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Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae)

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Nineteen new characters pertinent to the phylogeny of the spider suborder Araneomorphae are reviewed and tested against a previous data set, using quantitative cladistic techniques. An hypothesis of cladistic structure within Araneomorphae in the form of a quantitatively analysed cladogram is presented for the first time. The analysis supports orb weaving spiders (Orbiculariae: Deinopoidea and Araneoidea) as a monophyletic group (apparently sister to Dictynoidea) and Linyphiidae as an araneoid family. Likely precursors of orbs are discussed, as are relevant fossil evidence and possible times of origin.

1. Introduction

Coddington (1990) reviewed the higher level cladistic structure of true spiders (Araneomorphae) and ontogenetic evidence relevant to the homology of sclerites in the male spider palp, with the aim of clarifying orbweaver phylogeny. The analysis resulted in a cladogram for 32 orb weaving taxa, including most araneoid families, Deinopidae, and most uloborid genera. The analysis used 87 binary and multistate characters: 23 characters from male genitalia, 5 from female genitalia, 35 from somatic morphology, and 24 from behavior. Because many characters were multistate,

a larger total of 199 informative comparisons were actually made. Character data were taken from the literature as well as original observation.

Analysis of potential outgroups resulted in a relatively weakly supported and unresolved trichotomy with Amaurobioidea and/or Dictynoidea (sensu Forster 1970) as the sister taxon or taxa to Orbiculariae (=Deinopoidea+Araneoidea). No single spider family seems likely to be the sister group of Orbiculariae. The results strongly supported the monophyly of Orbiculariae ((Uloboridae, Deinopidae), Araneoidea), based on 13–14 synapomorphies (3–4 morphological; 10 behavio-

ral) and that of Araneoidea (including Linyphiidae), based on 10 synapomorphies. Nestiidae-Theridiidae remained unplaced within Araneoidea.

This report extends the previous study by testing new evidence from spinneret morphology, other morphological data, and new behavioral evidence against relevant characters from the previous study to explore the cladistic structure among potential cribellate outgroups to Orbiculariae. The analysis probes whether Amaurobioidea (exemplified here by Amaurobiidae and Titanocidae) or Dictynoidea (exemplified here by Dictynidae) is more likely to be the sister group to Orbiculariae. Although as far as I know the cladogram does not conflict with any quantitative cladistic analysis for spiders, the small number of taxa studied and the high categorical level of the comparison make the cladogram only a first conjecture of araneomorph relationships. Recent publications that present evidence or arguments relevant to orbweaver monophyly (Coddington 1989, Eberhard 1987, 1988, Kooor 1987, Kooor & Peters 1988, Millidge 1988) are also considered.

Before addressing points raised by these authors, some methodological issues deserve comment. I use cladistic analysis because it reflects descent with modification and thus is well-designed to reconstruct phylogeny, and because it is an explicit, repeatable, easily understood method. Competent cladistic analyses include six elements:

- 1) three (at least) taxon statements;
- 2) explicit character homologies;
- 3) transformation series polarized by outgroup comparison (or ontogeny);
- 4) a data matrix;
- 5) a cladogram;
- 6) a measure of fit between the matrix and the cladogram.

From a cladistic point of view, claims of "convergence" demand background evidence of a particular cladistic structure to be valid. Cladistic analyses should be regarded as the simplest quantitative explanations for particular data sets, not as attempts to "prove" hypotheses.

The diversity and conflicting nature of comparative information available for Araneomorphae are also important reasons to prefer a quan-

titative analysis. Already much comparative data are at hand. A partial list includes sperm structure, tapetal structure, tarsal organs, autospasy patterns, silk glands, tracheal systems, spinnerets and spigots, palp morphology, bothrial morphology, trochanteral notches, hair types, female reproductive systems, colulus/cribellum morphology, male tibial apophyses, epiandrous fusules, gastric caecae, web-building, drag-line spinning, mating position, circulatory system morphology, and karyotypes. Most of these characters systems of Araneomorphae show enough homoplasy (due to secondary loss, independent gain, errors of interpretation) so that quantitative analysis of character distributions becomes essential. Compiling and evaluating this accumulated information objectively demands a quantitative approach.

2. Materials and methods

2.1. Characters

This analysis uses 61 characters (19 spinneret/spigot characters, 30 other morphological characters, and 12 behavioral characters) across 19 taxa representing 18 families (Table 1). Forty-two characters are drawn from Coddington (1990) and are discussed there. The 45 characters from the latter study not included here dealt with intra-araneoid relationships or intra-uloborid relationships, and thus are irrelevant in the present context. Information on spinnerets and glands is drawn from original research and Kooor (1987) and works cited therein, although polarities and homologies of features differ from her interpretations in some cases.

Congruence of the 19 new characters with the data of Coddington (1990) has not been tested (Table 1: 1–9; 11–12; 15–17; 46–49; 61). Multistate characters were coded as linear transformation series, excepting characters 1 and 32, which were left unordered. The matrix was analysed with the implicit enumeration option in Hennig86 ver. 1.5 (Farris 1988). Fig. 1 presents the results, a single most parsimonious cladogram (length 109; c.i. 0.68; r.i. 0.85). I resolved ambiguous optimizations individually, usually favoring secondary loss to explain homoplasy.

