reduced-orb design (Robinson and Robinson, 1975).

⁹Similar failures to cross certain radii occur in a few other distantly related araneids such as *Zygiella* and relatives, and *Cyclosa* spp., and in the uloborid *Uaitemuri* (Santos and Gonzaga, 2017; Eberhard, in press).

¹⁰*Eustala* sp. pulled additional silk with legs IV just before making the final attachment of the sticky line at the junction of the radius with the temporary spiral; such pulls, when performed by typical orb weavers, often occurred just before attaching to the radius. This may thus represent an additional case of an ancestral trait performed in a new context.

¹¹Laying the sticky line on top of the radius, rather than strictly crossing it as in typical orbs, could be classified as a new behaviour.

¹²The changes in directions of movement might be equivalent to turnbacks in the sticky spiral in normal orbs; in this case, the classification of the transition would be ‘change frequency of ancestral behaviour’.

¹³This behaviour was common but facultative. It only occurred in ‘floating’ webs built over water (and sometimes only in certain sectors of these webs); in other webs it was omitted.

¹⁴Some details of the ancestral behaviour involved in making an attachment to a radius (grasping the radius with legs oIII and oIV and bringing it close to the spinnerets) probably did not occur when the spider made an attachment to the water surface, but these details were not described.

¹⁵This classification assumes that the line laid on the descent to the water was sticky spiral line, a difficult detail to resolve in field observations of these small spiders.

¹⁶Some of these details are from descriptions of the behaviour of other anapid species (Eberhard, 1987); this was counted as a single derivation in the closely related families Anapidae and Symphytognathidae (Lopardo et al., 2011).

¹⁷A few radii were modified during radius construction (‘false starts’) by the tetragnathid *Leucauge mariana* (Eberhard, in press), but this behaviour was entirely absent in the uloborid *Uloborus diversus* (Eberhard, 1972) and the araneid *Micrathena duodecimspinosa* (Eberhard, in press). This behaviour of anapids and tetragnathids is probably independently derived in *L. mariana*, where it would represent an additional case of ‘Ancestral behaviour expressed in a new context’.

¹⁸This derived trait may occur in the entire family.

¹⁹Omission of the temporary spiral may have evolved only once in the related families Anapidae and Mysmenidae; but a temporary spiral was built by *Patu*, and also in the closely related Symphytognathidae (Eberhard, 1987), so the number of losses is uncertain (the strict consensus phylogeny of Lopardo et al. (2011) suggests two independent losses).

²⁰Lack of contact with the inner loop of sticky spiral may have been derived only once (as assumed here) in the closely related families Theridiosomatidae, Anapidae, Symphytognathidae and Mysmenidae (see phylogeny of Lopardo et al., 2011); presumably these spiders used the distance from the hub (or from the previous loop of temporary spiral) as a cue to guide temporary spiral construction; if so, then ‘transfer of an ancestral trait to a new context’ also occurred.

²¹Ancestral behaviour for this derived group was taken to be that of other symphytognathoids.

Table A1.

(Continued.)

²²Description of supplementary radius construction by Hiramatsu and Shinkai (1993) was clear on this point; that of Eberhard (1987) was not clear regarding doubling of the line, but the mention of a lack of a dramatic sag is compatible with this detail.

²³Presumably spiders used the distance from the temporary spiral to guide sticky spiral construction; if so, then ‘transfer of an ancestral trait to a new context’ also occurred.

²⁴The derived aspect of the behaviour is which legs were used to obtain information on the site of the inner loop, not whether information was obtained.

²⁵The ancestral behaviour is assumed to be that of the same spider when it built prey capture orbs. Farther in the past, the ancestral behaviour was a single attachment, so the derived behaviour represents recovery of an ancestral trait.

²⁶*Uloborus conus* moved to the orb’s edge, descended and attached the dragline to a leaf below, climbed up the line and apparently broke the attachment to the frame and carried the broken end to the hub and attached it to hub; it then descended this line, broke and shifted its attachment to the leaf, and returned to the hub. Some shifting of attachment points to the substrate, and of radial lines to each other, occurred during the exploration stage in typical uloborids (Eberhard, 1972, 1990b, in press). But these movements were expressed by *U. conus* in a new temporal and spatial context: after finishing the sticky spiral, at different sites, far below the orb.

²⁷This complex behaviour could be, alternatively, divided in up to three behaviours: building a vertical line from a frame line to the vegetation below; climbing this line and breaking its attachment to the frame; and shifting the upper attachment from the frame to the hub. This would represent, respectively, two ‘new behaviour’ and one ‘ancestral behaviour expressed in a new context’ transitions.

