Chapter 2

PHYLOGENY AND CLASSIFICATION OF SPIDERS

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ARACHNIDA

Spiders are one of the eleven orders of the class Arachnida, which also includes groups such as harvestmen (Opiliones), ticks and mites (Acari), scorpions (Scorpiones), false scorpions (Pseudoscorpiones), windscorpions (Solifugae), and vinegaroons (Uropygi). All arachnid orders occur in North America. Arachnida today comprises approximately 640 families, 9000 genera, and 93,000 described species, but the current estimate is that untold hundreds of thousands of new mites, substantially fewer spiders, and several thousand species in the remaining orders, are still undescribed (Adis & Harvey 2000, reviewed in Coddington & Colwell 2001, Coddington *et al.* 2004). Acari (ticks and mites) are by far the most diverse, Araneae (spiders) second, and the remaining taxa orders of magnitude less diverse. Discounting secondarily freshwater and marine mites, and a few semi-aquatic or intertidal forms, all extant arachnid taxa are terrestrial. Arachnida evidently originated in a marine habitat (Dunlop & Selden 1998, Dunlop & Webster 1999), invaded land independently of other terrestrial arthropod groups such as myriapods, crustaceans, and hexapods (Labandeira 1999), and solved the problems of terrestrialization (desiccation, respiration, nitrogenous waste removal without loss of excess water, and reproduction) in different ways. Although the phylogeny of Arachnida is still controversial (Coddington *et al.* 2004), specialists agree that the closest relative of Araneae is a group of orders collectively known as Pedipalpi: Amblypygi, Schizomida, and Uropygi (Shultz 1990).

PHYLOGENETIC THEORY AND METHOD

Systematics is the study and classification of the different kinds of organisms and the relationships among them. Good classifications are predictive: knowing one feature predicts many others. If one knows that an animal has spinnerets on the end of the abdomen, it will also have fangs and poison glands (lost in a few spiders), eight legs, two body regions, male palpi modified for sperm transfer, and it will spin silk: in short, it is a spider. All spiders share these features because they inherited them from a common ancestor, but today's spiders have evolved to differ among themselves. For example, the earliest spiders had fangs that worked in parallel (orthognath, like tarantulas and their allies), but later in spider evolution one lineage developed fangs that worked in opposition (labidognath, like the majority of spiders in North America). Much later within the labidognath lineage, some evolved the ability to coat silk lines with a viscid, semi-liquid glue, useful for entrapping and subduing prey. This nested pattern of branching lineages (phylogeny), results from evolutionary descent with modification (Fig. 2.1). The vast majority of similarities and differences among species are due to phylogeny. Jumping spiders (Salticidae) all have huge anterior median eyes because they are relatively closely related, and wolf spider (Lycosidae) eyes exhibit their characteristic eye pattern for the same reason. Phylogeny explains more biological pattern than any other scientific theory (e.g., ecology, physiology, ethology, etc.), and therefore classifications based on phylogeny will be maximally predictive. Besides huge front eyes, jumping spiders also share many other anatomical, behavioral, ecological, and physiological features. Most important for the field arachnologist they all jump, a useful bit of knowledge if you are trying to catch one. Taxonomic prediction works in reverse as well: that spider bouncing about erratically in the bushes is almost surely a salticid.

Another reason that scientists choose to base classification on phylogeny is that evolutionary history (like all history) is unique: strictly speaking, it only happened once. That means there is only one true reconstruction of evolutionary history and one true phylogeny: the existing classification is either correct, or it is not. In practice it can be complicated to reconstruct the true phylogeny of spiders and to know whether any given reconstruction (or classification) is "true." Indeed, scientists generally regard "truth" in this absolute sense as beyond their reach. Instead they strive to make their hypotheses as simple as possible, and as explanatory as possible. Simpler and more general hypotheses win. They win through comparison of predictions made by the hypothesis to factual observation. Scientific hypotheses (e.g., explanations, classifications, taxonomies, phylogenies) are constantly tested by discovery of new traits and new species. To the extent that the hypothesis is good, it accommodates and comfortably explains new data. If the new data do not fit the theoretical expectations, sooner or later a new hypothesis or a revised version of the old one takes its place. In biological classification, and phylogeny reconstruction in particular, scientists have developed a number of technical terms to describe the various ways that classifications or phylogenies do, or do not, correspond to fact (Fig. 2.1). Any group in a classification is said to be a taxon (plural taxa) or clade, and in theory corresponds to one common ancestral species and all of its descendants. Such clades are said to be monophyletic ("mono" = single, and "phylum" = race).

