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SYSTEMATICS AND EVOLUTION OF SPIDERS (ARANEAE)*

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INTRODUCTION

In the last 15 years understanding of the higher systematics of Araneae has changed greatly. Large classical superfamilies and families have turned out to be poly- or paraphyletic; posited relationships were often based on symplesiomorphies. In this brief review we summarize current taxonomic and phylogenetic knowledge and suggest where future efforts might profitably be concentrated. We lack space to discuss fully all the clades mentioned, and the cited numbers of described taxa are only approximate. Other aspects of spider biology have been summarized by Barth (7), Eberhard (47), Jackson & Parks (72), Nentwig (105), Nyffeler & Benz (106), Riechert & Lockley (134), Shear (149) and Turnbull (160).

Diversity, Paleontology, Descriptive Work, Importance

The order Araneae ranks seventh in global diversity after the five largest insect orders (Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera) and Acari among the arachnids (111) in terms of species described or an-

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ticipated. Spiders are among the most diverse groups on earth. Among these taxa, spiders are exceptional for their complete dependence on predation as a trophic strategy. In contrast, the diversity of insects and mites may result from their diversity in dietary strategies—notably phytophagy and parasitism (104).

Roughly 34,000 species of spiders had been named by 1988, placed in about 3000 genera and 105 families (117). A small percentage of those species names will turn out to be synonyms. Families with over 1000 species described are Salticidae (jumping spiders; ca. 490 genera, 4400 species); Linyphiidae (dwarf or money spiders, sheet web weavers; ca. 400 genera, 3700 species), Araneidae (common orb weavers; ca. 160 genera, 2600 species); Theridiidae (cob web weavers; ca. 50 genera, 2200 species); Lycosidae (wolf spiders; ca. 100 genera, 2200 species), Gnaphosidae (ground spiders; ca. 140 genera, 2200 species); and Thomisidae (crab spiders; ca. 160 genera, 2000 species). Although the aforementioned families are cosmopolitan, the linyphiids are most diverse in the north temperate regions, whereas the others are most diverse in the tropics or show no particular pattern. Fourteen spider families are monotypic at the generic level, and 15 are known from 10 or fewer species.

Because spiders are not thoroughly studied, estimates of total species diversity are difficult. The faunas of Western Europe (especially England) and Japan are most completely known (136, 137, 166). The Nearctic fauna is perhaps 80% described (33), New Zealand perhaps 60–70% (36, 51, 52, 54, 55, 60, 61), and Australia perhaps 20% (131). Other areas, especially Latin America, Africa, and the Pacific region are much more poorly known. In several recent revisions of Neotropical orb weavers, 60–70% of the species in available collections were new. But for each 50 previously known species about 75 names exist, as common species had been given different names in different countries (96–99). Recent revisions by Baehr & Baehr (4, 5) of Australian hirsutiids had 93% new species. In a monograph on the poorly known south temperate family Orsolobidae (57), 85% of the species were new. Finally, available collections are biased toward medium- and larger-sized species from easily accessible habitats. There are very few places on earth where even desultory searching does not yield new species of spiders. About one third of all genera (1090 in 83 families) occur in the Neotropics. If the above statistics suggest that 20% of the world fauna is described, then about 170,000 species of spiders are extant.

PALEONTOLOGY The earliest spider fossil is *Attercopus fimbriunguis* from the Middle Devonian (380–374 million years BP) Gilboa site in New York State (146). The spinner spigots of this fossil resemble those of recent mesotheles but also share features with primitive opisthotheles (150). Other

fossil spiders formerly attributed to the Paleozoic either are not spiders or else are too incomplete to permit certain identification.

Two species of orb weaving spiders are known from Early Cretaceous limestone in Spain (144). These animals can be placed in modern families or superfamilies—Tetragnathidae and Deinopoidea. Eskov (48, 49) described a new family of orb weavers, the Juraraneidae, and a new archaeid subfamily from the Lower-Middle Jurassic. Given the placement of Orbiculariae and Palpimanoidea in current phylogenetic systems (see below), Araneae may have originated in late Silurian or Early Devonian, with the major radiation of Araneomorphae in late Paleozoic or early Mesozoic times. Jeram et al (74) report trigonotarbid, sister to Pedipalpi plus Araneae, from the Upper Silurian of England. Selden (145) offers a brief but intriguing review of the fossil record of Arachnida and Araneae, evaluating its support for various cladistic hypotheses at the ordinal level.

Amber fossils of about 400 species of Eocene to Miocene age are known, mainly from Baltic or Dominican amber. The latter are mainly small species of the family Theridiidae and males of the tetragnathid genus *Nephila*. Altogether 45 families are represented in Baltic and Dominican amber, of which 2–3 are extinct and of which 30 are found in both ambers. Spiders from Dominican amber mostly belong in recent genera (165).

DESCRIPTIVE TAXONOMIC WORK Descriptive taxonomic work on spiders is not much different from that on any poorly known arthropod group not susceptible to automated or mass sampling techniques. Few specimens of most species are available. Accurate identification is only feasible with adult specimens. Perhaps half of all named species were originally described from a single specimen. Spiders are predators, and adults of many species are rare. Roughly half of all species taken from single tropical sites are singletons, even in large samples (32). Although characteristic of tropical arthropod communities, this rarity may also be due to spiders living in habitats difficult for humans to access, such as tree canopies (28, 89).

Lack of material affects the taxonomist in many ways. Collections often contain one sex but not the other, and associating isolated males and females can be difficult. In some species of the orb-weaving genera *Witica* and *Micrathena*, males and females had originally been placed in different genera because they looked extremely different (93, 94).

Variation is always apparent among even a few specimens of a species, especially if from widely separated localities. However, variation in tiny samples is intractable statistically. One must always question whether this variation indicates separate species or reflects geographical or individual variation. Variation in spiders also arises from their propensity to mature in any of several molts. Some *Nephila* adult males are twice the length of others

(34). Female spiders also undergo a variable number of molts and may mature at different sizes (73). Despite allometric growth and variable morphology, the dimensions of adult genitalia from the same population vary less than do their coloration, body dimensions, or proportions (37, 91). Many papers are concerned with variation (6, 37), but few deal with the genetics of this variation or heredity of color patterns (109, 132).

Early taxonomic work focussed on faunas and new species descriptions, often the bounty of travelers and explorers. Revisionary work was hindered in the past because holotypes (voucher specimens for names of new species) were rarely loaned through the mail. Now large collections and loans of valuable specimens are routine. At present the best taxonomic research is done in the context of revisionary studies. In contrast, isolated papers on "new" species in unrevised groups may result in a new crop of synonyms. High quality revisions still present all relevant comparative data on all species known in a genus, but they are also heavily illustrated to facilitate identification of species by nonspecialists.

