# [a]TOWARDS A PHYLOGENY OF ENTELEGYNE SPIDERS (ARANEAE, ARANEOMORPHAE, ENTELEGYNAE)

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**ABSTRACT.** We propose a phylogeny for all entelegyne families with cribellate members based on a matrix of 137 characters scored for 43 exemplar taxa and analyzed under parsimony. The cladogram confirms the monophyly of Neocribellatae, Araneoclada, Entelegynae, and Orbiculariae. Lycosoidea, Amaurobiidae and some included subfamilies, Dictynoidea, and Amaurobioidea (sensu Forster & Wilton 1973) are polyphyletic. Phyxelidinae Lehtinen is raised to family level (Phyxelididae, NEW RANK). The family Zorocratidae Dahl 1913 is revalidated. A group including all entelegynes other than Eresoidea is weakly supported as the sister group of Orbiculariae.

The true spiders or Araneomorphae (*araneae verae* of Simon 1892) comprise more than 30,000 described species. The classification of this group has undergone a revolution in the last 30 years, sparked by Lehtinen's (1967) comprehensive reassessment of araneomorph relationships and steered by Hennig's phylogenetic systematics (Hennig 1966; Platnick & Gertsch 1976). Spider classification, portrayed by some authors as chaotic (Head 1995; Elgar et al. 1990; Vollrath & Parker 1997: Prenter et al. 1997) is actually one of the better-understood megadiverse orders (Coddington & Levi 1991): including the results reported here, 100 of the 108 currently recognized families (93%) have been placed cladistically, that is, in a higher taxon based on evidence assessed phylogenetically. New character systems compared across worldwide samples of taxa have led to many new and thought-provoking hypotheses in araneomorph phylogeny. The strongest test of such hypotheses is how simply they can account for the available data, i.e., most parsimonious cladograms based on matrices of taxa by characters. Tests specifically designed at the family level and above are increasingly common:

Raven (1985) and Goloboff (1993a) for Mygalomorphae (15 families); Coddington (1986, 1990a, b) for Orbiculariae (13 families) and Entelegynae; Platnick et al. (1991) on haplogynes (17 families) and Araneomorphae; Griswold et al. (1994, 1998) for Araneoidea (12 families), and Griswold (1993) for Lycosoidea and related families (11 families).

The latter studies targeted large but relatively well-defined lineages. It is now feasible to probe how these large lineages are related. We chose exemplars from all cribellate families, reasoning that taxa retaining this plesiomorphic feature are more likely to straddle the basal nodes of the phylogeny of higher groups than are their relatives that have lost the cribellum: therefore they are most likely to reflect phylogenetic groundplans. Although phylogenetically ancient, the cribellum is a complex feature unlikely to have evolved more than once. Most major araneomorph clades have cribellate members (exceptions are Palpimanoidea and Dionycha). A phylogeny of these basal taxa should mirror the relationships of the large clades they exemplify. As Lehtinen (1967: 202) declared, "because of the central position of the Cribellate groups in Araneomorphae, a detailed revision of them is a short cut to a rough classification of the whole suborder."

A parsimonious cladogram based on an explicit taxon-character matrix is concise, logical, and testable. Our analysis tests many suprafamilial hypotheses of the last 30 years and is the first attempt to relate them using quantitative phylogenetic techniques: Amaurobioidea (*sensu* Forster & Wilton 1973), Amaurobiidae and included subfamilies (*sensu* Lehtinen 1967), Dictynoidea and Desidae (*sensu* Forster 1970), Entelegynae (*sensu* Coddington 1990b; Coddington & Levi 1991), Lycosoidea (Homann 1971; *sensu* Griswold 1993); Orbiculariae (*sensu* Coddington 1986, 1990a, b); and the 'RTA clade' (*sensu* Coddington & Levi 1991).

## TAXA AND CHARACTERS

Table 1 comprises 43 exemplars from 21 of the 22 araneomorph families with cribellate members. As outgroups we included HYPOCHILIDAE (*Hypochilus*), AUSTROCHILIDAE (*Hickmania* and *Thaida*), and FILISTATIDAE (*Filistata* and *Kukulcania*, Filistatinae). From eresoids, we included OECOBIIDAE (*Oecobius* and *Uroctea*) and ERESIDAE (*Eresus* and *Stegodyphus*). From Orbiculariae we included DEINOPIDAE (*Deinopis* and *Menneus*), ULOBORIDAE (*Octonoba* and *Uloborus*) and an araneoid groundplan. Recent phylogenetic study of this superfamily (Griswold et al. 1998) gives us confidence that the reconstructed groundplan accurately reflects the primitive conditions for Araneoidea. From ''dictynoids'' we included DICTYNIDAE (*Dictyna* and *Nigma*, *Lathys*, and *Tricholathys* representing Dictyninae, Cicurinae, and Tricholathysinae, respectively), DESIDAE (*Badumna candida*, *B. longinquua*, and *Matachia*, formerly Matachiinae), and NICODAMIDAE (*Megadictyna*). From ''amaurobioids'' we included AMAUROBIIDAE (*Amaurobius* and *Callobius* (Amaurobiinae), *Metaltella* (Metaltellinae), *Retiro* and *Pimus* (Macrobuninae), *Phyxelida*, *Vytfutia*, and *Xevioso* (Phyxelidinae)), AMPHINECTIDAE (*Maniho*), NEOLANIDAE (*Neolana*), AGELENIDAE (*Neoramia*), and TITANOECIDAE (*Goeldia* and *Titanoeca*). From lycosoids and related groups we included CTENIDAE (*Acanthoctenus*), MITURGIDAE (*Raecius* and *Uduba*, Uliodoninae), PSECHRIDAE (*Psechrus*), STIPHIDIIDAE (*Baiami* and *Stiphidion*); TENGELLIDAE (*Tengella*), and ZOROPSIDAE (*Zoropsis*).