In the preceding examples, spiders (Araneae), labidognath spiders (now called Araneomorphae), sticky-silk spinners (Araneoidea), jumping spiders (Salticidae) and wolf spiders (Lycosidae) are all thought to be monophyletic groups, clades, and taxa. Each of these groups is distinguished by one or more uniquely evolved features or innovations. Such characters are said to be "derived," because they are transformations of a more primitive trait. Orthognath chelicerae is the original, primitive (plesiomorphic) condition for spiders, and labidognath chelicerae is the later, derived (apomorphic) condition. The only acceptable evidence for monophyletic groups are shared, derived characters, or synapomorphies ("syn" = shared, "apomorphy" = derived morphology) such as the evolution of viscid silk in Araneoidea (Fig. 2.1).
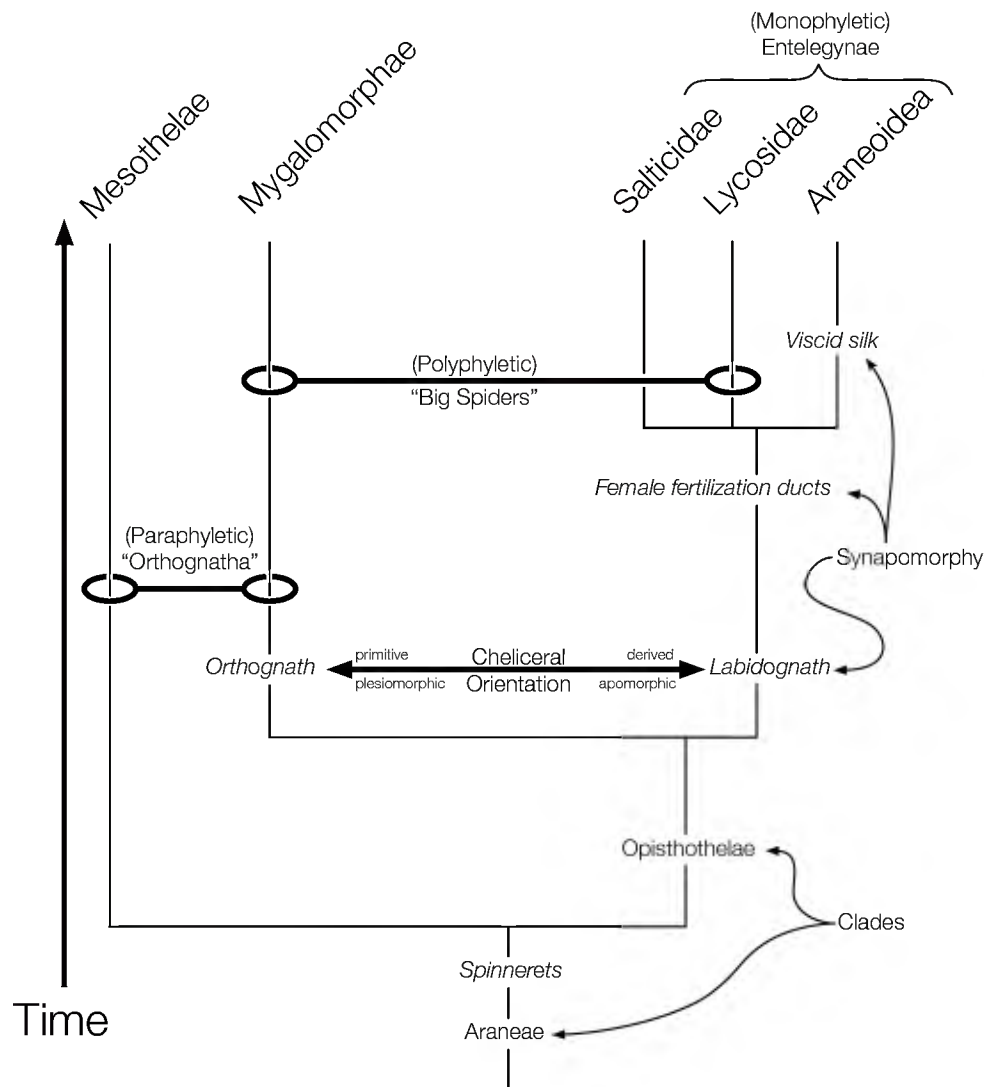
Sometimes systematists (scientists who infer phylogeny and use the results to classify organisms) make mistakes and group taxa based on primitive characters or plesiomorphies. Such groups, containing a common ancestor and some but not all of its descendants, are then termed paraphyletic. In Figure 2.1, the grouping "Orthognatha" is paraphyletic because it is based on a primitive character, orthognath or paraxial chelicerae, and because it includes the common ancestor of all spiders but excludes some

descendants, i.e. the Labidognatha. Even worse, sometimes groups don't even include any common ancestor at all and are then termed polyphyletic ("Big Spiders," Lycosidae + Mesothelae in Fig. 2.1 would be polyphyletic). Polyphyletic groups are usually based on convergent features and paraphyletic groups on primitive features.

Classifications (and phylogenies) need not be strictly binary or dichotomous: in Figure 2.1 the three-way fork uniting Araneoidea, Lycosidae, and Salticidae intentionally doesn't indicate which is most closely related to which. If nodes are dichotomous, the two daughter lineages are often called sister taxa, or, informally, sisters.

In practice systematists infer phylogeny by compiling large tables or matrices of taxa and their traits or features. Traits may be anything presumed to be genetically determined and heritable, such as morphology, physiology, behavior, or, increasingly, DNA sequences. The ideal approach would encapsulate all comparative knowledge about the group in question. Based on evidence external

to the analysis (or even an a priori assumption) one taxon in the analysis is specified to join at the root of the tree, and powerful computer algorithms are used to find the most plausible tree (or branching diagram, also termed a cladogram) that unites all taxa and best explains the data. Systematists adopt the initial null hypothesis that all similarities are due to phylogeny. The fit between the tree and the data decreases to the extent that one must suppose the "same" trait arose two or more times independently (convergent evolution) or was lost secondarily. An example of the former might be "big." Not all "big" spiders are each other's closest relatives (but some are). An example of the latter is the absence of true abdominal segmentation in all spiders. Spiders are arthropods and arthropods typically have segmented abdomens; spider relatives also have segmented abdomens. Rather than suppose that all arthropods with segmented abdomens gained the condition independently, and thus that spiders reflect the ancestral unsegmented arthropod, it becomes very much simpler

