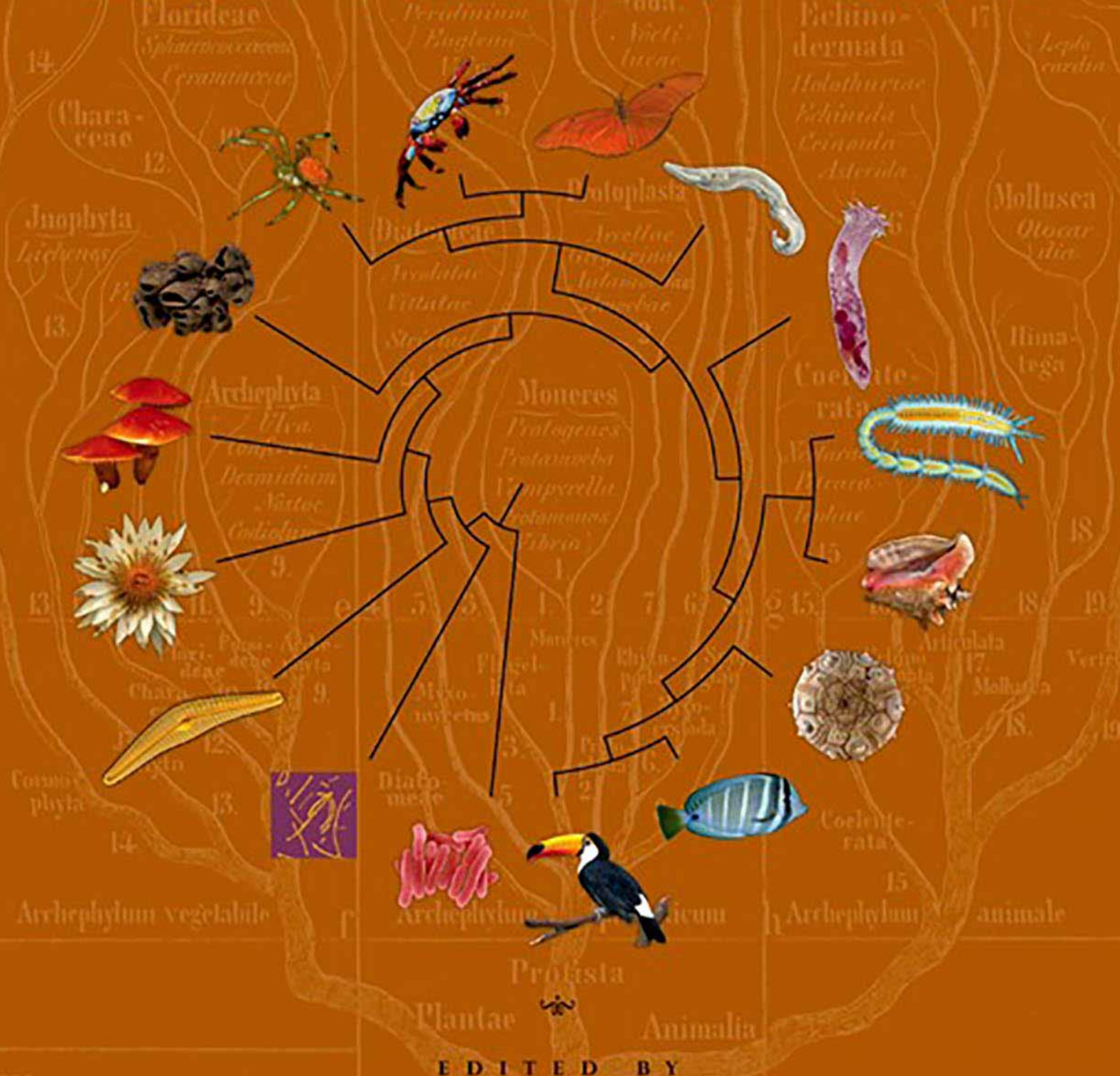


ASSEMBLING THE TREE OF LIFE



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Arachnida



Assembling the Tree of Life

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Although the earliest arachnids were apparently marine, arachnid diversity has been dominated by terrestrial forms from at least the Devonian. Even though arachnid fossils are scarce (perhaps only 100 pre-Cenozoic taxa), representatives of all major arachnid clades are known or cladistically implied from the Devonian or earlier, suggesting very early origins (Selden and Dunlop 1998). The more recent great radiation of insects, in contrast, seems to be Permian (Kukalová-Peck 1991, Labandeira 1999). Taxonomically, arachnids today are composed of approximately 640 families, 9000 genera, and 93,000 described species (table 18.1), but untold hundreds of thousands of new mites and spiders, and several thousand species in the remaining orders, are still undescribed. Arachnida include 11 classically recognized recent clades, ranked as "orders," although some acarologists regard Acari as a subclass with three superorders. Acari (ticks and mites) are by far the most diverse, with Araneae (spiders) second, and the remaining orders much less diverse. Discounting secondarily freshwater and marine mites, and a few semiaquatic spiders and one palpigrade, all extant arachnid taxa are terrestrial. Arachnids evidently arose in the marine habitat (Dunlop and Selden 1998, Selden and Dunlop 1998, Dunlop and Webster 1999), invaded land independently of other terrestrial arthropod groups such as myriapods, crustaceans, and hexapods (Labandeira 1999), and solved the problems of terrestrialization (skeleton, respiration, nitrogenous waste, locomotion, reproduction, etc.) in different ways.

Arachnids and Chelicerata

The monophyly of extant Euchelicerata—the arachnids and their marine sister group, the horseshoe crabs or merostomes—is consistently indicated by both morphology and molecular data (Snodgrass 1938, Wheeler 1998, Zrzavý et al. 1998, Giribet and Ribera 2000, Giribet et al. 2001, Shultz 2001). However, their relationship to the "sea spiders" (Pycnogonida), an enigmatic and morphologically highly specialized group of marine predators, remains controversial. Pycnogonids are variously seen as sister to euchelicerates (Weygoldt and Paulus 1979, Weygoldt 1998, Giribet and Ribera 2000, Shultz and Regier 2000, Regier and Shultz 2001, Waloszek and Dunlop 2002) or as sister to euchelicerates and all remaining arthropods (Zrzavý et al. 1998, Giribet et al. 2001).

Phylogeny of Arachnida

Arachnid monophyly is supported by at least 11 synapomorphies, among which extraintestinal digestion (although some mites and all members of Opiliones are particulate feeders), slit sense sensilla (absent in palpigrades), a single medial genital opening, and an anteroventrally directed mouth are particularly convincing (Weygoldt and Paulus 1979, Shultz 1990, 2001). If fossils are considered, arachnid monophyly is less certain mainly because of the character conflict

Table 18.1

Arachnid Diversity at the Family, Genus, and Species (Described and Estimated) Levels.

	Families	Genera	Species	
			Described	Estimated
Arachnida	650	9500	100,000	~1 million
Acari	~430	~3300–4000	~50,000	0.5–1 million
Araneae	109	3471	37,596	76,000–170,000
Opiliones	43	1500	5000	7500–10,000
Pseudoscorpiones	24	425	3261	3500–5000
Scorpiones	17	163	1340	4,000
Solifugae	12	141	1084	1,115
Amblypygi	5	17	142	?
Schizomida	2	39	237	?
Palpigradi	2	6	78	100
Uropygi	1	16	101	?
Ricinulei	1	3	55	85

From Adis and Harvey (2000), Harvey (2003), Platnick (2002), Fet et al. (2000).

created by marine scorpions and eurypterids. Paleontologists consider some fossil scorpions to have been marine (Jeram 1998, Dunlop 1998, Dunlop and Webster 1999, Dunlop and Selden 1998), which, if true, implies either that terrestrial scorpions invaded land independently, or that they returned to the seas secondarily. If the former, the similar arachnid innovations for terrestrial life may be convergent rather than homologous (Jeram 1998, Dunlop and Selden 1998, Dunlop and Webster 1999). Some paleontologists have argued that scorpions are derived merostomes (Dunlop 1999, Dunlop and Selden 1998, Jeram 1998, Dunlop and Braddy 2001), but the paucity of informative characters and the poor or incomplete preservation of the (very) few fossils that exist make conclusions ambiguous and tentative. Paleontologists now recognize three extinct arachnid orders: the clearly tetrapulmonate Trigonotarbita (50 species, including Anthracomartia; Dunlop 1996b), Haptopoda (one species), and Phalangiotarbita (26 species), the latter two orders of uncertain affinities (Selden and Dunlop 1998, Dunlop 1996b, 1999). The paleontological arguments tend to emphasize a few characters (e.g., absence of respiratory structures on the genital somite and subdivision of the abdomen into a proximal broader section and a distal tail) while discounting contrary evidence, especially that not preserved in fossils. Cladistic analyses based on morphological data for extant taxa place scorpions deep inside the recent arachnid clade, possibly related to Opiliones, pseudoscorpions, and solifuges (Shultz 1990, 2000, Wheeler and Hayashi 1998, Giribet et al. 2002), but this clade becomes ambiguously resolved when fossil scorpions and eurypterids are coded, possibly because of the large amount of conflicting character states, because of the aquatic habitat and missing data imposed by the fossils (Giribet et al. 2002). The extinct eurypterids are also chelicerates and are apparently closer to arachnids than to

xiphosurans (Weygoldt and Paulus 1979). Molecular data sometimes place scorpions as true arachnids (Wheeler et al. 1993, Giribet et al. 2001, 2002) but can nest horseshoe crabs within "true" arachnids as well (Wheeler 1998, Wheeler and Hayashi 1998, Edgecombe et al. 2000, Giribet et al. 2002).

The phylogeny of Arachnida itself is contentious, but not as contentious as a perusal of the recent literature might suggest. Specialists may disagree on analytical methodology and interpretation of fossil morphology but largely agree that more data are needed before incongruence should be taken seriously. Classical morphological analysis more or less strongly suggests various clades: Acaromorpha (= ricinuleids–mites), Haplocnemata (= pseudoscorpions–solifuges), Camarostomata (= whip scorpions–schizomids), and Tetrapulmonata (four-lunged arachnids: Araneae, Uropygi, Schizomida, Amblypygi). Besides the controversy over scorpions mentioned above, the positions of Palpigradi, Opiliones, Ricinulei, and Acari are unsettled (Weygoldt and Paulus 1979, Weygoldt 1998, Shultz 1990, 1998, Wheeler et al. 1998, Giribet et al. 2002). Weygoldt and Paulus's early analysis was the first explicit phylogenetic treatment of arachnid relationships, selecting characters that they considered to be of phylogenetic importance while dismissing contradictory evidence as convergence or secondary loss without regard to parsimony. Later authors analyzed morphology and/or molecular evidence cladistically (or using other numerical analytical methods). Parsimony analysis of morphological data from extant groups by different researchers generally agrees with the topology presented in figure 18.1. However, most of the morphological phylogenetic analyses of Arachnida published so far are based on groundplan codings for each order instead of using multiple representatives of each order showing the particular combinations of character states in those terminals. This alternative way of coding terminals has been recently discussed by Prendini (2001a), and it is

However, given the conflict in molecules alone, it seems wiser to recommend the morphological cladogram of Shultz (fig. 18.1) as a working hypothesis for arachnid phylogeny.