We omitted Gradungulidae because the cribellate genera are extremely rare in collections and its placement in Austrochiloidea seems firm (Forster, Platnick & Gray 1987; Platnick et al. 1991). Voucher specimens for exemplars are deposited in the California Academy of Sciences (CAS) with the exception of *Vytfutia* (Deeleman coll.) and male *Raecius* (NHMV). Character data taken from the literature include the suite of classical characters from spider internal anatomy (characters 43–49: Platnick 1977; ex Millot 1931, 1933, 1936; Marples 1968 [these have been recorded for hypochiloids, austrochiloids, and such a wide variety of haplogyne and entelegyne Araneoclada that we are confident that the assumed states for entelegyne exemplars in Table 1 are justifiable]) and character 114, presence/absence of the muscle M29 in the male palp (assumed for all taxa in Table 1 following Huber 1994). Silk ultrastructure data are taken from Eberhard & Pereira (1993) and from unpublished observations (R. Carlson in lit.).

Characters, character states, and codings are listed in Table 1. Some features are most succinctly described by reference to a taxon for which they are typical, e.g, 'dictynid conductor.' For figures of entelegyne genitalia see especially Lehtinen (1967), Coddington (1990a) and Griswold (1993); for features of spinnerets see especially Platnick et al. (1991) and Griswold et al. (1998). Character evolution is summarized on the cladogram (Fig. 1) optimized via Clados (Nixon 1992) and MacClade (Maddison & Maddison 1992).

## METHODS AND ANALYSIS

Spigot classification follows Coddington (1989); all specimens were critical point dried before scanning electron microscope (SEM) examination of spinning organs. Behavioral observations were made on living animals in the field or lab.

The matrix (all characters unordered and equally weighted) was analyzed with three phylogenetic packages: Nona 1.6 (Goloboff 1993b), Hennig86 1.5 (Farris 1988), and PeeWee 2.6 (Goloboff 1997), using a wide variety of randomized and directed search strategies. Nona (using both 'amb =' and 'amb-' options for clade support) and Hennig86 found the same three topologies, including Fig. 1 (length 376, ci 0.43, ri 0.69). The two alternate topologies involved local rearrangements of Ni-

codamidae and Eresoidea. The strict consensus has one 4-tomy at the entelegyne node, otherwise identical to Fig. 1.

We used successive and implied weighting (Carpenter 1988; Goloboff 1993c) to further evaluate the data. Successive weighting in Nona (length 16,346, ci 0.63, ri 0.80) preferred Fig. 1. Successive weighting in Hennig86 (length 1127, ci 0.79, ri 0.88) found Fig. 1 as well as two other trees one step longer. Pee-Wee at concavity functions of 3 and 4 (fits 962.6 and 1009.0, length 378) found one tree in which *Retiro* and *Pimus* swapped places, otherwise identical to Fig. 1. Concavity 5 (fit 1041.6, lengths 376, 378) found Fig. 1 as well as the tree found at concavities 3 and 4. Concavity 6 (fit 1067.8, length 376) found only Fig. 1. Because Fig. 1 was the only topology judged optimal by all criteria (equal, successive, and implied weights), we recommend it as the working hypothesis for entelegyne relationships. Table 1 gives the number of steps, consistency index, retention index, weight (*ex* Hennig86), and fit (*ex* Pee-Wee, concavity 4) for all characters on Fig. 1.

In addition to mapping character support at nodes, we also examined cladogram robustness with branch support indices (Bremer 1994) calculated with Nona using the parameters 'h25000; bsupport8;'. The ''Bremer Support'' (''Decay Index'') for a given node in the shortest unconstrained tree is the number of additional steps required in the shortest trees for which that node collapses. The following Bremer Support values were found for the clades on Fig. 1: Austrochiloidea (5), Araneoclada (1), Entelegynae (1), Haplogynae (8), Eresoidea (1), *Stegodyphus-Eresus* (8), *Uroctea-Oecobius* (4), Canoe Tapetum Clade (0), Orbiculariae (2), *Deinopis-Octonoba* (3), *Deinopis-Menneus* (4), *Uloborus-Octonoba* (5), *Megadictyna-Zoropsis* (0), Divided Cribellum Clade (1), Titanoecoids (1), *Titanoeca-Goeldia* (2), *Vytfutia-Phyxelida* (2), *Xevioso-Phyxelida* (2), RTA Clade (1), Dictynidae (2), *Tricholathys-Nigma* (1), *Dictyna-Nigma* (3), Amaurobioids (1), Fused Paracribellar Clade (2), Stiphidioids (1), *Stiphidion-Baiami* (5), Agelenoids (2), *Maniho-Badumna c* (2), *Maniho-Metaltella* (2), Desidae (1), *Badumna l-Badumna c* (5), *Retiro-Zoropsis* (1), Amaurobiidae (1), *Pimus-Callobius* (2), *Amaurobius-Callobius* (3), *Tengella-Zoropsis* (4), *Raecius-Zoropsis* (2), *Raecius-Uduba* (2), Lycosoidea (2), and *Acanthoctenus-Zoropsis* (3).

## RESULTS

**Status of the Lycosoidea and their kin.**—Homann (1971, followed by Levi 1982) defined the Lycosoidea on the basis of a grate-shaped tapetum in the indirect eyes. Griswold (1993) produced a phylogeny for those families plus selected tengellids and miturgids that

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Table 1.—Character by taxon matrix. Rows represent characters. The first state listed is coded as ″0″, the second as ″1″, etc., ″?″ = unknown, ″-″ = non-applicable. Columns represent taxa. The final five columns give the number of steps, the consistency index, the retention index, weight, and fit on Fig. 1. Taxon abbreviations are Ac = *Acanthoctenus*; Am = *Amaurobius*; AP = Araneoidea; Ba = *Baiami*; Bd = *Badumna candida*; Ca = *Callobius*; De = *Deinopis*; Di = *Dictyna*; Er= *Eresus*; FP = *Filistata*; Go = *Goeldia*; Hi = *Hickmania*; Hy = *Hypochilus*; Ix = *Badumna longinquua*; Ku = *Kukulcania*; La = *Lathys*; Ma = *Matachia*; Me = *Megadictyna*; Mh = *Maniho*; Mn = *Menneus*; Mt = *Metaltella*; Ne = *Neoramia*; Ni = *Nigma*; Nl = *Neolana*; Oc = *Octonoba*; Oe = *Oecobius*; Ph = *Phyxelida*; Pi = *Pimus*; Ps = *Psechrus*; Ra = *Raecius*; Re = *Retiro*; Sg = *Stegodyphus*; St = *Stiphidion*; Te = *Tengella*; Th = *Thaida*; Ti = *Titanoeca*; Tr = *Tricholathys*; Ud = *Uduba*; Ul = *Uloborus*; Ur = *Uroctea*; Vy = *Vytfutia*; Xe = *Xevioso*; Zo = *Zoropsis*.