Fig. 2.1 Taxa are in regular, characters in italic font. Only synapomorphies (shared, derived characters) are valid evidence of monophyletic groups (clades). Paraphyletic groups are usually based on plesiomorphies, polyphyletic groups on convergences.
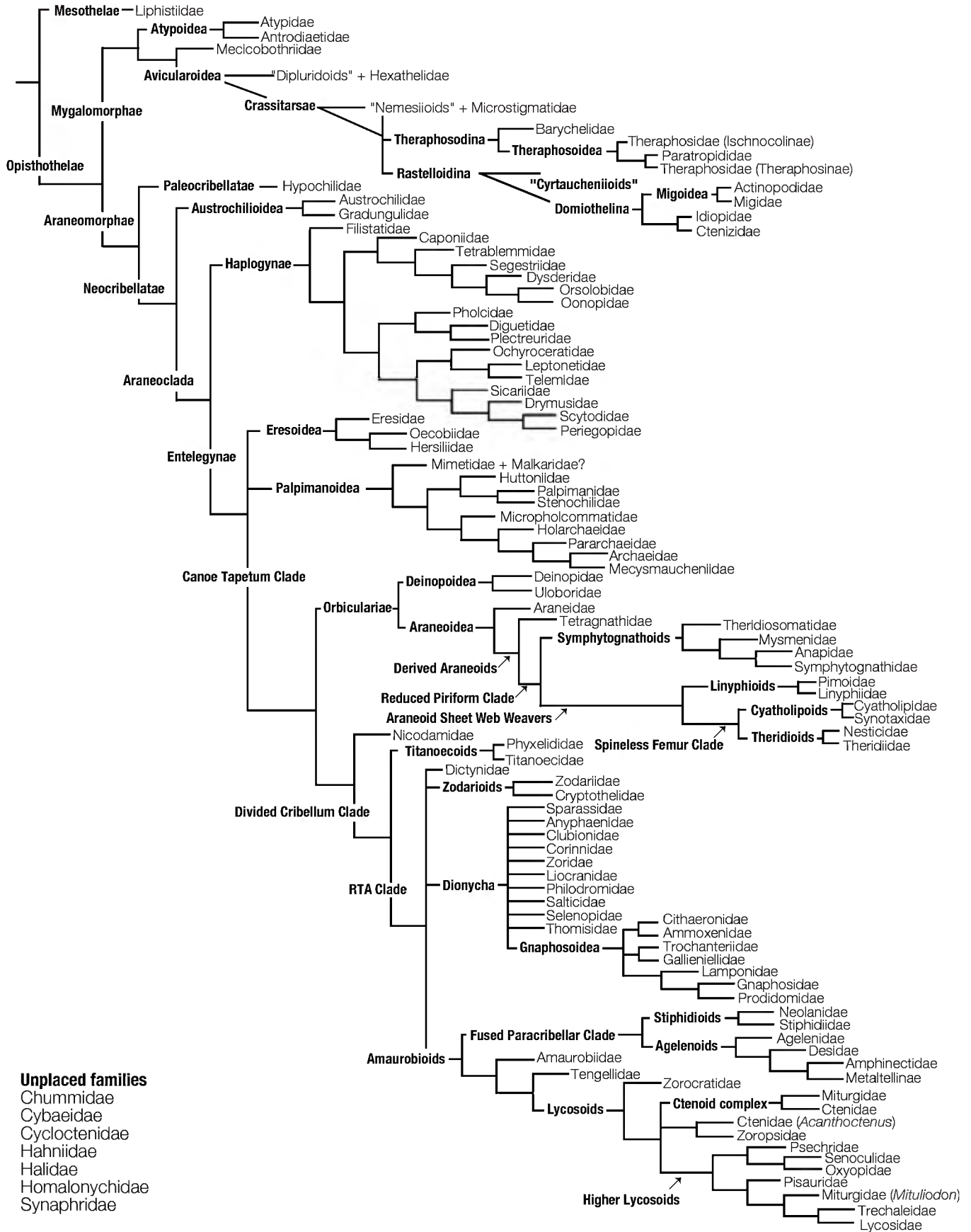
Mesothelae — Liphistiidae

Atypoidea — Atypidae
— Antrodiaetidae
Mecicobothriidae

Avicularioidea — "Dipluroids" + Hexathelidae

Mygalomorphae

Opisthothelae

Crassitarsae — "Nemesioids" + Microstigmatidae

Theraphosodina — Barychelidae
Theraphosoidea — Theraphosidae (Ischnocolinae)
— Paratropididae
Theraphosidae (Theraphosinae)

Rastelloidina — "Cyrtaucheniioids"
Domiothelina — Migoidea — Actinopodidae
— Migidae
Idiopidae
Ctenizidae

Paleocribellatae — Hypochilidae

Austrochilioidea — Austrochilidae
Gradungulidae

Araneomorphae

Neocribellatae

Haplogynae — Filistatidae
Caponiidae
Tetrablemmidae
Segestriidae
Dysderidae
Orsolobidae
Oonopidae

Pholcidae
Diguetidae
Plectreuridae
Ochyroceratidae
Leptonetidae
Telemidae
Sicariidae
Drymusidae
Scytodidae
Periegopidae

