

Selden, P.A. 1993 11 11: Fossil arachnids—recent advances and future prospects. *Memoirs of the Queensland Museum* 33(2): 389-400. Brisbane. ISSN 0079-8835.

Until 5 years ago, the arachnid fossil record was sparse. It was dominated by a comparative wealth of forms in Carboniferous Coal Measure sediments, and near-modern forms from Palaeogene Baltic amber. Both these relatively well-documented sources and the few reported finds elsewhere in the record suffered from erroneous interpretations. In recent years, new interpretations of existing fossils and a few spectacular new finds have filled in the gaps in the record and changed our knowledge and views of the course of arachnid evolution. Particular examples are: Devonian pseudoscorpions and spiders, book-lungs in Carboniferous scorpions, Triassic mygalomorph spiders, and Jurassic and Cretaceous araneomorph spiders. Phylogenetic systematic analyses of extant arachnids have produced evolutionary scenarios which conflict with the observed fossil record in parts. The newly expanded knowledge of the fossil record allows better tests for the cladograms. Future work on reinterpretation of known Carboniferous and Palaeogene fossils, on rare Mesozoic arachnids, and on arachnids in the earliest known terrestrial ecosystems in the Silurian will add to our knowledge of the fossil record of the arachnids and further enhance testing of phylogenetic hypotheses. □ *Aglaspida, Arachnida, Chelicerata, palaeontology, phylogeny, Pycnogonida.*

Paul A. Selden, Department of Geology, University of Manchester, Manchester M13 9PL, United Kingdom; 10 November, 1992.

For most of this century, one name dominated the literature on fossil arachnids, that of Alexander Petrunkevitch (1875-1964). Petrunkevitch (1955; in Størmer, 1955) summarized the arachnid fossil record to mid-century (Fig. 1) in the 'Treatise on Invertebrate palaeontology' and although he published on amber spiders after 1955, the broad view of the fossil record of chelicerates remained little changed until about a decade ago. Few workers either published on fossil arachnids or disputed Petrunkevitch's assignments during his lifetime. Only recently, during restudy of the fossils, have many errors and misinterpretations in his work come to light.

In the fossil chelicerate record published in the 'Treatise' (Fig. 1), the Merostomata (essentially aquatic chelicerates) are separated from the Arachnida. Second, most of the arachnid side consists of dashed lines converging towards the base of the Cambrian, indicating lack of fossil record and uncertainty of affinities respectively. Third, apart from one dubious palpigrade and some scorpions, there are no other records of Mesozoic (Triassic-Cretaceous) arachnids. Fourth, there is a clear pattern in the temporal distribution of the fossils: a concentration of records in the Upper Carboniferous, and many modern groups also occur in the Palaeogene (early Tertiary). The former records are from the

Coal Measures of Europe and North America, for example: Mazon Creek, Illinois; Coseley, England; and Nyrany, Czechoslovakia. The Palaeogene occurrences are mainly from Baltic amber. Although Trigonotarbita and a questionable record of Araneae had been known from the Devonian Rhynie Chert of Scotland since Hirst (1923), they were omitted from the diagram. (In addition, Petrunkevitch knew of undescribed Lebanese amber opilionids and some Cretaceous spiders from Manitoban amber).

Petrunkevitch developed theories on the evolution of arachnids, which resulted in his superordinal classifications of 1945 and 1949. He recognized a number of 'evolutionary trends', such as the movement of the mouth rearwards from the Xiphosura to the arachnids, and the reduction of the metasoma to a tail or pygidium. One of the most important characters used in his classifications is the width of the connection between prosoma and opisthosoma, i.e. reduction of the first abdominal somite to a pedicel. Petrunkevitch (1945) divided the class Arachnida into two subclasses, Latigastra and Caulogastra, on the basis of a broad or a narrow prosoma-opisthosoma connection respectively. Later, Petrunkevitch (1949) added the subclass Soluta to the scheme to include solely his new order Trigonotarbita which he considered exhibit both wide and narrow junctions. Another subclass, the