Kaston (76, 77) and Roth (139) have made it possible to key to genus most North American spider families. Comparable literature is available for England, Japan, and Western Europe. The work of Forster and collaborators (36, 51–55, 60, 61) provides the only concerted treatment of an Australasian fauna. Although dealing only with New Zealand and still incomplete, it is the reference for the whole region. As noted above, it will be a huge task to revise the many genera of spiders in unstudied areas of the world.

First revisions of spider groups rely heavily on good illustrations of genitalia, the most accessible and likely mark of specific identity. It has been known since Lister in the seventeenth century (Philip H. Schwann, personal communication) that spider species differ in their genitalia: the epigynum (female copulatory pores) and the male palp. Clerck (24) illustrated genitalia in his 1757 treatise on Swedish spiders, but later authors often ignored them in their eagerness to name new species. The critical question of why genitalia reflect species differences has been discussed by Eberhard (44), who favors sexual selection on genitalic morphology by female choice during copulation.

It is as yet impractical to start a revision or to identify voucher specimens with molecular or biochemical methods. Such methods are excellent to test genetic or phylogenetic hypotheses among or within named species, or to resolve cases in which morphological comparison is insufficient. Similarly, morphometric treatments of somatic characters are usually unnecessary to identify species with complex genitalia but are useful in the infraorder Mygalomorphae (128). They also offer much promise in answering specific research questions, such as partitioning variation into heritable and phenotypic components.

Spider taxonomists have been lucky to have a series of up-to-date taxonom-

ic catalogs. Bonnet (12) in France and Roewer (138) in Germany independently prepared catalogs that were complete up to 1939 and 1942, respectively. Brignoli (18) included species described from 1940 to 1981, and Platnick (117) those from 1981 through 1987.

ARANEOLOGISTS AND ARANEOLOGICAL COLLECTIONS The situation for systematic araneologists in North America is probably typical for the rest of the world. About seven araneologists did systematic work in the 1940s in North America, and the number of paid professional systematic araneologists is similar now (33). Those few are supplemented by about 25 professionals with largely nonresearch jobs and consequently limited time for systematic work. Paralleling the loss in taxonomic expertise world-wide, the job situation for systematic araneologists is poor enough that many have left the field and few are entering it. The age structure of systematic araneologists is therefore significantly skewed towards older workers, compared to nonsystematic araneologists in North America (33). The number of araneologists in nonsystematic disciplines has increased much more rapidly, and consequently the need for identifications and taxonomic advice has outstripped the ability of systematists to supply it (33, 135). About 24 arachnological societies exist around the world, 8 of which publish research journals (35). The Centre International de Documentation Arachnologique, with about 750 members, is the major international society for nonacarine arachnid researchers.

Major collections of spiders accumulated at many institutions in the past when natural history was more in vogue, but many of those institutions no longer employ systematic araneologists. Consequently, many collections have become nearly static and often are poorly maintained. The largest spider collections are at the American Museum of Natural History in New York and the Museum of Comparative Zoology at Harvard University.

ECOLOGICAL, ECONOMIC, AND MEDICAL IMPORTANCE Spiders are diverse and abundant terrestrial predators. New England has almost 700 species (77); Great Britain and Ireland about 600 (136, 137); the Berlin area of Germany about 500 (165). Larger areas for which estimates exist are Japan with about 1100 (166), North America with about 4000 (33), and Australia with about 9000 (131). No comparable estimates exist for tropical regions, but a few hectares of tropical wet forest have numbers comparable to those cited above for immensely larger temperate areas (32). Bristowe (21) found about five million spiders per hectare in an abandoned field in Sussex, England. Linyphiid densities reached 29,000 individuals per cubic meter among filter-beds of an English sewage treatment plant; they fed principally on enchytraeid worms and dipteran larvae (42). As generalist predators,

spiders are abundant in all terrestrial ecosystems. Turnbull (160) reported abundances ranging from 0.64 to 842 per square meter.

Control by spiders of insect populations in agricultural and epidemiological settings is receiving more attention as integrated pest management replaces the use of chemical pesticides (13, 14, 106, 133, 134). Spider neurotoxins are much used in neurobiological research (72), and they may have potential as insecticides (157). Fiber scientists study silks (164).

At least four genera are consistently responsible for medically serious or life-threatening bites: the Australian funnel-web mygalomorph *Atrax* (Hexathelidae), the brown recluse *Loxosceles* (Loxoscelidae), the widow spiders *Latrodectus* (Theridiidae), and the tropical wolf spiders *Phoneutria* (Ctenidae). Other ctenid genera occurring in the tropics are probably also responsible for serious bites. Sao Paulo has 100 serious bites a year (103). At least 20 other genera have been responsible for bites requiring medical attention (142).

PRIOR PHYLOGENETIC WORK ON SPIDERS

Before the 1880s, spider classification was based on broad categories of lifestyles. Important and widely accepted suprafamilial categories were Tubitelae (tube-dwellers), Orbitelae (orb web weavers), Saltigradae (jumpers), and Citigradae (runners). The classification became distinctly more artificial in the latter nineteenth century. A consensus developed to construct monothetic classifications based on strict character dichotomies. For example, groups were defined by two *or* three claws, presence *or* absence of a cribellum, paraxial *or* diaxial chelicerae, one *or* two pairs of booklungs. Taxa based on plesiomorphies, "not," or "absent" characters came to exist at all levels of the taxonomy. Examples of higher level "taxa" were Trionycha (three claws is primitive for spiders), Cribellatae (the cribellum is primitive for the suborder Araneomorphae), Tetrapneumoniae (four booklungs is primitive for spiders), Orthognatha (paraxial chelicerae is primitive for spiders), and Haplogynae (all female spiders primitively lack fertilization ducts). Consequently, about half of the major suprafamilial taxa were paraphyletic.

Unfortunately, these erroneous groups were adopted by Eugène Simon, the most knowledgeable araneologist to date. His *Histoire Naturelle des Araignées* (156) was encyclopedic, detailed, and widely accepted; it has not yet been equalled or even approached. Catalogers such as Roewer (138) preserved most of the hierarchy embodied in Simon's system, while amplifying it and changing ranks to accommodate increased knowledge. Although several authors criticized Simon's system in one respect or another (20, 113, 114), it remained the consensus view until a furor erupted over a monograph on cribellate spiders (84).