Character abbreviations: ALS = anterior lateral spinnerets; annul. = annulate; C = conductor; cent. = central; CR'ed = cut and reeled; dict = dictynid; E = embolus; embr. = embraces; extra = in addition to C and MA; iL1 = inside first leg; iL4 inside fourth leg; long. = longitudinal; L3 = third leg; L4 = fourth leg; MAP = major ampullate; mAP = minor ampullate; membr. = membraneous; met = metaltelline; Oe = oecobiid; oL1 = outside first leg; opp. = opposite; papill. = papillate; PMS = posterior median spinnerets; post. = posterior; PY = pyriform; scl. = sclerotized; spinn. = spinneret; STP = sclerotized tegular process; squam. = squamate; strob. = strobilate; Th = *Thaida*; trans. = transverse; trich. = trichobothria; Ulo = uloborid.

Table 1.

| | | St | CI | RI | Wt | Fit |
|---|---|---|---|---|---|---|
| | HTHFKSEUODMUOAMDNTLTGVXPNSBNMMMBIRPACTRUPZA | | | | | |
| **Legs** | yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | St | CI | RI | Wt | Fit |
| 1. Femoral trichobothria.: absent; present; | 00000000000110000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 2. Tarsal organ: exposed; capsulate; | 00011111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 3. Tarsal trichobothria: absent; present; | 00000000000000001100000111111111111111111 | 2 | .50 | .95 | 4 | 8 |
| 4. Tarsal trichobothrial rows: 1; 2+; | -----------------00-----0000000000000011011 | 2 | .50 | .75 | 3 | 8 |
| 5. Metatarsal trichobothria: 1-2; >2; | 00011000000000000011000001111111111111111 | 3 | .33 | .89 | 2 | 6.6 |
| 6. Tarsal trichobothria: normal; longer distally; | ------------------10-----1111011001111000000 | 4 | .25 | .66 | 1 | 5.7 |
| 7. Palpal tibial trichobothria: absent; present; | 0000000000?0?00000000000001101111101111000000 | 3 | .33 | .77 | 2 | 6.6 |
| 8. Trich. base: smooth; trans. ridge; long. ridge; | 00000110100000000001111100?0000000111111111 | 5 | .20 | .75 | 1 | 5 |
| 9. Trichobothrial base: simple; notched; | 01100000000000000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 10. Trochanteral notch: absent; present; | 00000000000000100000000000010101000000100001 | 6 | .16 | .00 | 0 | 4.4 |
| 11. Tarsal claws: 3; 2; | 00000000000000000000000000000000000000011 | 1 | 1.00 | 1.00 | 10 | 10 |
| 12. Claw tufts: absent; present; | 00000000000000000000000000000000000000111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 13. Calamistral rows: 2; 1; 3: | 0112211-11111-1111111111111111111111------ | 2 | 1.00 | 1.00 | 10 | 10 |
| 14. Calamistrum: linear; oval; | 0000000-00000-00000000000000000000000111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 15. Calamistrum origin: basal; median; | 0110000-00?00-00000000110000000000000000000 | 2 | .50 | .66 | 3 | 8 |
| 16. Male palpal femoral thorns: absent; present; | 01000000000000000000001110000000001100000000 | 4 | .25 | .40 | 1 | 5.7 |
| 17. Female palpal femoral thorns: absent; present; | 00000000000000000000011100000000001000000000 | 2 | .50 | .66 | 3 | 8 |
| 18. Feathery hairs: absent; present; | 010000000111100000000000001101000000000010000 | 5 | .20 | .50 | 1 | 5 |
| 19. Hair: plumose; pseudoserrate; serrate; | 00000000111120000000000000000000000000000 | 2 | 1.00 | 1.00 | 10 | 10 |
| 20. Metatarsal preening combs: absent; present; | 00000000000000000000010000111100011000000 | 4 | .25 | .50 | 1 | 5.7 |
| 21. Tibial ventral spine number: <7; >7; | 00000000000000000000000000000000000000011 | 1 | 1.00 | 1.00 | 10 | 10 |
| 22. Male metatarsus I: unmodified; modified; | 00000000000000000000011100000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 23. Male tibial crack: absent; present; | 00000000000000000000000000000000000001010 | 2 | .50 | .50 | 2 | 8 |
| 24. Serrate accessory claw setae: absent; present; | 00000000111111000000000000000000000000000 | 2 | .50 | .80 | 4 | 8 |
| 25. Female posterior leg scopula: absent; present; | 0000000000?000000000000000000000000000111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 26. Deinopoid tarsal comb: absent; present; | 00000000011101000000000000000000000000000 | 2 | .50 | .75 | 3 | 8 |
| | HTHFKSEUODMUOAMDNTLTGVXPNSBNMMMBIRPACTRUPZA | | | | | |
| **Carapace** | yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | St | CI | RI | Wt | Fit |
| 27. Carapace shape: oval; square; round; | 000001122000000000000000000000000000000000 | 2 | 1.00 | 1.00 | 10 | 10 |
| 28. Clypeal hood: absent; present; | 01100110000000000000000000000000000000000 | 2 | .50 | .66 | 3 | 8 |
| 29. Thickened setae at fang base: absent; present; | 0110000001?000111111111111110111111111111 | 4 | .25 | .70 | 1 | 5.7 |