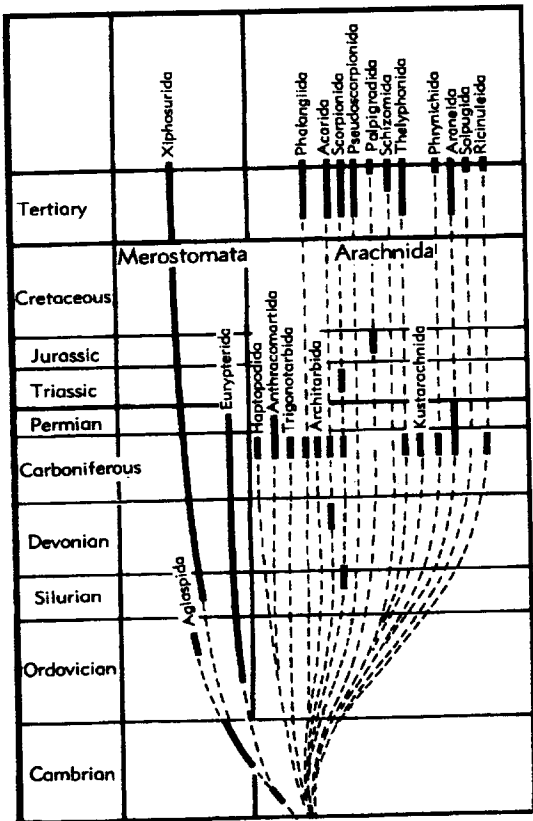


FIG. 1. Stratigraphic ranges of Chelicerata and Aglaspidida and presumed phylogenetic relationships (from Størmer, 1955).

Stethostomata, was created at this time to accommodate the orders Anthracomartida and Haptopoda which supposedly have a broad prosoma-opisthosoma junction and a unique coxosternal region. Petrunkevitch's (1949) classification scheme, used in the 'Treatise', has not stood the test of time. Weygoldt and Paulus (1979) noted its use in some textbooks but pointed out severe deficiencies in the scheme when other characters are taken into account.

Petrunkevitch was a devout proponent of the idea of the 'decoupling' of macroevolution and microevolution. He envisaged major features (those which define higher taxa) originating by mutation or other accelerated evolution, whereas minor morphological differences (those which separate species, for example) could provide only long, slow evolution and rarely produced higher taxa (Petrunkevitch, 1952, 1953). Petrunkevitch (1955) envisaged extinction occurring when irre-

versible evolutionary trends took groups down blind alleys—useful trends which proved lethal when taken to extreme or when environmental conditions changed. Characters could therefore be described as 'major' or 'minor', depending on the taxonomic rank they diagnose. Provided the 'rank' of a character is not decided *a priori*, there is no problem; however, difficulties arise when character states do not clearly change at taxon boundaries. For example, in a diagnosis of the subclass Soluta Petrunkevitch, 1949 is: 'abdomen composed of 8 to 11 segments' (Petrunkevitch, 1955, p. P107). Petrunkevitch described this variability as the character being in a 'labile' state. So, the subclass Soluta is diagnosed on the *labile condition* of the abdominal segmentation, the presence of *either* a broad *or* a narrow junction between the opisthosoma and prosoma (see above), and the *overall resemblance* of the coxosternal region to that in spiders [my italics]. Petrunkevitch (1955) argued that solutes are not spiders because of the combination of characters in the group, and additionally they showed a single series of marginal plates on the opisthosoma. Obviously, such a group could also be considered a collection of quite different animals placed together through their shared possession of a spider-like coxosternal region.

Restudy of fossil solutes reveals that the problem lies mainly in Petrunkevitch's inability to correctly interpret fossil material. The number of segments in the Soluta is invariably 11 (Shear *et al.*, 1987) but the number Petrunkevitch interpreted in each specimen differed according to its preservation. Thus, where a 2-segmented pygidium was preserved, then 2 additional segments were counted over specimens which did not preserve this organ, and the short first abdominal segment is not always visible in fossils. Similarly, the interpretation of the prosoma-opisthosoma junction depended on how closely these tagmata were conjoined in the fossil.

