

## CHAPTER 7

### Fossil Taxa and Relationships of Chelicerates

*Paul A. Selden and Jason A. Dunlop*

#### ABSTRACT

Chelicerata belong in Arachnomorpha and comprise Xiphosura, Eurypterida, and Arachnida. Pycnogonida, Aglaspida, Chasmataspida, and a number of merostomoid taxa, e.g., *Sanctacaris*, are regarded as possible chelicerate relatives but are not included in Chelicerata. Autapomorphies are presented for xiphosurans, eurypterids, and the recognized arachnid orders, and the fossil record, mode of life, and probable phylogenetic affinities of each group are discussed. The fossil record of the chelicerate taxa is compared to published phylogenies. Current controversies in arachnid phylogeny include whether scorpions are closer to eurypterids than to other arachnids, though in either case scorpions and non-scorpion arachnids terrestrialized independently. Some phylogenies predict aquatic Silurian opilionids. The problems of recognizing early occurrences of crown groups, because their stem groups acquired their autapomorphies through geological time, are discussed. A strong consensus among published arachnid phylogenies recognizes a taxon, Tetrapulmonata, comprising Trigonotarbida (extinct), Araneae, Amblypygi, Uropygi, and Schizomida.

Chelicerata is a major arthropod clade defined by an anterior prosoma bearing six pairs of appendages including pre-oral chelicerae, an opisthosoma of twelve segments, and a post-anal telson. Chelicerates have been traditionally divided into two classes: the aquatic Merostomata (Xiphosura + Eurypterida) and the terrestrial Arachnida, though many authors consider Merostomata to be a paraphyletic grade of aquatic chelicerates (Kraus 1976). Chelicerates underwent an initial radiation in the Cambrian, with the arachnids radiating later, in the Silurian (Lindquist 1984); most arachnid orders were established by Carboniferous times. Dunlop and Selden

(1997) discussed the relationships of chelicerates with other arthropods; in this chapter we provide brief sketches of each chelicerate group (fig. 7.1) and some chelicerate relatives, and then we discuss how the fossil record accords with recent phylogenies of the Chelicerata.

## CHELICERATE RELATIVES

Heymons (1901) introduced the name Chelicerata for arachnids, eurypterids, and xiphosurans. From a modern perspective, chelicerates appear to be a distinctive, clearly definable taxon, with the exception of the questionable inclusion of the Pycnogonida (see below). When fossil taxa are considered, however, the limits of Chelicerata are more vague. A number of Paleozoic forms, such as Aglaspidida Raasch, 1939, are superficially similar to xiphosurans but lack diagnostic features such as chelicerae; they may bear antennae, or their appendages are unknown. The case for inclusion or exclusion of these groups in Chelicerata is discussed below.

### Pycnogonida Latreille, 1810

Pycnogonids (sea spiders) are exclusively marine arthropods that resemble Chelicerata in having a chelate first appendage (chelifore). The prosoma consists of a series of tubular segments with lateral extensions each bearing a walking leg; there is a minute opisthosoma. An anterior proboscis precedes the chelifore; the second appendage is palplike. Appendage 3 (oviger) is modified in the male to carry ova during incubation. There are usually four pairs of walking legs, but some species bear one or two additional walking legs and corresponding trunk segments. The first prosomal segment bears, in addition to the first three pairs of appendages, a dorsal tubercle with eyes. Some deep-sea forms are blind.

King (1973) summarized the three main hypotheses about pycnogonid affinities. Pycnogonids may be related to: (1) crustaceans, since their protonymph larva resembles the nauplius larva, and they share certain embryological features; (2) chelicerates, because of their pre-oral chelifores and gut diverticula that extend into the leg coxae; or (3) neither of these groups.

Hedgpeth (1955a) referred Recent pycnogonids to Pantopoda and the monotypic *Palaeopantopus* Broili, 1928, from the Lower Devonian of Germany to *Palaeopantopoda*. Another monotypic arthropod, *Palaeoisopus*, also from the Lower Devonian of Germany, resembles pycnogonids, but its affinities are obscure (Hedgpeth 1955b). The fossil record does not help to determine the exact systematic position of the pycnogonids. Bergström et al. (1980) redescribed the fossil pycnogonids and suggested that they were derived from primitive merostomes.

### Aglaspidida

Aglaspidida is a distinct group of Lower Paleozoic arthropods that show similarities to both xiphosurans and trilobites. Aglaspidids have a phosphatic exoskeleton and

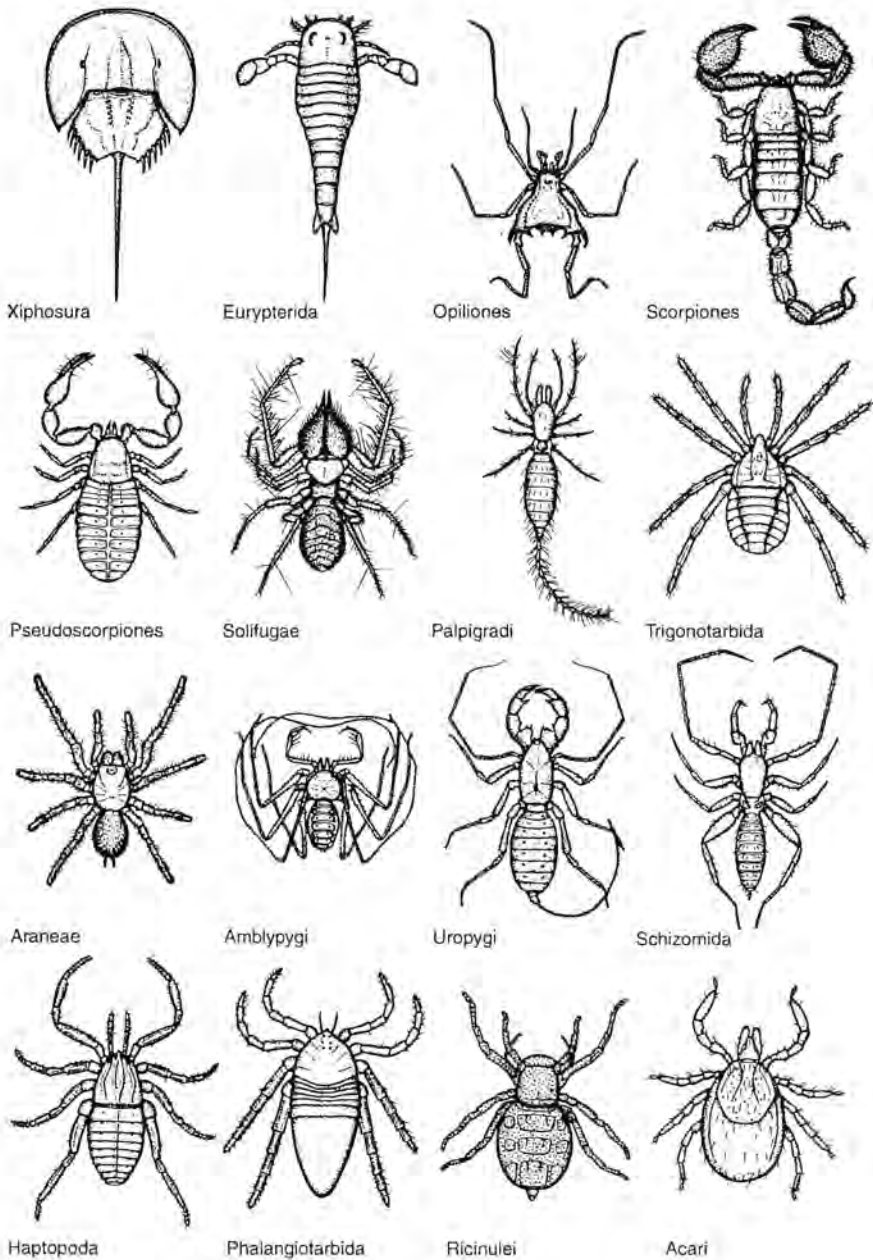


FIGURE 7.1

Sketch diagrams of a number of taxa described in the text. Xiphosura: *Limulus polyphemus*, Eurypterida: *Baltoerypteris tetragonophthalmus*, Opiliones: *Gonyleptus* sp., Scorpiones: *Scorpio martus*, Pseudoscorpiones: *Lasiochernes pilosus*, Solifugae: *Galeodes arabs*, Palpigradi: *Koenenia mirabilis*, Trigonotarbida: *Lissomatus schucherti*, Araneae: *Poecilotheria regalis*, Amblypygi: *Charinus milloti*, Uropygi: *Mastigoproctus giganteus*, Schizomida: *Schizontus peradyenensis*, Haptopoda: *Plesiosiro madeleyi*, Phalangiotarbida: *Goniotarbus tuberculatus*, Ricinulei: *Ricinoides feae*, Acari: *Ixodes ricinus*.

leglike appendages on both the prosoma and opisthosoma. The carapace has genal spines and the lateral margins of the tergites curve strongly backward. The group was classified as merostomes by Raasch (1939) and regarded as a separate order of the Xiphosura by Størmer (1955). Bristowe (1971), Manton (1977), and Weygoldt and Paulus (1979) placed aglaspidids within the Chelicerata. Weygoldt and Paulus (1979) regarded Aglaspidida as the sister taxon to all other chelicerates (Euchelicerata). Aglaspidids were removed from Chelicerata by Briggs et al. (1979) on the grounds that there were only four or five pairs of cephalic appendages, the first of which could not be demonstrated to be chelate. They did not refer them to another higher taxon. Their removal from Chelicerata was criticized by Bergström (1980) who argued that the number of head segments (and hence head appendages) was variable in early chelicerates and other arthropods. The extinct aglaspidids are probably not chelicerates since they bear neither chelicerae nor other features that would ally them more closely with the Chelicerata than with any other arthropod group (Briggs et al. 1979).

A number of Lower Paleozoic taxa representing potential candidates for basal chelicerates, e.g., *Paleomerus*, were referred to the Aglaspidida (Raasch 1939). This referral was disputed by Bergström (1971) since these genera do not have phosphatic exoskeletons, tergites drawn laterally into pleural spines, or genal spines like typical aglaspidids. The appendages of *Paleomerus*, *Strabops*, and *Neostrabops* are unknown.

#### Chasmataspida Caster and Brooks, 1956

Chasmataspids are a monotypic group from the Ordovician and were originally referred to the Xiphosura (Caster and Brooks 1956). Chasmataspids have a semicircular prosoma, a short pre-abdomen (buckler) of three segments and an elongate post-abdomen of nine segments. The appendages are poorly known. The Devonian fossil *Diploaspis* was referred to Chasmataspida by Størmer (1972). *Diploaspis* has a pair of paddles, but also appears to have a 3 + 9 opisthosomal segmentation, which argues against it being a eurypterid. Bergström (1980) removed *Diploaspis* from Chasmataspida, suggesting that it might represent a group from which arachnids evolved, leaving Chasmataspida as a monotypic order consisting only of the genus *Chasmataspis*. The prosoma of *Chasmataspis* resembles that of aglaspidids, and initial observations suggest these taxa may be sister groups, though restudy of this material, together with *Diploaspis* and the merostomoids, is required.