| 30. Male chelicerae: normal; bowed; | 00000000000000011000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 31. Chelicerae: normal; small; | 00000001100000000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 32. Chelicerae: free; fused at base; | 00011000000000000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 33. Cheliceral teeth: present; absent; | 00011001100000000000000000000000000000000 | 2 | .50 | .66 | 3 | 8 |
| 34. Cheliceral chela: absent; present; | 00011000000000000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 35. Cheliceral boss: absent; present; | 0000011000?011011111111111111111111111111 | 4 | .25 | .66 | 1 | 5.7 |
| 36. Cheliceral boss: small; large; | -----00---?-00-111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 37. Chilum: absent; median; bilateral; | 0??00??00???020?00?11122211?22122?111222222 | 7 | .28 | .68 | 1 | 4.4 |
| 38. Tapetum: primitive; canoe; grate; absent; | 0000033003333311111111111111111111111111222 | 5 | .60 | .86 | 5 | 6.6 |
| 39. Posterior eye row: straight; recurved; | 01111001010001111111111110111111111111100 | 5 | .20 | .55 | 1 | 5 |
| 40. Serrula tooth rows: multiple; single; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | --- |
| 41. Sigilla: present; absent; | 01100111111111111111111111111111111111111 | 2 | .50 | .50 | 2 | 8 |
| 42. Medial cheliceral concavity: present; absent; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | --- |
| 43. Venom gland: cheliceral; carapace; absent; | 01111111112211111111111111111111111111111 | 2 | 1.00 | 1.00 | 10 | 10 |
| 44. Coxal gland duct: convoluted; simple; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | — |
| 45. 5th endosternite invagination: present; absent; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | — |
| 46. Midgut cheliceral diverticula: present; absent; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | --- |
| 47. Pharynx muscle origin: carapace; rostrum; | 01111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | — |
| | HTHFKSEUODMUOAMDNTLTGVXPNSBNMMMBIRPACTRUPZA | | | | | |
| **Abdomen** | yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | St | CI | RI | Wt | Fit |
| 48. Intestine: M-shaped; straight; | 00011111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 49. Heart ostia number: 4; 3 or 2; | 00011111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 50. Anal tubercle: small; large; | 00000001100000000000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 51. Posterior spiracles: 2; 1; | 01011111111111111111111111111111111111111 | 2 | .50 | .00 | 0 | 8 |
| 52. Posterior spiracles: wide; narrow; | -1-0011111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 53. Post. respiratory system: booklungs; tracheae; | 000111111111111111111111111111111111111111 | 1 | 1.00 | 1.00 | 10 | 10 |
| 54. Median tracheae: simple; branched; | -0---00000?110111110001000000011110000000000 | 6 | .16 | .58 | 0 | 4.4 |
| 55. Lateral tracheae: simple; branched; absent; | -----00000?00002222000000000001110000000000 | 2 | 1.00 | 1.00 | 10 | 10 |
| 56. Epiandrous spigots: present; absent; | 00?0000010???00111110?100?1?10000010000?11?11 | 5 | .20 | .66 | 1 | 5 |
| 57. Epiandrous spigots: dispersed; 2 bunches; | 00?00000-0???00----0?-11???-------011------ | 2 | .50 | .66 | 3 | 8 |
| | HTHFKSEUODMUOAMDNTLTGVXPNSBNMMMBIRPACTRUPZA | | | | | |
| **Spinneret morphology** | yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | St | CI | RI | Wt | Fit |
| 58. Spinn. cuticle: annul.; ridged; squam.; papill.; | 011113311111121111111111111111111111111111 | 3 | 1.00 | 1.00 | 10 | 10 |
| 59. Cribellum: present; absent; | 00000001000001000000000000000000000000000 | 2 | .50 | .00 | 0 | 8 |
| 60. Cribellum: entire; divided; | 0001111-10000-0000011111111110111101101111 | 6 | .16 | .61 | 1 | 4.4 |
| 61. Cribellate spigots: uniform; clumped; | 00000?0-00000-0000000000000000000000011001 | 2 | .50 | .50 | 2 | 8 |
| 62. Cribellate spigots: strobilate; claviform; | 000011?0-0?000-00000000000000000000000000 | 1 | 1.00 | 1.00 | 10 | 10 |
| 63. Tartipores: absent; present; | 011001111111111111111111111111111111111111 | 2 | .50 | .50 | 2 | 8 |
| 64. ALS field margin: narrow; broad; | 00000000000000000000?0011111111110011000000 | 2 | .50 | .90 | 4 | 8 |
| 65. ALS MAP: clustered; dispersed; | 00011111-0000000000000000000000000000000 | 2 | .50 | .75 | 3 | 8 |
| 66. ALS MAP number: >3; 3; 2; 1; | 022110003003332333223222222222223222222222 | 9 | .33 | .60 | 2 | 4 |
| 67. ALS MAP nubbin: absent; present; | 01100100011110111001100000000011101000000 | 19 | .11 | .50 | 0 | 3.3 |
| 68. ALS MAP nubbin: one; extra; | -11--0---11000-000--00-----------101-1------ | 4 | .25 | .50 | 1 | 5.7 |
| 69. ALS piriform margin: rounded; flat; sharp; | 00000000021100110000000000000011000000020 | 5 | .40 | .57 | 2 | 5.7 |

Table 1.—Continued.