Although this review focuses more on the controversies than the consensus, some nodes in figure 18.1 are well supported. The tetrapulmonates share the subchelate condition of the mouthparts, the unique 9 + 3 axoneme sperm morphology, the narrow or petiolar connection between cephalothorax and abdomen, the reduction to four prosomal endosternal components, and the complex coxo-trochanteral joint. According to a recent anatomical study of the musculoskeletal system, Pedipalpi share 31 morphological synapomorphies (Shultz 1999), although many of these characters are not independent, and the extent of homoplasy in other arachnids is unclear. Camarostomata is also strongly supported by at least six synapomorphies. Haplocnemata (= Pseudoscorpiones-Solifugae) also has substantial morphological support. Dromopoda (= Scorpiones-Pseudoscorpiones-Solifugae-Opiliones) and Micrura (= Tetrapulmonata-Ricinulei-Acari) have been considered the weakest nodes morphologically (Weygoldt 1998).

Mites and Ticks (Acari or Acarina)

Mites are the "go anywhere, do anything" arachnids (Walter and Proctor 1999). They occur on every continent, including Antarctica, where they dominate the endemic terrestrial fauna (Pugh 1993). On land, they form a minute, scurrying plankton that coats the vegetation, from the canopies of the tallest rainforests down into the soil, at least as deep as roots can penetrate (Walter 1996, Walter and Behan-Pelletier 1999). Every bird, mammal, reptile, and social insect species plays host to symbiotic mites, as do many amphibians, slugs, spiders, scorpions, opilionids, myriapods, and non-social insects. Animal- and plant-associated mites are commonly commensals that scavenge a living on their hosts'

surfaces, and sometimes provide beneficial services, but all too often are parasites capable of damaging or killing their hosts. Although originating on land, mites have reinvaded and radiated into both freshwater (around six invasions, >5000 described species) and marine systems (around three invasions, hundreds of known species) from the intertidal to the deepest marine trenches (Walter and Proctor 1999).

More than 50,000 species of the "subclass" Acari have been described and distributed across three superorders, six orders, more than two dozen suborders and "cohorts" (~infrasuborders), >400 families, and 3000–4000 genera (see Table 18.2). Roughly 90 fossil species have been described (Selden 1993a). Like the artificial assemblage that we call reptiles, mites are easily recognized as such, but the monophyly of Acari is open to question. Mites have long been studied in isolation from other arachnids, and characters that once appeared to unite the Acari are now known to be more general. For example, the hexapod larva and the headlike capitulum (gnathosoma) were once thought unique to mites, but both are also found in ricinuleids (Lindquist 1984). Other supposedly unique characters, such as the ventral fusion of the palpal coxae, occur in many arachnids (e.g., ricinuleids, schizomids, pseudoscorpions) and may even have evolved twice within mites (Walter and Proctor 1999). Modern phylogenetic methods, especially using molecules, have only recently been applied to Acari, but most of these studies have been restricted to economically important parasites (Navajas and Fenton 2000).

Although Acari are not clearly monophyletic (van der Hammen 1989), each of the three acarine superorders probably is (Grandjean 1936). Opilioacarans are fairly large (2–3 mm) tracheate mites, superficially resembling small opilionids, which retain a number of plesiomorphic characters. Like early derivative acariform mites and most opilionids, opilioacarans ingest solid food, using large, three-segmented chelicerae to grasp small arthropods or fungi, and

Table 18.2
Systematic Synopsis and Distribution of Major Mite Lineages.

Class Arachnida, Acari (Acarina): mites and ticks

Superorder Opilioacariformes: Order Opilioacarida—1 family, 9 genera, ~20 species

Superorder Acariformes: mitelike mites

Order Sarcoptiformes: Endeostigmata, "Oribatida," Astigmata—230 families, >15,000 described species, including the paraphyletic oribatid mites (~1100 genera in >150 families); stored product mites; house dust, feather, and fur mites; and scabies and their relatives

Order Trombidiformes: Sphaerolichida, Prostigmata—125 families, >22,000 described species, including spider mites and their relatives (Tetranychidae); earth mites and their relatives (Eupodoidea); gall and rust mites (Eriophyoidea); soil predators and fungivores; hair, skin, and follicle mites (Cheyletoidea); straw itch mites (Pyemotidae); chiggers, velvet mites, water mites, and their relatives (Parasitengona)

Superorder Parasitiformes: ticks and ticklike mites

Order Ixodida (Metastigmata)—ticks—3 families, <900 described species

Order Holothyrida: holothyrids—3 families, <35 described species

Order Mesostigmata (Gamasida): Monogynaspida + Trigynaspida *sensu lato* (often treated as 3–4 separate suborders)—70 families, <12,000 described species, including poultry mites, nasal mites, bird mites, and rat mites (Dermanyssoidea); major soil predators; biocontrol agents (Phytoseiidae); tortoise mites (Uropodoidea)

serrated hypertrophied palpal coxal setae (rutella) on either side of the buccal opening to saw the food into bite-sized chunks that can be swallowed. Fossil opilioacarans are unknown, although Dunlop (1995) speculates that they may be related to the curious Carboniferous Phalangiotarbida. Opilioacariformes may be a sister group to Parasitiformes, but convincing synapomorphies have yet to be demonstrated. A sister-group relationship of Opilioacariformes and Parasitiformes has been recently proposed based on molecular data (Giribet et al. 2002).

Acariformes are supported by several synapomorphies unique within Arachnida, including prodorsal trichobothria, the loss of all primary respiratory structures or remnants (e.g., the ventral sacs in Palpigradi), the fusion of the tritosternum to the palpal coxal endites to form a subcapitulum, and genital papillae (osmoregulatory structures). Acariformes share the nonfeeding, hexapod prelarval stage, the rutella, and particulate feeding with Opilioacariformes. Particulate feeding also occurs in Opiliones (see above) and in horseshoe crabs.

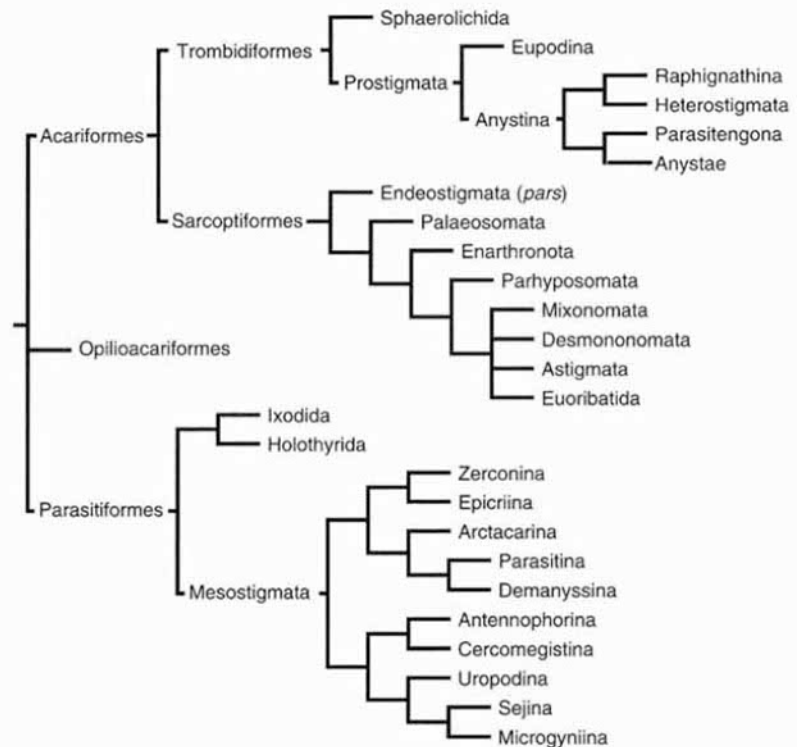
Acariformes consist of two orders, Sarcoptiformes and Trombidiformes, both corroborated by a morphological cladistic analysis (O'Connor 1984) that established the relationship between the suborders Sphaerolichida (two families previously attributed to the basal suborder Endeostigmata) and Prostigmata. Although no comprehensive analysis of Prostigmata has been published, five cohorts (fig. 18.2) are well supported by morphological characters. Of these, only Heterostigmata have received a thorough morphological cladistic analysis (Lindquist 1986), but parts of Parasitengona

are currently under molecular and morphological review (e.g., Soeller et al. 2001).

Prostigmatans display anterior dorsal stigmatal openings and feed only on fluids. Almost half of all known mite species belong to Prostigmata, including major radiations of mites parasitic on vertebrates, invertebrates, and plants (Table 18.2). All of the major acarine plant parasites belong here, including the smallest known terrestrial animals, gall mites (Eupodina: Eriophyoidea) as small as 0.07 mm in length as adults (Walter and Proctor 1999). In contrast, Parasitengona contains more than 7000 described species of terrestrial and aquatic mites, including some of the largest known (16 mm long).

Some traditional subdivisions of the Sarcoptiformes are obviously paraphyletic, but few cladistic analyses, even of a preliminary nature, have been published. Astigmata, often given subordinal rank, is monophyletic (Norton 1998) but derived from within the traditional suborder Oribatida (also Oribatei, Cryptostigmata), thereby rendering Oribatida paraphyletic. Oribatida consist of the beetle mites that form a dominant part of the soil fauna. Sarcoptiformans were among the earliest terrestrial animals and probably invaded land directly from the ocean by way of interstices in moist beach sand as minute animals that exchanged gases across their cuticles (Walter and Proctor 1999). By the Early Devonian (380–400 million years ago), sarcoptiformans were diverse members of the soil fauna, and 11 species are known from the Gilboa shales and Rhynie Chert (Norton et al. 1988, Kethley et al. 1989). Based on extensive fecal remains, it appears that sarcoptiform mites were major components of

Figure 18.2. Phylogeny of Acari.



the detritivore system in Palaeozoic coal swamps (Labandeira et al. 1997). A later radiation in association with animals (Astigmata: Psoroptida) has produced a dazzling diversity of nest, feather, fur and skin inhabitants and a source of some interesting host-symbiont analyses (e.g., Klompen 1992, Dabert et al. 2001).