²⁸Normal uloborid sticky spiral placement is guided by sticky lines already in place (Eberhard, 1972; Eberhard & Barrantes, 2015). In repairing webs, however, both the araneid *Micrathena* sp. nr. *lucasi* and the uloborid *Uloborus diversus* revealed an additional ability to move in an approximately circular direction without being guided by circular sticky lines (Eberhard, in press); *U. conus* may have used this ancestral ability to move in a more or less circular path irrespective of the many lines it encountered in the new context of building the cone spiral.

²⁹During the exploration stage, spiders also broke single lines, reduced their tensions, and then reconnected them. In still another context (destruction of a sector of an old web prior to repair), *U. diversus* broke multiple radii at once and then connected them to the dragline. In both of these cases the transition would be ‘ancestral behaviour performed in a new context’.

³⁰Similar shifting of the sites of attachment of non-sticky lines was common in other uloborids during the exploration stage of construction of typical orbs before orb construction per se began; but shifting never occurred after radius construction had ended.

³¹It is uncertain whether a prey capture web or a moulting web was ancestral (both sequences would involve transfer of an ancestral behaviour to a new context); it is also possible, though seemingly less likely, that the two were derived independently.

³²There are no experimental data regarding the cues that induce typical uloborids to attach sticky spiral lines to frame lines.

Table A1.
(Continued.)

³³The webs were similar in other two species in this genus (Opell, 1982). The evolutionary lineage of *Hyptiotes* is thought to have separated prior to the derivations of the genera with typical orbs whose behaviour has been observed (*Uloborus*, *Philoponella* and *Zosis*) (Opell, 1979, 1982, pers. comm.; Coddington, 1990). Nothing is known of the behaviour of other, more basal orb-weaving uloborid genera such as *Waitkera* and *Tangaroa*, which also built orbs. It is thus possible (though seemingly unlikely) that some of the differences in the behaviour of *Hyptiotes* are ancestral in Uloboridae.

³⁴Based on the account of Marples & Marples (1937); my own observations of *H. cavatus* were not clear on this point.

³⁵This complex behaviour could be subdivided into two or more traits with no obvious homologies with typical orbs, representing ‘new behaviour’ transitions.

³⁶The first radius was taken to be homologous with the earliest radii in typical orbs built before the proto-hub was removed, on the basis of the spider breaking and reeling up the new radial line. The last two radii were taken to be homologous with secondary radii in typical orbs, based on their not being broken and reeled up while the spider returned to the hub (a detail observed directly in *H. cavatus*), and inferred from the lack of mention of break and reel behaviour in *H. paradoxus* by Marples & Marples (1937), who did mention cut and reel behaviour for the earlier radius.

³⁷Hub lines were part of secondary radius construction in all other uloborids, but not in some araneoids, so the omission may also represent recovery of an ancestral trait.

³⁸This detail was certain only for *H. cavatus*.

³⁹Some orb-weaving uloborids maintained contact (*Uloborus*), while others did not (*Philoponella*, *Zosis*) (Eberhard, 1982). *Zosis geniculata* used kinesthetic cues as well as contact with temporary spiral lines to determine attachment sites for the sticky spiral (Eberhard & Barrantes, 2015).

⁴⁰It was not certain whether oI or iI (or both) touched the sticky spiral.

⁴¹Ancestral uloborid orb weavers presumably tapped laterally with leg oI, as this behaviour occurs in *Uloborus*, *Philoponella* and *Zosis*; leg iI was used to tap in Tetragnathidae (Eberhard, 1982).

⁴²Coddington (1986b) tentatively equated this single line to all the primary radii of a typical uloborid or araneid orb; but the radii that *D. sp.* laid while producing the two lateral frame lines, as seen in others such as the araneid *Micrathena undecimspinosa* (Eberhard, in press), could also be included as primary radii.

⁴³The spider never used this line as a bridge when moving between radii, in contrast with the use of the temporary spiral of typical orb weavers. The line may simply be vestigial and non-functional, or it may have a new function, such as giving added support to legs III when they pushed when the spider was thrusting the web toward prey.

⁴⁴The broken line was apparently not reeled up (Figure 5B of Coddington, 1986b), in contrast with typical radial lines (Coddington, 1986b).

Table A1.

(Continued.)