| | | | St | CI | RI | Wt | Fit |
|---|---|---|---|---|---|---|---|
| 70. PMS mAP: absent; present; | 0111111011111111111111111111111111111111 | | 2 | .50 | .00 | 0 | 8 |
| 71. PMS mAP number: 1; >1; | -110011-00000000000000000000000100000011 | | 4 | .25 | .50 | 1 | 5.7 |
| 72. PMS mAP position: median/anterior; posterior; | -000000-000011010000000000000000000000000 | | 3 | .33 | .00 | 0 | 6.6 |
| 73. PMS mAP nubbins: absent; present; | -000011000000100000000011000000000000010111 | | 5 | .20 | .50 | 1 | 5 |
| 74. PMS mAP nubbins: 1; 2; | -----10------0--------00--------------0-000 | | 1 | 1.00 | 1.00 | 10 | — |
| 75. PMS aciniform: present; absent; | 0000011000000000000000000000000000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 76. PMS aciniform number: >3; 1-3; | 00010--0000000000010000000010000000000010 | | 5 | .20 | .00 | 0 | 5 |
| 77. PMS paracribellars: absent; present; | 0111100-01111-11111001111111111110111000000 | | 5 | .20 | .66 | 1 | 5 |
| 78. PMS paracribellar: at apex; mid-field; | -0000----0000--00010--000000111011-000------ | | 3 | .33 | .60 | 2 | 6.6 |
| 79. PMS paracribellar: bunched; encircling; | -1000----0000-111----111------0----00------ | | 3 | .33 | .66 | 2 | 6.6 |
| 80. PMS paracribellar shafts: single bases; grouped; | -0000----0000-01110--000111111011-001------ | | 4 | .25 | .72 | 1 | 5.7 |
| 81. PMS paracribellar bases: round; long, narrow; | -0000----0000-00000--111------0---000------ | | 1 | 1.00 | 1.00 | 10 | 10 |
| 82. PMS paracribellar: deinopoid; strobilate; floppy; | -0022----0000-11111--111111111111-111------ | | 2 | 1.00 | 1.00 | 10 | 10 |
| 83. PMS cylindrical spigots: absent; present; | 00000111111111?101111111111111110111?11111111 | | 3 | .33 | .66 | 2 | 6.6 |
| 84. PMS cylindrical spigot number: 1-2; many; | -----11001111070-1000110000000-110000011111 | | 7 | .14 | .60 | 0 | 4 |
| 85. PLS cuticular finger: absent; present; | 00000000000000?00000001000010000000000000 | | 2 | .50 | .00 | 0 | 8 |
| 86. PLS aggregate gland spigot: absent; present; | 000000000000001000000000000000000000000000 | | 1 | 1.00 | 1.00 | 10 | — |
| 87. PLS paracribellar: absent; present; | 0101100000000-110001101011101111110111000000 | | 9 | .11 | .55 | 0 | 3.3 |
| 88. PLS paracribellar number: 1; 2-3; | -0-11---------00---01-0-1?1-11011-111------ | | 4 | .25 | .40 | 1 | 5.7 |
| 89. PLS paracribellar: separate; + modified spigot; | -0------------00---0--0-000-00011-010------ | | 2 | .50 | .50 | 2 | 8 |
| 90. PLS modified spigot: absent; present; | 11?00000011111110010111111111111111101?11? | | 6 | .16 | .44 | 1 | 4.4 |
| 91. PLS modified spigot: in field; segregated; | 00?------11111000--0-0000000000000000-0?00? | | 1 | 1.00 | 1.00 | 10 | 10 |
| 92. PLS apical segment: domed; conical; elongate; | 00?0000221?1101000000000111011011-000?00101 | | 8 | .25 | .53 | 1 | 4 |
| 93. PLS apical enlarged seta: absent; present; | 00?0000000?00000000000?11000000000-000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |

| **Male Genitalia** | HTHFKSEUODMJQAMDNTLTGVXPNSBNMMMBIRPACTRUPZA yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | | St | CI | RI | Wt | Fit |
|---|---|---|---|---|---|---|---|
| 94. Tibial retroapical process: absent; present; | 00000000000000010110010011111111111111-11 | | 3 | .33 | .89 | 2 | 6.6 |
| 95. Tibial retroapical process: simple; complex; | ----------------0-00--0--0001111010000000-00 | | 2 | .50 | .75 | 3 | 8 |
| 96. Tibial ventroapical process: absent; present; | 000000000000000000000000000000001111011000 | | 2 | .50 | .80 | 4 | 8 |
| 97. Tibial dorsal process: absent; apical; proximal; | 00000000000000221001111200022020211111000000 | | 8 | .25 | .57 | 1 | 4 |
| 98. Tibial dorsal process: simple; complex, folded; | ----------------000--110000---00-0-0000------ | | 1 | 1.00 | 1.00 | 10 | 10 |
| 99. Tibial prolateral process: absent; present; | 00000000000000000000000000000000001011000000 | | 2 | .50 | .50 | 2 | 8 |
| 100. Paracymbium: absent; present; | 10000000000000100000000000000000000000000 | | 2 | .50 | .00 | 0 | 8 |
| 101. Cymbial dorsal scopula: absent; present; | 00000000000000000000000000000000000000011111 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 102. Pyriform bulb; absent; present; | 00011000000000000000000000000000000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 103. Tegular locking lobe: absent; present; | 00000000000000000000000000000000000110111 | | 3 | .33 | .66 | 2 | 6.6 |
| 104. Subtegular locking lobe: absent; present; | 00000000000000000000000000000000000110111 | | 2 | .50 | .75 | 3 | 8 |
| 105. Conductor: present; absent; tegular groove; | 00111000000000000002200000000000000000000 | | 3 | .66 | .66 | 4 | 8 |
| 106. Conductor: sclerotized; hyaline; | 00---000000000000000--000000000001101111011 | | 3 | .33 | .71 | 2 | 6.6 |
| 107. Scl. C: embr. E; opp. E; cent.; Ulo; Oe; Th; | 05---00442233320000--110200110000--1----1-- | | 11 | .45 | .45 | 2 | 4 |
| 108. C embr. E: apex only; desid; dict; met; apical; | 0----00---------2222----1-14--3111---------- | | 4 | 1.00 | 1.00 | 10 | 10 |
| 109. Median apophysis present; absent; | 00111110011000111110000001100000000000100 | | 8 | .12 | .50 | 0 | 3.6 |
| 110. Median apophysis: convex; concave; | 00------00--000-----000000--0000110010010-01 | | 4 | .25 | .25 | 0 | 5.7 |
| 111. Median apophysis: fixed; flexibly attached; | 00-----00--001-----111010---1101111111111-11 | | 5 | .20 | .50 | 1 | 5 |
| 112. 'Extra' tegular processes: absent; present; | 01-----11--000-----110000--0110001111011-10 | | 8 | .12 | .41 | 0 | 3.6 |
| 113. 'Extra' tegular process: conical; STP; membr.; | -0-----00----------00-0-----00---1111-11-2- | | 2 | 1.00 | 1.00 | 10 | 10 |
| 114. Palpal tarsus M29 muscle: present; absent; | 00000111111111111111111111111111111111111111 | | 1 | 1.00 | 1.00 | 10 | 10 |