Parasitiformes are supported by a number of unique character states, including a plate above or behind leg IV bearing a stigmatal opening and peritreme, a biflagellate tritosternum, a sclerotized ring formed by fusion of the palps around the chelicerae (possibly representing a fusion of a ricinuleid-like cucullus to the palpal coxae), horn-shaped corniculi (possibly homologous with the rutella) that support the salivary stylets, a recessed sensory array on leg I (called Haller's organ in ticks), and by the use of the chelicerae to transfer sperm. Additional characters supporting Parasitiformes include suppression of the prelarval stage and widespread fluid feeding (the general condition among arachnids).

The internal relationships of Parasitiformes are the best studied of any of the three acarine superorders, but this is faint praise indeed. Relationships among ticks (Ixodida) and between ticks and other suborders are the best resolved (e.g., Klompen et al. 1996). However, some exemplary morphological and molecular analyses of parts of Mesostigmata are starting to appear (e.g., Naskrecki and Colwell 1998, Cruickshank and Thomas 1999). The monophyly of ticks, perhaps the most familiar of all mites because of their large size and bloodthirsty habits, is supported by several modifications of the chelicerae and hypostome for blood-feeding. Molecular evidence suggests that holothyrids, large (2–7 mm long), reddish to purplish armored mites, are close relatives of ticks. Holothyrids are rare, known only from Gondwanan continents and Indo-Pacific Islands, where they scavenge on fluids from dead arthropods (Walter and Proctor 1998). A uniquely formed all-encompassing dorsal shield and lateral peritrematal plate support the monophyly of Holothyrida.

The group consisting of (Holothyrida + Ixodida) is the sister to Mesostigmata. Characters supporting the monophyly of the latter are mostly developmental, for example, suppression of the tritonymphal stage and of the genital opening until the adult, and the appearance of sclerotized plates on the opisthosoma in nymphs. Mesostigmata can be split into two suborders, each with five cohorts based on variation in the female genital shield. In Monogynaspida (Gamasina), the plesiomorphic condition of four genital shields (found in Holothyrida and Cercomegastina) is reduced to a single genital shield by fusion of the laterals (latigynials) to the median genital shield and the loss of the anterior genital shield. Trigynaspida *sensu lato* shows a general trend toward fusion of the latigynials with other shields, and is only weakly supported. Trigynaspines often have restricted distributions but are prominent members of tropical forest faunas, as are members of Uropodina. A group comprising Uropodina, Sejina, and Microgyniina is supported by the development of a heteromorphic deutonymph (i.e., a differently formed

phoretic stage) that disperses on insects via an anal attachment organ.

Within Monogynaspida, the cohort Dermanyssina is clearly separated by the presence of a secondary insemination and sperm-storage system in the female and an inseminatory sperm finger on the male chelicera. Dermanyssines occur on all continents, including Antarctica. About half of the described species are free-living predators in soil litter, rotting wood, compost, herbivore dung, carrion, nests, house dust, or similar detritus-based systems. These predators are usually abundant and voracious enough to regulate the populations of other small invertebrates and are often used in biocontrol. A few mesostigmatans have switched from external digestion of prey to ingesting fungal spores and hyphae. Others feed on pollen, nectar, and other plant fluids. Pollen feeding is common in the Phytoseiidae, a family that has successfully colonized the leaf-surface habitat and accounts for about 15% of described species of Mesostigmata. Many Ascidae (Naskrecki and Colwell 1998) and Ameroseiidae have become venereal diseases of plants, that is, pollen- and nectar-feeding flower mites vectored by insect or bird pollinators. The Dermanyssoidea contain several massive radiations of vertebrate and invertebrate parasites, including such well-known pests as the bird and rat mites and the varroa mite of bees.

Ricinuleids (Ricinulei)

Ricinulei are an enigmatic group of curious, slow-moving arachnids that possess a series of unique modifications, including a hinged plate, the cucullus, at the front of the prosoma, which acts as a hood covering the mouthparts; a locking mechanism between the prosoma and the opisthosoma (shared with the fossil trigonotarbid) that can be uncoupled during mating and egg-laying; and a highly modified male third leg that is used for sperm transfer during mating. This leg structure is analogous to the modified pedipalp of male spiders, and provides a series of species-specific character states helpful in delimiting taxa.

Ricinulei are probably the sister group of mites (Lindquist 1984, Weygoldt and Paulus 1979, Shultz 1990, Wheeler and Hayashi 1998, Giribet et al. 2002). Savory (1977) proposed a relationship to Opiliones, even suggesting paraphyly of Opiliones by including Ricinulei, but that hypothesis remains quite dubious. More recently, addition of the extinct order Trigonotarbidia as well as molecular data suggested a possible relationship to tetrapulmonates (Dunlop 1996a, Giribet et al. 2002). Internal relationships of extant Ricinulei have been explored by Platnick (1980).

Hansen and Sørensen (1904) provided the first comprehensive taxonomic account of this order, in which they recognized a single family, Cyptostemmatoidae, with eight species grouped in the genera *Cryptostemma* and *Cryptocellus*. The order, as currently defined, contains just a single recent

family, Ricinoididae, with three genera (Harvey 2003). *Ricinoides* (10 species) occurs in the rainforests of western and central Africa. *Cryptocellus* (27 species) and *Pseudocellus* (18 species) occur in forest and cave ecosystems of Central America as far north as Texas and as far south as Peru. Selden (1992) proposed a classification for the order that divided it into two suborders, Palaeoricinulei for the two families of Carboniferous ricinuleids (15 species total) and the Neoricinulei for Ricinoididae.

Palpigrades (Palpigradi)

Palpigrades or micro-whip scorpions are one of the most enigmatic arachnid orders, with just 78 species in six genera and two families (Harvey 2003), and an unresolved phylogenetic position because of doubts regarding the many reductional apomorphies these small animals possess. Only one fossil species is known (Selden and Dunlop 1998). Their phylogenetic placement based on molecular data is similarly equivocal (Giribet et al. 2002). Palpigrades bear a long, multi-segmented flagellum, three-segmented chelicerae, sub-segmented pedipalpal and pedal tarsi, and a host of other modifications, including lack of slit sensillae, a dorsal hinged joint between the trochanter and femur on the walking legs (Shultz 1989), and a pair of anteromedial sensory organs (Shultz 1990). Palpigrades occur primarily in endogean habitats—soil, litter, under rocks, in caves and other subterranean voids—but the remarkable genus *Leptokoenenia* occurs in littoral deposits of Saudi Arabia and Congo.

Until recently only a single family, Eukoeneiidae, was recognized, but Condé (1996) transferred *Prokoenenia* and *Triadokoenenia* to a separate family, Prokoeneiidae. These two families can be distinguished by the presence (Prokoeneiidae) or absence (Eukoeneiidae) of abdominal ventral sacs on sternites IV–VI. This arrangement has not been tested cladistically, nor has the monophyly of each of the six genera. The genera are disproportionately sized: *Eukoenenia* consists of 60 named species, and the remaining five genera possess a total of just 18 species. Although the differences between families and genera are well understood (Condé 1996), their interrelationships have never been examined cladistically.

Spiders (Araneae)

Spiders currently consist of 110 families, about 3500 genera, and more than 38,000 species (Platnick 2002). Roughly 600 fossil species have been described (Selden 1996, Selden and Dunlop 1998). Strong synapomorphies support the clade: cheliceral venom glands, male pedipalpi modified for sperm transfer, abdominal spinnerets and silk glands, and lack of the trochanter-femur depressor muscle (Coddington and Levi 1991). The advent of the scanning electron microscope in the 1970s rejuvenated spider systematics: micro-

structures on the cuticle (sensory tarsal organs, the kinds and distributions of silk spigots on spinnerets) are now fundamental to phylogenetic research. Roughly 67 quantitative cladistic analyses of spiders have been published to date, covering about 905 genera (about 25% of the known total), on the basis of approximately 3200 morphological characters. Nine of these studies focus on interfamilial relationships (Coddington 1990a, 1990b, Platnick et al. 1991, Goloboff 1993, Griswold 1993, Griswold et al. 1998, 1999, Bosselaers and Jocqué 2002, Silva Davila 2003). Many of the others that focus on single families, however, include multiple outgroups that overlap from one study to another (Coddington 1986a, 1986b, Jocqué 1991, Rodrigo and Jackson 1992, Hormiga 1994, 2000, Davies 1995, 1998, 1999, Harvey 1995, Hormiga et al. 1995, Gray 1995, Ramírez 1995a, 1995b, 1997, Pérez-Miles et al. 1996, Ramírez and Griswold 1997, Scharff and Coddington 1997, Sierwald 1998, Huber 2000, 2001, Platnick 1990, 2000, Davies and Lambkin 2000, 2001, Griswold 2001, Griswold and Ledford 2001, Wang 2002, Schütt 2003). The trend has been to address unknown parts of the spider tree, thus yielding a first-draft, higher level phylogeny for the order, rather than repeating or intensifying lower level analyses. On the one hand, overlap and congruence have been fortuitously sufficient to permit “adding” results together manually; on the other, they are so sparse that many details in figure 18.3 are certain to change with more data and more detailed taxon sampling. Molecular work, at least above the species level, is still almost nonexistent (but see Huber et al. 1993, Hausdorf 1999, Piel and Nutt 1997, Hedin and Maddison 2001). Some molecular results are strongly contradicted by morphology, such as rooting the spider clade among arachnids on an araneomorph rather than a mesothele (Wheeler and Hayashi 1998).

The comparative data for the most inclusive groupings of spiders have been known for more than a century, but the data were not rigorously analyzed from a phylogenetic point of view until the mid-1970s (Platnick and Gertsch 1976). This analysis clearly showed a fundamental division between two suborders: the plesiomorphic mesotheles (one family, Liphistiidae; two genera; about 85 species) and the derived opisthotheles. Although mesotheles show substantial traces of segmentation, for example, in the abdomen and nervous system, the opisthothele abdomen is usually smooth and the ventral ganglia fused. Opisthotheles is composed of two major lineages: the baboon spiders (or tarantulas) and their allies (Mygalomorphae, 15 families, about 300 genera, 2500 species) and the so-called “true” spiders (Araneomorphae, 94 families, 3200 genera, 36,000 species) (Platnick 2003).