The Collapse of the Cribellatae

Lehtinen (84) focussed on the Cribellatae, one of the artificial taxa mentioned above. The cribellum is an anterior median spinneret homolog, a flat plate bearing hundreds of densely packed spigots that produce persistently sticky silk (43). Lehtinen argued that all araneomorph spiders were once cribellate and that any ecribellate araneomorph was so secondarily. At that time roughly a fourth of all spider families were exclusively cribellate and regarded as one monophyletic lineage. Even though close relationships had been suggested between cribellate and ecribellate lineages (113, 114), they were highly controversial because they struck at the fundamental taxonomic dichotomy in the infraorder Araneomorphae. Paraphyly of the Cribellatae implied a wholesale review of araneomorph classification and phylogeny.

Lehtinen's argument received empirical support from the discovery of many clear cribellate-ecribellate close relatives in the New Zealand fauna (52) and an objective consideration of the most obvious European example, Urocteidae-Oecobiidae (8, 82). Whereas there were relatively few other cribellate-ecribellate sister taxa in the north temperate fauna, austral faunas, even within genera, were evidently full of them.

During the same period, cladistic theory began to revolutionize systematics. None of the authors of this rather "fact-based" challenge to the old araneomorph systematics used a cladistic approach, but it has been commonly used since then to rework and justify many of those arguments. The validity of Orthognatha, Tetrapneumoniae, Trionychae, Haplogynae, Ctenizidae, Argiopidae, Agelenidae, Amaurobiidae, and Clubionidae, to name a few of the larger taxa, was obviously questionable. Lehtinen's work was not consistently phylogenetic (he recognized many paraphyletic groups), and there were enough loose ends and mistaken details to obscure the fundamental insight with controversy. However, in retrospect his challenge to the old system was unmistakably mortal.

Monophyly and Cladistic Relations of Araneae

The monophyly of Araneae is supported by several complex and unique synapomorphies. The most important are abdominal appendages modified as spinnerets, silk glands and associated spigots, cheliceral venom glands, male pedipalpal tarsi modified as secondary genitalia (sperm transfer organs), and loss of abdominal segmentation (external traces are clear in Mesothelae and faint in a few Mygalomorphae; all possible sister taxa to Araneae are segmented). Spiders also lack the trochanterofemoral depressor muscle in the walking legs (152).

The traditional view (163) has placed spiders as sister to Amblypygi (tail-less whip scorpions). Shultz (152) added many new characters to the cladistic analysis of arachnid orders, emphasizing especially muscles and joints.

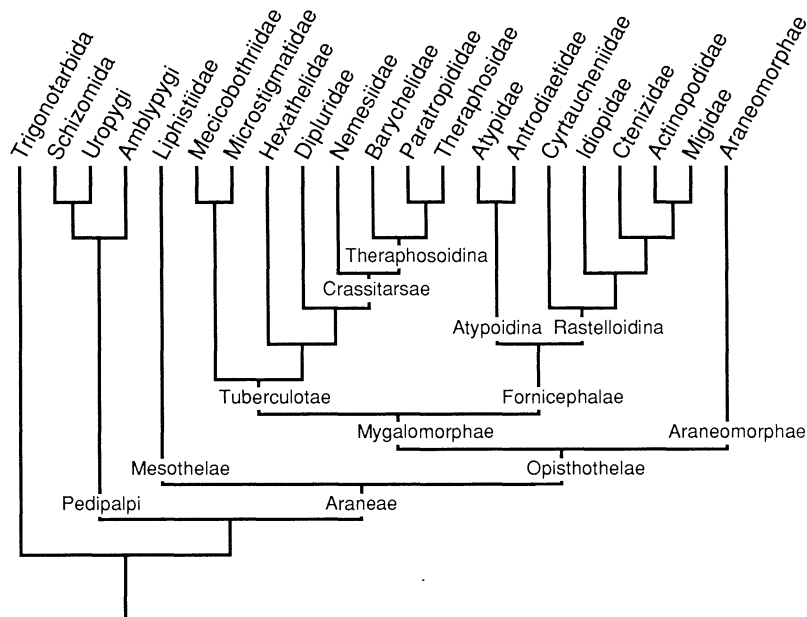


Figure 1 Cladistic hypothesis for Araneae and outgroups emphasizing cladistic structure of infraorders Mesothelae and Mygalomorphae. See Figure 2 for Infraorder Araneomorphae

Araneae emerged as sister to the Pedipalpi (Amblypygi, Schizomida, Uropygi) as a whole (Figure 1), based on six synapomorphies for Pedipalpi, and eight that linked Araneae to it. Shear et al (151) and Selden et al (146) agreed that Araneae was sister to Pedipalpi and further suggested that the extinct order Trigonotarbita was sister to the two together. Homann (71) argued that the plagula ventralis, a small sclerite associated with the cheliceral fang, was also a Pedipalpi-Araneae synapomorphy. Pedipalpi itself contains only about 200 species in three orders. The validity of the Pedipalpi-Araneae hypothesis is important for evolutionary studies on spiders. Reconstructing the ground plan for spiders now requires consideration of variation within all Pedipalpi rather than just Amblypygi.

CLADISTIC STRUCTURE OF ARANEA

Three major monophyletic groups of spiders exist: Mesothelae, Mygalomorphae, and Araneomorphae. Although most workers recognized them as different groups, for many years their interrelationships were not so clear.

Many authors (62, 76) recognized the taxon Orthognatha as including Mesothelae and Mygalomorphae. However, in perhaps the first explicitly cladistic treatment of spiders, Platnick & Gertsch (121) showed that paraxial

chelicerae (the “ortho” in Orthognatha) were primitive; Orthognatha was therefore paraphyletic. Instead Mygalomorphae and Araneomorphae are united as infraorders within Opisthothelae based on several characters such as terminally positioned spinnerets, coalesced neuromeres, and reduction of external evidence of abdominal segmentation. This work was an early example of the application of cladistic reasoning to a problem for which taxonomists did not lack data so much as they lacked any coherent rationale for preferring one solution over another.

Mesothelae

The suborder Mesothelae contains the single family Liphistiidae (2 genera; ca. 40 species), limited to China, Japan, southeast Asia, and Sumatra (123). Liphistiids confirm the metameric ancestry of spiders (tergites, sternites, dorso-ventral musculature, etc), dispersed (versus coalesced) ventral ganglia, and four distinct pairs of anteriorly placed spinnerets (versus fewer terminal spinnerets). One is left unsure whether many unique mesothele features, such as male genitalic morphology or pseudo-segmented spinnerets, are the plesiomorphic condition for all spiders or mesothele autapomorphies. This dilemma is particularly vexing in work on the evolution of spinnerets and spigots (110, 150).