Petrunkevitch described *Trigonmartus pustulatus*, and noted (1913, p. 104): 'The cephalothorax being much harder, kept more or less its shape, and what appears on it as a median crest was in reality a median groove. The irregular, polygonal depressions were evidently thickened areas of the chitin and formed in life low elevations.' But, two pages before he had diagnosed the new genus thus: 'Carapace triangular with a median crest in the posterior half, covered with irregular polygonal depressions.' Thus he had recognized that the fossils were

external moulds but diagnosed the genus as if they were casts. The error perpetuated until 1955 when, in the 'Treatise' (p. P112), the diagnosis became 'Carapace triangular, high, with median crest and a pustulose surface, without eyes. Abdomen with pustulose surface' Thus, pustules were recognized but the median crest remained, without explanation for the emendation. Furthermore, eyes exist in *Trigonomartus* (Petrunkevitch, 1913, pl. 9, fig. 49, in the same place as in *Aphantomartus* (Pocock 1911, Pl. II, fig. 6). These two genera were synonymized by Selden and Romano (1983). As well as misinterpreting fossils, Petrunkevitch produced some illogical taxonomic arguments. In 1945, he erected the Aphantomartidae for eophryinids with 7 abdominal tergites (i.e. *Aphantomartus areolatus* Pocock, 1911). In 1949, he erected the Trigonomartidae, and, recognizing that *Aphantomartus* had 8 abdominal tergites, not 7, he stated (p. 256): 'This means that the Family Aphantomartidae becomes a synonym of Trigonomartidae, the number of abdominal segments having served as the only character of distinction.' Why not place the contents of the new 'Trigonomartidae' in the existing Aphantomartidae? Aphantomartidae has priority and was redefined by Selden and Romano (1983). Furthermore, illustrations purporting to differentiate *Aphantomartus* and *Trigonomartus* (Petrunkevitch 1955, figs 80, 1 and 3) are unrepresentative and merely emphasise different characters of the same genus. Fig. 80, 3 is not *Aphantomartus areolatus*, as stated in the text, but a copy from Pruvost (1919, fig. 42) of *A. pococki*, with eyes drawn on incorrectly!

Consider also the Phalangiotarbida. Kjellesvig-Waering redescribed this group just before his death in 1979, and the MS was being prepared for posthumous publication (see Kjellesvig-Waering, 1978). In the MS, Kjellesvig-Waering, a renowned taxonomic 'splitter', reduced Petrunkevitch's 10 genera and 13 species to four genera and five species. He stated in the introduction to his MS: 'Seldom, if ever, has a fossil group with such uncomplicated, mostly easily determinable morphological characters, been subjected to such misunderstanding and careless and erroneous work as has the order Phalangiotarbida Haase, 1890. The main reason for this state has been the complete failure of some of the workers in this group to understand fundamental paleontological principles of preservation, for example, molds and casts, external and internal, along with results of compaction and consequent reflection

or impression of ventral into dorsal surfaces and vice versa.' Kjellesvig-Waering's conclusions on functional morphology and phylogeny, both in this MS and his other work, are not without dispute, but his long experience with the taxonomy of fossil chelicerates was generally reliable. Kjellesvig-Waering wrote in his MS: 'The question of whether Phalangiotarbida Haase, 1890, or Architarbida Petrunkevitch, 1945 is the proper name for this order of arachnids has not been settled, although it is difficult to understand why any question should have arisen in the first place.' What Petrunkevitch did was to substitute an existing name with one based on better preserved specimens of the order: 'What is more reasonable than to regard the Family Architarbidae as the most characteristic one of the Order and to emphasize this fact by using a proper derivative of the generic name for the Order?' (Petrunkevitch, 1945, p. 11).

The above examples show that much work is needed on fossil arachnids already in collections, in addition to study of the many new fossils awaiting description.