Mygalomorphs resemble mesotheles. They tend to be fairly large, often hirsute animals with large, powerful chelicerae that live in burrows and, apparently, rely little on silk for prey capture, at least compared with many araneomorph spiders. Within mygalomorphs, the atypoid tarantulas are probably sister to the remaining lineages (Raven 1985, Goloboff 1993), although some evidence supports the mono-

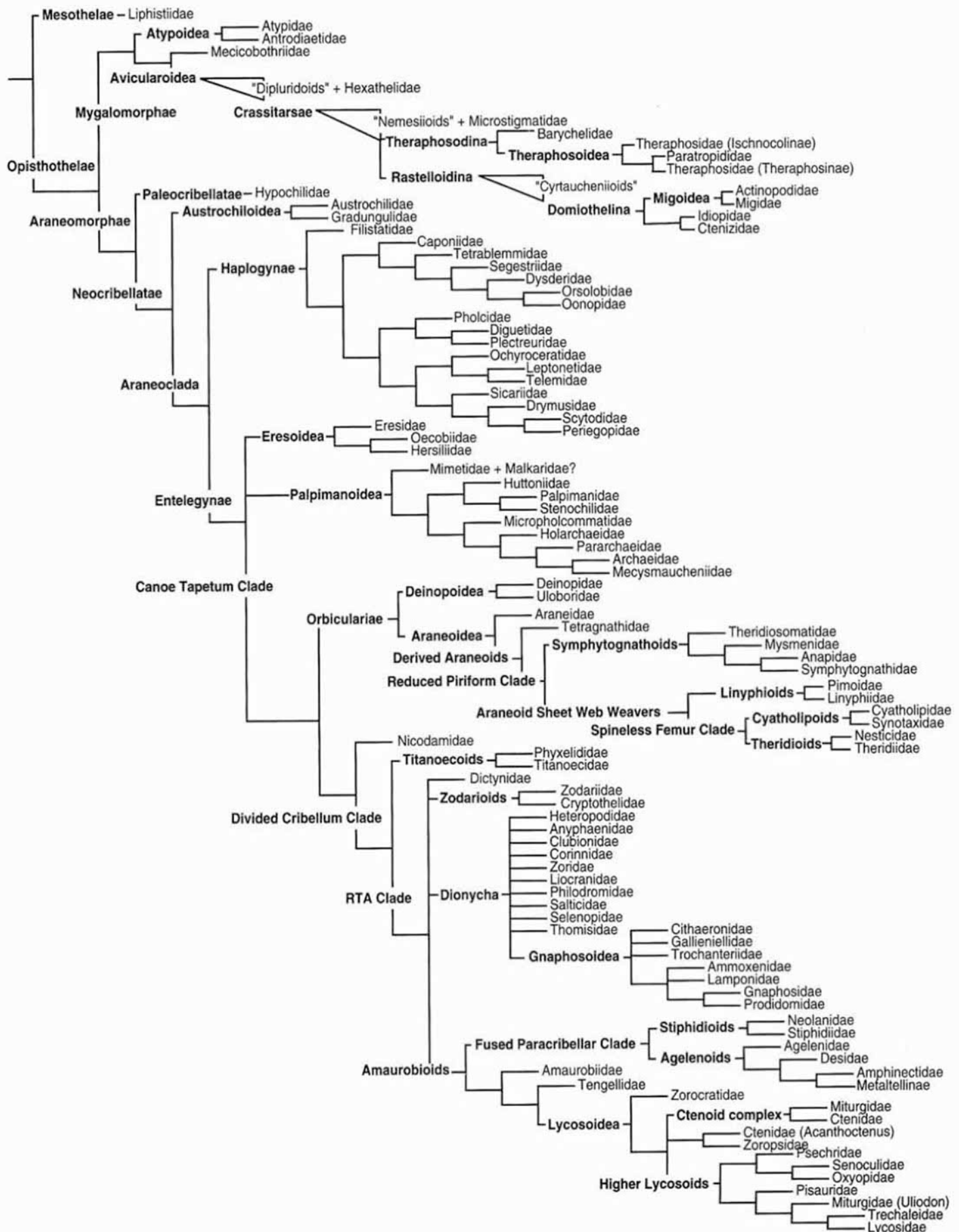


Figure 18.3. Phylogeny of Araneae.

phyly of Mecicobothriidae and the atypoids. The atypoid sister group is Avicularioidea, of which the basal taxon, Dipluridae, seems to be a paraphyletic assemblage. One of the larger problems in mygalomorph taxonomy concerns Nemesiidae, currently 38 genera and 325 species (Goloboff 1993, 1995). The group is conspicuously paraphyletic. The remaining mygalomorph families are relatively derived and more closely related to each other than to the preceding. Two seemingly distinct groups are the theraphosodines [baboon spiders or true "tarantulas" and their allies (Pérez-Miles et al. 1996), typically vagabonds] and the rastelloidines (typically trap door spiders). Because of the evident paraphyly of several large mygalomorph "families" (Dipluridae, Nemesiidae, Cyrtaucheniidae), the number of mygalomorph family-level lineages will probably increase dramatically with additional research.

Araneomorphs include more than 90% of known spider species; they are derived in numerous ways and are quite different from mesotheles or mygalomorphs. Although repeatedly lost, a strong synapomorphy of this clade is the fusion and specialization of the anterior median spinnerets into a flat spinning plate (cribellum) with hundreds to thousands of spigots that produce a dry yet extremely adhesive silk (cribellate silk). Many araneomorph lineages independently abandoned the sedentary web-spinning lifestyle to become vagabond hunters, but the plesiomorphic foraging mode seems to be a web equipped with dry adhesive silk (austrorhachids, Filistatidae among the haplogynes, oecobiids and eresids among eresoids, many entelegyne groups). Within Araneomorphae, the relictually distributed Hypochilidae (two genera, 11 species) are sister to the remaining families (Platnick et al. 1991). Some austrorhachid genera have lost webs, and most haplogynes are also vagabonds. These haplogyne taxa tend to live in leaf litter or other soil habitats (Caponiidae, Tetrablemmidae, Orsolobidae, Oonopidae, Telemidae, Leptonetidae, Ochyroceratidae, etc.; Platnick et al. 1991). The haplogyne cellar spiders (Pholcidae) are exceptional for their relatively elaborate, large webs. Some of the most common and ubiquitous commensal spider species are pholcids.

The entelegyne "node" in spiders is supported by several synapomorphies (Griswold et al. 1999). Among other things, the copulatory apparatus fundamentally changed in both males and females. One theory is that the change was driven by cryptic female choice: the tendency of females to choose males on the basis of their effectiveness in genitalic stimulation during copulation (Eberhard 1985). Females evolved a complex antechamber to their gonopore and acquired a second opening of the reproductive system to the exterior coupled with an unusual "flow-through" sperm management system in which deposited sperm are stored in separate chambers for later use in fertilizing eggs. Females also evolved a special sort of silk used only in egg sacs, which is almost universally present among entelegynes although its function

is unknown. Male genitalia became hydraulically rather than muscularly activated and more elaborate; the interaction with the equally complicated female genitalia became more complex. This "hydraulic bulb" of the male genitalia is so flexible during its operation that males have evolved various levers and hooks that seem to serve mainly to stabilize and orient their own genitalia during copulation. One of these, the "retrolateral tibial apophysis" has given its name to a fairly large clade of entelegyne families (the "RTA clade"; Coddington and Levi 1991, Griswold 1993, Sierwald 1998). Non-entelegynes, in contrast, have relatively simple male and female genitalia in which the female anatomy is one or two pairs or an array of blind receptacula, and the male intromittent organ is a smooth and simple hypodermiclike structure operated by tarsal muscles.

Among entelegynes the "eresoid" families seem basal. No clear synapomorphies define this group; in various analyses, eresoids may be paraphyletic (Coddington 1990a, Griswold et al. 1999). Perhaps the hottest current controversy in entelegyne systematics concerns the Palpimanoidea (10 families, 54 genera). Before their relimitation as a monophyletic group (Forster and Platnick 1984), palpimanoid families were dispersed throughout entelegyne classification: mimetids, archaeids, and micropholcommatids in particular were considered to be araneoids. The two classic features defining Palpimanoidea are setae shortened and thickened to function as cheliceral teeth (very rare in spiders) and the concentration of cheliceral glands on a raised mound. However, these two features are homoplasious within palpimanoids, and evidence is building that some palpimanoid taxa are araneoids after all (Schütt 2000).

One of the larger entelegyne lineages is the Orbiculariae. It unites two robustly monophyletic superfamilies (Araneoidea, 12 families, 980 genera; and Deinopoidea, 2 families, 23 genera) mainly but not entirely on the basis of web architecture and morphology associated with web spinning (Coddington 1986b and references therein). Both groups spin orb webs. Ethological research on orb weavers shows that orbs are constructed in fundamentally similar ways, although the deinopoid orb uses the plesiomorphic cribellate silk, whereas araneoids use the derived viscid silk (Griswold et al. 1998). Araneoidea are by far the larger taxon and includes many ecologically dominant web-weaving species. Interestingly, derived araneoids (the "araneoid sheet web weavers," six families, 685 genera) no longer spin orbs (some may not even spin webs) but rather sheets, tangles, and cobwebs (Griswold et al. 1998). There is a strong trend among araneoids to reduce and stylize the spinning apparatus (Hormiga 1994, 2000).

The sister taxon of Orbiculariae remains a mystery, although the most recent research suggests that most other entelegyne lineages are more closely related to each other than any is to the orb weavers (Griswold et al. 1999). Thus, the orbicularian sister group at present seems likely to be a very

large, hitherto unrecognized lineage consisting of amaurobioids (Davies 1995, 1998, 1999, Davies and Lambkin 2000, 2001), "wolf" spiders [Lycosoidea (Griswold 1993)], two-clawed hunters (Dionycha; Platnick 1990, 2000), and other, smaller groups (Jocqué 1991). Many of these lineages are relic-tual austral groups whose diversity is very poorly understood.