Liphistiid monophyly is supported by five morphological synapomorphies, including a unique cuticular modification that apparently functions to detect leg flexion (122, 123). Because liphistiids are the sister group to the remaining spiders, their biology may give some indication of the ecological setting in which spiders evolved. Liphistiids are tube-dwelling sit-and-wait predators that construct rudimentary trap doors. Some make silk “trip-lines” radiating away from the burrow entrance that extend the sensory radius of the animal. They are active mainly at night, live for several years, have very low vagility, and consume a catholic diet of mainly walking prey. Females molt after sexual maturity. Because the internal spermathecal lining is shed during a molt, presumably they must mate again to continue to lay fertile eggs. While females rarely leave their burrows, adult males wander in search of the females. Their respiratory system consists only of booklungs, a possible obstacle to high activity levels (2, 3). This predisposition to forgo high activity levels and mobility (which characterize pterygote insects at least) for a low-cost, sit-and-wait strategy is a common, plesiomorphic, and perhaps constraining pattern in spider evolution.

Mygalomorphae

Mygalomorphs include the baboon spiders or tarantulas (Theraphosidae), trap-door spiders (Ctenizidae, Actinopodidae, Migidae, etc), purse-web spiders (Atypidae), funnel web spiders (Hexathelidae), and several other groups

with no common name (Figure 1). With 15 families (ca. 260 genera, 2200 species) (117), Mygalomorphae are more diverse than Mesothelae, although they do not approach the diversity of araneomorphs. Mygalomorph monophyly rests mainly on spinneret and male genitalic characters. They lack any trace of the anterior median spinnerets present in mesotheles, whereas at least primitive araneomorphs retain the cribellum as a homolog of those spinnerets. In mygalomorphs the anterior lateral spinnerets are much reduced if not absent altogether; in araneomorphs these spinnerets are the largest and best developed. The male pedipalpal genital bulb is fused in most mygalomorphs, but primitive araneomorphs and mesotheles have two to three divisions. Homann (71) wrote that only mygalomorphs have a small ancillary dorsal sclerite near the fang tooth. Raven (129) reviews other possible mygalomorph synapomorphies as well.

The family Theraphosidae or "tarantulas" contains almost three times as many species as any other mygalomorph family (ca. 800 species). It is not clear why they are so speciose: the most obvious synapomorphy for the family is dense tarsal scopulae on the last two pairs of legs as well as the first. This feature may aid in locomotion or in prey-handling (see below under *Dionycha*). Theraphosids are famous for their large size (at 10 cm body length the South American *Theraphosa leblondi* is probably the largest spider), but some are only a centimeter, and the smallest mygalomorph is less than a millimeter. The Australian *Atrax* (Hexathelidae) is extremely venomous and dangerous to humans.

Like mesotheles, mygalomorphs usually live in tube retreats or burrows. The popular stereotype of tarantulas as vagabond predators is inaccurate (38). Instead many tube dwellers extend the range over which they can sense prey by constructing silk lines away from the retreat entrance or arranging debris in radial patterns. These elaborations rarely gain the animal more than a few centimeters in range, although the foraging area can equal that accessed by typical web spiders. Some diplurids, however, build extensive and elaborate capture webs that approach a meter in diameter (38). Mygalomorphs are also capable of spinning at least slightly adhesive silk (39, 159). Although use of silk by mygalomorphs is more diverse than commonly appreciated (38), it is not so developed as in some araneomorphs. Mygalomorphs display a limited diversity of silk glands and spigot types (78, 79, 110).

Raven (129) recently reviewed and revamped the systematics of mygalomorphs. For the first time, a cladogram for families, subfamilies, and many generic groupings was proposed. The prior classification included 9–11 families (18, 149) and, in general, lacked justification. Earlier cladistic analyses had contested the monophyly of the Atypoidea (63, 116) and linked Actinopodidae and Migidae (124). Perhaps the worst cladistic problem was the sympleiomorphic Ctenizidae, a large, amorphous "dumping ground" classically

known as the trap-door spiders (130). At the family level, most of Raven's changes involved relimiting the Ctenizidae and recognizing groups formerly subsumed in it, although he did synonymize one family name. Figure 1 reproduces the cladistic structure among mygalomorphs presented by Raven.

His results show two major lineages, Fornicephalae (7 families, ca. 60 genera, 700 species), and the more speciose Tuberculotae (7 families, ca. 200 genera, 1500 species). Almost all the diversity in Tuberculotae is due to Theraphosidae (ca. 80 genera, 800 species). The Fornicephalae include two subsidiary branches, the atypoids and the rastelloids. It is interesting that one apomorphy of the atypoids is the great reduction or absence of tarsal trichobothria, mechanoreceptors sensitive to vibration and near-field sound. The rastelloids are united by the possession of a rastellum or digging rake on the chelicerae—they are all tube-dwellers and most make trap doors. A number of more subtle features unite the Fornicephalae as a whole, such as an arched head region, stout tarsi, and the first two pair of legs being more slender than the last. Tuberculotae, in contrast, have a sloping thoracic region, a serrula (saw-like row of teeth) on the maxillae that probably help to grasp and crush food items, and a distinct eye tubercle. Within these mygalomorphs, one well-defined group is the Crassitarsae (Nemesiidae and three families comprising Theraphosoidina), which share tarsal scopulae and a reduced median tarsal claw. Monophyly of Theraphosodina is based on presence of claw tufts (see also *Dionycha*, below) and the form of the tibial hook used by the male to catch the chelicerae of the female during mating.

The scope and results of Raven's work are impressive. He exposed many long-standing absurdities, and his work has become the point of departure for mygalomorph higher level systematics. It also substantiates the more general impression that uniquely derived and unreversed synapomorphies are not common in spiders. Inferring phylogeny is not so much a question of finding characters as it is of allocating homoplasy. Raven used 39 characters of which only 7 were fully consistent on his tree; three groupings at the family level were supported only by homoplasious characters.