Araneoclada

Eresoidea — Eresidae
Oecobiidae
Hersiliidae

Entelegynae

Palpimanoidea — Mimetidae + Malkaridae?
Huttoniidae
Palpimanidae
Stenochilidae
Micropholcommatidae
Holarchaeidae
Pararchaeidae
Archaeidae
Mecysmaucheniidae

Canoe Tapetum Clade

Deinopoidea — Deinopidae
Uloboridae

Orbiculariae

Araneoidea — Araneidae
Tetragnathidae

Symphytognathoids — Theridiosomatidae
Mysmenidae
Anapidae
Symphytognathidae

Derived Araneoids ↗

Linyphioids — Pimoidae
Linyphiidae

Reduced Piriform Clade ↗

Cyatholipoids — Cyatholipidae
Synotaxidae

Araneoid Sheet Web Weavers ↗

Theridioids — Nesticidae
Theridiidae

Spineless Femur Clade ↗

Nicodamidae

Titanoecoids — Phyxelididae
Titanoecidae

Dictynidae

Zodarioids — Zodariidae
Cryptothelidae

Divided Cribellum Clade

Sparassidae
Anyphaenidae
Clubionidae
Corinnidae
Zoridae
Liocranidae
Philodromidae
Dionycha — Salticidae
Selenopidae
Thomisidae

RTA Clade

Gnaphosoidea — Cithaeronidae
Ammoxenidae
Trochanteriidae
Gallieniellidae
Lamponidae
Gnaphosidae
Prodidomidae

Stiphidioids — Neolanidae
Stiphidiidae

Fused Paracribellar Clade

Agelenoids — Agelenidae
Desidae
Amphinectidae
Metaltellinae

Amaurobioids

Amaurobiidae
Tengellidae
Zorocratidae

Lycosoids — **Ctenoid complex** — Miturgidae
Ctenidae
Ctenidae (*Acanthoctenus*)
Zoropsidae

Psechridae
Senoculidae
Oxyopidae
Pisauridae
Miturgidae (*Mituliodon*)
Trechaleidae
Lycosidae

Higher Lycosoids ↗

Unplaced families
Chummidae
Cybaeidae
Cycloctenidae
Hahniidae
Halidae
Homalonychidae
Synaphridae

Fig. 2.2 Phylogeny of Araneae

to suppose that the original arthropod was segmented and that it was spiders that changed to lack abdominal segmentation. The tree that requires the fewest hypotheses of convergent evolution and/or secondary loss is preferred as the current working hypothesis. Of course new taxa and characters can be added, so that in practice the preferred tree can -and usually does -change at least a little bit with each new analysis. The best classifications are derived from phylogenetic analyses, but to date rather few groups of spiders have been analyzed phylogenetically.

SPIDER PHYLOGENY

Spiders currently comprise 110 families, about 3,600 genera, and nearly 39,000 species (Platnick 2005). Paleontologists to date have described roughly 600 fossil species (Selden 1996, Dunlop & Selden 1998), but these have primarily been significant in dating lineages; thus far fossils have not seriously challenged or refuted inferences based on the recent fauna. Strong evidence supports spider monophyly: cheliceral venom glands, male pedipalpi modified for sperm transfer, abdominal spinnerets and silk glands, and lack of the trochanter-femur depressor muscle (Coddington & Levi 1991). Roughly 67 quantitative phylogenetic analyses of spiders at the generic level or above have been published to date, covering about 905 genera (about 25% of the known total), on the basis of approximately 3,200 morphological characters (summarized in Coddington & Colwell 2001 and Coddington et al. 2004). On the one hand, overlap and agreement among these studies is just sufficient to permit "stitching" the results together manually (Fig. 2.2); on the other, they are so sparse that many relationships in Fig. 2.2 are certain to change as more information accumulates and more taxa are studied. Figure 2.2 is not itself the result of a quantitative analysis but is, essentially, an amalgamation of individual cladograms published for particular lineages. Although there are several spider phylogenies above the species level based on DNA (Huber et al. 1993, Garb 1999, Gillespie et al. 1994, Piel & Nutt 1997, Hedin & Maddison 2001, Vink et al. 2002, Maddison & Hedin 2003a, b, Arnedo et al. 2004), this field is still in its infancy.

The basics of spider comparative morphology have been known for over a century, but the first explicitly phylogenetic treatment of spider classification was not published until the mid-1970's (Platnick & Gertsch 1976). This analysis resolved a long-standing debate by clearly showing a fundamental division between two suborders: the plesiomorphic mesotheles (the southeast Asian Liphistiidae with two genera and about 85 species) and the derived opisthotheles (everything else). Whereas mesotheles show substantial traces of segmentation, for example in the abdomen and nervous system, the opisthothele abdomen shows no segmentation (although color patterns in many spider species still reflect ancient segmentation patterns) and the ventral ganglia, or nerve centers, are fused. Opisthotheles include two major lineages: the baboon spiders (tarantulas) and their allies (Mygalomorphae, 15 families worldwide with about 300 genera and 2,500 species) and the so-called "true" spiders (Araneomorphae, 94 families worldwide with about 3,200 genera and 36,000 species) (Platnick 2005).