#### Merostomoidea Størmer, 1944

A range of Lower Paleozoic aquatic arthropods that superficially resemble xiphosurans in having a body comprised of two tagmata was referred to the class Merostomoidea by Størmer (1944). These include *Sidneyia*, *Helmetia*, *Emeraldella*, *Ha-*

*belia*, *Molaria*, and *Cheloniellon*. They show variable numbers of segments in each tagma and a range of appendages including antennae in some forms and leglike opisthosomal limbs in others (Bergström 1980). Merostomoids almost certainly do not form a monophyletic group; recent studies have indicated they are scattered within the group Arachnomorpha, which includes Chelicerata and Trilobita (Wills et al. 1995).

*Sanctacaris* Briggs and Collins, 1988, from the Middle Cambrian Burgess Shale of British Columbia, was suggested as plesiomorphic sister taxon (plesion) to all other Chelicerata on the grounds of having two tagmata with six pairs of appendages on the first tagma, a cardiac lobe, and the anus at the rear of the last trunk segment. Briggs and Collins (1988) proposed a new diagnosis of Chelicerata, more appropriate to fossil material. Arguing against a close association of *Sanctacaris* with Chelicerata are: lack of chelicerae, an opisthosoma of eleven segments (twelve is the number regarded as plesiomorphic for Chelicerata [Shultz 1990]) and a broad, rather than styliform, telson, which is generally considered to be the plesiomorphic state. In a more recent cladistic analysis, *Sanctacaris* was grouped with other Burgess Shale merostomoids (Wills et al. 1995).

## CHELICERATA HEYMONS, 1901

### Xiphosura Latreille, 1802

Xiphosura (horseshoe crabs) are the only extant, primarily aquatic chelicerates. They are widely regarded as the most primitive chelicerates and commonly cited as outstanding examples of "living fossils" because of their apparent conservative morphological change since the Paleozoic. One living species (*Limulus polyphemus*), which can grow up to 0.6 m long, occurs on the Atlantic coast of North America, and three species of *Tachypleus* and *Carcinoscorpius* occur in southeast Asia and the Philippines. Xiphosurans are characterized by a horseshoe-shaped carapace, two to five chelate appendages, modification of appendage 6 into a "pusher" and modification of the first opisthosomal appendages into chilaria.

Though previously allied with Eurypterida in the Merostomata Dana, 1852, most authors now place Xiphosura with either the Scorpiones (Bergström 1979, 1980; Bergström et al. 1980; van der Hammen 1985, 1986) or as the sister group to all other chelicerates (except *Sanctacaris*) (Grasshoff 1978; Boudreaux 1979; Paulus 1979; Weygoldt and Paulus 1979; Weygoldt 1980), thereby rendering Merostomata an unnatural group (Kraus 1976).

About thirty fossil genera are known. A carapace dating from the Lower Cambrian from Öland, Sweden, *Eolimulus alatus* (Moberg 1892), was referred to Xiphosura, though it might equally well be an aglaspidid or some other arthropod. Flower (1968) placed *Lemoneites*, from the Ordovician of New Mexico, in the



Aglaspidida but remarked on the number of similarities with Synziphosurina Packard, 1886. Synziphosurines (Ordovician—Upper Devonian) are primitive xiphosurans with a horseshoe-shaped carapace and a segmented opisthosoma of freely articulating segments divided into pre- and post-abdominal regions. A recent cladistic analysis (Anderson and Selden 1997) has shown that Synziphosurina is paraphyletic.

### Eurypterida Burmeister, 1843

Eurypterids flourished from Ordovician to Permian times in aquatic environments worldwide. Most eurypterids were marine, but some Silurian and later forms lived in fresh water and some may have been amphibious. Approximately 300 species have been described, ranging from 0.1 m to 2 m in length; the latter were the largest arthropods that ever lived. Most were predators, and their prey included the early vertebrates. Eurypterids are characterized by an elongate body bearing a telson, a carapace with median ocelli and a pair of compound eyes, three-segmented chelicerae and five further pairs of prosomal appendages with gnathobasic coxae, and five pairs of opisthosomal appendages (*Blattfüsse*) modified as opercula for respiratory organs. Autapomorphies of the Eurypterida are: a median opisthosomal (genital) appendage, a platelike metastoma (probably homologous with the first pair of opisthosomal appendages, i.e., the xiphosuran chilaria) and so-called gill tracts (*Kiemenplatten*) on opisthosomal sternites 1–5, within branchial chambers.

Eurypterids were placed by Woodward (1865) with the Xiphosura in the class Merostomata Dana, 1852, but in most recent studies Xiphosura have been considered to be the sister group to all other Chelicerata (except *Sanctacaris*) and not to Eurypterida alone (e.g., Kraus 1976). Eurypterida is a monophyletic group, though some authors (e.g., Tollerton 1989) have regarded the hibbertopteroids (= Cyrtocutenida) as a sister group of equal rank to all other eurypterids. Most authors (e.g., Clarke and Ruedemann 1912; Caster and Kjellesvig-Waering 1964) divided the main eurypterid line into two taxa: Pterygotina and Eurypterina. Pterygotines have enormous chelicerae for food capture and simple walking legs; eurypterines have small chelicerae and commonly spinose anterior limbs for food gathering. An alternative division into those forms in which the sixth appendage is leglike (Stylonuracea) and those in which it is formed into a paddle for swimming (Eurypteracea) was proposed by Størmer (1955). A cladistic analysis was attempted by Plotnick (1983) at the generic level, and Tollerton (1989) has produced the most recent systematic account of the group.

### Opiliones Sundevall, 1833

Opilionids are among the most diverse extant chelicerates with approximately 4000–5000 living species worldwide. They range in size from less than 1 mm to

about 22 mm. They are omnivorous animals and are the only arachnids known to ingest solid food (Petrunkevitch 1955). Their morphology ranges from the round-bodied, long-legged phalangoids to the shorter-legged, spiny laniatores and the mitelike cyphophthalmids. Opilionids are characterized by a prosoma that is broadly joined to the opisthosoma, the division between the two often being indistinct. The chelicerae are three-segmented and chelate, and in some taxa the pedipalps are raptorial. Opilionids respire with tracheae opening through a single pair of spiracles on the second opisthosomal segment. Autapomorphies proposed for the Opiliones are: an elongate and tactile leg pair 2, a trochanterofemoral joint with a vertical bi-condylar articulation, tracheal stigmata on the genital segment, a male penis and female ovipositor, loss of the lateral eyes, and prosomal defensive glands.

Though a distinctive group, the position of Opiliones within Chelicerata is poorly defined. Some authors (e.g., Yoshikura 1975; Weygoldt and Paulus 1979) placed them in a derived position as the sister group to Acari. Van der Hammen (1989) argued that opilionids were related to Xiphosura and Scorpiones, and more recently Shultz's (1990) analysis placed them as the plesiomorphic sister taxon to Scorpiones, Pseudoscorpiones, and Solifugae (see below). Of particular phylogenetic interest are the cyphophthalmid opilionids and the opilioacarid mites. Some authors have cited these similar groups as providing strong evidence for Acari and Opiliones representing sister groups, though Acari are normally placed as the sister group of Ricinulei.

Opiliones occur in the Lower Carboniferous rocks of East Kirkton, near Edinburgh, Scotland (Wood et al. 1985), in Upper Carboniferous strata of France (Thevenin 1901; undescribed fossils from Montceau-les-Mines) and Illinois (Petrunkevitch 1913), and in the Lower Cretaceous of Koonwarra, Victoria, Australia (Jell and Duncan 1986). They are much better known from Tertiary ambers (Koch and Berendt 1854). The order Kustarachnida Petrunkevitch, 1913, should be included with Opiliones, following reassessments by Beall (1986) and Dunlop (1996).

### Scorpiones Hemprich and Ehrenburg, 1810

Approximately 1500 living species of scorpions inhabit tropical and temperate parts of the world, and about 110 fossil species are known. Scorpions are the oldest known arachnids, ranging from Silurian (Llandovery) strata onward, and have a good fossil record, especially in the Paleozoic. Living scorpions range from 9 mm to 210 mm, and some fossil scorpions may have reached 1 m. All living scorpions are terrestrial predators, but some Silurian to Carboniferous forms were aquatic. Scorpion biology has been summarized by Polis (1990).

Scorpions are characterized by three-segmented, chelate chelicerae (the observation that some fossil forms had four segments is erroneous), chelate pedipalps, and an opisthosoma divided into a broad mesosoma and a narrow metasoma, the latter with ankylosed segments. Scorpions respire through four pairs of book lungs opening on opisthosomal segments 2-5. Autapomorphies proposed for the Scorpiones

are pectines, spermatozoa with free flagella throughout their development, opisthosomal venom glands, a pretarsal levator muscle originating in the tibia, and large endites on the coxae of walking legs 1 and 2.

A monograph of fossil scorpions was prepared by Kjellesvig-Waering (1986), but this posthumous publication was marred by compilation defects, and the classification scheme proposed therein was controversial. For example, the linchpin of Kjellesvig-Waering's classification was the supposed Devonian gilled scorpion described as *Tiphoscorpio hueberi*. Restudy of this material (Selden and Shear 1992; Shear and Selden 1995) revealed that it is not a scorpion but an arthropleurid myriapod. Stockwell (1989), in an unpublished thesis, produced a more acceptable classification scheme of Scorpiones, based on an exhaustive cladistic analysis that included fossils. This was adopted by Selden (1993a,b) and Jeram (1994).

Scorpions are the oldest arachnid group; the oldest known scorpion is *Dolichophonus loudonensis* (Laurie, 1889) from the Llandovery of the Pentland Hills, near Edinburgh, Scotland. The Early Silurian record of scorpions could be interpreted as representing the earliest terrestrial animals because all modern scorpions are terrestrial. However, all Silurian fossil scorpions occur in marine or marginal marine sediments, and morphological features suggest an aquatic mode of life. Petrunkevitch (e.g., 1953) considered that all fossil scorpions were terrestrial, but other workers (e.g., Pocock 1902; Wills 1947; Størmer 1970; Rolfe and Beckett 1984; Kjellesvig-Waering 1986) argued for an aquatic habitat for Silurian scorpions at least. Evidence for aquatism among fossil scorpions includes: gills and digitigrade tarsi as well as the absence of terrestrial modifications such as coxal apophyses, stigmata, book lungs, trichobothria, highly developed pectines, and plantigrade tarsi. There is considerable overlap in the ranges of aquatic and terrestrial scorpions, but the first terrestrial forms had appeared by the Devonian (Selden and Jeram 1989). It is not always easy to decide whether a given fossil had an aquatic or terrestrial mode of life; the original environment of the enclosing sediment is commonly the best clue. Well-preserved book lungs have been found in a Carboniferous (Viséan) scorpion from East Kirkton, near Edinburgh, Scotland (Jeram 1990). Few new records of fossil scorpions have turned up in recent years although in the otherwise sparsely recorded Mesozoic scorpions from the Triassic of France (Gall 1971) and the Cretaceous of Brazil (Campos 1986) are currently under study.