Table 1. Character data for Fig. 1, grouped by category. Each row codes one character as follows: "Character name: 'state' (0); 'state' (1); 'state' (2);", etc. Missing or inapplicable states are coded as "--." The last two columns give the consistency index of the character for the tree in Fig. 1, and the character number assigned in Coddington (in press). Familial representatives in order of listing are: Hypochilus (Hypochilidae); Thaida (Austrochilidae); Loxosceles (Scytodidae); Kukulcania (Filistatidae); Oecobius (Oecobiidae); Stegodyphus (Eresidae); Callobius (Amaurobiidae); Titanoeca (Titanoecidae); Psechrus (Psechridae); Dictyna (Dictynidae); Deinopis (Deinopidae); Octonoba (Uloboridae); Araneus (Araneidae); Leucauge (Tetragnathidae); Theridiosoma (Theridiosomatidae); Helophora, Frontinella (Linyphiidae); Latrodectus (Theridiidae); Gaucelmus (Nesticidae).

	HTLKOSCTPDDOALTHFLG yaouetaisieceheraa	C.I.	Coddington (1990)
Spigot characters			
1. ALS maj. ampullate #: many; 2; 1;	012000111202222222	0.40	
2. ALS ampullate nubbin: abs; pres;	0000000011111111	1.00	
3. ALS pyriform margin: otherwise; sharp;	0000000011111000	0.50	
4. ALS ampullates: dispersed; clustered;	01-00011111111111	0.50	
5. PMS aciniform brush: pres; abs;	-----00011111	1.00	
6. PMS aciniform #: many; 3; 2;	00-00-0000000112211	1.00	
7. PMS minor amp. nubbins: abs; 2; 1; lost;	000000000001223332	0.75	
8. PMS minor amp. #: multiple; 1;	00-00011111111111	1.00	
9. PMS minor amp. position: med/ant; post;	00-00000000111111	1.00	
10. PMS paracribellum: abs; pres;	01-000100111-----	0.33	Fig. 3 (23)
11. PMS cylindrical #: 2 or less; many;	00--01000110000000	0.50	
12. PLS aciniforms: random; elongate rows;	00000-0000000111100	0.50	
13. PLS mod. spig.: abs; pres; pseudofl.; flag.;	0000011110223333333	0.75	Fig. 108 (46)
14. PLS aggregates: abs; pres; huge;	000000000001111122	1.00	Fig. 108 (47-48)
15. PLS paracribellar(s): abs; pres;	01-000110100-----	0.33	
16. PLS cylindrical #: 2 or less; many;	00--010000110000000	0.50	
17. Aciniform A: pres; abs;	-----001-111-	1.00	
18. Cribellum: entire; divided;	00-111111000-----	0.50	Fig. 3 (10)
19. Cribellum: pres; lost;	001000000000111111	0.50	Fig. 3 (10)
Morphology			
20. Gut: straight; M-shaped;	00111111111111-----	1.00	Fig. 2 (1)
21. Heart ostia #: 4; 3 or 2;	00111111111111-----	1.00	Fig. 2 (2)
22. Endosternite extension: pres; abs;	01111111111111-----	1.00	Fig. 2 (14)
23. 5th endosternite invagination: pres; abs;	01111111111111-----	1.00	Fig. 2 (15)
24. Cheliceral lamina: abs; pres;	001100000000000000	1.00	Fig. 3 (3)
25. Tegulum-subtegulum: free; fused;	001100000000000000	1.00	Fig. 3 (4)
26. Conductor: pres; abs;	001100000000000000	1.00	Fig. 3 (5)
27. Tracheae: abs; few stout trunks; branched;	0011--111212111111	0.66	Fig. 3 (7)
28. Tarsal trichob. row: abs; pres;	000000111000000000	1.00	Fig. 3 (8)
29. Metatarsal trichobothria: 1-2; >2;	000100111000000000	0.50	Fig. 3 (9)
30. Spinneret cuticle: annulate; ridged; squamate;	011111111111222222	1.00	Fig. 3 (24)
31. Calamistral rows: 2; 1;	011101011111-----	0.33	Fig. 3 (25)
32. Tapetum: primitive; canoe; grate; abs;	000003112133111111	0.75	See text
33. Paracymbium: abs; pres;	000000000001111111	1.00	Fig. 108 (4)
34. Petiole fused to subtegulum: abs; pres;	000000000001001100	0.50	Fig. 108 (6)
35. Embolus stalk: abs; pres;	000000000001001100	0.50	Fig. 108 (21)
36. Araneoid radix: abs; pres;	000000000001001100	0.50	Fig. 108 (22)
37. Female genitalia: haplogyne; entelegyne;	000011111111111111	1.00	Fig. 108 (24)
38. Labium: Length > width; width > length;	000010000000111111	0.50	Fig. 108 (33)
39. Gnathocoxal sex glands: abs; pres;	000000000001001100	0.50	Fig. 108 (34)
40. Macrosetal comb: abs; pres;	000000000011000000	1.00	Fig. 108 (38)
41. Tarsus IV comb: abs; pres;	000000000000000011	1.00	Fig. 108 (39)
42. Duct levator muscle: abs; pres;	000000000-111---1-	1.00	Fig. 108 (44)
43. Duct sphincter: abs; pres;	000000000-111---1-	1.00	Fig. 108 (45)