Some of Raven's results are, of course, controversial. Speaking only of interfamilial relationships, perhaps the most significant controversy concerns the dismemberment of the Atypoidea (Atypidae, Antrodiaetidae, Mecicobothriidae). Araneologists often considered the atypoids as the most primitive mygalomorphs (23). Platnick (116) and Raven (129, 130) argued that atypoids were a symplesiomorphic group, although they accept the linkage of Atypidae and Antrodiaetidae. Eskov & Zonshtein (50) countered that mecicobothriids do form a monophyletic group with the atypoids and that Atypoidea in their sense are indeed sister to the remaining mygalomorphs, termed Theraphosoidea. However, Eskov & Zonshtein explicitly accepted grades in their scheme, and they excluded many apparently informative characters to

arrive at a considerably less parsimonious explanation of mygalomorph relationships. The debate is productive and focused on characters, a direct benefit of competing explicit phylogenetic hypotheses.

Araneomorphae

The infraorder Araneomorphae, sometimes referred to as “true” spiders, includes all remaining taxa, some 90 families, 2700 genera, and 32,000 species described.

Diversification rates in spiders between sister taxa (by definition of equal age) tend to be unequal. Mesothelae has a few dozen known species, Opisthothelae has 34,000. Mygalomorphae has roughly 2,000 species, Araneomorphae has the rest. Hypochilidae (9 species) are sister to the Neocribellatae (32,000 species), and Austrochiloidea (23 species) are sister to the Araneoclada (59, Figure 2). Entelegynae includes roughly 30,000 species, whereas Haplogynae numbers only about 2500 (Figure 2). Diversification rates within “higher” Entelegynae have been somewhat more equal. Orbiculariae (orb weavers and their descendants; ca. 10,300 species) may be sister to all taxa that have a retrolateral tibial apophysis on the male palp (“RTA Clade,” Figure 2, ca. 18,000 species). Within Araneoidea, Araneidae (ca. 2600 species) are apparently sister to the rest (ca. 7200 species) although the position of the large family Linyphiidae is still controversial. However, Deinopoidea (ca. 300 species) is putatively sister to Araneoidea (26, 30).

As noted above, plesiomorphic araneomorphs are unique in retaining the cribellum, a functional homolog of the anterior median spinnerets that produces extremely sticky silk. It is tempting to speculate that the diversity of araneomorph spiders is related to this important innovation. However, cribellate taxa are not very speciose, and for nearly all cribellate-ecribellate sister clades the cribellate lineage is less diverse. Examples are Filistatidae versus the remaining haplogynes (ca. 90 species versus 2400; Figure 2) and Deinopoidea versus Araneoidea (300 species versus 10,000; Figure 2). Only about 180 araneomorph genera in 22–23 families still contain cribellate members, although the diverse Australian cribellate fauna is mostly undescribed. However, that fauna may be another example of atypically high Australian diversity within an otherwise relict and depauperate clade (e.g. marsupials).

ARANEOCLADA This large group is defined by numerous synapomorphies. The most salient may be the transformation of the posterior booklungs into tracheae, the first appearance of a tracheal system in spiders. Here again, when a large group is defined by a synapomorphy with such an important function, it is tempting to suppose some linkage between diversification rates and evolutionary innovation. Although not as extensive as the tracheae of

higher insects, the tracheal system in spiders does correlate with higher metabolic rates and better water conservation (2).

The most recent cladistic work in spiders has focused on araneocladan groups. The higher taxa Haplogynae (17 families), Orbiculariae (13 families), Dysderoidea (4 families), Palpimanoidea (10 families), Lycosoidea (10 families), Gnaphosoidea (7 families), Deinopoidea (2 families), and Araneoidea (11 families) have all received recent cladistic treatment (30, 31, 56, 57, 65, 88, 118, 119, 154). Important exceptions are the clubionoid assemblage, the dictynoid assemblage, dionychan subgroups, and the amaurobioid assemblage (but see 10, 64), all of which suffer from varying degrees of polyphyly or paraphyly. Generally concordant cladistic hypotheses relating most of these large groups have recently been presented (31, 119). Figure 2 summarizes these arguments.

HAPLOGYNAE Any female reproductive system that lacked fertilization ducts was called haplogyne, a "non" category that rightly received much criticism (15, 16, 19, 115). Although the Haplogynae were originally defined on the basis of this plesiomorphy, cladistic evidence suggests that the Filistatidae, Dysderoidea, and "scytodoids" (Figure 2) are a monophyletic group after all (30, 31, 119). Alberti & Weinmann (1) reported peculiar sperm morphology distributed among Filistatidae, Oonopidae, Dysderidae, and Scytodidae that may turn out to be phylogenetically informative when all relevant groups are studied. In addition, the fused and pyriform bulb in the male palp has been reinterpreted as derived (80, 143), although it was formerly considered primitive by analogy to the mygalomorph condition. The tripartite palps of Paleocribellatae, Austrochiloidea, and Mesothelae are critical to this inference (59, 81). Other characters supporting the monophyly of the Haplogynae are a basal fusion of the chelicerae, a lamina along the fang groove instead of teeth, and the enigmatic absence of "tartipores" (150), apparently the vestigial traces of spinneret spigots present in previous instars (167).

Within Haplogynae, the cribellate Filistatidae are apparently sister to the entirely ecribellate remainder. The monophyly of the Dysderoidea (four families, ca. 120 genera) was rigorously justified by Forster & Platnick (57) on the basis of two clear synapomorphies: a novel posterior bursa in the female genitalia to store sperm, and the anterior position of the abdominal tracheal trunk. Haplogynae exhibit many diverse morphologies related to sperm storage, obviously an important functional problem (53). The functional significance of a relatively anterior versus posterior spiracle is unclear. So far as is known, most dysderoids usually live in leaf litter or similar protected habitats. Some such as segestriids spin relatively simple webs with trip lines radiating from the tubular retreat; most presumably are vagabonds.

Platnick et al (119) found several features that placed two enigmatic families, Tetrablemmidae ("armored" spiders; 87, 147) and Caponiidae (no

common name) close to the dysderoids. Tetrablemmids are related to the classical dysderoids by the loss of the anterior median eyes. Caponiidae are related to this clade by the advancement of the posterior tracheal spiracle to just behind the gonopore.

The remaining haplogynes, informally labelled “scytodoids” in Figure 2, are defined by the loss of the AME, a parallelism with the situation just noted for Tetrablemmidae-Dysderoidea. It includes the cellar spiders (Pholcidae) and diguetids, both of which spin elaborate webs, the spitting spiders (Scytodidae) and recluse spiders (Loxoscelidae), as well as lesser known groups. It differs from Scytodoidea as defined by Brignoli (16) by the transfer of Caponiidae and Tetrablemmidae to the dysderoids, and the placement of several small groups about which Brignoli was uncertain. Other hypotheses concerning haplogyne relationships (15, 88, 158) considered fewer taxa and characters, lacked data matrices, and were nonquantitative and less parsimonious. Subtle alternative explanations for character distributions (and implied groupings) are difficult to detect unless a quantitative approach is used.