Mygalomorphs look much more like mesotheles than araneomorphs. They tend to be rather large, often hirsute animals with large, powerful chelicerae. Nearly all lead quite sedentary lives, usually in burrows, which they rarely leave, and they rely little on silk for prey capture. Some do fashion "trip-lines" from silk or debris, which effectively increase their sensory radius beyond the immediate area

of the burrow entrance, and some diplurid species do spin elaborate sheet webs, but they lack one key innovation present in araneomorphs: the piriform silk essential to cement silk to silk, or silk to substrate. Whereas any araneomorph can dab a tiny dot of piriform cement to anchor its dragline and almost instantly trust its life to the bond, mygalomorphs must spin structures several centimeters across to anchor silk to substrate, and that is a long and laborious process. Without piriform silk, substantial innovations in web architecture are essentially impossible.

Mygalomorphs rarely balloon, and therefore their powers of dispersal are limited to walking. Usually, the juveniles do not walk far, and so mygalomorph populations are highly clumped: when you find one, its siblings and cousins are generally not far away. Mygalomorph known species diversity is barely 7% of araneomorph diversity, so the diversification rates of these two sister taxa clearly differ, but the reasons remain mysterious. The contrast in dispersal mechanisms may be a partial explanation, but it also may be that mygalomorph species are simply much more difficult to discriminate morphologically. Araneomorphs lead much more vagile lives (including dispersal by ballooning), and the group is much more diverse.

Within mygalomorphs, the atypoid tarantulas (Atypidae, Antrodiaetidae) seem to be the sister group of the remaining lineages (Raven 1985a, Goloboff 1993), although some evidence suggests including Mecicobothriidae in the atypoids. The sister group to the atypoids is the Avicularioidea, of which the basal Dipluridae may be a paraphyletic assemblage (Goloboff 1993). One of the larger problems in mygalomorph taxonomy worldwide concerns the paraphyletic Nemesiidae, currently 38 genera and 325 species (Goloboff 1995). The remaining mygalomorph families (represented in North America only by Ctenizidae, Cyrtaucheniidae, and Theraphosidae, Fig. 2.2) divide into two distinct groups: the theraphosodines – baboon spiders or true "tarantulas" and their allies (Pérez-Miles et al. 1996) and the typically trap-door dwelling rastelloidines (Bond & Opell 2002). Less work has gone into mygalomorph phylogeny, and because the diverse Dipluridae, Nemesiidae, and Cyrtaucheniidae seem to be paraphyletic, the number of mygalomorph families may increase substantially. For all their size and antiquity, mygalomorphs have remarkably uniform morphology. Because fewer reliable, distinctive features can be compared, mygalomorph phylogeny has been a difficult and frustrating subject. Perhaps molecular data will advance the subject.

Araneomorphs include over 90% of known spider species: they are derived in numerous ways and appear quite different from mesotheles or mygalomorphs. Mesotheles are the only spiders with an anterior median pair of distinct spinnerets and mygalomorphs have lost them completely. A complex, important synapomorphy of araneomorphs is the fusion and reduction of the anterior median spinnerets to a cribellum, a flat sclerotized plate that bears hundreds to thousands of silk spigots that produces very fine, dry, yet extremely adhesive, silk (cribellate silk). Spider dragline silk is justly famous because it is tougher than Kevlar (Craig 2003, Gosline et al. 1986, 1999, Scheibel 2004), but in many ways, cribellate silk is even more amazing. Its stickiness seems to be based on electron-electron interactions (van der Waals forces) between the silk and the surface to which it sticks (Hawthorn & Opell 2002). Insofar as other natural and man-made glues operate on gross chemical principles, this atomic-level universal glue mechanism also seems worthy of biotechnological attention.

Other animals use silk throughout their lives, but no other group of animals even comes close to the diversity,

intricacy, and elegance of silk use by spiders (Eberhard 1990, Craig 2003). Systematists first became aware of this richness through comparative studies of behavior (Eberhard 1982, 1987b, 1990, Coddington 1986b, c), and only later by paying attention to the morphology that produced all that diversity. Although cytologists had been studying spider silk glands since the early 20th century (Kovoor 1987), it was not until the advent of the scanning electron microscope, and the cladistic reinterpretation of cytological data in the light of spigot diversity (Coddington 1989) that systematists began to plumb the immense variation in spinneret spigots and silks for phylogenetic research. Now spigots, silks, and silk use are some of the richest sources of comparative data in spiders (e.g., Platnick 1990a, Platnick et al. 1991, Eberhard & Pereira 1993, Griswold et al. 1999a).

Although many araneomorph lineages independently abandoned the sedentary web-spinning lifestyle to become vagabond hunters, the plesiomorphic foraging mode seems to be a web equipped with cribellate silk. Paleocribellatae contains just one family, Hypochilidae (two genera, 11 species). It is a famous North American taxon because it is sister to all remaining araneomorphs (Neocribellatae), and therefore retains a fair number of primitive traits (Platnick et al. 1991, Catley 1994). Within Neocribellatae, the monophyly of Haplogynae is weakly based on cheliceral (chelicerae fused with a lamina instead of teeth), palpal (tegulum and subtegulum fused rather than free), and spinneret characters (vestiges of spigots in former molts lacking) (Platnick et al. 1991, Ramírez 2000). The cribellate Filistatidae (three North American genera) is is sister to the remaining haplogynes, and a quantitative phylogeny of the family has been published (Ramírez & Grismado 1997). All haplogynes except Filistatidae evidently lost the cribellum, but Pholcidae (Huber 2000), Diguetidae, Ochyroceratidae, and, debatably, Scytodidae and Segestriidae still build prey-catching webs. The cellar spiders (Pholcidae) are exceptional for their relatively elaborate, large webs. Some pholcid genera have independently invented viscid silk (Eberhard 1992). Some of the most common and ubiquitous synanthropic spider species are pholcids, so one should not assume that a taxon that branched off relatively early in evolution is necessarily primitive, poorly adapted, or non-competitive. The remaining haplogyne families live either in tubes (Dysderidae) or are vagabonds that tend to occur in leaf litter or other soil habitats and are not commonly encountered by the casual collector. Because they are still poorly known, many of the new spider species discovered each year tend to come from haplogyne families.