THE FOSSIL RECORD (Fig. 2)

ARACHNID RELATIVES

The extinct aglaspidids are probably not chelicerates since they bear neither chelicerae nor other features which would ally them with the Chelicerata over any other arthropod group (Briggs *et al.*, 1979). The fossil record does not help to determine the systematic position of the enigmatic pycnogonids. Chelicerae are not a prerequisite for a chelicerate. *Sanctacaris* Briggs and Collins, 1988 from the Middle Cambrian Burgess Shale of British Columbia lacks chelicerae but was included in the phylum because of a combination of characters unique to Chelicerata: six pairs of prosomal appendages, cardiac lobe, prosoma and opisthosoma, and anus at rear of last trunk segment. *Sanctacaris* was described as sister to all other chelicerates, but may not be the oldest chelicerate because a dubious xiphosuran carapace of Lower Cambrian age, *Eolimulus alatus* (Moberg, 1892) was recorded from Öland, Sweden. Xiphosura are the most primitive chelicerates in existence and, though previously allied with the Eurypterida in the Merostomata, most authors place Xiphosura with either the Scorpionida (Bergström, 1979, 1981; Bergström *et al.*, 1980; van der Hammen, 1985, 1986) or as sister to all other chelicerates (except

Sanctacaris) (Grasshoff, 1978; Boudreaux, 1979; Paulus, 1979; Weygoldt and Paulus, 1979; Weygoldt, 1980), thereby rendering *Merosotomata* an unnatural group.

SCORPIONS

Scorpions are the arachnid group with the earliest known ancestors; the most ancient known scorpion is *Dolichophonus loudonensis* (Laurie, 1889) from the Llandovery of the Pentland Hills, near Edinburgh, Scotland. Kjellesvig-Waering (1986) proposed a controversial classification scheme. Stockwell (1989) produced a more acceptable classification scheme of Scorpionida which included fossils, but it has yet to be published formally. A linchpin of Kjellesvig-Waering's classification was the supposed Devonian gilled scorpion described as *Tiphoscorpio hueberi*. Restudy of this material (Selden and Shear, 1992) revealed that it is not a scorpion but an arthroploid myriapod!

The early Silurian record of scorpions could be interpreted as representing the earliest terrestrial animals since 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 all fossil scorpions were terrestrial, but other workers (e.g. Wills, 1947; Stormer, 1970; Rolfe and Beckett, 1984; Kjellesvig-Waering, 1986) argued for an aquatic habitat for Silurian scorpions at least. Evidence for aquatism among fossil scorpions are: 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 overlap in the ranges of aquatic and terrestrial scorpions but the first terrestrial forms probably appeared the Devonian (Selden and Jeram, 1989). It is not 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, but a recent find is worthy of especial note: well preserved book lungs in a Carboniferous (Visean) 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 reported from the Triassic of France (Gall, 1971), and the Cretaceous of Brazil (Campos, 1986) are currently under study.

PSEUDOSCORPIONIDA

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 Lebanon (Whalley, 1980) and Manitoba (Schawaller, 1991). However, the most important fossil pseudoscorpions are well preserved specimens of *Dracochela deprehendor* (Shear *et al.*, 1989; Schawaller *et al.*, 1991), in the Upper Devonian mudstones of Gilboa, New York. Only protonymph and tritonymph are known which, though modern in many aspects, cannot be assigned with confidence to extant taxa because both diagnostic characters in the fossils and cladistic assessment of extant forms are lacking.