ENTELEGYNÆ Entelegynae includes all the remaining superfamilies and about 70 families. Entelegyne female genitalia have paired copulatory pores that usually open on a sclerotized plate, the epigynum. Grooves, projections, and cavities of the epigynum offer the male a complex structure to affix his palpal bulb during copulation. How copulating pairs that lack these structures solve the problem of orienting their complicated genitalia during copulation is unknown, and therefore the mechanical significance of the epigynum is difficult to assess. Separate fertilization ducts lead from the spermathecae to the gonoduct; thus the reproductive system opens twice to the outside. Presumably this “flow-through” sperm management system is also an important functional difference from the haplogyne condition, but precise comparative data on well-chosen groups are lacking. Entelegyny is more uniform morphologically than haplogyny and is apparently only rarely lost among higher spiders. Reversal to a “haplogyne” condition occurs in a few genera of Uloboridae, Tetragnathidae, Anapidae, and at least three times within the Palpimanoidea (119). Interpretation of this character system is subject to lively debate (30, 31, 53, 57, 119). Eberhard (46) also discovered details of cribellate silk spinning behavior that seem to confirm entelegyne monophyly.

OTHER ENTELEGYNES Several entelegyne families remain unplaced in Figure 2 (see legend). The large family Zodariidae (ca. 50 genera, 420 species) recently received cladistic treatment (75), although its affinities remain elusive. Miturgidae are also a large family (ca. 20 genera, 150 species), but their monophyly is dubious (64, 65).

Eresoidea Oecobiidae and Hersiliidae share elongate posterior spinnerets used in a distinctive attack behavior—they rapidly circle around prey to wrap and immobilize it with silk. Eresidae are a distinct family, and it contains some odd genera (e.g. *Wajane*); its phylogenetic placement is controversial. Based on a selection of taxa and characters chosen to answer another question, the conclusions of Platnick et al (119) were that the oecobiid lineage and eresids were sister taxa based on secondary loss of the paracribellum, a distinctive set of silk spigots. Coddington (31) instead found that eresids and oecobiids (hersiliids were not considered) were adjacent outgroups to the remaining Entelegynae. Both studies agreed that they were basal within Entelegynae. Both Oecobiidae and Eresidae are cribellate. They are pivotal in Figure 2 because, although entelegyne, they lack derived eye tapeta (69), a retrolateral tibial apophysis, and the derived trichobothrial pattern (see below). Ethological studies of mating positions during copulation roughly confirm the positions of Oecobiidae and Eresidae as basal within the Entelegynae (161). These families appear cladistically intermediate between two great groups of “lower” and “higher” neocribellate spiders.

“HIGHER ENTELEGYNES” The “higher” entelegynes have specialized spigots in females that are used to make egg-sacs (29, 78, 119). Where studied, cylindrical glands serve these spigots, also only present in female spiders. Eggsac characteristics can deter parasitoid attacks (68) and decrease desiccation (108); perhaps cylindrical fibers contribute to these functions. The same group has either the canoe-shaped tapetum or the yet more derived grate-shaped tapetum in the indirect eyes, as opposed to the primitive tapetum (69, 83). By influencing how photons reflect within the eye, tapetal structures can strongly influence optical performance (11).

Palpimanoidea Classically the palpimanoids included only three closely related haplogyne families—Huttoniidae, Palpimanidae, and Stenochilidae. The latter is now included within Palpimanidae. Forster & Platnick (56) redefined the superfamily to include the haplogyne archaeids, mecysmaucheniids, the entelegyne Holarchaeidae, Pararchaeidae, Mimetidae, and the mostly entelegyne Micropholcommatidae. Two synapomorphies define the group—cheliceral glands on an elevated mound and cheliceral “peg” teeth (modified setae). These new additions were previously placed in Araneoidea. Malkaridae were recently recognized as the sister taxon of the Mimetidae (40, 120, 165), thus adding an additional entelegyne group to this superfamily.

Although these four groups (the classical palpimanoids, the four “archaeoid” families, Mimetidae-Malkaridae, Micropholcommatidae) are each clearly monophyletic, the resulting Palpimanoidea is heterogeneous. Mimetids and some archaeoid taxa specialize as predators of other spiders.

Araneophagy occurs in other palpimanoids and thus may corroborate monophyly (F. Murphy, personal communication). Palpimanids, huttoniids, and the archaeoid families live in leaf litter and probably don't spin webs; otherwise their habits are poorly known. The entelegyne mimetoid families are basal within Palpimanoidea. Parsimony thus suggests that entelegyny is plesiomorphic for Palpimanoidea and that haplogyny in this case is secondary (119). Forster (53) has argued that the morphological transformations required by the latter hypothesis are implausible compared with multiple origins of the entelegyne condition. Once again, all possible resolutions to this problem require homoplasy. The diverse genitalic morphologies subsumed under the term "haplogyne" (53, 56, 57) need to be cladistically analyzed. The male genitalia of Mimetidae are reminiscent of araneoids in some respects, though few potential synapomorphies have been proposed (30, 148). If further research shows mimetids, archaeoids, and micropholcommatids to be araneoids, then haplogyny might be the primitive state for the classical palpimanoids, thus contesting their placement within Entelegynae. Even if the former families are not palpimanoids, at least some Palpimanidae have canoe tapeta (69), thus still favoring placement within the "higher" entelegynes.

Within "higher" entelegynes, the "RTA Clade" and Orbiculariae are united by the presence of distinct pseudoflagelliform spigots on the posterior lateral spinnerets (Figure 2; 119). This spigot contributes the fibers that support the sticky cribellate silk in Deinopoidea and presumably in other cribellates as well. The homology of this spigot with distinctive spigots in Austrochiloidea and Filistatidae has not been established (119). Should homology be confirmed, the justification for this node will rest solely on special similarities between the pseudoflagelliform spigot in the "RTA Clade" and the cribellate orbicularians.

"RTA CLADE" The retrolateral tibial apophysis on the male palpal tibia is another higher level synapomorphy among spiders, ubiquitous among *Dionycha*, *Lycosoidea*, *amaurobioidea*, and *dictynoids* (10, 30, 31, 64, 65, 154). Haplogynes, orbicularians (except linyphiid erigonines), *Oecobiidae*, and *Eresidae* (*Wajane* is an exception) lack the structure. In two cases the tibial apophysis stabilizes the highly expansible palp during copulation (9, 155). Heimer (66) suggests that the paracymbium, an araneoid synapomorphy, may have a similar function. How other spiders lacking either structure solve the same functional problem is unknown. Comparative studies of copulatory position roughly confirm the RTA clade (161).