The araneomorph Entelegynae is supported by several important, yet poorly understood synapomorphies (Griswold et al. 1999a) in reproductive and spinning systems. Entelegynes have more complex reproductive systems in which the female genitalia (epigynum) has external copulatory openings. In all other spiders copulation takes place through the gonopore. This secondary set of openings provides a "flow-through" sperm management system: the male deposits sperm in the epigynum that connects to spermathecae that connect to the uterus. This has major implications for reproductive behavior and the relation between the sexes (Eberhard 2004). For one thing, the flow-through system means the first male to mate with a female usually sires most of the spiderlings (Austad 1984). The copulatory ducts that lead from the epigynum to the spermathecae are often extremely contorted in entelegyne females. This has led to hypotheses that such complexity actually make it more difficult for males to inseminate females (Eberhard 1985, 1996). For whatever reason, fer-

tilization ducts in entelegyne spiders have been secondarily lost only five times and in mostly small groups: twice in distal palpimanoid families (this may be primary absence rather than secondary loss, Huber 2004), a small sub-clade of uloborids, some anapids, and a rather uniform, if speciose, sub-clade of tetragnathids (Hormiga et al. 1995). A second consistent but enigmatic entelegyne synapomorphy is cylindrical gland silk. These glands and spigots appear only in adult females, and it is thought that the silk is used only in egg sacs, but the specific contribution of cylindrical gland silk to egg sac function remains unknown.

Male entelegyne genitalia are also greatly modified. Plesiomorphic male spider genitalia are usually simple, tapering, pyriform bulbs. Pyriform bulbs lack apophyses or, if apophyses are present, they are small and quite simple (e.g., Fig. 2.3). Other parts of the male palp, such as the cymbium, patella, and tibia, are likewise unadorned. In contrast, entelegyne male genitalia can be bewilderingly complex. The bulb has two or three divisions (always subtegulum and tegulum, sometimes with an elaborate embolic division). The tegulum usually has two apophyses (conductor and median apophysis) in addition to the embolus. Any or all of these in entelegynes can be wonderfully complex, with knobs, levers, grooves, hooks, serrations, sinuous filaments, and spiraling parts (e.g., Figs. 2.4-2.5). Unraveling the homology of entelegyne male genitalia is a major problem (Coddington 1990). Entelegyne bulbs also work differently. The plesiomorphic bulb ejaculates via muscles that force the sperm out. Entelegyne bulbs lack those muscles and work hydraulically instead. The male pumps blood into the bulb to raise its internal pressure, which serves both to expand and "uncoil" its various parts. Glands empty their contents into the sperm duct and force the sperm out (Huber 2004). For sperm transfer to occur, this complicated structure must interact precisely with the correspondingly complex female genitalia (Huber 1994, 1995). In addition, the various parts of an entelegyne bulb are usually connected only by thin, flexible membranes that inflate like balloons during copulation. As a whole the bulb is so flexible that at least some of the male's complexity doubtless serves only to stabilize and orient his own genitalia during copulation.

2.4

2.3

2.5

Female epigyna have corresponding ledges, pockets, ridges and protuberances externally, and often labyrinthine ductwork internally. One hypothesis is that the female complexity is essentially defensive, the result of antagonistic co-evolution (Chapman *et al.* 2003): females as a whole invest so much more in their offspring than do males (even in spiders), that they should choose mates carefully (Alexander *et al.* 1997). Female genitalic complexity may be a "challenge" to males such that only high-quality males succeed, or succeed much better than low-quality males. Males, in turn, have evolved complex and highly flexible genitalia, the better to win over choosy females. This explanation assumes, of course, that overall quality of males is tightly correlated with male copulatory prowess. In any event, the difficulty of attaching to and navigating female genitalia may give the female more time to assess the male and break off mating if she chooses.

Three small families, known as "eresoids," have thus far always clustered near the base of Entelegynae in phylogenetic analyses: Oecobiidae, Hersiliidae, and Eresidae (Coddington 1990, Griswold *et al.* 1999a). Only the first two occur in North America. Their phylogenetic relationships are controversial. Oecobiids (Glatz 1967) and hersiliids (Li *et al.* 2003) share a unique attack behavior: they are the only spiders known to run swiftly around the stationary prey encircling it with silk as they go. The behavior could also be convergently evolved, although in accordance with the null hypothesis of phylogenetics, until proven otherwise, we presume the similarity is explained by descent. Certainly no obvious features tie any of these families closely to any other entelegynes. Because they are entelegyne yet share no more derived apomorphies with other entelegyne clades, they seem to be the basal entelegyne group.