The phylogenetic structure among non-orbicularian entelegynes, therefore, is highly provisional at this point. Because of a long-standing emphasis on symplesiomorphy, many of the classical entelegyne families (most seriously Agelenidae, Amaurobiidae, Clubionidae, Ctenidae, and Pisauridae) were paraphyletic. Dismembering these assemblages into monophyletic units has been difficult because the monophyly of related families is also often doubtful (e.g., Amphinetidae, Corinnidae, Desidae, Liocranidae, Miturgidae, Tenggellidae, Stiphidiidae, Titanoecidae). Therefore neither the RTA clade, nor the two-clawed hunting spider families (Dionycha) may be strictly monophyletic, although in each is certainly a large cluster of closely related lineages. Dionychan relationships are quite unknown, although some headway has been made in the vicinity of Gnaphosidae (Platnick 2000). 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 (Bosselaers and Jocqué 2002). The nodes surrounding Entelegynae will certainly change in the future.

In sum, phylogenetic understanding of spiders has advanced remarkably since the early 1980s. We are on the cusp of having at least a provisional, quantitatively derived hypothesis at the level of families, but on the other hand, the density and consistency of the data for subsidiary taxa will remain soft for some years to come.

Whip Spiders (Amblypygi)

Whip spiders, also known as tailless whip scorpions, are a conspicuous group of mostly medium to large, dorsoventrally flattened arachnids distributed throughout the humid tropics and subtropics with a few species occurring in the arid regions of southern Africa. Although most species are epigean, several troglobite species are known.

Monophyly of Amblypygi is supported by several features, including the morphology and orientation of the pedipalps, the enormously elongated antenna-like first legs that act as tactile organs, and the presence of a cleaning organ on the palpal tarsus. The order belongs to Pedipalpi as the sister to Camarostomata (Uropygi + Schizomida) (Shultz 1990, 1999, Giribet et al. 2002), although some treatments place them as the sister to Araneae (e.g., Platnick and Gertsch 1976, Weygoldt and Paulus 1979, Wheeler and Hayashi 1998).

Current understanding of the internal phylogeny and classification of Amblypygi is almost entirely the work of Weygoldt (1996, 2000), who recognized five families, placed in two suborders, Paleoamblypygi and Euamblypygi. Paleoamblypygi contain a single West African species, *Paracharon caecus* (Paracharontidae), as well as five Carboniferous species that remain unplaced in a family. Paleoamblypygi differ in various features, including an anteriorly produced carapace and reduced pedipalpal spination. The Euamblypygi consist of the remaining whip spiders, including the circumtropical Charinidae, which contains three genera and 43 species. Charinidae may not be monophyletic (Weygoldt 2000). The remaining three families comprise Neoamblypygi, which is in turn divided into the Charontidae and Phrynoidea; the latter includes the Phrynidae and Phrynichidae. The Charontidae consist of two genera and 11 species from Southeast Asia and Australasia. The Phrynidae contain four genera and 55 species from the Americas, with a single outlying species from Indonesia (Harvey 2002a). The Phrynichidae contain 31 species in seven genera from Africa, Asia, and South America.

Whip Scorpions (Uropygi)

Whip scorpions are large, heavily sclerotized arachnids that have changed little since the Carboniferous. They primarily inhabit tropical rainforests but some, such as the well-known North American *Mastigoproctus giganteus*, occupy arid environments. Like other members of the Pedipalpi, tarsus I is subsegmented and is used as a tactile organ. They possess a number of distinctive features, including palpal chelae with the movable finger supplied with internal musculature (Barrows 1925), a long, multisegmented flagellum, raptorial pedipalps, and a long rectangular carapace. The abdomen bears a pair of glands that discharge at the base of the flagellum and are used to direct a spray of acetic acid (vinegar) at potential predators (Eisner et al. 1961; Haupt et al. 1988). On account of this unusual ability, whip scorpions are known as vinegaroons (or vinegarones) in the southern United States.

Uropygi are consistently placed as sister to Schizomida, and the gross morphology of its members suggests monophyly. Dunlop and Horrocks (1996) suggested that the Carboniferous uropygid *Proschizomus* may represent the sister to Schizomida, rendering Uropygi paraphyletic. The sole family Thelyphonidae is divided into four subfamilies: Hypoconinae (4 genera, 25 species: Southeast Asia, South America, west Africa), Mastigoproctinae (4 genera, 18 species: Americas, Southeast Asia), Typopeltinae (1 genus, 10 species), and Thelyphoninae (7 genera, 48 species: Southeast Asia and Pacific) (Rowland and Cooke 1973, Harvey 2003). Eight fossil species have been described (Selden and Dunlop 1998, Harvey 2003). Only Typopeltinae and

Thelyphoninae are well supported by apomorphic character states; Hypoctoninae and Mastigoproctinae appear to be solely defined by plesiomorphies (M. Harvey, unpubl. obs.).

Schizomids (Schizomida)

Schizomids are small (<1 cm), weakly sclerotized arachnids that can be recognized by the presence of a short abdominal flagellum that generally in females consists of three or four segments and in males is single segmented. The shape and setation of the male flagellum are species specific (e.g., Rowland and Reddell 1979, Harvey 1992b, Reddell and Cokendolpher 1995), probably reflecting its use during courtship and mating, in which it is gripped in the mouthparts of the female (Sturm 1958).

The order contains two families, the Central American Protoschizomidae and the widely distributed Hubbardiidae. Three fossil species have been described (Selden and Dunlop 1998). Protoschizomidae are represented by two genera and 11 species from Mexico or Texas, many from caves (Rowland and Reddell 1979, Reddell and Cokendolpher 1995). The Hubbardiidae consist of two subfamilies. Megaschizominae are represented by two species of *Megaschizomus* from Mozambique and South Africa. The widespread Hubbardiinae consists of 205 species in 35 genera (Harvey 2003), the vast proportion of which have been named in the last 40 years because of an increased awareness of previously overlooked character systems such as female genitalia. Cokendolpher and Reddell (1992) presented a cladistic analysis of the basal clades of Schizomida but refrained from including individual hubbardiine genera, whose systematics are still in a state of flux.

Harvestmen (Opiliones)

Commonly known as "daddy longlegs," harvestmen, shepherd spiders, or harvest spiders (among other names), the Opiliones were well known to North Temperate farmers and shepherds because of their abundance at harvest time. These are the only nonacarine arachnids known to ingest vegetable matter, but generally they prey on insects, other arachnids, snails, and worms. They can ingest particulate food, unlike most arachnids, which are liquid, external digesters. The order is reasonably well studied, although many of the Southern Hemisphere families are still poorly understood taxonomically.

Opiliones contain 43 families, about 1500 genera, and about 5000 species, but many more species await discovery and description. Most members of Opiliones are small to medium in size (<1 mm to almost 2.5 cm in the European species *Trogulus torosus*) and inhabit moist to wet habitats on all continents except Antarctica. Laniatores include large (>2 cm), colorful, well-armored Opiliones, most diverse in tropical regions of the Southern Hemisphere, but many

laniatorids are also very small. Eupnoi and Dyspnoi are more widely distributed and are especially abundant in the Northern Hemisphere. Members of Cyphophthalmi are distributed worldwide but are among the smallest (down to 1 mm) and most obscure members of the Opiliones.

Opilionids are typical arachnids with two basic body regions, and their junction is not constricted, giving them the appearance of "waistless" spiders. The cephalothorax generally has a pair of median simple eyes surmounting the ocular tubercle. Cyphophthalmi either lack eyes entirely or have a pair of eyes (some stylocellids), possibly lateral eyes. The anterior rim of the cephalothorax bears the large openings of a pair of secretory organs, known as repugnatorial glands. These differ in position and type among different groups within Opiliones, being most obvious in the suborder Cyphophthalmi, whose members take the shape of cones, named ozophores. The cephalothorax bears one pair of chelate three-segmented chelicerae for manipulating the food particles, one pair of pedipalps of either tactile or prehensile function, and four pairs of walking legs. The legs can be enormously long (>15 cm) in some Eupnoi and Laniatores species. Laniatorid palps are usually large and equipped with parallel rows of ventral spines that act as a grasping organ. The second pair of walking legs is sometimes modified for a tactile or sensory function.

The abdomen is clearly segmented in most species, although some segments may appear fused to different degrees. One pair of trachea for respiration opens ventrally on the sternite of the first abdominal segment. The genital aperture and its associated structures (operculum) open on the same segment. The anal region is very often modified; certain Cyphophthalmi males have anal glands, secondary sexual characters that are probably secretory. Females may have a long ovipositor with sensory organs on the tip that is used to check the soil quality for egg deposition. Males have a muscular or hydraulically operated penis, or copulatory organ. Some mites have vaguely similar structures, but otherwise ovipositors and penises are unique to Opiliones. Fertilization is thus internal and direct.

The monophyly of Opiliones is strongly supported by the presence of five unambiguous synapomorphies: (1) the presence of repugnatorial glands, (2) the special vertical bi-condylar joint between the trochanter and femur of the walking legs, (3) the paired tracheal stigmata on the genital segment, (4) the male penis, and (5) the female ovipositor (Shultz 1990, Giribet et al. 2002). Opilionid taxonomy supposes a basic division between Cyphophthalmi (no common name, six families) and the remaining harvestmen ("Phalangida"), consisting of Eupnoi (six families), Dyspnoi (seven families), and Laniatores (24 families). Eupnoi and Dyspnoi have been traditionally grouped in Palpatores (fig. 18.4).

Cyphophthalmids are small (1–6 mm), hard-bodied, soil animals that superficially resemble mites. Six families are recognized (Shear 1980, 1993, Giribet 2000), although some

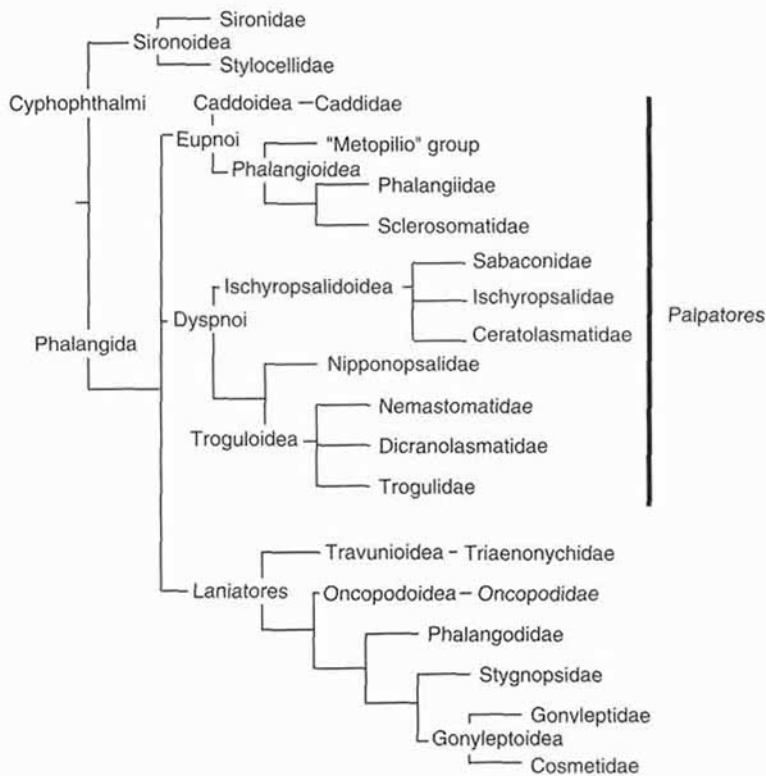


Figure 18.4. Phylogeny of Opiliones.

do not withstand cladistic tests (Giribet and Boyer 2002). "Palpatores" are diverse and heterogeneous; their monophyly is disputed. The component Eupnoi and Dyspnoi, however, are well-supported monophyletic clades, each with two superfamilies. Eupnoi includes Caddoidea (one family) and Phalangioidea (five families), and Dyspnoi includes Ischyropsalidoidea (three families) and Troguloidea (four families). The caddoids and especially the phalangoids include the typical "daddy long legs" of the Holarctic region, although Gondwanan families of both groups also exist. Ischyropsalidoidea and troguloids are diverse but more poorly known. Laniatores, in contrast, are heavily sclerotized, usually short-legged, often fantastically armored animals with diversity concentrated in the Southern Hemisphere.