| **Female Genitalia** | HTHFKSEUODMJQAMDNTLTGVXPNSBNMMMBIRPACTRUPZA yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | | St | CI | RI | Wt | Fit |
|---|---|---|---|---|---|---|---|
| 115. Female genitalia: haplogyne; entelegyne; | 000001111111111111111111111111111111111111111 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 116. Epigynum: absent; present; | 0100011111111111111111111111111111111111111 | | 2 | .50 | .66 | 3 | 8 |
| 117. Epigynum teeth: absent; present; | -0---0000000000000000000001111110010000000 | | 2 | .50 | .83 | 4 | 8 |
| 118. Convoluted vulva: absent; present; | 00000000000000000000000000001100000000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 119. Posterior receptaculum: absent; present; | 01100000000000000000000000000000000000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |

| **Behavior and Silk** | HTHFKSEUODMJQAMDNTLTGVXPNSBNMMMBIRPACTRUPZA yhiiugrreenlcPeiiraioyehltaehtadxeimaeadsoc | | St | CI | RI | Wt | Fit |
|---|---|---|---|---|---|---|---|
| 120. Cribellate silk axial lines: present; absent; | 0?00000?-00000-011?? 0???0?0?? 0010?? 00000?? 0? | | 2 | .50 | .50 | 2 | 8 |
| 121. Cribellate silk reserve warp: present; absent; | 0?1000?-00011-010?? 0???0?0?? 0010?? 00000?? 0? | | 4 | .25 | .25 | 0 | 5.7 |
| 122. Cribellate silk nodules: absent; present; | 0?1001?-11111-111?? 1??? 1?1?? 1111?? 1111??? 1? | | 2 | .50 | .50 | 2 | 8 |
| 123. Cribellate fibrils: cylindrical; flat; | 0?0110?-00000-000?? 0??? 0?0?? 0000?? 0000??? 0? | | 1 | 1.00 | 1.00 | 10 | 10 |
| 124. Cribellate silk: uniform; puffed; | 0?0000?-?1111-011?? 0??? 0?0?? 0000?? 0000??? 0? | | 2 | .50 | .80 | 4 | 8 |
| 125. Web posture: inverted; erect; | 000111?? 100000011?? 1?? 10000110111? 11111101- | | 7 | .14 | .57 | 0 | 4 |
| 126. Orb web architecture: absent; present; | 00000000011111000000? 00000000000000000000- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 127. Deinopid web architecture: absent; present; | 00000000011000000000000000000000000000000000 | | 1 | 1.00 | 1.00 | 10 | 10 |
| 128. Combing leg support: fixed L3; mobile L4; | 0??? 01?-11111-11????? 111?????? 1?? 1?? 1111111? | | 1 | 1.00 | 1.00 | 10 | 10 |
| 129. Frame construction: absent; present; | 00?? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 130. Radius construction: absent; CR'ed; doubled; | 0??? 0?? -? 1? 221?????????? 0???--0????????? 0? 0-- | | 2 | 1.00 | 1.00 | 10 | 10 |
| 131. Hub construction: absent; present; | 0??? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 132. Temporary spiral construction: absent; present; | 0??? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 133. Sticky spiral construction: absent; present; | 0??? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 134. Sticky silk localization: absent; oL1; iL4; | 0??? 0?? -? 2? 111?????????? 0???--0????????? 0? 0-- | | 2 | 1.00 | 1.00 | 10 | 10 |
| 135. L4 sticky silk shift: absent; present; | 0??? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 136. Non-sticky-sticky line grip: otherwise; w L4; | 0??? 0?? -? 1? 111?????????? 0???--0????????? 0? 0-- | | 1 | 1.00 | 1.00 | 10 | 10 |
| 137. Wrap attack: absent; present; | 00?? 10??? 11111100?????? 1? 0??? 0?? 0? 00000?? 0? | | 3 | .33 | .71 | 2 | 6.6 |

Hypochilus
Thaida
Hickmania
Filistata
Kukulcania
Stegodyphus
Eresus
Uroctea
Oecobius
Araneoidea
Deinopis
Menneus
Uloborus
Octonoba
Megadictyna
Titanoeca
Goeldia
Vytfutia
Xevioso
Phyxelida
Lathys
Tricholathys
Dictyna
Nigma
Neolana
Stiphidion
Baiami
Neoramia
Maniho
Metaltella
Matachia
Badumna l
Badumna c
Retiro
Pimus
Amaurobius
Callobius
Tengella
Raecius
Uduba
Psechrus
Acanthoctenus
Zoropsis

Paleocribellatae
Austrochiloidea
Haplogynae
Eresoidea
Orbiculariae
Nicodamidae
Titaneocoids
Dictynidae
Stiphidioids
Agelenoids
Desidae
Amaurobiidae
Lycosoidea
Neocribellatae
Araneoclada
Entelegynae
Canoe Tapetum Clade
Divided Cribellum Clade
RTA Clade
Fused Paracribellar Clade
Amaurobioids

shared with Lycosoidea a derived, oval cal-amistrum. Figure 1 corroborates the oval cal-amistrum (14) as a synapomorphy for this group. The former miturgid genera *Campos-tichomma, Zorocrates*, *Zorodictyna*, *Raecius*, and *Uduba* (clade BB in Griswold 1993) com-prise the family Zorocratidae Dahl 1913. Syn-apomorphies of Zorocratidae are: male tibial crack (23), clumped cribellar spigots (61), and a male palpal tibial ventroapical process (96). Zorocratidae are sister to Lycosoidea (Fig. 1) based on posterior median spinnerets with many cylindrical spigots (84) and a dorsal scopula on the cymbium (101). Stiphidiidae (*Baiami* and *Stiphidion* in Fig. 1) were for-merly included in Lycosoidea, but in this anal-ysis are more closely related to the Ageleni-dae, Amphinectidae, Desidae, and Neolanidae, based on a suite of rather homo-plasious characters. Perhaps the strongest ev-idence is the clumped rather than dispersed arrangement of the paracribellar spigots on the PMS (80). Jointly these characters overrule the grate-shaped tapetum, which therefore ap-pears to have evolved independently in sti-phidiids. Lycosoidea will probably be further modified by detailed study of lineages now included in Ctenidae.