	HTLKOSCTPDDOALTHFLG yaouetaisicreheraa	C.I.	Coddington (1990)
44. Hair: plumose; pseudoserrate; serrate;	00-0000000112222222	1.00	Fig. 108 (49)
45. Juxtaposed lateral eyes: abs; pres;	0000000000001111111	1.00	Fig. 108 (61)
46. Clypeus: low; high;	0000000000000111111	1.00	
47. Male palpal tibia: no apophyses; w apophyses;	0000001111000000000	0.50	
48. Abdominal tubercles: abs; pres;	0000000000110000000	1.00	
49. Serrate accessory claw setae: abs; pres;	0000000001111111111	1.00	
Behavior			
50. Frame construction: abs; pres;	0000000000111110000	0.50	Fig. 108 (67)
51. Radius construction: abs; CR'ed; doubled;	0000000000121110000	0.66	Fig. 108 (69)
52. Hub construction: abs; pres;	0000000000111110000	0.50	Fig. 108 (73)
53. Temporary spiral construction: abs; pres;	0000000000111110000	0.50	Fig. 108 (77)
54. Sticky spiral construction: abs; pres;	0000000000111110000	0.50	Fig. 3 (16)
55. SS localization: abs; oL1; iL1;	0000000000111220000	0.66	Fig. 108 (78)
56. SS wrap attack: abs; pres;	0000000000000000011	1.00	Fig. 108 (79)
57. NS-SS grip: otherwise; w L4;	0-0000000011111----	1.00	Fig. 108 (81)
58. L4 SS shift: abs; pres;	0-0000000011111----	1.00	Fig. 108 (82)
59. Cribellate silk: otherwise; puffed;	000000000011-----	1.00	Fig. 108 (83)
60. Wrap attack: absent; pres;	0000000000111000000	0.50	Fig. 108 (85)
61. Combing leg support: fixed L3; mobile L4;	0--01-111111-----	1.00	

2.2. Taxa

At some level, an “exemplar” approach will always be necessary to reach conclusions about araneomorph phylogeny. Results are more quickly had but selective sampling is never optimal and can mislead. Such studies obviously assume that character codings represent the ground plan for the taxon, which should instead be found by cladistic analysis at a lower level.

Exemplars of families or higher taxa in this study are: *Hypochilus* (Paleocribellatae: Hypochilidae); *Thaida* (Austrochiloidea: Austrochilidae, Gradungulidae); *Loxosceles* (Scytodoidea: Scytodidae, Pholcidae, Tetrablemmidae, etc.); *Kukulcania* (Filistatidae); *Oecobius* (Oecobiidae); *Stegodyphus* (Eresidae); *Callobius*, *Titanoeca* (Amaurobioidea: Amaurobiidae, Titanoecidae, Agelenidae, etc.); *Psechrus* (Lycosoidea: Psechridae, Zoropsidae, Pisauridae, Lycosidae, Ctenidae, etc.); *Dictyna* (Dictynoidea: Dictynidae, Hahniidae, Desidae, etc.); *Deinopis* (Deinopidae); *Octonoba* (Uloboridae); *Araneus* (Araneidae); *Leucauge* (Tetragnathidae, including metines and nephilines); *Theridiosoma* (symphytognathoids: Theridiosomatidae, Mysmenidae, Anapidae,

Symphytognathidae); *Helophora*, *Frontinella* (Linyphiidae); *Gaucelmus* (Nesticidae); *Latrodectus* (Theridiidae). Two typical linyphiid genera are included to emphasize intrafamilial patterns, given the recent suggestion that linyphiids are not araneoids at all, but rather sister to Agelenidae (Millidge 1988). Although not included here, Cyatholipidae groups with Linyphiidae, and Anapidae, Mysmenidae, and Symphytognathidae with Theridiosomatidae. While I could have used “hypothetical” ground plans for these higher taxa, presenting data from real taxa is more empirical, even though some taxa may not adequately represent their intended higher taxon (e.g. *Loxosceles*, *Callobius*, *Psechrus*, *Dictyna*). In the following discussion “theridioid” stands for the theridiid assemblage, i.e. *Synotaxis* et al., Nesticidae, Hadrotarsidae, and Theridiidae (Forster et al. 1990). “Lower” neocribellates mean Filistatidae, Oecobiidae, and Eresidae (and their cribellate relatives). “Higher” neocribellates mean the remaining cribellate taxa (and their relatives).

As Lehtinen (1967) insightfully recognized, the problem of the basic structure of araneomorph phylogeny is probably the same as the problem of cribellate phylogeny. Correctly solving the latter

should solve the former in broad outline. Exclusively cribellate lineages are omitted here for two reasons. First, the sister group of the primitively cribellate Orbiculariae is unlikely to be entirely cribellate. This argument minimizes homoplasy in the loss of the cribellum. Although obviously lost several times at generic levels, loss at the familial level is much less homoplasious. Second, most evidence already points towards cribellates as outgroups (Coddington 1986a). Given the size of the problem, the lack of contrary evidence, and parsimony considerations, it is reasonable to begin the search for the orbicularian sister group among cribellate lineages.

2.3. Terminology

Although it is simpler to use gland names for spigots, this usage begs the controversial question of gland homologies (Kovoor 1987). Accurate terminology relating glands and spigots among themselves and to each other is currently beyond our grasp. In this paper use of the same term for spigots implies homology among spigots, but not necessarily among the glands they serve and glands in different taxa already given the same name. Abbreviations are AC, aciniform; AG, aggregate; ALS, anterior lateral spinneret; FL, flagelliform; MAP major ampullate; mAP minor ampullate; CY, cylindrical; PA, paracribellar; PF, pseudoflagelliform; PI, piriform; PMS, posterior lateral spinneret; PLS posterior lateral spinneret; SS, sticky silk; NS, non-sticky silk.

3. Results

Characters 1–19 concern spinnerets or spigots. Kovoor (1987) recently reviewed silk system morphology in general and prior literature. Coddington (1989) surveyed the spigot morphology of selected taxa with SEM.

Character 1

Among cribellates, Orbiculariae (pers. obs.) and Dictynidae (*Archaeodictyna*, *Dictyna*, *Tricholathys*, pers. obs.; Mallos, Jackson 1982) have a single major ampullate spigot on the ALS. Other cribellate taxa usually have two. Multiple ALS

ampullate spigots in a segregated field in Deinopidae apparently is autapomorphic. A single ALS MAP thus appears to be a synapomorphy for at least Dictynidae among the Dictynoidea plus Orbiculariae.