The distribution of trichobothria (fine sensory hairs) on the metatarsi and tarsi is another important character (30, 31, 85, 86). The plesiomorphic araneomorph pattern seems to be absence or near absence on the metatarsi and tarsi (although present on mygalomorph and mesothele tarsi). The derived

condition is single or multiple rows of trichobothria, often increasing in length toward the leg tip. Trichobothria detect slight air movements and may help to detect prey and predators (7). This feature apparently supports the monophyly of the RTA clade.

Amaurobioidea and Dictynoidea These superfamilies are among the largest cladistic problems at the family level. It is no coincidence that they are mainly cribellate groups. Although certainly entelegyne, no strong synapomorphies have yet been found to define them or to resolve their exact placement. This difficulty partly stems from heterogeneity within families. Agelenidae, Desidae, Dictynidae, Hahniidae, Miturgidae, and Amaurobiidae, to name the largest, probably will be more or less drastically redefined. Some spin large funnel webs, some small cribellate sticky webs, some are wanderers. Griswold (64) offered a succinct definition of Amaurobiidae but could not allocate the excluded genera to other families on objective grounds, thus leaving them effectively *incertae sedis*. In a revision of nearctic Cybaeidae, Bennett (10) discussed the composition of Dictynoidea and found several features (secondary gland pores in the female genitalia, a male palpal patellar apophysis, loss of male palpal tegular apophyses) to define all or most of the Dictynoidea. Aygyronetidae, a monotypic family including only the European water spider, are probably close to the Cybaeidae (84). Hahniids may share palpal apomorphies with dictynids and cybaeids, but this argument is still preliminary. Almost no recent work has concerned the very diverse amphinectids and desids. Lehtinen's Amaurobioidea lacked well-defined and defended synapomorphies (84). Forster and Wilton (52, 61) defined Amaurobioidea on the basis of unbranched abdominal median tracheae, and Dictynoidea on the basis of branched tracheae. Coddington (30) argued that by outgroup comparison the unbranched condition was plesiomorphic, but that the branched condition could indicate monophyly of Dictynoidea. The placement of many families in Amaurobioidea and Dictynoidea continues more by tradition than explicit justification (see legend to Figure 2).

Lycosoidea The classical lycosoid synapomorphy is the specialized structure of the tapetum of the lateral and posterior eyes—known as a “grate-shaped tapetum” (69). The feature is a transformation of the “canoe” tapetum, itself a transformation of the “primitive” type. The roughly ten lycosoid families (ca. 235 genera, 3700 species) include both cribellate and ecribellate taxa. As usual, this situation required a wholesale reevaluation of the higher level systematics (65). As for all true spiders, the plesiomorphic lifestyle apparently was as a sedentary web spinner. This still characterizes a few taxa (the cribellate Psecridae and Tengellidae). Most members of this superfamily, including nearly all of the speciose family Lycosidae, have forsaken the web habit for a more cursorial hunting style.

Lycosoid relationships have been recently studied (41, 64, 65, 153, 154). Griswold gives the most complete phylogenetic treatment of the superfamily, and his arrangement is used in Figure 2. He and Sierwald have shown that Lycosidae (wolf spiders), Pisauridae (nursery web spiders), rhoicinines (no common name), and Trechaleidae (no common name, see 22 and 154) share synapomorphies of male palp structure. Griswold (65) also proposed the small cribellate family Tengellidae as the sister group of Lycosoidea based on the presence of an oval rather than a linear calamistrum (the patch of hairs that functions with the cribellum to produce cribellate silk). In Figure 2 the families Acanthothenidae, Zoropsidae, Ctenidae, Psechridae, and Stiphidiidae contain cribellate members. Despite its scattered distribution on the cladogram, the cribellum still emerges as primitive for this mixed cribellate-ecribellate lineage.

Larger problems in lycosoid systematics include the definition and possible polyphyly of the large family Ctenidae, or tropical wolf spiders. For example, the cribellate genus *Acanthothenus*, often regarded as a ctenid, grouped with the cribellate family Zoropsidae in Griswold's analysis (on the basis of other characters than the retention of the cribellum). Similar questions about monophyly concern the Pisauridae, Bradystichidae, and Dolomedidae (153, 154).

DIONYCHA Primitively, all spiders were three-clawed. The derived two-clawed condition, in which the third claw is generally lost or very reduced and tufts of setae adorn the leg tip, characterizes the Dionycha. The monophyly of Dionycha has not yet been confirmed by a thorough analysis. These are primarily hunting animals that have forsaken webs as a foraging technique. The claw tuft, and/or the continuation of dense setae along the tarsus as a scopula, is known to improve traction on smooth surfaces (140). Another role of the scopula may be to improve prey manipulation during attacks. Some evidence suggests that removal of scopulae or claw tufts makes the animals less adept (141). The dionychan condition also occurs elsewhere in spiders, e.g. in Palpimanidae or Ctenidae, but sporadically at lower taxonomic levels. Several dionychan families remain unplaced in Figure 2 (see legend).

Gnaphosoidea and their relatives Three synapomorphies link the gnaphosoid families: flattened, irregularly shaped posterior median eyes, obliquely depressed endites, and heavily sclerotized anterior lateral spinnerets (118). The Gnaphosoidea currently includes seven families: Gnaphosidae ("ground" spiders; ca. 110 genera); Prodidomidae (ca. 30 genera); Gallieniellidae (3 genera); Ammoxenidae (1 genus); Cithaeronidae (1 genus); Trochanteriidae (5 genera) and Lamponidae (1 genus) (118). Gnaphosidae and Prodidomidae are thought to be sister taxa, but other gnaphosoid interrelationships remain ambiguous (118). Gnaphosids don't spin catching webs; presumably the other families related to them are also wanderers.

Penniman (112) suggested tentatively that Liocranidae or Corinnidae, formerly parts of the old Clubionidae, might, based on eye features, separately or together be the sister group to the Gnaphosoidea. The classical Clubionidae (or Clubionoidea) is therefore paraphyletic. He placed Anyphaenidae and Clubionidae as outgroups to this clade based on morphology of the sternum. This evidence has not been assessed by other workers, but the hypothesis is reasonable. Anyphaenidae, Clubionidae, and Salticidae lack cylindrical glands and spigots, otherwise characteristic of "higher" entelegynes (see above), and may therefore be united by this secondary loss (79, 119).