### Pseudoscorpiones de Geer, 1778

Pseudoscorpions (= Chelonethi) are small (1 mm to 7 mm), predatory arachnids with large, chelate pedipalps. Approximately 2500 living species have been described from around the world. Pseudoscorpions can be found typically in leaf litter, moss, and under stones. Their method of dispersal, phoresy, involves hitching a ride on a flying insect using the pedipalps. Pseudoscorpions have cheliceral silk glands with which they construct elaborate brood chambers. Pseudoscorpion biology has been summarized by Weygoldt (1969).



Some workers have placed scorpions and pseudoscorpions together on account of their overall similarity (e.g., Yoshikura 1975). However most recent studies have all placed pseudoscorpions and solifuges as sister groups united by the synapomorphies of two-segmented chelate chelicerae (Weygoldt and Paulus 1979), lack of a patella, presence of a rostrum in the mouthparts (van der Hammen 1989), and a chelicero-carapacial articulation (Shultz 1990).

Pseudoscorpions are characterized by their small, often rounded bodies and large chelate pedipalps. These animals lack median eyes and Malpighian tubules. They possess a brood sac and respire with tracheae opening through spiracles on the first two opisthosomal segments. The female has a ram's-horn organ for use in taking up the spermatophore. Autapomorphies proposed for Pseudoscorpionida are: absence of an anterior patellotibial muscle in the walking legs, cheliceral silk glands, and complex brood care.

Many pseudoscorpions are known from the Tertiary (mainly in ambers, e.g., listed in Schawaller 1982, table 1), and some are known from Cretaceous ambers of the Lebanon (Whalley 1980) and Manitoba (Schawaller 1991). An important find of fossil pseudoscorpions was the discovery of exceptionally well preserved specimens in the Upper Devonian mudstones of Gilboa, New York, described as *Dracochela deprehendor* (Shear et al. 1989; Schawaller et al. 1991). Only protonymphs and tritonymphs are known, which were referred to the superfamily Chthonioidea (Harvey 1992).

### Solifugae Sundevall, 1833

Solifugae (= Solpugida) are medium-sized (7 mm to 70 mm), swift-running, predatory arachnids. Approximately 900 living species are known from all arid and semi-arid regions of the world except Australia. They have a tracheal system rivaling that of insects, allowing them to be among the most active of the arachnids. With their large, chelate chelicerae, they have probably the largest jaws relative to body size of any animal, and large forms can overpower vertebrate prey.

The placement of Solifugae and Pseudoscorpiones as sister taxa was discussed above, though Grasshoff (1978) placed Solifugae as the sister group to all other arachnids + eurypterids + xiphosurans. This interpretation was based partly on the interpretation of their divided carapace as a plesiomorphic character, though this could also be seen as a secondary adaptation associated with small size and/or prosomal mobility.

Solifuges are characterized by a divided carapace, huge chelicerae, loss of lateral eyes, a constriction between the prosoma and opisthosoma, and an extremely hairy body and legs. They respire using an extensive tracheal system opening through spiracles on the midline of the abdomen and also in the prosoma. Solifuge pedipalps are stouter than the walking legs and have a tactile function. Autapomorphies proposed for the Solpugida include their complex respiratory organs and prosomal stigmata,

the presence of malleoli (racquet organs) on the underside of the posterior legs, loss of the endosternite, and a monocondylar femur-patella joint.

The Carboniferous solifuge *Protosolpuga carbonaria* Petrunkevitch, 1913, is in a poor state of preservation, but its morphology places it in the Solifugae rather than any other arachnid order (Selden and Shear 1996). Only two other fossil solifuges are known, both described recently: *Happlodontus proterus* Poinar and Santiago-Blay, 1989, from Oligocene Dominican amber, and *Cratosolpuga wunderlichi* Selden, 1996, from the Cretaceous of Brazil.

### Palpigradi Latreille, 1810

Palpigradi are tiny (up to 3 mm body length) arachnids found mostly in soil and interstitial environments (Monniot 1966). Approximately 125 living species are known. Palpigrades have a thin, colorless cuticle. They are blind, have no respiratory organs or Malpighian tubules, and have a divided carapace, a narrow prosoma-opisthosoma junction, and an opisthosoma ending in a long, jointed flagellum. Autapomorphies proposed for Palpigradi are: simple coxosternal region with a terminal mouth, paired anteromedial sensory organ and trochanterofemoral joint formed by a dorsal hinge in the walking legs.

Another name for Palpigradi is Microthelyphonida, which suggests a relationship with Thelyphonida (Uropygi and Schizomida), which they superficially resemble. However, palpigrades have three-segmented chelicerae, and their pedipalps are not chelate. Some authors have regarded palpigrades as primitive arachnids that approximate the hypothetical "archaearachnid" (Savory 1971), but many of their characters (e.g., divided carapace and separate sternites) may be a consequence of miniaturization rather than of the retention of plesiomorphic characters and should be treated with caution in phylogenetic analysis. Even so, most studies (Weygoldt and Paulus 1979; Shultz 1990) have classified palpigrades as relatively primitive arachnids.

The preservation potential of palpigrades is low; their small size, thin cuticle, and interstitial habitats make them difficult objects of study. *Sternarthron zitteli* Haase, 1890, from the Jurassic lithographic limestone of Solnhofen, Germany, was synonymized with the heteropteran insect *Propygodlampis* by Carpenter (1992), following Handlirsch (1906). Thus, the only good fossil palpigrade is *Palaeokoenenia mordax* Rowland and Sissom, 1980, from the "Onyx Marble" quarries (Pliocene) of Arizona.

### Trigonotarbida Petrunkevitch, 1949

Trigonotarbids are medium-sized (1 mm to 50 mm), extinct, spiderlike arachnids characterized by opisthosomal tergites divided into median and lateral plates. They respired with two pairs of book lungs opening on opisthosomal segments 2 and 3. Autapomorphies proposed for the Trigonotarbida are: loss of sternite 1, divided ter-

gites, and a locking mechanism between the prosoma and opisthosoma (a similar mechanism is found in Ricinulei, but may be convergent). Studies of well-preserved specimens of their chelicerae suggest they were active predators and probably ran down or ambushed prey. Some later forms had spinous legs for prey capture. Early trigonotarbids tended to be small, with stout legs. Later forms were often larger, spinous, and heavily tuberculated on their dorsal surface. Trigonotarbids represent probably the most diverse Paleozoic arachnids, second only to scorpions, and show a range of body forms reflected in their division into some ten families.

The first trigonotarbids to be described were referred to Pseudoscorpiones; later the group was allied to Opiliones. The order Anthracomarti was erected by Karsch (1882), and the order Trigonotarbi was carved from it by Petrunkevitch (1949). In the latter paper, Petrunkevitch recognized a fundamental division between Haptopoda (see below) and Anthracomarti (= subclass Stethostomata Petrunkevitch, 1949), defined by the fixed state of their characters, and Trigonotarbi (= subclass Soluta Petrunkevitch, 1949), defined on a combination of characters in a labile state. It has been pointed out by Shear et al. (1987) and Selden (1993b) that many of the differences between Soluta and Stethostomata suggested by Petrunkevitch (1949) are due to poor preservation and/or interpretation of the fossils, and the others compare to familial, or at most subordinal, differences in other arachnid groups. On this basis, Dunlop (1996) reunited Anthracomartida with the better defined Trigonotarbida under the latter name. Thus trigonotarbids show a division of opisthosomal tergites into three or more plates; anthracomartids are trigonotarbids with opisthosomal tergites divided into five plates. Following the discovery of two pairs of book lungs in some exceptionally preserved trigonotarbid material, their placement within the Tetrapulmonata Shultz, 1990 (see below), became apparent. Shear et al. (1987) classified Trigonotarbida as the sister group to all other tetrapulmonates.

Approximately fifty trigonotarbid species are known, from Silurian (Přídolí) to Permian (Asselian) strata of Euramerica (one fossil is known from Gondwana). Trigonotarbids are the commonest Paleozoic arachnids and one of the best known groups. They are among the first known land animals (Jeram et al. 1990). First described from Upper Carboniferous rocks (e.g., Buckland 1837; Fritsch 1901; Pocock 1902, 1911), Hirst (1923) described the first Devonian specimens, from the Rhynie Chert of Scotland, and Størmer (1970) described forms from the Middle Devonian of Alken an der Mosel, Germany. Trigonotarbids are one of the few arachnid groups found relatively frequently in Paleozoic terrestrial rocks; forms have been described recently from Argentina (Pinto and Hünicken 1980), Spain (Selden and Romano 1983), the Czech Republic (Oplustil 1985), and Germany (Jux 1982).

### Araneae Clerck, 1757

Araneae (spiders) are the most familiar of all arachnids and have generated the most research. Spiders are a very diverse group, with approximately 35 000 living species described. They range from 1 mm to 90 mm in length (250 mm leg span) and have

been found in many different habitats, from high latitudes and altitudes to tropical forests and deserts; some species live much of their lives submerged in marine or fresh water. The use of silk for prey capture in many taxa has doubtless contributed to the spiders' success. Foelix (1982) provided an excellent review of the biology of spiders. With the exception of the Mesothelae, Recent spiders are characterized by a lack of opisthosomal segmentation. All spiders show a narrow pedicel between the prosoma and opisthosoma, and their appendages are less modified than in other arachnid taxa (with the exception of the pedipalp of the adult male, which is greatly modified for sperm transfer). The plesiomorphic respiratory organs in spiders are a pair of book lungs on opisthosomal segments 2 and 3 in mesotheles, mygalomorphs, and one araneomorph family. Most araneomorphs have modified the second pair of lungs into tracheal systems, and some have replaced both lungs with tracheae. Autapomorphies proposed for the Araneae are opisthosomal silk-producing spinnerets, a naked cheliceral fang, cheliceral venom glands, a copulatory device on the male pedipalp, and the absence of the trochanterofemoral depressor muscle in the walking legs. Recent spider systematics were reviewed by Coddington and Levi (1991). Araneae is divided into two suborders: Mesothelae and Opisthothelae, the latter further subdivided into infraorders Mygalomorphae and Araneomorphae. Mesotheles show the greatest number of plesiomorphic character states, araneomorphs the most derived.