Character 2

Uloboridae and Araneoidea have the vestige, or “nubbin,” of the second ALS MAP persisting in the adult female. Deinopids also have nubbins, but more than one because they have more than one ALS ampullate spigot. Both states occur in Dictynidae. The ALS MAP nubbin is thus either an orbicularian or Orbiculariae-Dictynoidea synapomorphy.

Character 3

Coddington (1989) argued that sharp rather than rounded PI base distal margins were synapomorphic for Araneoidea. However, outgroup comparison to other cribellates beyond Orbiculariae shows that Deinopoidea (fairly sharp margins) and Araneoidea resemble each other more than outgroups (gently rounded spigot base distal margins). Character 3 is thus inferred to be an orb weaver synapomorphy. Sharp PI base margins are lost or ambiguous in linyphiids and theridioids because spigots in these taxa have reduced bases.

Character 4

Only filistatids, oecobiids (e.g. Uroctea), and eresids among Araneoclada have ampullate spigots dispersed among the pyriform spigot field, as far as I know. *Thaida* seems to have ampullate spigots restricted to the ALS mesal margin, otherwise characteristic of higher neocribellates. Scytodoids have highly derived ALS spinning fields, and don't help in interpreting the conflict. Study of other austrochiloids may resolve the homoplasy, but at this point a segregated and uniform PI spigot field appears to be a derived condition within Araneomorphae.

Characters 5–9

Mostly treated in Coddington (1989). Character 5 groups araneoid lineages studied thus far, exclusive of Araneidae. Two PMS AC spigots (6) also occurs in some theridiid genera (Forster et al. 1990), congruent with other characters dis-

cussed in Coddington (1990). Persistence of the PMS juvenile second mAP spigot as a nubbin in adult females (7) is probably synapomorphic for Araneoidea, although lost in derived lineages. Kooor (1987) documents that multiple PMS ampullate glands (8) are found in several lower neocribellate lineages, and spigot evidence is thus far concordant. Strictly posterior PMS mAP spigots (9) are characteristically araneoid. The mesal position in deinopoids may be due to autapomorphically high numbers of PMS CY spigots.

Characters 10–17

The PMS paracribellum (10) appears first in Thaida and is sporadically common in higher neocribellates (Peters & Kooor 1980). It is absent in the eresids, oecobiids, titanocids, and psechrids studied thus far (pers. obs.; Peters 1983). Peculiar spigots that may be paracribellar homologues are present in the correct positions in *Filistata* and *Kukulcania*. Although at this point the paracribellum is most parsimoniously synapomorphic for higher neocribellates and parallel in Austrochilidae, independent gain in austrochilids of that complex feature does seem unlikely (see below). Distribution of paracribellar spigots (e.g. a transverse row in phyxelidine and amaurobiine amaurobiids) may also be cladistically informative. Characters 11 and 16, multiple CY spigots on PMS and PLS, appear to be synapomorphies for Deinopoidea. Dictynids (pers. obs.) have multiple distinctive spigots on the PMS and PLS which may be cylindrical spigots, although disputed by glandular evidence (Kooor 1987). Characters 12 and 14 are discussed in Coddington (1989) and Forster et al. (1990).

Unique, more or less distal, modified spigots on the PLS (13) have now been found in non-orb weaving cribellate taxa, such as Titanocidae, Austrochilidae and Amaurobiidae. Kooor (1987) reports pseudoflagelliform glands in Psechridae, Zoropsidae, and Eresidae as well, and their absence in Dictynidae. I have not yet found distinctive spigots in the former taxa, nor in oecobiids. *Filistata* does have modified distal PLS spigots, but the morphology is quite different from the former cases. A modified PLS spigot in Dictynidae remains ambiguous because the PLS AC spigots are confusingly similar to the shape expected for the modified spigot. In non-orbicular-

ian cribellates this spigot has a rounded base with an elongate cylindrical shaft and a gently rounded tip — apparently the primitive condition. In Orbiculariae, the base is thick and tapered with sharp margins. The shaft is short (plesiomorphically), tapering to a fine, blunt tip. The same description applies to the araneid, tetragnathid, and symphytognathoid flagelliform spigot, although those of theridiids and linyphiids are derived. Thus, although the modified PLS spigot per se now appears to be a synapomorphy of higher generality than just orb weavers (contra Coddington 1986a), several derived details of the spigot morphology still seem congruent with Orbiculariae.

PLS “paracribellar” spigot morphology (15) is convincingly similar to that of PMS PA spigots. These spigots occur sporadically on the PLS of several higher neocribellates, with the notable exception of Orbiculariae. Kooor suggested that PLS acinous glands might be aggregate homologues, but the PLS paracribellar spigots might be considered, given the role of the PMS PA spigots in production of the cribellate sticky line (Peters 1984).

Kooor (1987) observed that aciniform A glands are widespread in uloborids and she found possible aciniform B glands in *Polonecia* (but not in other uloborids). Aciniform A and B glands occur in araneids, further corroborating their basal status in Araneoidea, but aciniform A's are absent in tetragnathids (including nephilines and metines), linyphiids, and theridiids (17). Character 17 lends support to previous hypotheses that the latter araneoid lineages are derived (Coddington 1986a, 1990), although it contests the previous linkage of linyphiids and araneids (see below). Characters 18–19 are discussed in Coddington (1990).