Only recently have workers focused on the internal phylogenetic structure of Opiliones. Five modern quantitative cladistic studies have been published to date, covering about 50 genera and directed mainly at interfamilial relationships (Shultz 1998, Giribet et al. 1999, 2002, Giribet and Wheeler 1999, Shultz and Regier 2001). In contrast to the situation in spiders, molecular data are strongly represented and largely agree with morphology. Despite the relatively small size of the group, no phylogeny to date has included all families. Martens and coworkers (Martens 1976, 1980, 1986, Martens et al. 1981) and Shear (1986) provided an early overview of aspects of opiloid phylogeny and emphasized the phylogenetic value of the male genital organs. Martens rejected the division between Cyphophthalmi and Phalangida,

instead suggesting the taxon "Cyphopalpatores," consisting of Cyphophthalmi nested within a paraphyletic Palpatores. The idea depended largely on penis morphology, but because a penis among arachnids is unique to Opiliones (convergent in some mites), the character transformation was polarized and ordered by evolutionary speculations rather than outgroups. If the features are left unordered, Cyphopalpatores disappear under parsimony (Shultz 1998, Giribet et al. 2002). All later work has decisively rejected the Cyphopalpatores hypothesis and agrees that Phalangida are monophyletic.

Opinions diverge on groups within Phalangida. Three monophyletic groups clearly exist: Eupnoi, Dyspnoi, and Laniatores, as recognized by Hansen and Sørensen (1904), but the monophyly of Palpatores is still disputed. Molecular data (18S rRNA and 28S rRNA) separately and combined with morphology suggest Dyspnoi as sister to Laniatores, thus rendering Palpatores paraphyletic (Giribet 1997, Giribet et al. 1999). The morphological codings employed in these studies were later criticized by Shultz and Regier (2001), who presented new molecular data to support Palpatores monophyly but dismissed the morphological evidence. A more inclusive analysis of morphology and molecular data including 35 genera of Opiliones recently reaffirmed Palpatores paraphyly, a result stable under a wide variety of analytical parameters (Giribet et al. 2002). This result also accords with a study of internal Cyphophthalmi relationships (Giribet and Boyer 2002). The studies of Shultz and Regier (2001) and of

Giribet et al. (2002) disagree on the internal resolution of Trogluloidea and Ischyropsalidoidea, possibly because of the sparser taxon sampling in Shultz and Regier's analysis or differences in information content between the genes used.

Phylogeny of Laniatores is still in its infancy. No analysis has yet included a large sample with the exception of a study on Gonyleptoidea (Kury 1993) and the more recent molecular (Shultz and Regier 2001) and total evidence (Giribet et al. 1999, 2002) analyses considering Opiliones as a whole. The Laniatores are a well-supported monophyletic group originally divided into two groups, Oncopodomorphi and Gonyleptomorphi, by Šilhavý (1961). Martens (1976) later divided Laniatores into the three superfamilies Travunioidea, Oncopodoidea, and Gonyleptoidea, although it has been suggested (A. B. Kury, unpubl. obs.) suggests that Gonyleptoidea could be paraphyletic with respect to Oncopodoidea, constituting a clade informally named "Grassatores." The tripartite relationship proposed by Martens (1976) for Laniatores was also corroborated by total evidence analyses (Giribet et al. 1999, 2002), but many laniatorean families remain untested and their phylogenetic affinities unexplored.

Fossil members of Opiliones are rare, and their fossil record is currently restricted to a few Paleozoic and Mesozoic examples plus a more diverse Tertiary record based principally on the Florissant Formation and on Baltic and Dominican ambers (for reviews, see Cokendolpher and Cokendolpher 1982, Selden 1993b). The majority of known fossil harvestmen strongly resemble members of Eupnoi and Dyspnoi. Laniatores is currently only known from Tertiary ambers, and all the Dominican amber harvestmen described so far are Laniatores (Cokendolpher and Poinar 1998). A single fossil of the suborder Cyphophthalmi is known from Bitterfeld amber, Sachsen-Anhalt, Germany (Dunlop and Giribet in press).

Scorpions (Scorpiones)

Although their placement in Arachnida remains controversial (Weygoldt and Paulus 1979, Shultz 1990, 2000, Sissom 1990, Starobogatov 1990, Wheeler et al. 1993, Dunlop 1998, Dunlop and Selden 1998, Jeram 1998, Weygoldt 1998, Wheeler and Hayashi 1998, Dunlop and Webster 1999, Dunlop and Braddy 2001, Giribet et al. 2002), scorpions are unquestionably monophyletic. The clade is supported by 11 synapomorphies, including pectines (ventral abdominal sensory appendages), chelate pedipalps, and a five-segmented postabdomen (metasoma) terminating with a modified telson, including a pair of venom glands internally and a sharp aculeus distally, which functions as a stinging apparatus for offense and defense (Shultz 1990, Wheeler et al. 1993, Wheeler and Hayashi 1998, Giribet et al. 2002).

The approximately 1340 extant (Recent) scorpion species in 163 genera and 17 families (Fet et al. 2000, Lourenço 2000, Prendini 2000, Fet and Selden 2001, Soleglad and

Sissom 2001, Kovařík 2001, 2002) constitute a monophyletic crown group with a post-Carboniferous common ancestor (Jeram 1994a, 1998). Fossil representatives comprise 92 species assigned to 71 genera and 42 families (Fet et al. 2000), of which only six species can be placed in two extant families. All Paleozoic scorpions form the stem group of this clade, with *Palaeopisthacanthus* the most crownward stem taxon (Jeram 1994b, 1998), sister to recent scorpions (Soleglad and Fet 2001). Paleozoic scorpions were far more diverse than present forms and are pivotal to resolving the phylogenetic placement of the order (Jeram 1998, Dunlop and Braddy 2001), but their phylogeny and classification are controversial and largely decoupled from that of Recent scorpions. Some classifications (Kjellesvig-Waering 1986, Starobogatov 1990) were typological and overly detailed (Sissom 1990, Fet et al. 2000). Kjellesvig-Waering (1986) placed Paleozoic scorpions into two suborders, five infraorders, 21 superfamilies, and 48 families; only *Palaeopisthacanthidae* was placed with the suborder containing Recent period scorpions. Starobogatov (1990) treated scorpions and eurypterids as two superorders and recognized two orders and seven suborders of scorpions. Other classifications, although based on phylogenetic analysis (Stockwell 1989, Selden 1993a, Jeram 1994a, 1994b, 1998), were hampered by the limited quantity and quality of data obtainable from fragmentary fossils. These treat scorpions as a class *Scorpionida*, with two extinct and one Recent order, the latter containing several suborders and infraorders, of which, again, only one contains all living representatives. In the latest classification of Paleozoic scorpions (Jeram 1998), hierarchical ranks are not established because the rank of the crown group is uncertain and there is no point of reference for the stem group clades.

Stockwell (1989) conducted the first quantitative phylogenetic analysis of Recent scorpions, excluding Buthidae, and proposed a new higher classification. Stockwell retrieved four major clades of Recent scorpions, ranked as superfamilies: Buthoidea (Buthidae and Chaerilidae), Chactioidea (Chactidae, Euscorpiidae, and Scorpipidae), Scorpionoidea (Bothriuridae, Diplocentridae, Ischnuridae, Scorpionidae, and Urodacidae), and Vaejovoidea (Iuridae, Superstitioniidae, and Vaejovidae). However, Stockwell used groundplans derived from often paraphyletic genera as terminals (Prendini 2001b), casting doubt on his cladistic findings and resulting classification. Further, only his proposed revisions to the suprageneric classification of North American Chactioidea and Vaejovoidea were actually published (Stockwell 1992), although others, notably Lourenço (1998a, 1998b, 2000), have since implemented some of his other unpublished revisions.

Only two significant family-level morphological analyses appeared since Stockwell (1989). One treats Scorpionoidea using exemplar species (Prendini 2000). The other treats the chactoid family Euscorpiidae using genera as terminals (Soleglad and Sissom 2001). Soleglad and Fet (2001) recently attempted to illuminate basal relationships among extant

scorpions (placement of the enigmatic Chaerilidae and monotypic Pseudochactidae), in an analysis based solely on trichobothrial characters, and Fet et al. (2003) presented an analysis of 17 buthid exemplar species based on 400–450 bp of 16S rDNA. A molecular analysis of the entire order, based on nuclear and mitochondrial DNA loci, to be combined with available morphological data, is underway (L. Prendini and W. Wheeler, unpubl. obs.).

Stockwell's (1989) unpublished cladogram remains the only comprehensive hypothesis for nonbuthid families and genera. Addressing the internal relationships of Buthidae (~50% and 43% of all generic and species diversity, respectively) is a major goal of future research. Although it will certainly change, the most reasonable working hypothesis of scorpion phylogeny is basically Stockwell's (1989) cladogram for nonbuthids as emended by Prendini (2000), Soleglad and Sissom (2001), and Soleglad and Fet (2001) and including the little that is known about buthid phylogeny (fig. 18.5). Most of Lourenço's (1996, 1998b, 1998c, 1999, 2000) proposed familial and superfamilial emendations cannot be justified phylogenetically (Prendini 2001b, 2003a, 2003b, Soleglad and Sissom 2001, Volschenk 2002) but are included here because they represent the most recent published opinion.