Approximately 600 fossil spider species have been described. The oldest spider is *Attercopus fimbriunguis* Shear, Selden, and Rolfe, 1987, from the Devonian of Gilboa, New York; supposed Devonian spiders from Rhyndie (Hirst 1923) and Alken an der Mosel (Størmer 1976) have been disproved (Selden et al. 1991). *Attercopus* is sister to all other spiders; the patella-tibia joint is a rocking joint but in a more plesiomorphic state than in other spiders, lacking the "compression zone Y" of Manton (1977). Autapomorphies of *Attercopus* are: fimbriate paired claws, spinules on the palpal femur, and lack of trichobothria; the latter feature is puzzling. Many Carboniferous spiders were originally referred to the Mesothelae on account of their segmented opisthosomas, but since this is a plesiomorphic character, and autapomorphies of mesotheles are absent in the fossils, this conclusion is unwarranted. However, a true fossil mesothele was described recently (Selden 1996), the first and oldest of this suborder. The oldest recorded mygalomorph is Triassic in age (Selden and Gall 1992). Reported Paleozoic araneomorphs (e.g., Pocock 1911; Størmer 1976) are actually misidentified other arachnids or other arthropods (Selden et al. 1991). The oldest described araneomorph is Jurassic in age (Eskov 1984). Recent finds of Cretaceous araneomorphs have emphasized the diversity of a spider fauna of modern aspect during this period. Some show too little morphological detail to be of value (Jell and Duncan 1986), but Selden (1990b) described some specimens from the Lower Cretaceous of northeast Spain, beautifully preserved in lithographic limestone. The specimens included a deinopoid and a tetragnathid, demonstrating that both cribellate and ecribellate orb weavers were in existence at this time. In broad

terms, by the Tertiary, the spider fauna was almost identical to that of today, and only three families are known to have become extinct since the Paleogene (Eskov 1990).

### Amblypygi Thorell, 1883

Amblypygi are medium-sized (15 mm to 45 mm) arachnids with flattened bodies and elongate legs that move in the horizontal plane and thus enable them to live in narrow crevices under bark, stones, and leaf litter. Approximately eighty extant species of Amblypygi live in the tropical regions of the world. They detect prey with the antenniform leg 1 and grab it with huge, spiny pedipalps. Few autapomorphies exist for Amblypygi (Shultz 1990); these are: a pretarsal depressor muscle without a patella head, vestigial labrum, large anterior coxal apodemes on all legs, divided tibiae, and an immovable patello-tibia joint. Amblypygi respire with book lung pairs on the second and third opisthosomal segments.

Amblypygids have long been recognized as close relatives of Uropygi, with which they were originally placed in the order Pedipalpi. Subsequently, they have been interpreted as the sister group of spiders (e.g., Weygoldt and Paulus 1979; van der Hammen 1989) on the synapomorphies of a pedicel and a sucking stomach. Shultz (1990) and Selden et al. (1991) placed Amblypygi as sister group to Uropygi + Schizomida principally on the synapomorphies of an antenniform leg pair 1 and subchelate pedipalps (see these authors for further synapomorphies).

Four fossil amblypygid species have been described from the Upper Carboniferous (Westphalian) of Europe and North America, with a gross morphology similar to modern forms (Dunlop 1994). Fossils are also known from the Cretaceous of Brazil (unpublished) and Tertiary ambers (e.g., Schawaller 1979). Amblypygi may be present in the Devonian of Gilboa; a possible pedipalp tarsus was figured by Shear et al. (1984) and *Ecchosis pulchribothrium* Selden and Shear, 1991, may belong in this group (Selden et al. 1991).

### Uropygi Thorell, 1882

Eighty-five living species of Uropygi (whip scorpions, vinegaroons) occur in tropical and subtropical zones, with the exception of Europe and Australia. They are closely related to schizomids. Uropygids are 15 mm to 80 mm in body length and are characterized by a pentagonal carapace, stout, chelate pedipalps, and slender legs with segmented tarsi. Leg 1 is antenniform. They respire using book lung pairs on opisthosomal segments 2 and 3. Autapomorphies proposed for the Uropygi by Weygoldt and Paulus (1979) are: a camerostome (fused palpal coxae), development involving a prenymp and four nymphal instars, and the male grabbing the female's opisthosoma during mating. However, these authors proposed these characters for what is essentially Uropygi + Schizomida. Shultz (1990) proposed pygidial



ommatoids, two pairs of small accessory lateral eyes, and internal musculature for the movable finger of the pedipalp as autapomorphies of Uropygi alone. Uropygids typically live in burrows and hunt using their sub-chelate pedipalps. The name whip scorpion comes partly from their habit of raising the opisthosoma in a defensive display called aggressive posturing by which they mimic a scorpion. The name vinegarron comes from their other defensive mechanism, spraying acetic acid from a pair of pygidial glands. Uropygi, with Amblypygi and Schizomida, have been united in Pedipalpi by some authors. The similarities and differences between Uropygi and Schizomida are discussed below.

Six well-preserved fossil species of Uropygi are known from Carboniferous (Namurian–Westphalian) rocks of Europe (e.g., Brauckmann and Koch 1983) and North America. All are placed in the modern family Thelyphonidae. Fossil uropygids are very similar in morphology to Recent forms.

### Schizomida Petrunkevitch, 1945a

Schizomids are small (2 mm to 15 mm) arachnids resembling the larger whip scorpions, but they have only a short flagellum, a single pair of book lungs, and a divided carapace. Schizomids lack eyes and have an antenniform leg 1 and semi-raptorial pedipalps. Approximately eighty species live in the temperate and tropical regions of Asia, Africa, and the Americas. They are predators in leaf litter or soil environments. Autapomorphies proposed for the Schizomida are a specialized pygidial flagellum in the male and an enlarged leg 4 femur.

Schizomida are included in Uropygi by some authors; for example, Shultz (1990) divided Uropygi into Thelyphonida and Schizomida. There is little doubt that schizomids represent miniaturized Uropygi.

Three species of schizomids have been described from the Pliocene "Onyx Marble" quarries of Arizona (Petrunkevitch 1945b) and one from the Oligocene of China (Lin et al. 1988). Undescribed specimens are known from the Oligocene Dominican amber.

### Haptopoda Pocock, 1911

This monotypic order was established on the basis of the subdivided tarsus of the first leg. Petrunkevitch (1949) cleaned and reexamined the specimens and redefined the order based on a new interpretation of the abdominal segmentation. Only nine specimens of the 12 mm long single species, *Plesiosiro madeleyi* Pocock, 1911, are known, all from a single British Upper Carboniferous (Westphalian B) locality. Haptopoda have an opisthosoma with a segment pattern similar to that of the Uropygi and a carapace with what may be a pair of median eyes and two lateral eye tubercles. The anterior legs are slightly spinous, and all legs have subdivided tarsi. The pedipalps are pediform, and the animal has a broad prosoma-opisthosoma junction.

Cheliceral morphology and respiratory organs are not clearly preserved, making referral to any higher taxon difficult. No distinct autapomorphies have been proposed for the Haptopoda. Some features are reminiscent of Uropygi, and an alternative possibility is that this is an unusual form of opilionid (Shear and Kukalová-Peck 1990). Since it shows the autapomorphies of neither group, its status as a distinct order appears deserved.

### Phalangiotarbida Haase, 1890

Phalangiotarbida (= Architarbida) is an extinct group known only from a few Upper Carboniferous (Westphalian) Euramerican localities (Petrunkevitch 1953, 1955), but where they do occur they can be locally abundant. Phalangiotarbrids have 10 mm to 20 mm long, flattened, oval bodies with stout walking legs, small pediform palps, and tiny chelicerae, possibly hidden in a pre-oral chamber above the coxae of leg 1. The sternum is divided, and the opisthosomal segmentation pattern with abbreviated anterior tergites and longitudinally divided sternites is unique among arachnids. Specific autapomorphies have not been proposed for the Phalangiotarbida, but they could include: abbreviated anterior tergites, a median eye tubercle bearing six eye lenses, and extreme reduction of the pedipalps and chelicerae. Twenty-six species are recorded. Their mode of life is unclear, but they have been interpreted as ambush predators on account of the orientation of their stout legs. It has been suggested that their morphology mimicked lycopod leaves (Beall 1984). The Phalangiotarbida were renamed Architarbi by Petrunkevitch (1945a), but this change was not justified (Selden 1993b).

Phalangiotarbrids have at times been likened to Opiliones (Pocock 1911), Haptopoda (Petrunkevitch 1913), Ricinulei, and anactinotrichid mites (van der Hammen 1979). Shultz (1990) tentatively suggested that they belonged in his taxon *Micrura*, comprising arachnids with a pygidium. An unpublished manuscript by Kjellesvig-Waering figured a supposed clasp-knife chelicera on one specimen. If this observation is correct, then these animals could belong in Tetrapulmonata. The lack of convincing synapomorphies with other arachnids makes placing phalangiotarbrids difficult, and restudy of this material to try to identify new characters would be helpful.

### Ricinulei Thorell, 1876

Ricinuleids are blind, slow-moving, predatory arachnids with a body length of 10 mm to 20 mm. Twenty-five living species in three genera are known from leaf litter and caves in tropical regions of West Africa and the Americas. The mouthparts are two-segmented, sub-chelate chelicerae, which are hidden beneath a movable hood (cucullus) that is hinged onto the anterior margin of the carapace. Ricinuleids have a thick cuticle, anteriorly located gonopore, pedipalps with a small terminal chela,

and a double trochanter on legs 3 and 4. Respiration is through tracheae, the spiracles opening at the rear of the prosoma. Autapomorphies proposed for the Ricinulei are the cucullus, a male copulatory organ on leg 3, an endosternite with one segmental component, divided tergites, and a coupling device between the prosoma and opisthosoma. The latter two characters have analogues in the Trigonotarbida.

Selden (1992) split the Ricinulei into the extant Neoricinulei (vestigial eyes; coxa 2 larger than coxae 3 or 4) and fossil Palaeoricinulei (eyed; coxa 2 smaller than coxae 3 or 4). Palaeoricinulei are further subdivided into Poliocheridae, with opisthosomal tergites similar to Neoricinulei, and Curculioididae, without opisthosomal tergites, but instead a single median dorsal dividing line or sulcus. Most recent authors have placed ricinuleids as the sister group to the Acari on account of similar mouthparts, comprising a "gnathosoma," and a hexapodous larva.

The first fossil ricinuleid was illustrated by Buckland in 1837, one year before the first extant species was described (Guerin-Méneville 1838). Fourteen fossil species of fossil Ricinulei are now known from the Upper Carboniferous (Namurian-Westphalian) of Europe and North America. A revision of the fossils (Selden 1992) revealed a greater diversity in the Carboniferous than today, but based on an essentially similar bodyplan. None is yet known from any other geological period. It appears that the group has remained in warm, humid habitats (equatorial forest litter and caves) throughout its geological history.