⁴⁵Further details are needed to decide whether this behaviour represents fixation of an occasionally expressed ancestral trait (as proposed by Coddington, 1986b and coded here), or whether it is a new behaviour resembling the pulls with legs IV during sticky spiral construction seen in araneoids. The unusually extensible non-sticky silk of deinopid webs (Coddington & Sobrevila, 1987), and the need to have these lines lax in the finished web so that they can be extended long distances probably favoured radius lengthening.

⁴⁶The same leg oIV is used for this function in the araneoid family Nephilidae and also in a few araneids (Eberhard, in press); as noted by Coddington (1986b) this probably represents a convergence, due to the mechanical constraints imposed by the combination of especially long legs and the small mesh of *Denopsis* sp. webs.

Table A2.

Apparent ancestral traits in construction behaviour of orb weavers, as determined by uniformity among uloborid and araneoid species or, in case in which there is variation within araneoids or uloborids, by using the other superfamily as an outgroup (data from summaries in Eberhard & Barrantes (2015) and Eberhard (in press)). Traits in italics were altered in modified orb species in Table A1; numbers in parentheses refer to the conservative (as in Table A1) and maximum estimates of the number of evolutionary lines (see footnotes in Table A1) in which each of these traits changed. Data are missing for some traits in modified orb species, so differences are conservative.

Frames

Vertical orbs are initiated with an approximately horizontal, 'bridge' line at top (1).

Each frame line is initiated with a radius attached at the hub, and the spider moves to the second exit radius along this line, via the hub (1)

One radius is added with the construction of each new frame line

The outer (primary) frames are all built before the first inner (secondary) frames

Radii

Radius length is not subsequently modified (1)

Radii are not subsequently reinforced (2)

Radii are not broken and reconnected to the hub after being built (1)

Radii are not later broken and discarded (1)

Radii are not lengthened by pulling additional silk with leg IV³ (1)

Radius doubling (or lack of doubling) is consistent throughout the web (1)

No radii are added following initiation of sticky spiral construction (1)

Each new radius is built at a 'final' angle with the exit radius; this angle is not later

Subdivided

Spider leaves the hub along the upper of two possible exit radii (vertical webs)

Spider uses the new radius rather than the exit radius to return to hub

Tertiary radii are laid only as part of temporary spiral construction

There is a positive intra-specific correlation between the number of radii and the size of the orb¹

There is a negative intra-specific correlation between inter-radial angles and radius length¹

Hub

Hub is not removed following sticky spiral construction² (1)

Hub is built from the centre outward

The spacing between loops is probably based on contact of leg III with the outer hub loop

There is only a single hub

Temporary spiral

There is a temporary spiral (1)

The temporary spiral ends in the outer portion of the web (1)

The site of outer loop of temporary spiral is used as a reference point (1)

The line is approximately spiral form (not circular) (1)

The temporary spiral to each radius it crosses at a single point (1)

The temporary spiral is removed during sticky spiral construction (1)

Table A2.

(Continued.)

The temporary spiral is built as a single continuous line
The temporary spiral is built from the hub outward
Memory of previous distances from outer loop is used as reference cue
Tension-related cues are not used as references
Sticky spiral
<i>The stick spiral is built as a single continuous line</i> (3)
<i>The sticky covering of line is continuous</i> (1)
<i>The attachments to radii are more or less uniform in strength</i> (1)
<i>The sticky spiral is attached only once to each radius it crosses</i> (2)
<i>Most segments are between radii; the sticky spiral is attached only occasionally to the frame</i> (1)
<i>The sticky spiral is attached only to web lines, not to the substrate</i> (1)
<i>The site of inner loop of sticky spiral is used as a reference point</i> (2)
<i>Contact with previously laid sticky lines occurs repeatedly and does not elicit termination</i> (1)
<i>'Extra' lengthening of line (pulls or combing movements with leg IV) is done mostly just prior to each attachment to a radius</i> (1)
<i>Sticky lines are single rather than double</i> (1)
<i>Radii are left intact during sticky spiral construction</i> (1)
The sticky spiral is built from outer edge moving inward
The distance from outer loop of temporary spiral is used as a reference cue
Memory of previous spaces is used as a reference cue
The amount of silk in reserve is used as a reference
The number of loops correlates positively with the number of radii
Tension-related cues are not used as references
Others
The size of the available space has similar, apparently independent effects on seven different traits of the hub, frames, radii and sticky spiral

¹Perhaps the same phenomenon.²At most, only the central portion of the hub is removed.³Somewhat uncertain (see Table A1).