**Amaurobiidae and included subfamilies (*sensu* Lehtinen 1967)**.—Defined classically by a plesiomorphy (presence of the cribel-lum), perhaps Amaurobiidae was most obvi-ously in need of relimitation after the collapse of the old Cribellatae. Lehtinen (1967) pro-posed nine subfamilies, seven of which are treated here: Matachiinae (*Badumna*, *Mata-chia*), Desinae (*Maniho*), Phyxelidinae (*Phy-xelida*, *Xevioso*; also *Vytfutia* following Gris-wold 1990), Stiphidiinae (*Baiami*, *Stiphidion*),

Macrobuninae (*Pimus*, *Retiro*), Metaltellinae (*Metaltella*) and Amaurobiinae (*Amaurobius*, *Callobius*). The cribellate Altellopsinae are known only from females (Lehtinen 1967: 338) and Rhoicininae are neither cribellate nor amaurobiids (Griswold 1993). Unless the lim-its of the family are expanded to include the lycosoids, one must conclude that Amaurobi-idae is the most seriously polyphyletic family discovered to date. Only Lehtinen's macro-bunines (paraphyletic) and amaurobiines ar-guably remain in Amaurobiidae (Fig. 1). Leh-tinen's desines and metaltellines are closely related and belong in Amphinectidae *sensu* Forster & Wilton 1973: this result corrobo-rates Davies (1998). As noted above, Stiphi-diidae *sensu* Forster & Wilton 1973 (*Stiphi-dion* and *Baiami* in Fig. 1) is sister to Neolanidae, not amaurobiids. Matachiines are desids *sensu* Forster & Wilton 1973 (Fig. 1); at least *Matachia* is strikingly similar to the ecribellate *Desis*. Phyxelidinae Lehtinen 1967 (formerly Amaurobiidae), which includes *Am-bohima*, *Kulalania*, *Lamaika*, *Malaika*, *Ma-tundua*, *Namaquarachne*, *Phyxelida*, *Pongo-lania*, *Themacrys*, *Vidole*, *Vytfutia* and *Xevioso*, constitutes a distinct family (Phyxel-ididae, NEW RANK). Phyxelididae (*Vytfutia, Xevioso* and *Phyxelida* in Fig. 1) is sister to Titanoecidae (*Titanoeca* and *Goeldia* in Fig. 1), not close to amaurobiids. Phyxelididae is corroborated by various synapomorphies: male (16) and female (17) palpal femur thorns, modified male metatarsus I (22), and long, narrow, closely packed and laterally flat-tened PMS paracribellar spigots (81).

**Amaurobioidea and Dictynoidea (*sensu* Forster & Wilton 1973)**.—Building upon an extensive study of the respiratory systems of

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Figure 1.—Cladogram for entelegyne spider exemplars. Character changes are noted on branches by character number, with ambiguous optimizations underlined. Characters optimized at the neocribellate node are ambiguous because Mygalomorphae, Mesothele, and Amblypygi are not considered in this matrix. Taxon names are to the right of their branch. Familial assignments of exemplars on this cladogram are: AGELENIDAE (*Neoramia*), AMAUROBIIDAE (*Amaurobius*, *Callobius*, *Pimus*, and *Retiro*), AMPHI-NECTIDAE (*Maniho* and *Metaltella*), AUSTROCHILIDAE (*Hickmania* and *Thaida*), CTENIDAE (*Acan-thoctenus*), DEINOPIDAE (*Deinopis* and *Menneus*), DESIDAE (*Badumna* c[*andida*], *Badumna* l[*onginquua*], and *Matachia*), DICTYNIDAE (*Dictyna*, *Nigma*, *Lathys*, and *Tricholathys*), ERESIDAE (*Eresus* and *Stegodyphus*), FILISTATIDAE (*Filistata* and *Kukulcania*), HYPOCHILIDAE (*Hypochilus*), NEOLANIDAE (*Neolana*), NICODAMIDAE (*Megadictyna*), OECOBIIDAE (*Oecobius* and *Uroctea*), PHYXELIDIDAE (*Phyxelida*, *Vytfutia*, and *Xevioso*), PSECHRIDAE (*Psechrus*), STIPHIDIIDAE (*Baiami* and *Stiphidion*), TENGELLIDAE (*Tengella*), TITANOECIDAE (*Goeldia* and *Titanoeca*), ULOBORIDAE (*Octonoba* and *Uloborus*), ZOROCRATIDAE (*Raecius* and *Uduba*), and ZOROPSIDAE (*Zoropsis*).

spiders, Forster (1970) and Forster & Wilton (1973) defined two superfamilies that contained all the families treated here as well as others. The Amaurobioidea (unbranched, slender tracheae) included Agelenidae, Amaurobiidae, Amphinectidae, Ctenidae, Cycloctenidae, Neolanidae, Psechridae, and Stiphidiidae. Figure 1 suggests a much more limited arrangement: Amaurobiidae is sister to only tengellids, zorocratids, and lycosoids. The Dictynoidea (at least median tracheae branched) included Amaurobioididae, Anyphaenidae, Argyronetidae, Cybaeidae, Dictynidae, Desidae, Hahniidae, and Nicodamidae. The unbranched condition (54) is primitive and thus Amaurobioidea should not be expected to be monophyletic. Branched tracheae (54), however, originates six times on Fig. 1 and although it helps to define families (Uloboridae, Dictynidae) it does not, as yet, clearly define a larger clade. Dictynidae is monophyletic and is sister (or part of the sister group) to most distal entelegynes, including Neolanidae, Stiphidiidae, Amphinectidae, Amaurobiidae, Desidae, Agelenidae, Tengellidae, Zorocratidae, and Lycosoidea.