### Acari Sundevall, 1833

The Acari (mites, ticks) may be the most diverse of living chelicerate orders, although more spiders have been named. Thirty thousand species have been described worldwide, but this may represent only a small proportion of their total diversity. Acari are small (80  $\mu$ m to 30 mm), primarily terrestrial arachnids that occupy a wide range of niches and include predators, parasites (of plants and animals), and detritivores. Acari are characterized by poorly defined body segmentation and a broad prosoma-opisthosoma junction. They respire with tracheae that can open on any body segment. Acari have an ovipositor and a hexapodous larva (see Lindquist [1984] for additional characters). The only autapomorphy proposed for Acari is the presence of a gnathosoma, a modified region of the prosoma bearing the chelicerae and pedipalps (Weygoldt and Paulus 1979). This character was considered synapomorphic for Acari + Ricinulei by Shultz (1990). The mouthparts of Acari are variable within the group, which reflects their diverse feeding habits.

There has been debate about whether or not the Acari are monophyletic (Lindquist 1984) or polyphyletic (van der Hammen 1989). Most authors agree that Anactinotrichida (Opilioacarida + Parasitiformes) and Actinotrichida form two fundamental branches of the Acari, but in a series of papers on the subject van der Hammen developed the idea of a separate origin of these groups (summarized in van der Hammen 1972). He argued from comparative morphology that Anactino-

trichida were more closely allied to Ricinulei than to other mites (van der Hammen 1979) and that Actinotrichida were closer to Palpigradi (van der Hammen 1982). The cladistic analyses of Lindquist (1984) and Shultz (1990) concluded that Acari is monophyletic and that Ricinulei is the sister group.

The oldest mites are Actinedida (Prostigmata) from the Lower Devonian (Pragian) Rhynie Chert of Scotland (Hirst 1923). Other Devonian Actinotrichida are known from Gilboa, New York (Norton et al. 1988; Kethley et al. 1989). A few Jurassic and Cretaceous Actinotrichida are known (e.g., Bulanova-Zachvatina 1974; Krivolutsky and Ryabinin 1976; Sivhed and Wallwork 1978), but the majority of fossil mites are oribatids from Baltic amber (e.g., Koch and Berendt 1854; Sellnick 1918, 1931). Anactinotrichida are very poorly represented in the fossil record; there are no fossil Opilioacarida or Holothyrida and only a few records of Ixodida (Scudder 1890, somewhat suspect) and Gamasida (Hirschmann 1971; Blaszak et al. 1995).

## CHELICERATE FOSSILS AND PHYLOGENIES

There have been many attempts to elucidate the evolutionary relationships within the Chelicerata. Some authors included fossil and Recent chelicerates in the same scheme, for example, Størmer (1944), Petrunkevitch (1949), Bristowe (1971), Savory (1971), Manton (1977), Grasshoff (1978), Beall and Labandeira (1990), and Starobogatov (1990). Others, for example, Firstman (1973), Yoshikura (1975), and van der Hammen (1989), excluded fossils from their analyses. The first attempt at a cladistic analysis of Chelicerata was made by Weygoldt and Paulus (1979). Recent studies of exceptionally well preserved Paleozoic chelicerates (Selden 1981; Shear et al. 1987; Jeram et al. 1990; Selden et al. 1991) have provided much greater detail of the morphology of these forms, such as Eurypterida, Scorpiones, and Trigonotarbida, and consequently they can be included in cladistic analyses with greater confidence (Shultz 1989, 1990; Selden 1990a, 1993b).

Figure 7.2 shows cladograms derived from the analyses of Shultz (1989, 1990), Weygoldt and Paulus (1979), and van der Hammen (1989). Details of the character states can be found in these papers. One point of disagreement between the cladograms lies in the placement of Opiliones. Weygoldt and Paulus's (1979) analysis (fig. 7.2c) placed Opiliones in a derived position as sister group to Ricinulei + Acari, while in the analyses of van der Hammen (1989) and Shultz (1990) Opiliones occupies a basal position and is sister group to Scorpiones + other groups. Whereas earlier authors (e.g., Savory 1971) considered Palpigradi to be primitive arachnids, it is interesting that all of the studies depicted in figure 7.2 show Palpigradi not to be primitive, though there is no agreement concerning their relationship to any other arachnid group. There is agreement concerning the close relationship of the following: Ricinulei + all or some Acari; Tetrapulmonata (Araneae, Amblypygi, Uropygi,

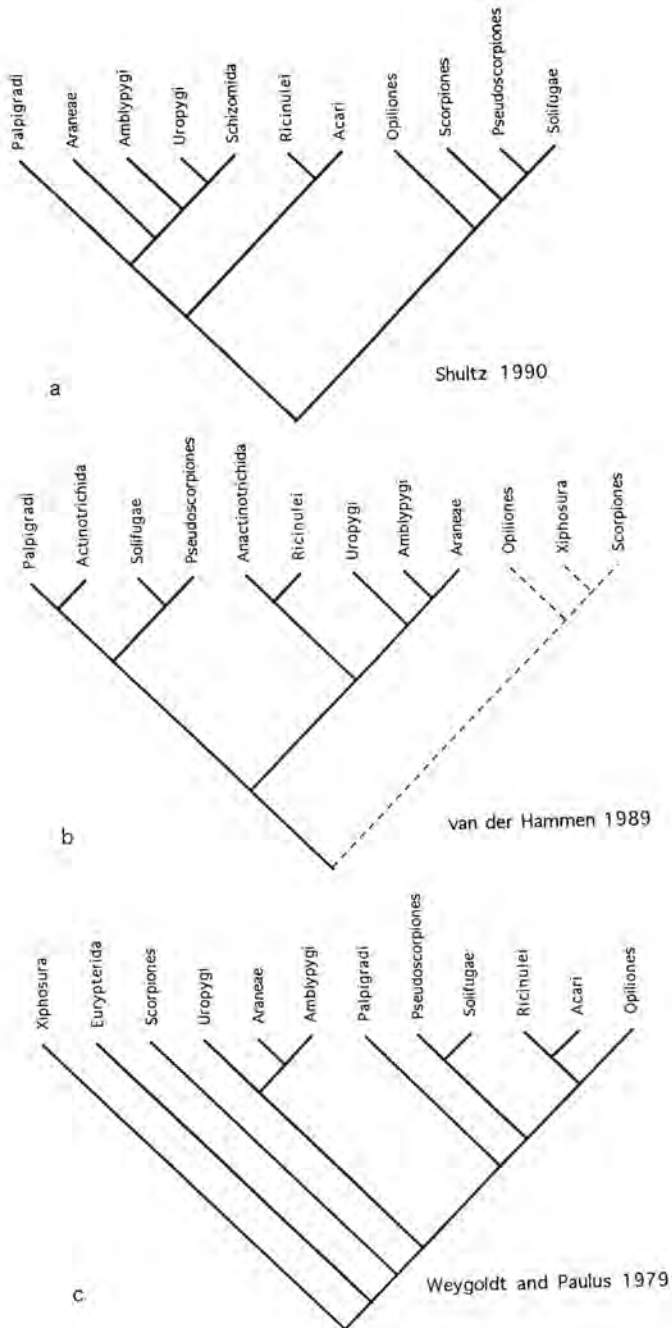


FIGURE 7.2

Cladograms of relationships among the arachnid groups as viewed by (a) Shultz (1990); (b) van der Hammen (1989); and (c) Weygoldt and Paulus (1979). Interrupted lines indicate uncertainty.



Schizomida); Solifugae + Pseudoscorpiones. How do these analyses correspond to the fossil record of Chelicerata?

Figure 7.3 shows an evolutionary tree produced by combining the fossil record of Chelicerata with a cladogram. The fossil record is the most up-to-date possible and uses both published and unpublished data. The cladogram combines the analyses of Wills et al. (1995) for major chelicerate groups and Shultz (1990) for arachnids. Fine vertical lines show range extensions of named taxa and ghost lineages (see Smith 1994 for explanation) that are predicted by the cladogram. The longest range extensions are predicted for Palpigradi, Anactinotrichida, and Schizomida (this is predicted by every analysis shown in fig. 7.2). This is not surprising since all of these animals are tiny, lightly sclerotized, and generally occur in habitats that are poorly represented in the fossil record. Thus, they not only have low fossilization potential but are also easily overlooked. Other predictions of this evolutionary tree are considered in detail below.

### Scorpions, Pseudoscorpions, and Solifuges

There are four opinions concerning the position of scorpions within the Chelicerata: Arachnida is monophyletic and scorpions are true arachnids (e.g., Shultz 1990); Scorpiones is the sister group to all other arachnids (e.g., Weygoldt and Paulus 1979); Scorpiones is the sister group to Eurypterida (e.g., Grasshoff 1978; Kjellesvig-Waering 1986); Scorpiones is the sister group to Xiphosura (van der Hammen 1989). Van der Hammen's scheme appears the most unusual; his analysis was not cladistic in its approach, and these relationships were considered tentative by its author. In its favor, however, is the finding of Anderson (1973) that scorpion embryology differs from that of other arachnids and is closer to that of Xiphosura and that while other arachnids could be derived from a xiphosuran-like embryology, they could not be derived from the scorpion pattern. In Shultz's (1989, 1990) scheme (fig. 7.2a), scorpions are sister to pseudoscorpions + solifuges, and Opiliones is the sister group to (Scorpiones (Pseudoscorpionida + Solifugae)). Shultz (1990) proposed the names Novogenuata for (Scorpiones (Pseudoscorpionida + Solifugae)), and Dromopoda for (Opiliones (Scorpiones (Pseudoscorpionida + Solifugae))). Dromopoda has the following synapomorphies: extensor muscles and specialized joints at femoropatellar and patellotibial joints, distinct transverse furrows on carapace (representing primitive tergite boundaries), reduced intercoxal sternal region, prosomal endosternite with two components, undivided leg 3 and 4 femora, pretarsal depressor muscle with a patellar head, and stomotheca (pre-oral chamber formed by pedipalp and anterior walking leg endites). A number of these characters are further modified in Solifugae. Weygoldt and Paulus (1979) proposed eye rhabdome morphology, sperm morphology, the presence of lyriform organs, and tactile leg 1 as synapomorphies of the non-scorpion arachnids. Kjellesvig-Waering (1986) argued for a common scorpion-eurypterid ancestor on the basis of similar morphology, e.g., abdominal plates, multifaceted lateral eyes (in early scorpions) and three-segmented