Characters 46–49, 61

Clypeal height (46) and the presence of ventral serrate accessory claw setae (49) were inadvertently omitted by Coddington (1990). Character 46 again suggests that araneids are basal in Araneoidea. Male palpal tibiae with apophyses (47) are mostly congruent (excepting Dictynidae/oidea) with the divided cribellum (18) and trichobothrial characters (29, 30). A less detailed analysis of orbicularian outgroups at first suggested these characters as evidence for a monophyletic

group including all Araneoclada exclusive of Dictynoidea and Orbiculariae (Coddington 1990), but in the present analysis that group dissolves to become a paraphyletic assemblage basal to Dictynoidea and Orbiculariae. Something like "Amaurobioidea" survives. The former alternative, however, adds only three steps to the cladogram in Fig. 1, emphasizing the fragile nature of some parts of the tree. Character 48 confirms the monophyly of Deinopoidea. Character 49 confirms the monophyly of Orbiculariae. Character 61 from Eberhard (1988) corroborates the monophyly of entelegyne Araneoclada.

4. Discussion

4.1. Comments on araneomorph phylogeny

The analysis of the data of Table 1 supports the monophyly of two controversial groups, Orbiculariae and Araneoidea. Fig. 1 suggests 16 synapomorphies for Orbiculariae, and Dictynidae/Dictynoidea as the outgroup (but see below). Araneoidea, including Linyphiidae, is monophyletic by 10 synapomorphies.

Searching for the sister taxon to Orbiculariae required consideration of most other major araneomorph lineages. Likely monophyletic groups include Araneoclada (all araneomorphs exclusive of tetra-pulmonate araneomorphs); Scytodoidea (including Filistatidae), Entelegynae (i.e. the group defined by changes in characters 37, 61), a group of higher neocribellates (defined by changes in characters 1, 4, 8, 32, 47), and Lycosoidea (taxa with grate-shaped tapeta in one or more eyes). Sperm ultrastructure evidence (Alberti & Weinmann 1985) may group Dysderoidea with Scytodoidea and Filistatidae, thus validating most of the old "Haplogynae" (though for different reasons). Outgroup comparison with Hypochilidae and Austrochiloidea suggests that the entire cribellum is primitive for Araneoclada. Divided cribella then characterize most extant cribellate groups except Orbiculariae and Dictynoidea (sensu Forster 1970). Some homoplasy is apparent in this character at the generic level, but the family placement of the discordant genera may be incorrect (e.g. Desidae: *Matachia*; Dictynidae: *Aebutina*). Roughly the same taxa with divided cribella gen-

erally have rows of tarsal trichobothria increasing in length. Is this huge group, more or less the old Amaurobioidea, monophyletic or paraphyletic? At present homoplasy in important characters makes the answer ambiguous.

In fact, homoplasy seems ubiquitous in those characters most useful for the inference of araneomorph phylogeny. Entelegyny (37) is another example of such a feature that is undoubtedly synapomorphic at some level. It may unite Oecobiidae and Eresidae with the rest of the entelegyne Araneoclada. On the other hand, everything basal to Oecobiidae in Fig. 1 seems to be primitively haplogyne. Haplogyny in some uloborids and some araneoids is then secondary.

Several results are especially noteworthy. Four characters place Dictynidae as the sister group of the orb-weavers: the single ALS MAP spigot (1); the reduction of the second ALS ampullate spigot to a nubbin (2); the equivocal inference of convergent evolution of the paracribellum (10); and the reversal to an entire cribellum from a divided condition (18). None of these synapomorphies are without homoplasy. The first and second because some dictynids (*Archaeodictyna*, *Dictyna*, *Tricholathys*) lack the vestigial MAP nubbin, unlike most Orbiculariae. Whether juveniles also lack the second MAP is unknown. Primitive araneoids (but not deinopoids) generally have both. The third because independent gain of the complicated paracribellum seems unlikely and, in any case, the change at this node is equivocal. The fourth because reversal in the cribellum condition depends on a gain of a divided cribellum early in araneocladan evolution. A disturbing number of characters suggest monophyly of animals with divided cribella (e.g. tarsal trichobothrial patterns, male tibial apophyses). If subsequent work vindicates these as synapomorphies, then the entire cribellum (18) as a synapomorphy for Dictynoidea + Orbiculariae becomes plesiomorphic.

It also seems to me that taxa such as Titanocidae and Amaurobiidae represent better ground plans than Dictynidae from the point of view of the spinneret evidence. They have the "pseudoflagelliform" spigot on the PLS, generally two PLS CY spigots, often one PMS MAP, and often one PMS CY spigot. It is still unclear if these features can be optimized to occur at the node subtending "Amaurobioidea" when other