SOLIFUGAE

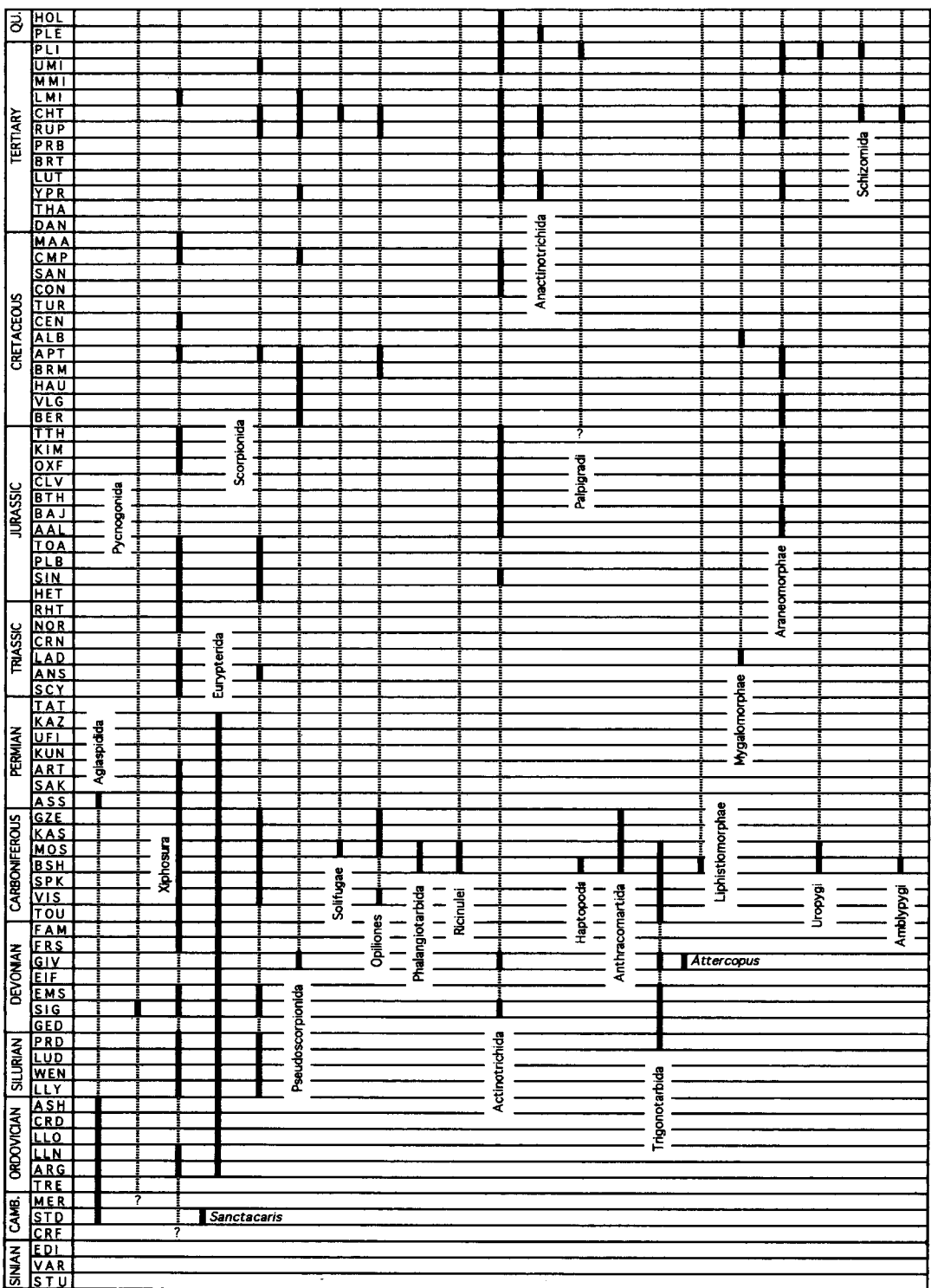
The Carboniferous solifuge, *Protosolpuga carbonaria* Petrunkevitch, 1913, was described as being in a very poor state of preservation. It is impossible to judge the validity of the identification from the published photograph and drawing. The only reliable fossil solifuge is *Happlodontus proterus* Poinar and Santiago-Blay, 1989, from Oligocene Dominican amber.