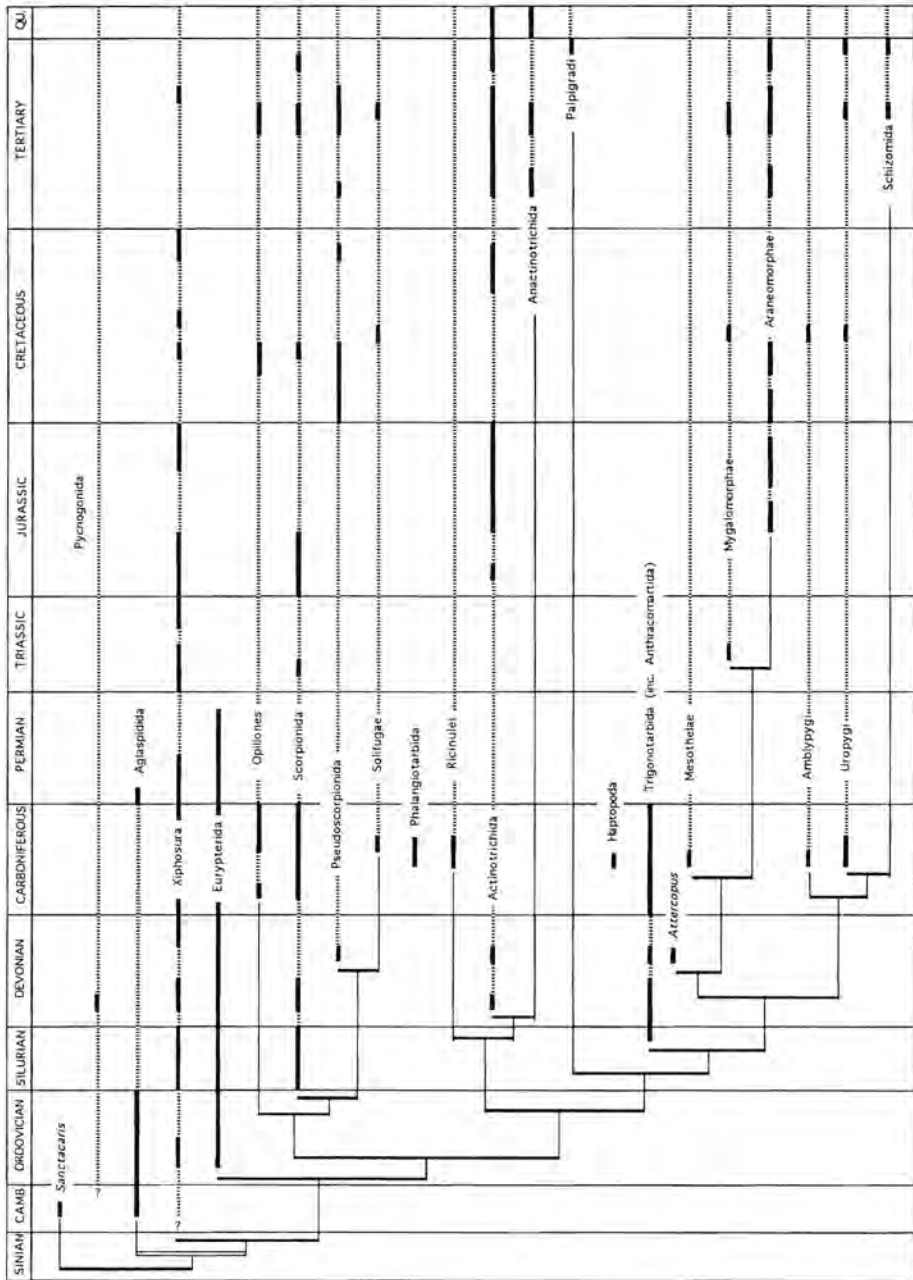


FIGURE 7.3

Evolutionary tree combining results of the most recent cladistic analyses of Chelicerata (Shultz 1990; Wills et al. 1995) with current knowledge of the fossil record of Chelicerata and relatives. Thick vertical lines denote actual occurrence in the stratigraphic stage(s) concerned; interrupted lines indicate presumed occurrence in intervening stages. ? denotes doubtful record. Open horizontal lines show relationships derived from cladistic analyses; thin vertical lines denote range extensions and ghost lineages predicted from the analyses. Note that taxon ranks are not equivalent; stratigraphic axis not to scale.

chelate chelicerae, which are plesiomorphic character states. Grasshoff (1978) placed scorpions and eurypterids together on account of their overall body shape, which he interpreted as an adaptation for swimming.

The light the fossil record sheds on this problem is that scorpions are the oldest arachnid group; the earliest specimens known are from Lower Silurian strata. The early scorpions were aquatic (see above), but since they clearly show scorpion apomorphies, they must have emerged onto land separately from other arachnid groups (see Selden and Jeram [1989] for a discussion). Thus, terrestrial arachnid characters, such as book lungs and trichobothria, are convergent adaptations to life on land.

## Opiliones

In Shultz's (1989, 1990) phylogenetic scheme, Opiliones are the sister group to his Novogenuata (see above), so their fossils should occur in strata at least as old as Lower Silurian. Since scorpions were aquatic at that time, presumably opilionids would have been, too. In van der Hammen's (1989) phylogeny, Opiliones came out as the sister group to Xiphosura + Scorpiones; since the oldest xiphosuran is Lower Ordovician or older, Opiliones would have been around in aquatic environments in the Lower Ordovician in this scheme. In Weygoldt and Paulus's (1979) scheme, Opiliones occupy a rather derived position.

The prediction of Silurian aquatic Opiliones was discussed by Selden (1990a). Shultz (1994), in a critique of the use of stratigraphic evidence to assess phylogenetic hypotheses, pointed out that the earliest members of the Opiliones clade, after it had diverged from Novogenuata, may not have had all of the apomorphies of the clade as now recognized. This is a common problem with fossils, since apomorphies are collected during evolution of the stem group, and the full complement might occur only in the crown group. Whether the name Opiliones is used for the total group (stem group + crown group) or the crown group alone is debatable. However, at the divergence of two clades, there must be at least one defining apomorphy for the two clades to be recognized; Shultz's (1994) contention that "the earliest members of two sister lineages may be indistinguishable from one another and from their immediate ancestors in morphology, behavior, genetics, etc." is unsustainable.

## Tetrapulmonata

This clade, comprising the orders Trigonotarbida, Araneae, Amblypygi, Uropygi, and Schizomida, is probably the best supported and least contentious area of arachnid phylogeny. As its name suggests, it is diagnosed by two pairs of book lungs that are situated on opisthosomal segments 2 and 3 (subsequently modified in some groups, e.g., many spiders and all schizomids have only one pair of lungs and some spiders have tracheae only). Tetrapulmonata is strongly supported by a range of other synapomorphies, including two-segmented, clasp-knife-like chelicerae, *plagula ventralis*, a sucking stomach, constriction of segment 7 (pedicel), 9 + 2 ax-

oneme arrangement in the spermatozoa, and prosomal endosternite with four segmental components.

Almost all phylogenetic studies (Firstman 1973; Grasshoff 1978; Weygoldt and Paulus 1979; van der Hammen 1989; Shultz 1990) have placed spiders, Amblypygi, Uropygi, and Schizomida together, and a number of names have been proposed for this taxon (see Shear et al. 1987), of which Tetrapulmonata Shultz, 1990, is the most appropriate and best defined. These studies differed only in whether Amblypygi was placed closer to Araneae (Firstman 1973; Grasshoff 1978; Weygoldt and Paulus 1979; van der Hammen 1989) or to Uropygi + Schizomida (Shultz 1990). Two pairs of book lungs were identified in the Rhynie Chert trigonotarbid arachnids (Claridge and Lyon 1961). Shear et al. (1987) and Selden et al. (1991) included Trigonotarbida in Tetrapulmonata. These authors' analyses supported placing Amblypygi as the sister group of Uropygi + Schizomida and placed Trigonotarbida as the sister taxon to all other tetrapulmonates.

Trigonotarbids are among the oldest terrestrial animals (Jeram et al. 1990), and the evolutionary tree (fig. 7.3) predicts that other tetrapulmonates should be found alongside trigonotarbids in early terrestrial ecosystems. The oldest spider is *Attercopus* from the Devonian of New York (Shear et al. 1987; Selden et al. 1991), and it is sister to other spiders that arose in the Devonian or earlier. The first mesothele occurs in the Late Carboniferous (Selden 1996), which predicts that opisthotheles (Mygalomorphae + Araneomorphae) should have originated by then. The long gap in the fossil record between the Late Carboniferous and the Triassic (first mygalomorph) and Jurassic (first described araneomorph) occurrences of fossil spiders is due largely to the poor preservation generally of fossils in Permian strata in parts of the world where specimens are regularly collected.

#### ACKNOWLEDGMENTS

We thank Lyall Anderson for information on Xiphosura, Simon Braddy for information on Eurypterida, and both for useful discussions. We thank Bill Shear for reading and commenting on the manuscript. We acknowledge support from the Natural Environment Research Council.

#### REFERENCES

- Anderson, D. T. 1973. *Embryology and Phylogeny in Annelids and Arthropods*. Oxford: Pergamon Press.
- Anderson, L. I. and P. A. Selden. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia* 30:19-31.
- Beall, B. S. 1984. Functional and ecological analyses of phalangiotarbid arachnids. *Geological Society of America, Abstracts with Programs* 15:440.
- Beall, B. S. 1986. Reinterpretation of the Kustarachnida. *American Arachnology* 34:4.