The Palpimanoidea is a controversial entelegyne group (10 families, 54 genera), of which only the pirate spiders (Mimetidae) occur in North America. For years mimetids were thought to be araneoids based on setal morphology, general appearance, and the overall complexity of their palps, but then were transferred to palpimanoids (Forster & Platnick 1984). Recent research, however, suggests that mimetids are araneoids after all, in which case Palpimanoidea is polyphyletic (Schütt 2000, 2003, Huber 2004).

Males can also have knobs or apophyses elsewhere on their palpi. About half of entelegyne species have one in particular, the "retrolateral tibial apophysis," that defines a clade of 39 entelegyne families (the "RTA clade": Sierwald 1990, Coddington & Levi 1991, Griswold 1993, Fig. 2.2). Huber (1994, 1995) found that the RTA usually, but not always, serves to anchor and orient the male bulb to the female genitalia prior to expansion of the hematodochae.

Orbiculariae is one of the largest entelegyne lineages. It consists of two superfamilies, Araneoidea (13 families, 1,000 genera), and Deinopoidea (2 families, 22 genera). The monophyly of Orbiculariae is controversial because the strongest apomorphies are all behavioral: both groups spin orbwebs (Coddington 1986c and references therein). Prior to strictly phylogenetic classification in spiders the two groups were thought to be only distantly related. The cribellate Deinopidae and Uloboridae were included in the "Cribellatae," and authors often commented on the detailed similarity of these orbs to those of the classical, ecribellate Araneidae (reviewed in Scharff & Coddington 1997). However, as noted above, the cribellum is primitive for Araneomorphae. On the one hand, araneoids or their ancestors must therefore have lost it and, on the other, groups based on plesiomorphies are false. When the old, polyphyletic Cribellatae collapsed (Lehtinen 1967, Forster 1967, 1970b), deinopids and uloborids had nowhere else to

go, as it were, and so the form of the web (and the striking similarities in behavioral details) constituted a strong block of synapomorphies. But if orbweavers were monophyletic, the six araneoid families that spin sheet or cobwebs must have lost the orbweb. Against this view is the hypothesis that the orbweb is an unusually efficient and profitable design to catch prey. In general the more adaptive a feature is, the more likely it is to evolve independently; perhaps the araneoid and deinopoid web forms are convergent. This view argues that the orbweb is so superior a predation strategy that any spider lineage capable of it would have evolved it independently (and never lost it). Little evidence thus far suggests that orbwebs are drastically better than other web architectures (although they are widely regarded as better-looking!). Indeed, ecological evidence points the other way (Blackledge *et al.* 2003). Another difficulty for the monophyly hypothesis is that the deinopoid orb is cribellate (dry adhesive silk), and the araneoid orb uses viscid silk. The "missing link," it is argued, would have had neither. The obvious rejoinder is that perhaps they had both at one point, but one of the good effects of modern quantitative analysis is that people spend less time arguing about irresolvable issues, and more time seeking new evidence. The orb web diphyly argument particularly needs evidence that deinopoids share strong synapomorphies with some non-orb weaving group. Evidence against orbweaver monophyly is starting to appear from molecular evidence (Hausdorf 1999, Wu *et al.* 2002), but these studies are small, omit many important taxa, and do not confirm each other's results.

Araneoidea (ca. 11,000 species) is much larger than Deinopoidea (ca. 300 species). Only one deinopid species occurs in North America (in Florida and, possibly, Alabama). Araneoids are ecologically dominant species throughout the world but especially in north temperate areas such as North America, where Linyphiidae swamps any other spider family in both species diversity and sheer abundance. Current phylogenetic results (Hormiga 1994b, 2000, Griswold *et al.* 1998) indicate that Linyphiidae and five other families form the monophyletic "araneoid sheet weaver clade," which thus implies that within Araneoidea, the orb was lost only once (or transformed into a "sheet" web). Linyphiidae spin sheets as do Pimoidae. The classic cobwebs of Theridiidae and Nesticidae would then be derivations from a basic sheet, which, considering the web of black widows, *Steatoda*, and other apparently basal theridiid genera (Benjamin & Zschokke 2002, Agnarsson 2004, Arnedo *et al.* 2004,), seems plausible. Araneoid sheet web weavers account for the bulk of araneoid species diversity (713 genera, 7,600 species worldwide). Perhaps sheet or cobwebs are not so bad after all (Griswold *et al.* 1998, Blackledge *et al.* 2003).

Although the most recent analysis suggests that the sister taxon of Orbiculariae is approximately all remaining entelegyne families (possibly including eresoids and palpimanoids), the evidence for this is quite weak for several reasons (Griswold *et al.* 1999a). First, non-orbicularian entelegyne families have received little phylogenetic research, so such overarching conclusions are premature. Second, the problem is intrinsically difficult. Resolving the entelegyne node requires an analysis that includes several representatives from all major entelegyne clades, including relevant enigmas such as Nicodamidae (Harvey 1995) and Zodariidae (Jocqué 1991a). That means a very large matrix and an even larger scope of characters. Such a matrix is not easily constructed, and will probably require collaboration of numerous specialists.

Although araneologists refer to large groups like the "amaurobioids" (Davies 1998a, 1999, Davies & Lambkin 2000, Wang 2002), "lycosoids" (wolf spiders, Griswold 1993), and "Dionycha" (two-clawed hunters, Platnick 1990a, 2000a, 2002), their monophyly is also tenuous at best. Amaurobioids (which currently contains lycosoids as a subgroup) are defined by a few small changes in spinneret spigot morphology only visible with the scanning electron microscope. Basal amaurobioid families present in North America are Desidae, Amaurobiidae, and Agelenidae (a mixture, by the way, of cribellate and ecribellate groups). The group is quite heterogeneous, including everything from hunters to elaborate web builders. Dictynidae may fall close to these families as well (e.g., Bond & Opell 1997).