Most authorities agree that the basal dichotomy among Recent scorpions separates buthids (Buthoidea) from nonbuthids, a hypothesis supported by morphological, embryological, toxicological, and DNA sequence data (Lamoral 1980, Stockwell 1989, Sissom 1990, Fet and Lowe 2000, Soleglad and Fet 2001, Fet et al. 2003, L. Prendini and W. Wheeler, unpubl. obs.). The divergence predates the breakup of Pangaea. Similarly, it is clear that the buthoid clade is monophyletic, although the monogeneric Microcharmidae (Lourenço 1996, 1998c, 2000) renders Buthidae paraphyletic (Volschenk 2002). Within Buthidae *sensu lato*, a basal dichotomy between

New and Old World genera has also been retrieved with toxicological and DNA sequence data (Froy et al. 1999, Tytgat et al. 2000, L. Prendini and W. Wheeler, unpubl. obs.).

The Buthidae are the largest and most widely distributed scorpion family (81 genera, 570 species). Buthids are characterized by eight chelal carinae, the type A trichobothrial pattern, and flagelliform hemispermatophore, whereas most also display a triangular sternum (Vachon 1973, Stockwell 1989, Sissom 1990, Prendini 2000). Buthidae include the majority of species known to be highly venomous to humans. Buthid scorpion toxins block sodium and potassium channels, preventing transmission of action potentials across synapses (Tytgat et al. 2000). At the clinical level, this results in severe systemic symptoms and signs of neurotoxicosis (extreme pain extending beyond the site of envenomation, disorientation, salivation, convulsions, paralysis, asphyxia, and often death). Toxins affecting sodium channels are better known and divided into two major classes, alpha and beta, according to physiological effects and binding properties (Froy et al. 1999). Alpha toxins occur among Old and New World buthids, whereas beta toxins occur only among New World buthids.

Examining the phylogenetic placements of the enigmatic Chaerilidae (one genus and 19 species, Khatoon 1999, Kovařík 2000) from tropical South and Southeast Asia, and recently described monotypic Pseudochactidae (Gromov 1998), known only from Central Asia, is critical for resolving basal relationships of scorpions. Both display autapomorphic trichobothrial patterns, dubbed type B (Vachon 1973) and type D (Soleglad and Fet 2001), respectively, along with a peculiar mix of buthid and nonbuthid character states. Chaerilidae additionally exhibit an autapomorphic, fusiform hemispermatophore (Stockwell 1989, Prendini 2000). Although Stockwell (1989) placed Chaerilidae as sister taxon of Buthidae, mounting evidence confirms earlier opinions

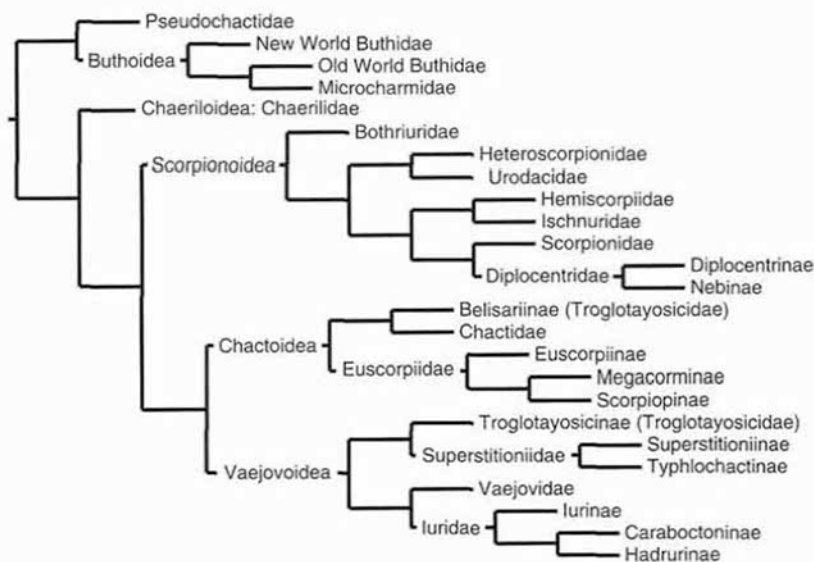


Figure 18.5. Phylogeny of Scorpiones.

that they are sister group of nonbuthids (Lamoral 1980, Lourenço 1985, Prendini 2000, Soleglad and Fet 2001), whereas Pseudochactidae may, instead, be sister group of buthids (Fet 2000, Soleglad and Fet 2001, Fet et al. 2003). Neither hypothesis based on evidence supports Lourenço's (2000) proposal to place Pseudochactidae with Chaerilidae in a unique subfamily, Chaeriloidea.

All remaining scorpions are characterized by the type C trichobothrial pattern and the lamelliform hemispermatophore, whereas most display 10 chelal carinae and a pentagonal sternum (Vachon 1973, Stockwell 1989, Sissom 1990, Prendini 2000). According to morphological and molecular evidence (Stockwell 1989, L. Prendini and W. Wheeler, unpubl. obs.), the type C scorpions comprise two distinct clades, corresponding to Stockwell's (1989) superfamilies Scorpionoidea and (Chactioidea + Vaejovoidea).

Relationships in the scorpionoid clade (37 genera and 380 species, or 23% and 29% of generic and species diversity) are better understood. All scorpionoid families are monophyletic according to morphological and molecular evidence (Stockwell 1989, Prendini 2000, L. Prendini and W. Wheeler, unpubl. obs.). Placement of Bothriuridae, a Gondwanan group with species in South America, Africa, India, and Australia, remains contentious. Bothriuridae was placed as sister to the chactoid-vaejovoid clade in some reconstructions (Lamoral 1980, Lourenço 1985) and, more recently (Lourenço 2000), in a unique superfamily Bothriuroidea. However, quantitative analyses (Stockwell 1989, Prendini 2000) place it as sister to the remaining scorpionoid families, monophyly of which is, in turn, well supported by embryological and reproductive characters, the most important being katoikogenic development. Embryos develop in ovariuterine diverticula and obtain nutrition through specialized connections with digestive caeca, rather than developing in the lumen of the ovariuterus (apoikogenic development) as in other scorpions. Katoikogenic scorpions occur mostly in the Old World and include some of the largest and most impressive scorpions. Relationships among the katoikogenic scorpionoid families, portrayed in figure 18.5, are well supported, except for the sister group relationship of Malagasy Heteroscorpionidae and Australian Urodacidae, which warrants additional testing (Prendini 2000).

Monophyly of the chactoid-vaejovoid clade (42 genera and 360 species, or 26% and 27% of generic and species diversity) appears well supported by morphological and molecular data (Stockwell 1989, L. Prendini and W. Wheeler, unpubl. obs.), but relationships among its component families, and monophyly thereof, are uncertain. Chactioidea and Vaejovoidea, as conceptualized by Stockwell (1989), may not withstand further analysis.

The chactoid-vaejovoid lineage includes the traditional and severely paraphyletic families Chactidae, Iuridae, and Vaejovidae. In an attempt to achieve monophyly, Stockwell (1989, 1992) removed Scorpipiidae from Vaejovidae, and Superstitioniidae and Euscorpiidae (to which he transferred

the chactid subfamily Megacorminae) from Chactidae. Soleglad and Sissom (2001) further altered these families by placing the scorpipioid genera into Euscorpiidae and transferring *Chactopsis* from Chactidae to Euscorpiidae. Chactid monophyly, particularly inclusion of the North American *Nullibrotheas* in an otherwise exclusively neotropical group, is untested. Euscorpiidae, comprising species from Europe, Asia, and the Americas, and Vaejovidae, including most North American species, now appears to be monophyletic. This cannot be said for Superstitioniidae, a family consisting almost entirely of eyeless, depigmented troglobites from Mexico that, in Stockwell's (1989, 1992) view, included two additional troglobites: *Troglotayosicus* from Ecuador and *Belisarius* from the Pyrenees (France and Spain). Sissom (2000) questioned their inclusion in Superstitioniidae. Lourenço (1998b) placed them in a new family, Troglotayosicidae, because of their eyeless, troglobite habitus. Notwithstanding that eyelessness may have evolved convergently in the caves of Ecuador and the Pyrenees, morphological and molecular evidence (Soleglad and Sissom 2001, L. Prendini and W. Wheeler, unpubl. obs.) indicates that *Belisarius* is more closely related to Euscorpiidae than to *Troglotayosicus*, which probably is a superstitioniid.

Iuridae, also in the chactoid-vaejovoid clade, include six genera from North America, South America, and southwestern Eurasia, formerly distributed among two families and four subfamilies. This heterogeneous group is united by a single synapomorphy—a large, ventral tooth on the cheliceral movable finger (Francke and Soleglad 1981, Stockwell 1989). However, mounting morphological and molecular evidence (L. Prendini and W. Wheeler, unpubl. obs.) suggests that it is paraphyletic. Few agree on placement of the monotypic North American *Anuroctonus* in the chactoid-vaejovoid clade at large, although it might be related to *Hadrurus*, also from North America (Stockwell 1989, 1992). The South American *Caraboctonus* and *Hadruroides* form a monophyletic group, as do the Eurasian *Calchas* and *Iurus*, but the Eurasian genera display significant trichobothrial and pedipalp carinal differences, suggesting that their putative relationship to the other genera is spurious.

Pseudoscorpions (Pseudoscorpiones)

Pseudoscorpions, false scorpions, or book scorpions are a cosmopolitan group that consists of 24 families, 425 genera, and 3261 species (Harvey 1991, 2002b, M. S. Harvey, unpubl. obs.). They represent a monophyletic clade strongly supported by several features, but only one, the presence of a silk producing apparatus discharging through the movable cheliceral finger, is deemed to be autapomorphic. Other important features include the presence of chelate pedipalps, loss of the median eyes, median claw absent from all legs but replaced by an arolium, and two-segmented chelicerae. They represent the sister group of Solifugae, together comprising the

Haplocnemata (Shultz 1990, Wheeler et al. 1993, Wheeler and Hayashi 1998, Giribet et al. 2002).