Salticidae or "jumping spiders" are the largest family of spiders, quite specialized, and proportionately enigmatic in their relationships. The most salient family synapomorphy is the highly specialized pair of anterior median eyes. These ocelli have impressive optical properties that enable the visually based, stalking attack for which jumping spiders are famous (11, 83). The chief cladistic problem has always been the difficulty of estimating intrafamilial cladistic structure, although some progress has been made (162). Loerbros (102) found evidence in palp structure and function to relate Salticidae and Thomisidae. Blest (11) sought the sister group of salticids among web-building spiders, thus arguing against Thomisidae. In a study of silk manipulation during the spinning of trail lines, Eberhard (45) found evidence to relate Salticidae, Gnaphosidae, and "Clubionidae," but that excluded Anyphaenidae and Thomisidae (more homoplasy).

The placement of Thomisidae within Dionycha is also unclear. Philodromidae, Sparassidae, and Selenopidae may eventually be placed near Thomisidae because they have laterigrade legs, which make their locomotion appear crab-like. The laterigrade condition makes hiding and maneuvering in narrow crevices easier. Based on eye structure, Homann (70) argued that Sparassidae and Philodromidae were sister taxa, but that Thomisidae were sister to Lycosoidea. In the light of Griswold's analysis of Lycosoidea, this hypothesis seems improbable, although Griswold did not include Thomisidae in his analysis. Once again, serious homoplasy is evident. Progress on dionychan relationships probably will be slow until all comparative data are considered simultaneously in one analysis.

ORBICULARIAE Reconstitution of the orb weavers, or Orbiculariae (25), also resulted from cladistic analysis of a classical cribellate-ecribellate dichotomy. Classically orb webs were thought to have evolved twice; once among the [paraphyletic] Cribellatae, and once among the [polyphyletic] Ecribellatae. The reputation of the orb as extremely adaptive confused the issue; some workers suggested as many as six separate origins of the orb geometry (67). Various authors considered a link between Uloboridae and

Araneidae or Araneoidea and explored its logical consequence; secondary loss of the orb among most of the remaining Araneoidea (17, 90, 107). Given the collapse of the Cribellatae and Ecribellatae as valid taxa, the orb web itself constituted initial evidence for monophyly. A series of detailed ethological and morphological investigations has failed to refute this hypothesis, thus corroborating that cribellate orb weavers (Deinopoidea) are the sister group of Araneoidea (26, 30, 31). If true, then the orb web evolved earlier than formerly believed and was subsequently lost in the large linyphiid and theridiid clades (31).

Orbiculariae are primitive spiders in many respects. Cribellate species preserve the plesiomorphic entire cribellum, and nearly all representatives preserve the apparently primitive pattern in trichobothrial distribution and tracheae. Although the fossil record of spiders is poor, orbicularians are among the earliest known entelegynes in the record (48, 50, 144, 145).

Deinopoidea The entirely cribellate Deinopoidea contains two families, about 25 genera, and some 300 species. All spin modified orbs. Some controversy existed in the past over placement of Deinopidae (ogre-faced spiders), but ethological work showed that they shared derived motor patterns unique to orb weavers, despite the derived web architecture (26). Uloborid genera have been revised recently (107), although recent work on their outgroups has suggested some changes in generic interrelationships (30). Uloborids are interesting phylogenetically because they may still retain many primitive aspects of orb weaver biology. In other aspects they are clearly derived, especially the complete loss of poison glands.

Araneoidea Araneoidea includes 11 families (ca. 740 genera, 10,000 species) or about a third of all described spiders. The most salient synapomorphies are the behavioral and morphological features that produce highly elastic viscid silk lines. Viscid silk is neither as sticky nor as durable as cribellate sticky silk, but it is faster and probably more economical to produce. Controversy over secondary loss of this ability as opposed to primary absence underlies most of the controversies about the composition of Araneoidea (e.g. the placement of various families here or in Palpimanoidea, see above). Araneoids are morphologically a rather compact group, despite their species-level diversity.

Taxonomic progress at the family level in Araneoidea has come mainly through relimitation and redefinition of the large families Araneidae and Theridiidae, the common orb weavers and cob web weavers (58, 100). The same fate may await Linyphiidae. Before the last decade, Araneidae usually included all ecribellate orb weavers and was thus defined by a plesiomorphy. Araneidae used to include the families Theridiosomatidae and Tetragnathidae.

The former araneid subfamilies Metinae and Nephilinae are now placed within Tetragnathidae (95, 101) based on apomorphies in male genitalia. Theridiidae used to include all or parts of the symphytognathoid families Anapidae, Mysmenidae, and Symphytognathidae (27, 125–127). Araneidae are now more compact and diagnosable (92), although still one of the largest spider families.

Unresolved problems in Araneoidea concern the affinities of the theridiid lineage (Synotaxidae, Nesticidae, Theridiidae, the “cob web” weavers) and the linyphiid lineage (Cyatholipidae and Linyphiidae, the “sheet web” spiders). Both groups are highly derived and thus difficult to place among the relatively more plesiomorphic araneoid groups. Somatic morphology and details of the spinning apparatus ally linyphiids with the “higher” araneoids, i.e. tetragnathids and the symphytognathoid families (31), but details in palp structure may place the linyphiids with the araneids (30). Despite much work, the placement of Theridiidae and its relatives within Araneoidea remains ambiguous.

CONCLUSIONS

Figures 1 and 2 compile the progress to date in proposing explicit cladograms that relate families of spiders. To what extent these often initial hypotheses will survive test by the addition of new taxa and evidence remains to be seen. Although strict phylogenetic reasoning has advanced spider systematics tremendously, conceptions of spider phylogeny in the past lacked more than a classical Hennigian basis. As quantitative analyses covering a broad range of character systems accumulate, it is apparent that character systems conflict. Phylogenies wholly consistent with supposed transformations in one character system are frequently inconsistent with others. Allocating this homoplasy is a serious problem and requires a quantitative approach, if only to establish an objective point of departure. Phylogenetic hypotheses based on single character systems that are oblivious to others are usually less useful. Likewise, comparative morphology is also less useful if authors fail to confront the phylogenetic implications of their hypotheses. In view of the weaknesses of these approaches, the most fruitful course will be for workers to consider carefully the phylogenetic implications of their own results in the context of other studies. Synthesis of comparative data is the core task of systematics; we hope that the cladograms compiled here will be useful to evolutionary biologists interested in spiders and in a common goal—the reconstruction and explication of evolutionary history.

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