Lycosoids were formerly thought to be defined by quite an unusual and convincing synapomorphy, the "grate-shaped" tapetum. The tapetum is a reflective layer within the eye that probably serves to increase sensitivity. In most lycosoids, the tapetal architecture is like a barbecue or street-drain grate -an arrangement of parallel bars and holes, whereas in other spiders the tapetum shows no particular pattern, or is in the form of a simple "canoe" (Canoe Tapetum Clade, Fig. 2.2). The reflection of the grate-shaped tapetum of the posterior median or lateral eyes can be visible at great distances in the field. At night it is common with a headlamp to see the green eye shine of a lycosoid 5, or even 15 meters away. In the latest analysis, however, the grate-shaped tapetum evolves twice (in stiphidiids and lycosoids *sensu stricto*). In North America, the lycosoid families are Ctenidae, Lycosidae, Miturgidae, Oxyopidae, Pisauridae, Trechaleidae, and Zoropsidae (introduced). Among these families a few genera still spin webs, but the majority have given up webs for a "vagabond" lifestyle.

The monophyly of "Dionycha" is equally tenuous. Dionycha is an old hypothesis -at one time many classifications divided entelegyne families into two-clawed (Dionycha) and three-clawed spiders (Trionycha). But three claws is primitive for a group even larger than all spiders, so a group defined by it would be paraphyletic. Two claws, however, is arguably a derived condition. This argument is weak (some spider groups placed elsewhere are two-clawed), and if strong evidence connected a dionychan family elsewhere, it would be preferred. As it happens, however, phylogenetically rigorous arguments link any dionychan group outside Dionycha, so the group stands solely on the simple fact of the two-clawed condition. One group within Dionycha, the Gnaphosoidea (7 families, Gnaphosidae and Prodidomidae in North America), does share an apomorphy with interesting functional implications (Platnick 1990a, 2000a, 2002): all have obliquely angled posterior median eyes with flat, rather than rounded lenses. As a flat lens cannot bend light, and there seems little reason otherwise to have eyes, the flat lens has always been a mystery. It turns out that at least the gnaphosid *Drassodes* uses these modified eyes to orient to polarized light, which in turn allows them to move about in the habitat and to return to the same spot (Dacke *et al.* 2001a, b).

The phylogenetic relationships of these non-orbicularian entelegynes, therefore, is poorly known. Because they were originally defined by plesiomorphies, many of the classical entelegyne families (most seriously Agelenidae, Amaurobiidae, Clubionidae, Ctenidae, and Pisauridae) were, and still probably are, paraphyletic. Dismembering these assemblages into monophyletic units has been difficult because the monophyly of their components or related families is also often doubtful (e.g., Amphinectidae, Corinnidae, Desidae, Liocranidae, Miturgidae, Tengellidae, Stiphidiidae, Titanoecidae). Corinnids, liocranids, zoropsids, and ctenids have been recently studied (Bosselaers & Jocqué 2002, Silva Dávila 2003), and neither analysis recovered a monophyletic Liocranidae, Corinnidae, or Ctenidae (indeed, rather the opposite). Bosselaers (2002) analyzed Zoropsidae, and it does seem to be monophyletic. The basic phylogenetic structure of Anyphaenidae was studied by Ramírez (1995a, 2003).

Therefore neither the RTA clade, nor the two-clawed hunting spider families (Dionycha) may be strictly monophyletic, although each presumably contains within it a large cluster of closely related lineages. Dionychan relationships are quite unknown, although some headway has been made in the vicinity of Gnaphosidae (Platnick 1990a, 2000a, 2002). In contrast, Lycosoidea was supposedly based on a clear apomorphy in eye structure, but recent results suggest that this feature evolved more than once, or, less likely, has been repeatedly lost (Griswold *et al.* 1998). The nominal families Liocranidae and Corinnidae are massively polyphyletic. The nodes surrounding Entelegynae will certainly change in the future.

In summary, most of the major clades in 20th century spider classifications were fundamentally flawed, which means books and overviews published prior to the last two decades have been superceded. Major lineages such as Trionycha, Cribellatae, Tetrapneumonae, Orthognatha, and Haplogynae (older definition) were all based on plesiomorphies. By the mid-1970's the higher-level classification of spiders had collapsed to the extent that catalogs of that era began to ignore higher classification (and still do). From that rubble has emerged the hypothesis presented in Figure 2.2, but events on the horizon suggest that its clarity may be shortlived. For one thing, a small cadre of workers from the mid 1980's on tried to cover as much ground as possible on the family-level, via studies that barely overlapped. Thus, the various studies underlying Figure 2.2, although quantitative, have not been tested by other workers, denser taxonomic sampling, or new sources of data. Figure 2.2 remains a first draft of spider phylogeny. As the latter processes proceed, our understanding of spider phylogeny will doubtless improve. The underlying observations are solid, and as more data accumulates, we can expect more stability in the results. In sum, phylogenetic understanding of spiders has advanced remarkably since the early 1980's. We are approaching a truly quantitative estimate of spider phylogeny at the family level, but phylogenies below that are going to require much denser taxonomic sampling and rigorous comparative study.