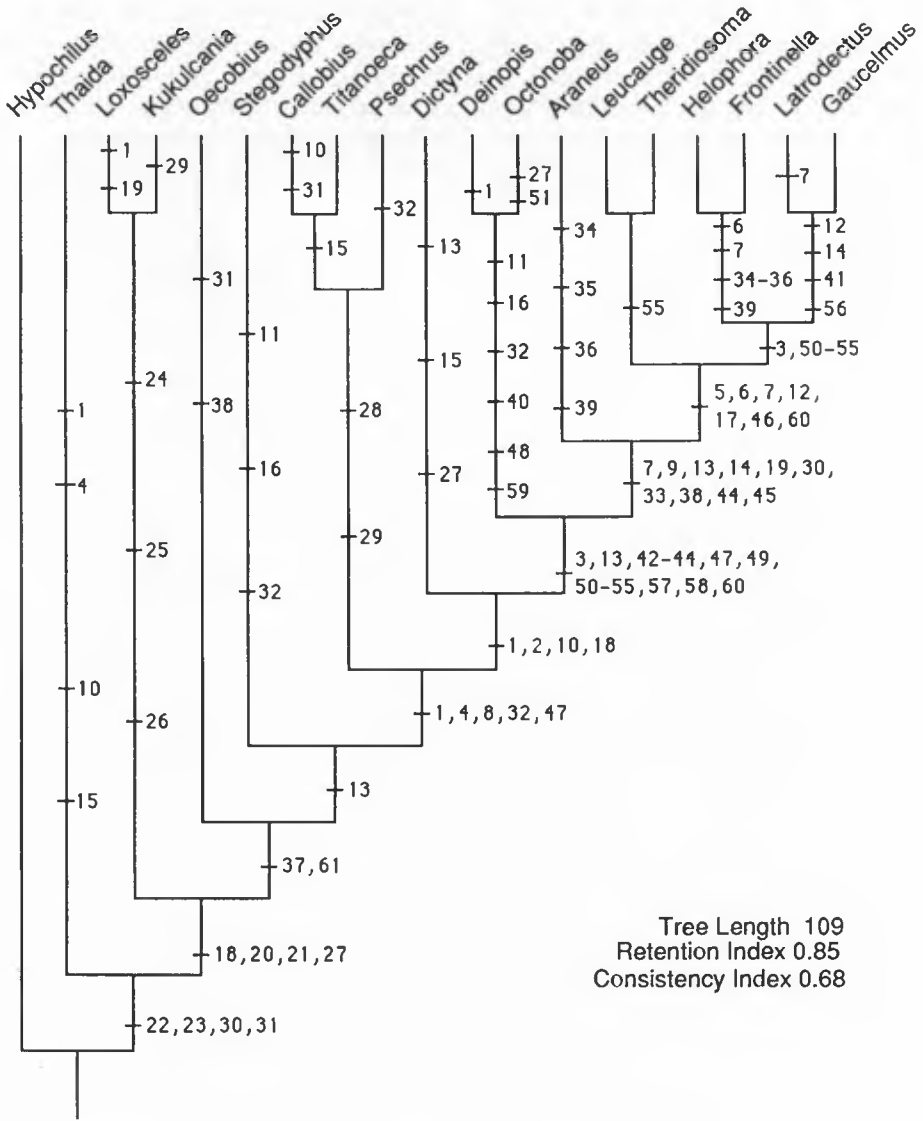


Fig. 1. Cladogram for taxa and characters in Table 1. Some of the mapped changes represent arbitrary resolutions of ambiguous character state optimizations at internal nodes.

taxa are considered. That, plus the single ALS MAP and vestigial nubbin, diagnoses the araneoid spinning complement. Deinopoidea are autapomorphic in having multiple PMS and PLS

CY spigots. More of this character complex is present in amaurobioids than dictynoids, which, at least in Dictynidae, have distinctly different (autapomorphic?) PMS and PLS spinning fields.

4.2. Monophyly of Orbiculariae

Kovoor & Peters (1988) recently objected to the monophyly of Orbiculariae, preferring instead to regard the orb web and associated morphologies as convergent. They concluded "it is impossible to conceive of the two sub-systems responsible for the production of capture threads in Uloboridae and Araneidae as homologous" and "since essential components of the orb webs in Uloboridae and Araneoida are produced by sub-systems of organs that cannot be regarded as homologous, we prefer the hypothesis that the orb web, i.e. the general pattern of this type of web, evolved independently in each of the two taxa under consideration." This objection can be resolved by careful consideration of the distinction between behavior itself and morphologies that behavior may employ, between plesiomorphy and apomorphy, and between secondary loss and primitive absence.

First of all, presumably most workers agree that homology in other aspects of orb web construction (e.g. radius, frame, hub, non-sticky spiral, etc.) is feasible. After all, if it were not, the classical controversy over monophyly would not have arisen. Secondly, the above argument apparently claims that all morphological systems used by a behavior pattern must be themselves homologous in order to infer behavioral homology. On purely ethological grounds one should recognize that many instinctual behaviors, as neuromotor patterns, can employ different morphologies and still remain homologous as behaviors, e.g. the leg used to locate the SS line during SS localization behavior within araneoids (55), or the leg used to support the combing leg during cribellate silk spinning (61).

The above objection thus concerns only the small portion of the total behavior pattern concerned with capture thread production, specifically the hypothesized loss of the plesiomorphic cribellate components of the capture thread (cribellar silk, paracribellar fibers), and the origin of the apomorphic araneoid components (viscid silk). Features plesiomorphic even for outgroups are irrelevant to placement of lineages, and especially so if, as in the case of any group of ecribellate araneomorph spiders, one knows from other evidence that the cribellum and associated structures have been secondarily lost. Known secondary

loss (at some level) of plesiomorphic cribellate features cannot be logically construed as positive evidence of convergence, or non-homology.

The problem is then the origin of derived araneoid features, not loss of plesiomorphic cribellate ones. Araneoids only use two components in their capture threads: flagelliform axial threads and aggregate gland glue. Empirical evidence supports the homology argument for pseudoflagelliform and flagelliform glands and spigots (or behavior or fibers): congruence with and distributions of other characters, disjunct character states, and similar placement, morphology, and function. While not identical, they seem at least as similar as other known sets of homologues that have survived a transformation as fundamental as that from the cribellate to the ecribellate condition in spiders.

The next issue is the origin of the araneoid aggregate gland. Positional criteria suggest that the aggregate gland originated from PLS glands. Kovoor suggested coalescence of acinous PLS glands; the discovery of PLS paracribellar spigots raises these as a possibility as well, although the histochemical transformations required are certainly complex; one would have to hypothesize loss in Deinopoidea, and it is not at all clear (Fig. 1) that PLS paracribellar glands are plesiomorphic for Orbiculariae. In any case, origin of the aggregate gland from gland types already present on orbicularian PLS is feasible.