- Beall, B. S. and C. C. Labandeira. 1990. Macroevolutionary patterns of the Chelicerata and Tracheata. In D. G. Mikulic, ed., *Short Courses in Paleontology*. Vol. 3, *Arthropod Palaeobiology*, pp. 257-284. Knoxville: Paleontological Society.
- Bergström, J. 1971. *Palaeomerus*: Merostome or merostomoid. *Lethaia* 4:393-401.
- Bergström, J. 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. In A. P. Gupta, ed., *Arthropod Phylogeny*, pp. 3-56. New York: Van Nostrand Reinhold.
- Bergström, J. 1980. Morphology and systematics of early arthropods. *Abhandlungen des naturwissenschaftlichen Vereins in Hamburg (NF)* 23:7-42.
- Bergström, J., W. Stürmer, and G. Winter. 1980. *Palaeoisopus*, *Palaeopantopus*, and *Palaeothea*: Pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. *Paläontologische Zeitschrift* 54:7-54.
- Blaszak, C., J. C. Cokendolpher, and V. J. Polyak. 1995. *Paleozercon cavernicolus*, n. gen., n. sp.: Fossil mite from a cave in the southwestern U.S.A. (Acari, Gamasida: Zerconidae), with a key to Nearctic genera of Zerconidae. *International Journal of Acarology* 21:253-259.
- Boudreaux, H. B. 1979. Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. In A. P. Gupta, ed., *Arthropod Phylogeny*, pp. 551-586. New York: Van Nostrand Reinhold.
- Brauckmann, C. and L. Koch. 1983. *Prothelyphonus naufragus* n. sp.: Ein neuer Geisselscorpion (Arachnida: Thelyphonida: Thelyphonidae) aus dem Namurium (unteres Oberkarbon) von West-Deutschland. *Entomologica Generalis* 9:63-73.
- Briggs, D. E. G., D. L. Bruton, and H. B. Whittington. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaeontology* 22:167-180.
- Briggs, D. E. G. and D. Collins. 1988. A Middle Cambrian chelicerate from Mount Stephen, British Columbia. *Palaeontology* 31:779-798.
- Bristowe, W. S. 1971. *The World of Spiders*. 2d Edition. London: Collins.
- Broili, F. 1928. Crustaceenfunde aus dem rheinischen Unterdevon. *Sitzungsberichte Bayerischen Akademie der Wissenschaften* 1928:197-201.
- Buckland, W. 1837. *The Bridgewater Treatises on the Power, Wisdom, and Goodness of God as Manifested in the Creation: Treatise IV., Geology and Mineralogy Considered with Reference to Natural Theology*. 2d Edition. London: William Pickering.
- Bulanova-Zachvatina, E. M. 1974. New genera of oribatid mites from the Upper Cretaceous of Taimyr. *Paleontologicheskii Zhurnal* 2:141-144.
- Burmeister, H. 1843. *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematischer Uebersicht aller zeither beschriebenen Arten*. Berlin: G. Riemeier.
- Campos, D. R. B. 1986. Primeiro registro fóssil de Scorpionoidea na Chapado do Araripe (Cretaceo Inferior), Brasil. *Anais da Academia Brasileira de Ciências* 58:135-137.
- Carpenter, F. M. 1992. Hexapoda. *Treatise on Invertebrate Paleontology, Part R, Arthropoda* 4. Vol. 3. Boulder, Lawrence: Geological Society of America, University of Kansas Press.
- Caster, K. E. and H. K. Brooks. 1956. New fossils from the Canadian-Chazyan (Ordovician) hiatus in Tennessee. *Bulletins of American Paleontology* 36:157-199.
- Caster, K. E. and E. N. K. Kjellesvig-Waering. 1964. Upper Ordovician eurypterids of Ohio. *Palaeontographica Americana* 4:301-358.
- Claridge, M. F. and A. G. Lyon. 1961. Lung-books in the Devonian Palaeocharinidae (Arachnida). *Nature* 191:1190-1191.



- Clarke J. M. and R. Ruedemann. 1912. The Eurypterida of New York. *New York State Museum Natural History Memoirs* 14:1–628.
- Clerck, C. 1757. *Svenska spindlar (Aranea Suecici) L. Salvii* (in Swedish and Latin). Stockholm.
- Coddington, J. A. and H. W. Levi. 1991. Systematics and evolution of spiders (Araneae). *Annual Reviews of Ecology and Systematics* 22:565–592.
- Dana, J. D. 1852. Crustacea. *United States Exploring Expedition, 1838–1842* 13:21.
- de Geer, C. 1778. *Mémoires pour servir à l'histoire des Insectes*. Vol. 7. Stockholm.
- Dunlop, J. A. 1994. An Upper Carboniferous amblypygid from the Writhlington Geological Nature Reserve. *Proceedings of the Geologists' Association* 105:245–250.
- Dunlop, J. A. 1996. Systematics of the fossil arachnids. *Revue Suisse de Zoologie* vol. hors série: 173–184.
- Dunlop, J. A. and P. A. Selden. 1997. The early history and phylogeny of the chelicerates. In R. A. Fortey and R. H. Thomas, eds., *Arthropod Relationships*, pp. 221–235. London: Chapman and Hall.
- Eskov, K. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984:645–653.
- Eskov, K. 1990. Spider Paleontology: Present trends and future expectations. *Acta Zoologica Fennica* 190:123–127.
- Firstman, B. 1973. The relationship of the chelicerate arterial system to the evolution of the endosternite. *Journal of Arachnology* 1:1–54.
- Flower, R. 1968. Merostomes from a Cotter horizon of the El Paso Group. *New Mexico State Bureau of Mines and Mineral Resources Memoir* 22:35–44.
- Foelix, R. F. 1982. *Biology of Spiders*. Cambridge, Mass.: Harvard University Press.
- Fritsch, A. 1901. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, 4:64. Prague.
- Gall, J.-C. 1971. Faunes et paysages du Grès à Voltzia du nord des Vosges: Essai paléocologique sur le Buntsandstein supérieur. *Mémoires du Service de la Carte Géologique d'Alsace et de Lorraine* 34:1–318.
- Grasshoff, M. 1978. A model of the evolution of the main chelicerate groups. *Symposia of the Zoological Society of London* 42:273–284.
- Guerin-Méneville, M. 1838. Note sur l'Acanthodon et sur le Cryptostemme, nouveaux genres d'Arachnides. *Revue Zoologique Société Cuvier* 1:10–12.
- Haase, E. 1890. Beiträge zur Kenntnis der fossilen Arachniden. *Zeitschrift der deutschen geologischen Gesellschaft* 42:629–657.
- Hammen, L. van der. 1972. A revised classification of the mites (Arachnidea, Acarida) with diagnoses, a key, and notes on phylogeny. *Zoologische Mededeelingen, Leiden* 47: 273–292.
- Hammen, L. van der. 1979. Comparative studies in Chelicerata, part 1: The Cryptognomae (Ricinulei, Architarbi, and Anactinotrichida). *Zoologische Verhandelingen, Leiden* 174:1–62.
- Hammen L. van der. 1982. Comparative studies in Chelicerata, part 2: Epimerata (Palpigradi and Actinotrichida). *Zoologische Verhandelingen, Leiden* 196:1–70.
- Hammen, L. van der. 1985. Functional morphology and affinities of extant Chelicerata in evolutionary perspective. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 76:137–146.

- Hammen, L. van der. 1986. Comparative studies in Chelicerata, part 4: Apatellata, Arachnida, Scorpionida, Xiphosura. *Zoologische Verhandelingen, Leiden* 226:1-52.
- Hammen, L. van der. 1989. *An Introduction to Comparative Arachnology*. The Hague: SPB Academic Publishing.
- Handlirsch, A. 1906. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Leipzig: Wilhelm Engelman.
- Harvey, M. S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). *Invertebrate Taxonomy* 6:1373-1435.
- Hedgpeth, J. W. 1955a. Pycnogonida. In R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part P, Arthropoda 2*, pp. P163-P170. Boulder, Lawrence: Geological Society of America, University of Kansas Press.
- Hedgpeth, J. W. 1955b. *Palaeoisopus*. In R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part P, Arthropoda 2*, pp. P171-P173. Boulder, Lawrence: Geological Society of America, University of Kansas Press.
- Heymons, R. 1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica* 33:1-244.
- Hirschmann, W. 1971. A fossil mite of the genus *Dendrolaelaps* (Acarina, Mesostigmata, Digamasellidae) found in amber from Chiapas, Mexico. In A. Petrunkevitch, ed., *Studies of Fossiliferous Amber Arthropods of Chiapas, Mexico*. University of California Publications, Entomology 63:69-70.
- Hirst, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire). *Annals and Magazine of Natural History* 9:455-474.
- Jell, P. A. and P. M. Duncan. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* 3:111-205.
- Jeram, A. J. 1990. Book-lungs in a Lower Carboniferous scorpion. *Nature* 342:360-361.
- Jeram, A. J. 1994. Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology* 37:513-550.
- Jeram, A. J., P. A. Selden, and D. Edwards. 1990. Land animals in the Silurian: Arachnids and myriapods from Shropshire, England. *Science* 250:658-661.
- Jux, U. 1982. *Somaspidion hammapheron* n. gen. n. sp.: Ein Arachnide aus dem Oberkarbon der subvaristischen Saumsenke NW Deutschlands. *Paläontologische Zeitschrift* 56:77-86.
- Karsch, F. 1882. Über einige neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden der Steinkohlenformation überhaupt. *Zeitschrift der deutschen geologischen Gesellschaft* 34:556-561.
- Kethley, J. B., R. A. Norton, P. M. Bonamo, and W. A. Shear. 1989. A terrestrial alicorhagiid mite (Acari: Acariformes) from the Devonian of New York. *Micropaleontology* 35:367-373.
- King, P. E. 1973. *Pycnogonids*. London: Hutchinson.
- Kjellesvig-Waering, E. N. 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica Americana* 55:1-299.
- Koch, C. L. and G. C. Berendt. 1854. *Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden, und Apteren der Vorwelt*. Berlin.
- Kraus, O. 1976. Zur phylogenetischen Stellung und Evolution der Chelicerata. *Entomologica Germanica* 3:1-12.
- Krivolutsky, D. A. and N. A. Ryabinin. 1976. Oribatid mites in Siberian and Far East amber. *Reports of the Academy of Science, USSR* 230:945-948.

- Latreille, P. A. 1802. *Histoire naturelle, générale, et particulière: Crustacés et des Insectes*. Vol. 3. Paris: Dufart.
- Latreille, P. A. 1810. *Considerations générales sur l'ordre naturel des animaux composant la classe des Crustacés, des Arachnides, et des Insectes*. Paris: Dufart.
- Laurie, M. 1889. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Transactions of the Royal Society of Edinburgh* 39:515-590.
- Lin, Q.-B., Y.-M. Yao, W.-D. Xiang, and Y.-R. Xia. 1988. An Oligocene micropalaeontofauna from Gubei District of Shandong and its ecological environment. *Acta Micropalaeontologica Sinica* 5:331-345.
- Lindquist, E. E. 1984. Current theories on the evolution of the major groups of Acari and on their relationships with other groups of Arachnida, with consequent implications for their classification. In D. A. Griffiths and C. E. Brown, eds., *Acarology*, 1:28-62. New York: John Wiley.
- Manton, S. M. 1977. *The Arthropoda: Habits, Functional Morphology, and Evolution*. Oxford: Clarendon.
- Moberg, J. C. 1892. Om en nyupptäckt fauna i block af kambrisk sandsten, insamlade af dr N. O. Holst. *Geologiska Föreningens i Stockholm Förhandlingar* 14:103-120.
- Monniot, F. 1966. Un palpigrafe interstitiel: *Leptokoenia scurra*, n. sp. *Revue d'Écologie et de Biologie du Sol* 3:41-64.
- Norton, R. A., P. M. Bonamo, J. D. Grierson, and W. A. Shear. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. *Journal of Paleontology* 62:259-269.
- Oplustil, S. 1985. New findings of Arachnida from the Bohemian Upper Carboniferous. *Věstník ústředního ústavu geologického* 60:35-42.
- Packard, A. S. 1886. On the Carboniferous xiphosurous fauna of North America. *Memoirs of the National Academy of Sciences* 3:143-157.
- Paulus, H. F. 1979. Eye structure and the monophyly of Arthropoda. In A. P. Gupta, ed., *Arthropod Phylogeny*, pp. 299-383. New York: Van Nostrand Reinhold.
- Petrunkévitch, A. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. *Transactions of the Connecticut Academy of Arts and Sciences* 18:1-137.
- Petrunkévitch, A. 1945a. Palaeozoic Arachnida of Illinois: An inquiry into their evolutionary trends. *Illinois State Museum, Scientific Papers* 3:1-72.
- Petrunkévitch, A. 1945b. *Calcitro fisheri*: A new fossil arachnid. *American Journal of Science* 243:320-329.
- Petrunkévitch, A. 1949. A study of Palaeozoic Arachnida. *Transactions of the Connecticut Academy of Arts and Sciences* 37:69-315.
- Petrunkévitch, A. 1953. Palaeozoic and Mesozoic Arachnida of Europe. *Memoirs of the Geological Society of America* 53:1-128.
- Petrunkévitch, A. 1955. Arachnida. In R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part P, Arthropoda* 2, pp. P42-P162. Boulder, Lawrence: Geological Society of America, University of Kansas Press.
- Pinto, I. D. and M. A. Hünicken. 1980. *Gondwanarachne*: A new genus of the Order Trigonotarbida (Arachnida) from Argentina. *Boletín de la Academia Nacional de Ciencias, Córdoba, Argentina* 53:307-315.
- Plotnick, R. E. 1983. Patterns in the evolution of the eurypterids. Ph.D. diss., University of Chicago.