**The 'RTA' Clade.**—Coddington & Levi (1991) suggested an informal but informative grouping for those spiders having a retrolateral tibial apophysis (RTA) on the male palp, including taxa thought to lack the RTA secondarily. A variety of tibial apophyses on the male palp exist, sometimes on the same animal, and here we code this diversity as four homologies rather than one. The RTA itself (94) still defines roughly the same lineage (Fig. 1), except that the absence of the RTA in Nicodamidae, Phyxelididae, and Titanoecidae is primitive, not secondary and thus excludes them from the RTA clade. An additional unambiguous synapomorphy is trichobothria on the tarsi (3). *Vytfutia* apparently evolved the RTA independently.

**Outgroup of the Orbiculariae.**—With more than 10,000 described species and a great variety of documented webs and other behaviors, the Orbiculariae comprise one of the largest and most interesting clades of spiders. Coddington (1990b) implied Dictynoidea as a possible Orbicularian sister group. Platnick et al. (1991) suggested that the Amaurobioidea (represented in their study by *Amaurobius*) and Dictynoidea (represented by *Dictyna*) together could be the sister group.

Coddington & Levi (1991) suggested that the 'RTA clade' (including Dictynoidea, Amaurobioidea, Dionycha, and Lycosoidea) was the orbicularian sister group. The first two studies lacked many relevant taxa, and the last was a review, not a new analysis. This study omits palpimanoids, but suggests that the sister group to Orbiculariae is essentially all entelegyne spiders other than eresoids. In retrospect, the difficulty in finding the sister group of orbweavers is understandable. The answer, suggested by all of these studies in one way or another, is not one or a few classical families, or even any pre-existing taxonomic hypothesis in spiders. It is, rather, a previously unknown suprafamilial clade whose precise characterization still requires much work. In one alternative parsimonious topology for this dataset, however, the orbicularian sister group is Nicodamidae (*Megadictyna*), based on serrate accessory claw setae (24), the entire cribellum (60), and inverted posture in the web (125). Given this possibility, further field studies of nicodamid behavior and web construction would be welcome.

**New entelegyne groups.**—As before (Coddington & Levi 1991; Scharff & Coddington 1997; Griswold et al. 1998) we propose informal names for a few clades so that they may be discussed and tested by other workers prior to formal taxonomic recognition. All entelegynes distad of eresoids we call the ''canoe-tapetum clade'' (Fig. 1). On this cladogram the canoe tapetum arises unambiguously at this node and certainly represents an important restructuring of the spider visual system. The clade is also supported by the appearance of the modified silk spigot on the PLS (90), called the pseudoflagelliform in deinopoids, but now known to have homologs in many other lineages. This spigot presumably contributes additional axial fibers to the cribellate silk, as noted by Eberhard & Pereira (1993), and may represent an important event in the evolution of capture threads.

It seems logical to redefine the Amaurobioidea to include all families in the sister clade to Dictynidae (Fig. 1). Likewise, the clade including Titanoecidae and Phyxelididae could be called the ''titanoecoids.'' ''Agelenoids'' could refer to Agelenidae, Amphinectidae, and Desidae.

Similarly it seems worthwhile to recognize the ''fused paracribellar clade'' as well as the

"divided cribellum clade" (Fig. 1). The functional role of paracribellar fibrils in capture threads is not known with certainty, but these taxa have the paracribellar shafts fused so that many spigots emerge from the same shaft–a striking morphology (80). The same clade is also defined by wide ALS piriform field margins (64)–another spinning field feature whose functional significance is still unknown. Likewise, the divided cribellum (60) is scarcely free from homoplasy, but one of its origins does define a large clade of spiders (Fig. 1).

## DISCUSSION

These results constitute the most detailed proposal to date for basic entelegyne relationships. Added to previous analyses (refs. in Coddington & Levi 1991), 100 of the 108 current spider families are now placed in higher taxa intermediate between suborder and superfamily. *Incertae sedis* families are only Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, the remaining Miturgidae, and Zodariidae. The higher taxa Palpimanoidea and Dionycha (if monophyletic) also need to be placed in the general schema. Both groups are entirely ecribellate and so many informative characters cannot be scored. Palpimanoidea was placed by Platnick et al. (1991) as sister group of the clade Orbiculariae plus the RTA clade, which group was supported by the presence of the PLS pseudoflagelliform gland spigot (90). Nothing in our additional data challenges this conclusion. On the whole, these results sharpen rather than contest earlier work by providing a much more detailed and factually based hypothesis for test.

A notable result is the unavoidable homoplasy in character systems traditionally relied upon in araneomorph classification. For example, branched median tracheae (54) arise six times, the divided cribellum (60) evolves three times and reverts to entire three times (Dictynidae, *Matachia* and *Raecius*). Loss and regain of epiandrous spigots (56) occurs. Although the median apophysis (109) is homologous wherever it occurs, eight unambiguous losses are required. Once again understanding spider phylogeny seems to be, as succinctly put by Coddington & Levi (1991: 575), "not so much a question of finding characters as it is of allocating homoplasy." Spider data, however, is not abnormally homoplasious.

Based on regression coefficients calculated by Sanderson & Donoghue (1989) 43 taxa yield on average ci values of about 0.35; the value observed here (0.43) is rather better.

Several tasks remain before the first, rough, cladistic reconnaissance of Araneae could be said to be "complete." The major groups Palpimanoidea (Forster & Platnick 1984) and Dionycha (sensu Coddington & Levi 1991) as well as families mentioned above, are not placed on this cladogram. At infrafamilial levels, many cribellate enigmas remain unstudied, e.g., *Poaka* (Psechridae?) and *Aebutina* (Dictynidae?). The generality of these results is uncertain because in many cases the monophyly of families containing cribellate and ecribellate members is untested (especially Agelenidae and Dictynidae). Nevertheless, in its breadth of taxa and characters this study represents progress towards a comprehensive family-level phylogeny for the true spiders.

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