Thus, the objection raised by Peters & Kovoor faces several difficulties: first it misconstrues secondary loss of the cribellum and some associated features in araneoids as positive evidence of non-homology; second, it must explain the origin of the aggregate glands in a way that excludes an orbicularian ancestry; third, it does not address recent theoretical advances in homology research (Patterson 1982) such as the equivalence of apomorphy and homology, congruence of character distributions, disjunction of character states, and simplicity of explanation. As Fig. 1 shows, according to the latter criteria the convergence argument must explain away a great deal of data.

An additional difficulty for the monophyly hypothesis may be the feasibility of a hypothetically intermediate cribellate-ecribellate orbweaver. Although entirely speculative, one may imagine a transition in which the reduction of the cribellum

and calamistrum proceeds in parallel with development of glands excreting viscid material on the PLS. Such a creature presumably would have continued to produce PLS axial fibers, possibly adorned with cribellate silk and viscid material from the nascent PLS glands, or perhaps the weakly viscid silk was used initially in a different context, such as prey-wrapping. If one assumes modern uloborid biology as a ground plan, such a transition even seems advantageous because uloborid juveniles build rather dysfunctional orbs without cribellate silk but which do have a thin covering of (probably) aciniform dry silk. Variation that made a source of sticky silk available early in uloborid ontogeny might have prospered. Early ontogenetic change is a common macroevolutionary mechanism.

The best one can do with questions of classical homology is to show that particular transitions are feasible; homology is best regarded as subject to refutation, but not to proof. Given that the improbable similarity in uloborid and araneoid spinning morphologies and behaviors demands some explanation, one kind of evidence is especially necessary to prefer convergence over homology. That is distinct sets of synapomorphies that separately relate uloborids and araneoids to non-overlapping groups of spiders that don't spin orb webs. However, the convergence "argument" thus far is entirely negative. It has failed to present an alternative explanation (cladogram) for the available data, nor even evidence favoring one. The present analysis results in roughly 16 synapomorphies for Orbicularia. Although monophyly explains the data better (more congruently, more simply) than all other phylogenetic hypotheses for these taxa and these data, like homology it can't be finally, irrefutably "proven." New data or new taxa may modify the results in various ways. However, until alternative hypotheses based on explicit synapomorphy schemes are proposed, one must conclude that the monophyly hypothesis best explains the available data.

4.3. Monophyly of Araneoidea

Millidge (1988) argued that linyphiids are the sister group of Agelenidae (or some large group including agelenids), and repudiated the mono-

phyly of araneoids. Those arguments did not include explicit synapomorphies for Agelenidae, Linyphiidae, or the two together. Although he discussed many features, he apparently claims synapomorphic status for only three: a sheet web; a tegular ridge; and an embolic division attached to the tegulum by a stalk. The first character is too poorly defined (in contrast to the orb web or other taxon-specific architectures) to be used as a synapomorphy at the level of Linyphiidae-Agelenidae. No behavior patterns or architectural features that I know of group these two families but exclude other "sheet" web weavers such as psechrids, eresids, pholcids, etc. The second character is an intriguing possibility, but Millidge did not demonstrate that it was plesiomorphic for both Linyphiidae and Agelenidae, a basic requirement if it were synapomorphic for the two families. The third feature is characteristic of Araneidae as well, and, while it may be synapomorphic for Araneidae and Linyphiidae (Coddington 1986a), it apparently cannot be synapomorphic for Linyphiidae and Agelenidae exclusive of the Araneidae.

Fig. 1 supports Araneoidea by 10 synapomorphies, of which Linyphiidae, despite their highly derived status, still exhibit 9 (PMS mAP nubbins are lost). The agelenid-linyphiid sister relationship can also be refuted by noting that it requires 22 steps of additional homoplasy for the data of Table 1, assuming that Agelenidae would group with the anaeroboids in Fig. 1. Thus, even if the comprehensive distribution of the three putative synapomorphies for Agelenidae-Linyphiidae were as claimed (which they are not), the cladogram of Fig. 1 is still objectively a simpler explanation. The Agelenidae-Linyphiidae hypothesis must explain each araneoid synapomorphy as independent instances of convergence.

Millidge's refutations of araneoid synapomorphies cite isolated instances of states similar to the araneoid condition, found more or less at random among araneomorph families. Consideration of Fig. 1 (or any cladogram) shows that random, uncorrelated instances of homoplasy have little effect on relationships supported by even a few co-varying homologies. To take one example, his argument that pholcids also make "sticky" silk is irrelevant to the araneoid condition for at least two reasons. Presuming that pholcids use the scyto-

doid modified ALS MAP gland/spigot system to make viscid silk, it cannot be homologous to the araneoid PLS aggregate gland/spigot system because araneoids retain the unmodified ALS MAP gland/spigot system. Second, even if the two morphological systems did not fail the conjunction and similarity criteria, concordance with other araneoid synapomorphies would still force explanation of the pholcid condition as homoplasy. The same logic applies to Millidge's discussions of other araneoid synapomorphies. Because the proposed refutations of putative araneoid synapomorphies do not agree among themselves on an alternative cladogram, the refutations themselves lack force.