- Poock, R. I. 1902. *Eophrynus* and allied Carboniferous Arachnida. Part 1. *Geological Magazine* 9:439–448.
- Poock, R. I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. *Monographs of the Palaeontographical Society* 64:1–84.
- Poinar, G. O. and J. A. Santiago-Blay. 1989. A fossil solpugid, *Happlodontus proterus*, new genus, new species (Arachnida: Solpugida) from Dominican amber. *Journal of the New York Entomological Society* 97:125–132.
- Polis, G. A., ed. 1990. *Biology of Scorpions*. Stanford: Stanford University Press.
- Raasch, G. O. 1939. Cambrian Merostomata. *Special Papers of the Geological Society of America* 19:1–146.
- Rolfe, W. D. I. and C. M. Beckett. 1984. Autecology of Silurian Xiphosurida, Scorpionida, and Phyllocarida. In M. G. Bassett and J. D. Lawson, eds., *Autecology of Silurian Organisms: Special Papers in Palaeontology* 32:27–37.
- Rowland J. M. and W. D. Sissom. 1980. Report on a fossil palpigrade from the Tertiary of Arizona, and a review of the morphology and systematics of the order (Arachnida: Palpigrida). *Journal of Arachnology* 8:69–86.
- Savory, T. H. 1971. *Evolution in the Arachnida*. Watford: Mellow.
- Schawaller, W. 1979. Erstnachweis der Ordnung Geisselspinnen in Dominicanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Amblypygi). *Stuttgarter Beiträge zur Naturkunde aus dem Staatlichen Museum für Naturkunde in Stuttgart*, series B, 50:1–12.
- Schawaller, W. 1982. Spinnen der Familien Tetragnathidae, Uloboridae, und Dipluridae in Dominicanischem Bernstein und allgemeine Gesichtspunkte (Arachnida, Araneae). *Stuttgarter Beiträge zur Naturkunde aus dem Staatlichen Museum für Naturkunde in Stuttgart*, series B, 89:1–19.
- Schawaller, W. 1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber. *Palaeontology* 34:971–976.
- Schawaller, W., W. A. Shear, and P. M. Bonamo. 1991. The first Palaeozoic pseudoscorpions (Arachnida, Pseudoscorpionida). *American Museum Novitates* 3009:1–17.
- Scudder, S. H. 1890. Illustrations of the Carboniferous Arachnida of North America. *Memoirs of the Boston Society of Natural History* 4:443–456.
- Selden, P. A. 1981. Functional morphology of the prosoma of *Baltoerypteris tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Transactions of the Royal Society of Edinburgh, Earth Sciences* 72:9–48.
- Selden, P. A. 1990a. Fossil history of the arachnids. *Newsletter of the British Arachnological Society* 58:4–6.
- Selden, P. A. 1990b. Lower Cretaceous spiders from the Sierra de Montsech, northeast Spain. *Palaeontology* 33:257–285.
- Selden, P. A. 1992. Revision of the fossil ricinuleids. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 83:595–634.
- Selden, P. A. 1993a. Arthropoda (Aglaspidida, Pycnogonida, and Chelicerata). In M. J. Benton, ed., *The Fossil Record* 2, pp. 297–320. London: Chapman & Hall.
- Selden, P. A. 1993b. Fossil arachnids: Recent advances and future prospects. *Memoirs of the Queensland Museum* 33:389–400.
- Selden, P. A. 1996. Fossil mesothele spiders. *Nature* 379:498–499.
- Selden, P. A. and J.-C. Gall. 1992. A Triassic mygalomorph spider from the northern Vosges, France. *Palaeontology* 35:211–235.

- Selden, P. A. and A. J. Jeram. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 80:303–310.
- Selden, P. A. and M. Romano. 1983. First Palaeozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock, (Stephanian; Prov. León, N.W. Spain), with remarks on aphantomartid taxonomy. *Boletín del Instituto de Geología e Mineralogía de España* 94:106–112.
- Selden, P. A. and W. A. Shear. 1992. A myriapod identity for the Devonian "scorpion" *Tiphoscorpio huerberi*. *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck, Supplement* 10:35–36.
- Selden, P. A. and W. A. Shear. 1996. First Mesozoic solpugid (Arachnida), from the Cretaceous of Brazil, and a redescription of the Palaeozoic solpugid. *Palaeontology* 39:583–604.
- Selden, P. A., W. A. Shear, and P. M. Bonamo. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaeontology* 34:241–281.
- Sellnick, M. 1918. Die Oribatiden der Bernsteinsammlung der Universität Königsberg. *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg* 59:21–42.
- Sellnick, M. 1931. Milben im Bernstein. *Bernsteinforschungen* 2:148–180.
- Shear, W. A., P. M. Bonamo, J. D. Grierson, W. D. I. Rolfe, E. L. Smith, and R. A. Norton. 1984. Early land animals in North America. *Science* 224:492–494.
- Shear, W. A. and J. Kukalová-Peck. 1990. The ecology of Palaeozoic terrestrial arthropods: The fossil evidence. *Canadian Journal of Zoology* 68:1807–1834.
- Shear, W. A., W. Schawaller, and P. M. Bonamo. 1989. Record of Palaeozoic pseudoscorpions. *Nature* 341:527–529.
- Shear, W. A. and P. A. Selden. 1995. *Eoarthropleura* (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 196:347–375.
- Shear, W. A., P. A. Selden, W. D. I. Rolfe, P. M. Bonamo, and J. D. Grierson. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbita). *American Museum Novitates* 2901:1–74.
- Shultz, J. W. 1989. Morphology and locomotor appendages in Arachnida: Evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* 108:335–365.
- Shultz, J. W. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6:1–38.
- Shultz, J. W. 1994. The limits of stratigraphic evidence in assessing phylogenetic hypotheses of Recent arachnids. *Journal of Arachnology* 22:169–172.
- Sivhed, U. and J. A. Wallwork. 1978. An Early Jurassic oribatid mite from southern Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 100:65–70.
- Smith, A. B. 1994. *Systematics and the Fossil Record*. Oxford: Blackwell Scientific Publications.
- Starobogatov, Y. I. 1990. The systematics and phylogeny of the lower chelicerates (a morphological analysis of the Paleozoic groups). *Paleontologicheskii Zhurnal* 1:4–17.
- Stockwell, S. A. 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). Ph.D. diss., University of California, Berkeley.
- Størmer, L. 1944. On the relationships and phylogeny of fossil and recent Arachnomorpha: A comparative study on Arachnida, Xiphosura, Eurypterida, Trilobita, and other fossil Arthropoda. *Skrifter Utgitt av Det Norske Videnskaps-Akademi i Oslo, I. Matematisk-Naturvidenskapelig Klasse* 5:1–158.



- Størmer, L. 1955. Merostomata. In R. C. Moore, ed., *Treatise on Invertebrate Paleontology, Part P, Arthropoda* 2, pp. P4–P41. Boulder, Lawrence: Geological Society of America, University of Kansas Press.
- Størmer, L. 1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany, part 1: Arachnida. *Senckenbergiana Lethaea* 51:335–69.
- Størmer, L. 1972. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany, part 2: Xiphosura. *Senckenbergiana Lethaea* 53:1–29.
- Størmer, L. 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany, part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. *Senckenbergiana Lethaea* 57:87–183.
- Sundevall, J. C. 1833. *Onceptus Arachnidum*. Londini, Gothorum.
- Thevenin, A. 1901. Sur le découverte d'arachnides dans le terrain houiller de Commentry. *Bulletin de la Société Géologique de France* 4:605–611.
- Thorell, T. H. 1876. Sopra alcuni Opilioni (Phalangidea) d'Europa e dell'Asia occidentale, con un quadro dei generi europei di quest'ordine. *Anali del Museo Civico di Storia Naturale di Genova*, series 1, 8:452–408.
- Tollerton, V. P. 1989. Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843. *Journal of Paleontology* 63:642–57.
- Weygoldt, P. 1969. *The Biology of Pseudoscorpions*. Cambridge, Mass.: Harvard University Press.
- Weygoldt, P. 1980. Towards a cladistic classification of the Chelicerata. *8th International Congress of Arachnology, Wien*, 1980:331–334.
- Weygoldt, P. and H. F. Paulus. 1979. Untersuchungen zur Morphologie, Taxonomie, und Phylogenie der Chelicerata. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 17:85–116.
- Whalley, P. E. S. 1980. Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. *Bulletin of the British Museum (Natural History), Geology* 33:157–164.
- Wills, L. J. 1947. A monograph of British Triassic scorpions. *Monograph of the Palaeontographical Society* 101:1–137.
- Wills, M. A., D. E. G. Briggs, R. A. Fortey, and M. Wilkinson. 1995. The significance of fossils in understanding arthropod evolution. *Verhandlungen der deutschen zoologischen Gesellschaft* 88:203–215.
- Wood, S. P., A. L. Panchen, and T. R. Smithson. 1985. A terrestrial fauna from the Scottish Lower Carboniferous. *Nature* 314:355–356.
- Woodward, H. 1865. A monograph of the British Fossil Crustacea. *Monograph of the Palaeontographical Society* 19:1–43.
- Yoshikura, M. 1975. Comparative embryology and phylogeny of Arachnida. *Kumamoto Journal of Science, Biology* 12:71–142.