Chamberlin (1931) provided the first modern classification of the order, recognizing the groups Heterosphyronida and Homosphyronida. The former consisted solely of the Chthonioidea, whereas the latter consisted of two suborders, Diplosphyronida (Neobisioidea and Garypoidea) and Monosphyronida (Fealloidea, Cheiridioidea, and Cheliferoidea). Beier (1932a, 1932b) adopted this classification but changed the subordinal names to Chthoniinea, Neobisiinea, and Cheliferiinea. These complementary classifications remained in place, with various new families being added or synonymized, until Harvey (1992a) presented a cladistic analysis of the group based upon 200 morphological and behavioral characters. Harvey's analysis (fig. 18.6) hypothesized a different arrangement, with the suborder Epiocheirata, composed of the superfamilies Chthonioidea and Fealloidea, representing the sister to the remaining Icheirata. Epiocheiratans lack a venom apparatus in the chelal fingers, and adults and later nymphal instars always possess a small unique diploid trichobothrium on the distal end of the fixed chelal finger. Chthonioidea are dominated by the cosmopolitan Chthoniidae (30 genera, 612 species). Tridenchthoniidae (15 genera, 70 species) is largely tropical, whereas Lechytiidae (*Lechyti*, 22 species) is sporadically distributed. Whereas the superfamily Chthonioidea and the families Tridenchthoniidae and Lechytiidae are each clearly monophyletic, Chthoniidae probably are not. The Pseudotyranchochthoniinae and some other apparently basal taxa such as *Sathrochthonius* may warrant removal from the family. Fealloidea are curiously distributed with Pseudogarypidae (seven species, two genera) in North America and Tasmania, and Feallidae (11 species, one genus), on continents bordering the Indian Ocean. These distributions are undoubtedly

vicariant (Harvey 1996). The group was once more widely distributed, because three species of *Pseudogarypus* are known from Oligocene Baltic amber deposits.

The larger suborder, Icheirata, is characterized by the presence of a venom apparatus in the chelal fingers (later lost in one finger in several lineages) and absence of the diploid trichobothrium. Icheirata contains Hemictenata (Neobisioidea) and Panctenata (Olpioidea, Garypoidea, Sternophoroidea, and Cheliferoidea).

Neobisioidea are a basal clade containing Bochicidae (10 genera, 38 species) and Ideoroncidae (9 genera, 54 species), successively followed by the Hyidae (three genera, nine species), Gymnobisiidae (four genera, 11 species), Neobisiidae (33 genera, 499 species), Syarinidae (16 genera, 96 species), and Parahyidae (one genus, one species). Olpioidea contain two families, Olpiidae (52 genera, 324 species) and Menthidae (four genera, eight species), but there is little support for the monophyly of the former. Garypoidea consist of the basal Geogarypidae (three genera, 59 species), the Holarctic Larcidae (two genera, 12 species), the Garypidae (10 genera, 75 species), and two families previously placed in Cheiridioidea: Cheiridiidae (six genera, 71 species) and Pseudochiridiidae (two genera, 12 species). Cheiridioidea were recently reinstated as a separate superfamily by Judson (2000) but without a full reanalysis of the character set provided by Harvey (1992a).

The remaining taxa are placed in Ellassommatina—consisting of the monofamilial Sternophoroidea (three genera, 20 species), a group of pallid, flattened, corticolous species distributed in various disparate regions of the world (Harvey 1991)—and Cheliferoidea. The perceived relationship of Sternophoridae with Cheliferoidea is only tentatively supported (Harvey 1992a), and knowledge of the mating be-

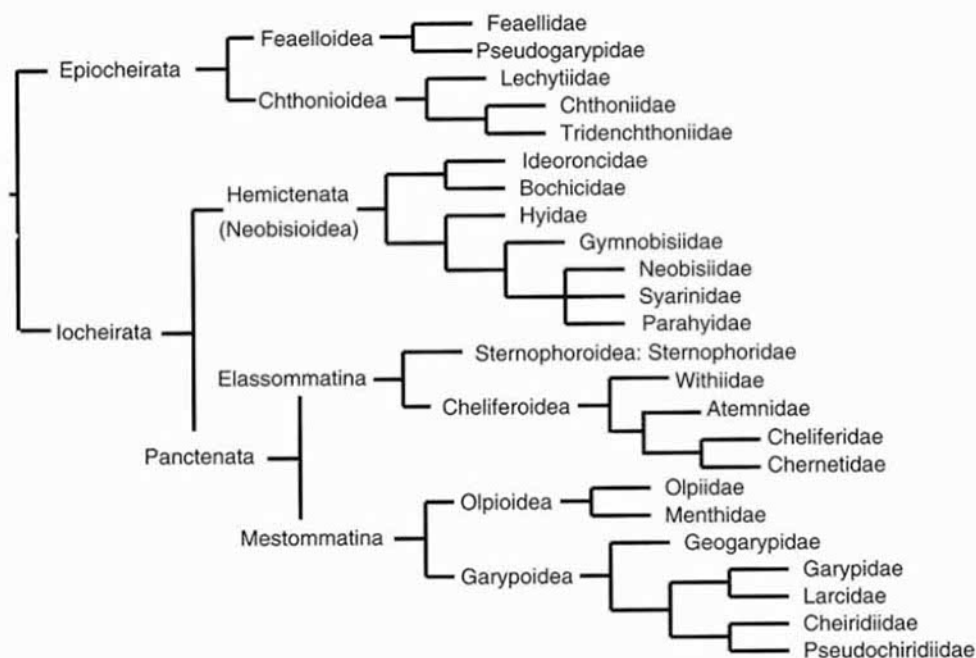


Figure 18.6. Phylogeny of Pseudoscorpiones.

havior of sternophorids may assist in determining their phylogenetic status. Cheliferoidea consist of Withiidae (34 genera, 153 species), Cheliferidae (59 genera, 274 species), and Chernetidae (111 genera, 646 species). The resolution of this clade depends on mating behavior and spermatophore morphology (Proctor 1993). Cheliferoids are the only pseudoscorpions with sperm storage receptacula (spermathecae) in females.

The fossil fauna consists of 35 named species, most of which were found as inclusions in Tertiary ambers. Cretaceous pseudoscorpions are known (Schawaller 1991), but the earliest known taxon is *Dracochela deprehendor* from Devonian shales in New York (Schawaller et al. 1991).

Harvey (1992a) confirmed the monophyly of most families, but the original analysis is currently being extended to include more taxa to test further the monophyly and internal phylogeny of various clades.

Solifuges, Camel Spiders (Solifugae)

Solifuges or solpugids are a bizarre group of specialized, mostly nocturnal, errant hunting arachnids notable for their huge powerful chelicerae and voracious appetite (Punzo 1998). Besides their large powerful chelicerae, solifuges are unique in having sensory malleoli (or racket organs) on the fourth coxae and trochanters, and many other peculiar features (prosomal stigmata, male cheliceral flagellae, palpal coxal gland orifices, adhesive palpal organs, a monocondylar walking leg joint between the femur and patella).

The Solifugae contain 1,084 species in 141 genera and 12 families (Harvey 2003): Ammotrechidae (22 genera, 81 species), Ceromidae (three genera, 20 species), Daesiidae (28 genera, 189 species), Eremobatidae (eight genera, 183 species), Galeodidae (eight genera 199 species), Gylippidae (five genera, 26 species), Hexisopodidae (two genera, 23 species), Karschiidae (four genera, 40 species), Melanoblossiidae (six genera, 16 species), Mummuciidae (10 genera, 18 species), Rhagodidae (27 genera, 98 species), and Solpugidae (17 genera, 191 species). Only three fossil species are known (Selden and Dunlop 1998). They primarily occur in Old and New World semi-arid to hyperarid ecosystems but are absent from Australia and Madagascar. The Southeast Asian melanoblossiid *Dinorhax rostrumspittaci* is unusual in residing in rainforest, whereas the peculiar mole solifuges (Hexisopodidae) from the deserts of southern Africa are highly modified for burrowing through soil (Lamoral 1972, 1973).

Relationships within the order are very poorly understood, largely because of the chaotic familial and generic classification promulgated by Roewer (1932, 1933, 1934) and continued with many reservations by later workers (e.g., Muma 1976, Panouse 1961, Turk 1960). The current classification is a flat structure devoid of any phylogenetic signal (Harvey 2002b, 2003). There has been no detailed phylogenetic work on any solifuge group, let alone a synop-

sis, and no monophyly arguments exist for any family, although some (e.g., Hexisopodidae) seem to be defined by obvious autapomorphies. The group urgently needs higher level cladistic analysis.

Conclusions

The last decade has seen substantial progress in research on major arachnid clades. Considering family rank as indicating "major" lineages, at least preliminary hypotheses are available for five of the 13 "orders" (Araneae, Amblypygi, Opiliones, Scorpiones, and Pseudoscorpiones), but an additional four (Ricinulei, Palpigradi, Uropygi, and Schizomida) have only one or two clades ranked as families, so relationships at that level are trivial. Solifugae (12 families, 141 genera) and Acari (~400 families, ~4000 genera) remain as substantial lineages without explicit family-level phylogenies. Although solifuge taxonomy is so completely artificial that it is difficult to know how to begin, the main reason is lack of workers: only two or three solifuge specialists exist worldwide. Mites similarly suffer from a lack of taxonomists, but the few acarologists must deal with a much greater taxonomic tangle. There are so many autapomorphic mite lineages and so much diversity that relationships are obscured, resulting in an overly split higher classification. The very small size of mites makes molecular work difficult, although not impossible (e.g., Dabert et al. 2001), and they are so morphologically diverse (and often highly simplified) that morphological work is no easier.

The current conflict between molecules and morphology at the ordinal level in arachnid phylogeny is intriguing but probably temporary. Deeper nodes in arachnid phylogeny are hard to recover consistently with 18S and 28S rRNA sequence data. Curiously, the same loci do provide robust signal on still deeper nodes (e.g., arthropods; see Wheeler et al., ch. 17 in this vol.), as well as shallower nodes such as Opiliones (Giribet et al. 2002) and Scorpiones (L. Prendini and W. Wheeler, unpubl. obs.). The problem, therefore, seems to be, on the one hand, exploratory—loci robustly informative for these presumably Lower Palaeozoic divergences are as yet unknown—and on the other, technical, because the few loci that seem to have worked in other taxa at comparable levels have not been studied in arachnids. Edgecombe et al. (2000) also point out that the "anomalous" nodes in molecular results are usually weakly supported. The sheer quantity of molecular data make a single, most parsimonious tree almost inevitable, but that obscures the often very tenuous support for some nodes. Because fewer comparisons are usually possible, morphological data are more likely to produce multiple most parsimonious trees so that dubious nodes disappear in the strict consensus tree. No doubt as more genes are analyzed and taxon sampling improves, the discrepancies will decrease and the congruence of the total evidence will improve.

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