Figure 1 suggests a different placement for linyphiids than in Coddington (1990). This result may be due to the sparse representation of araneoid groups in Table 1. Restoring nephilines, tetragnathines, anapids, mysmerids, and symphytognathids to the data set might also restore linyphiids to the vicinity of araneids. On the other hand, the linyphiid-araneid synapomorphies listed in Coddington (in press) were taken from the literature, and I cannot really evaluate the proposed homologies (especially "gnathocoxal sexual glands"). In the present analysis it is largely parsimonious interpretation of the loss of orb web building behaviors that groups linyphiids with theridioids. Loss is a weak reason to group taxa.

4.4. On convergence in web form

To appreciate the cladistic meaning of claiming convergence on orb webs, and the phylogenetic evidence necessary to claim it, consider a less notorious web architecture such as the funnel web. Why are not all funnel webs homologous? Funnel webs (*Atrax*, *Diplura*, *Tengella*, *Agelenopsis*) are arguably less diverse in architecture than orbs (*Deinopis*, *Araneus*, *Mysmena*). Architectural dissimilarity therefore does not explain the absence of funnel web homology hypotheses. Rather, other character systems overwhelmingly place at least some of the above taxa in groups also including non-funnel web weavers. No convincing phylogenetic series of funnel web builders exists to make homology of funnel webs from *Atrax* to *Agelenopsis* cladistically feasible (much

less to Linyphiidae). Funnel webs are convergent across Araneomorphae because other character systems refute homology by lack of congruence.

The opposite seems true of the two groups of orb weavers. Araneoidea and Deinopoidea have generally been regarded as unquestionably monophyletic but isolated lineages (e.g. Lehtinen 1967). Other "orphaned" cribellate groups such as Filistatidae, Acanthoctenidae, or Oecobiidae have tended to find their nearest relatives among ecribellates, so why not deinopoids and araneoids? The answer to this "why not" question is the heart of the evidential controversy over orb weaver monophyly. Relevant evidence has been reviewed in detail (Coddington 1986a-c, 1989, 1990) and, allowing for residual homoplasy, it supports monophyly. In contrast, in the decade since Brignoli (1979) first raised the monophyly issue in something like its modern form, no body of evidence has been found to link deinopoids and araneoids separately to non-orb weaving lineages. Confirmed polyphyly of the group sharing the trait at issue is fundamental to convergence arguments. Until such evidence appears, the "convergence" argument is illogical.

4.5. Origin of the orb

Eberhard (1987) discussed aspects of cribellate building, and reported potential "proto-orb" behaviors in non-orb weaving cribellates, e.g. a tendency to lay sticky lines at an angle to radial non-sticky lines, and to lay sticky lines from the periphery of the web inwards. The tendency to lay lines radially from a retreat usually makes a cribellate web look vaguely orb-like (Kullmann 1972). As emphasized by Coddington (1986a), the most suggestive "proto-orbs" are spun by cribellate spiders. However, this barely radial architecture does not correlate with the appearance of regular spirals, the other striking aspect of orbs. Similarly, laying sticky silk lines in broader (*Psecrus*) or narrower (*Titanoeca*, *Stegodyphus*, Dictynidae) switchbacks at angles to radial lines also does not correlate with appearance of spirals. Consequently one may infer that neither radial lines, nor centripetal sticky silk construction (Coddington 1986a) was the key step facilitating the origin of the orb. If one must guess, it seems more likely

that the reduction of the dry scaffolding — the more or less continuous platform that supports the spider while spinning cribellate silk — may have been critical for the evolution of spirals (or initially, incomplete pendulum swings). In orb weavers the reduction and stereotypy of such “platform construction” on the radial structure may have resulted in non-sticky spiral construction. In basal orb weaving groups the latter behavior provides cues important to sticky spiral construction. On the other hand, cribellate spiders spinning sheets dense enough to permit irregular paths probably will all be found to spin irregular sticky lines.

These kinds of behaviors were predicted earlier on the assumption that if the origin of the orb lay in cribellates rather than araneoids, then various vaguely suggestive precursors were likely to be found among cribellates (Coddington 1986a). Of course, orb weaver radius, frame, and sticky spiral construction behaviors are still unique to orb weavers; none of these easily definable motor patterns have been observed in non-orb weaving cribellates to date. However, if orb weavers are monophyletic then outgroup comparison predicts that intermediates in behavior and morphology should be found among cribellates, not cribellates. Eberhard's behavioral data, and the morphologies described by Kovoov (1987) and Coddington (1989, 1990) are consistent with this view. Discovery of cladistically concordant intermediate stages augments, rather than weakens, the transformational hypothesis.

Given that current evidence suggests that orb weaving behavior is relatively primitive, rather than the non-homologous terminal stages in two independent transformation series, then its origin may be ancient. Although neither web architecture nor behavior fossilizes, the origin of insect flight (wings) may mark the date, because orbs may well have evolved in tandem with insect flight. The preponderance of winged prey in orb webs (and the absence of crawling or walking prey; saltatory prey is equivocal) supports this idea. Carpenter & Burnham (1985) place the evolution of wings in the Lower Carboniferous. Fossil evidence for orb weavers this old is lacking, although Selden's discovery of Early Cretaceous uloborid and araneoid orbweavers (Selden 1990) is far older than the convergence hypothesis, simply

construed, would have predicted. The Lower-Middle Jurassic Juraraneidae described by Eskov (1988) date orb weavers back even further. The first appearance of orb weaver fossils are thus the earliest cribellates known and the earliest araneoid known, respectively. They are neither the youngest or among the youngest, as the convergence hypothesis would predict. Given Jurassic araneoids, orb weavers must be at least somewhat older. A pre-Jurassic date seems necessary, a mid-Paleozoic date feasible. In conclusion, available evidence still offers virtually no support to the beguiling notion of orb webs as terminal, recent stages in evolutionary trends convergent on highly selected and extremely adaptive regular geometries.

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