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, Amaurobioidea 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:

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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: Amaurobioida (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), ASTROCHILIDAE (Hickmania and Thalida), and FILISTATIDAE (Filistata and Kukulcania, Filistatinae). From eresoids, we included OECOBIIDAE (Oecobius and Urocea) and ERESIDAE (Eresus and Stegodyphus). From orbiculariae we included DEINOPIDAE (Deinopsis and Menneus), ULOBORIDAE (Octonoba and Uloborus) and an araneoid groundplan. Recent phylogenetic study of this superfamilly (Griswold et al. 1998) gives us confidence that the reconstructed groundplan accurately reflects the primitive conditions for Araneoidea. From “dictynoids” we included DICHTYNIIDAE (Dictyna and Nigma, Lathys, and Tricholathys representing Dictyninae, Cicerinae, and Tricholathysinae, respectively), DESIDAE (Badumna candida, B. longinqua, and Matica, formerly Matachinea), and NICODAMIDAE (Megadictyna). From “amaurobioids” we included AMAUROBIIDAE (Amaurobius and Callobius (Amaurobiinae), Metaelte (Metaeltelinae), Retiro and Pimus (Macrobuninae), Phyxelida, Vythia, and Xeviso (Phyxelidinae)), AMPHINECTIDAE (Maniho), NEOLANIIDAE (Neolana), AGELENIDAE (Neorania), and TITANOECIDAE (Goeldia and Titanoeeca). From lycosooids and related groups we included CTENIDAE (Acanthoctenus), MURGIDAE (Raecius and Uduba, Uliodoninae), PSECHRIDAE (Psechrus), STIPHIDIIDAE (Batania 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 Vythia (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 Araneoidea 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 spinnersets 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 PEE-WEE 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 Eresioidea. 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. Pec-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 Pec-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), Araneoidea (1), Entelegyneae (1), Haplogyneae (8), Eresioidea (1), Stegodyphus-Eresus (8), Uroctea-Oecobius (4), Canoe Tapetum Clade (0), Orbiculariae (2), Deinopis-Octonoba (3), Deinopis-Menoneus (4), Uloborus-Octonoba (5), Megadictyna-Zoropsis (0), Divided Cribellum Clade (1), Titanoccoids (1), Titanoeca-Goeldia (2), Vytfutia-Physelixida (2), Xevioso-Phyxelida (2), RTA Clade (1), Dictyniae (2), Tricholatys-Nigma (1), Dictyna-Nigma (3), Amaurobioids (1), Fused Pararibellar Clade (2), Stiphidioids (1), Stiphidion-Baiami (5), Ageleoniids (2), Manihoden (2), Manihoden c (2), Manihoden-Metalittal (2), Desidae (1), Badumna l-Badumna c (5), Retiro-Zoropsis (1), Amaurobiidae (1), Pimus-Callibius (2), Amaurobius-Callibius (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
<table>
<thead>
<tr>
<th>Character</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posterior eye row: straight; recurved;</td>
<td></td>
</tr>
<tr>
<td>Cheliceral boss: small; large;</td>
<td></td>
</tr>
<tr>
<td>Serrula tooth rows: multiple; single;</td>
<td></td>
</tr>
<tr>
<td>Intestine: M-shaped; straight;</td>
<td></td>
</tr>
<tr>
<td>Posterior spiracles: 2; 1; wide; narrow;</td>
<td></td>
</tr>
<tr>
<td>Median tracheae: simple; branched;</td>
<td></td>
</tr>
<tr>
<td>Tartipores: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Cribellate spigots: strobilate; claviform;</td>
<td></td>
</tr>
<tr>
<td>Cribellate spigots: uniform; clumped;</td>
<td></td>
</tr>
<tr>
<td>Carapace shape: oval; square; round;</td>
<td></td>
</tr>
<tr>
<td>Cheliceral teeth: present; absent;</td>
<td></td>
</tr>
<tr>
<td>Calamistral rows: 2; 1; 3;</td>
<td></td>
</tr>
<tr>
<td>Claw tufts: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Ctenidial tufts: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Tarsal claws: 3; 2;</td>
<td></td>
</tr>
<tr>
<td>Female palpal femora! thorns: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Female posterior leg scopula: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Serrate accessory claw setae: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Metatarsal preening combs: absent; present;</td>
<td></td>
</tr>
<tr>
<td>Tarsal trichobothria: normal; longer distally;</td>
<td></td>
</tr>
<tr>
<td>Trichobothrial base: simple; notched;</td>
<td></td>
</tr>
<tr>
<td>Female posterior trochanter: absent; present;</td>
<td></td>
</tr>
</tbody>
</table>
| Abdomen: }
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, Mesothelae, 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: AGELINIDAE (Neoania), AMAUROBIIDAE (Amaurobius, Callobius, Pimus, and Retiro), AMPHIBATIDAE (Manilo and Metalteria), AUSTROCHILIDAE (Hickmania and Thaidia), CTENIDAE (Acanthocephus), DEINOPIDAE (Deinopis and Memnesus), DESIDAE (Badunna clandida), Badunna longinquua, and Matachla), DICTYNIDAE (Dictyna, Nigma, Lathys, and Tricholathys), ERESIDAE (Eresus and Stegodyphus), FILISTATIDAE (Filistata and Kulakancia), HYPOCHILIDAE (HyPOCHilus), NEOLANIDAE (Neoanal), NICODAMIDAE (Megadictyna), OECOBIDAE (Oecobius and Uroctea), PHYLXELIDACEAE (Phyxelida, Vythutia, and Xevioso), PSECHRIDAE (Psechrus), STIPHIIDAE (Baiami and Stiphidion), TENGELIDAE (Tengella), TITANOECIDAE (Goeldia and Titanoeca), ULOBORIDAE (Octonoba and Uloborus), ZOROCRATIDAE (Raeucius 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 tenebrids, zorocratids, and lycosoids. The Dicynoidea (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 Titanococidae is primitive, not secondary and thus excludes them from the RTA clade. An additional unambiguous synapomorphy is trichobothria on the tarsi (3). Vytflavia 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 superfamilial 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 Titanococidae and Phyxelididae could be called the “titanocoids.” “Agele- noids” 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 superfamilies. 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., Pouka (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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