OPILIONES

Until recently, Opiliones had a fairly typical arachnid fossil record, being known only from Upper Carboniferous strata and Tertiary ambers. In 1985 a specimen was discovered in Lower Carboniferous rocks of East Kirkton, near Edinburgh, Scotland (Wood *et al.*, 1985), and a year later, one was described from the Lower Cretaceous of Koonwarra, Victoria, Australia (Jell and Duncan, 1986). Both of these unnamed specimens are long-legged opilionids but no further identification is possible (pers. obs.).

The order Kustarachnida Petrunkevitch, 1913 is included with the Opiliones, following Beall (1986).

FIG. 2. Current knowledge of the fossil record of Aglaspidida, Pycnogonida and Chelicerata; data in Selden (1993). Solid lines denote actual occurrence in the stage(s) concerned; interrupted lines indicate presumed occurrence in intervening stages. ? denotes doubtful record. Note that taxon ranks are not equivalent; occurrences of important genera *Sanctacaris* (most plesiomorphic chelicerate) and *Attercopus* (oldest and most plesiomorphic spider) are shown separately. Stratigraphic resolution is to stage; abbreviations in second column refer to standard stage names (see e.g. endpapers of Briggs and Crowther, 1990).



PHALANGIOTARBIDA

The situation of the phalangiotarbid has been described above. This group is only known from the Upper Carboniferous but fossils are widespread in European and North American coalfields.

RICINULEI

Ricinulei are known only from the Upper Carboniferous of Europe and North America, and the New and Old World tropics at the present day (their range extends outside the tropics mainly by cavernicole species). A recent revision of the fossils (Selden, 1992) revealed a greater diversity in the Carboniferous than today, but based on an essentially similar body plan. It appears that the group has remained in warm, humid habitats (equatorial forest litter and caves) throughout its geological history.

MITES

The oldest mites are Actinedida (Prostigmata) from the Lower Devonian Rhynie Chert of Scotland (Hirst, 1923). Other Devonian Actinotrichida are known from Gilboa, New York (Norton *et al.*, 1988, 1989; Kethley *et al.*, 1989). A few Jurassic and Cretaceous Actinotrichida are known (e.g. Bulanova-Zakhvatkina, 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, somewhat suspect, records of Ixodida (e.g. Scudder, 1890) and Gamasida (e.g. Hirschmann, 1971). Fossil mites are probably found routinely in palynological preparations but are unreported. With the growth of micropalaeontological techniques in the study of fossil arthropods it is likely that many more fossil mites will be identified.

PALPIGRADI

The preservation potential of palpigrades is even lower than that of mites. Their small size, thin cuticles and interstitial habitats makes them difficult objects of study when Recent or fossil. *Sternarthron zitteli* Haase, 1890, from the Jurassic lithographic limestone of Solnhofen, Germany, is doubtful; the only good fossil palpigrade is *Palaeokozenia mordax* Rowland and Sissom, 1980, from the 'Onyx Marble' quarries (Pliocene) of Arizona.

HAPTOPODA

This monotypic order was established by Pocock (1911) 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. The group would repay restudy along with Anthracomartida and Trigonotarbida.

ANTHRACOMARTIDA

Together with Haptopoda, this order forms Petrunkevitch's 1949 subclass Stethostomata. In a discussion of the rationale for separating Stethostomata from Soluta (Shear and Selden, 1986; Shear *et al.*, 1987), it was concluded that the only feature separating anthracomartids from trigonotarbids is two versus one rows of marginal tergal plates on the opisthosoma. Again, this common Upper Carboniferous group needs careful restudy.

TRIGONOTARBIDA

Trigonotarbids are the best known extinct arachnid group on account of their excellent preservation in the Devonian Rhynie Chert of Scotland and Gilboa mudstones of New York and are among the first known land animals (Jeram *et al.*, 1990). First described from Upper Carboniferous rocks (Buckland, 1837; Fritsch, 1901; Pocock, 1902, 1903, 1911), Hirst (1923) described the first Devonian specimens (from Rhynie), and Størmer (1970) described forms from the Middle Devonian of Alken-an-der-Mosel, Germany. Trigonotarbida is one of the few arachnid groups found relatively frequently in Palaeozoic terrestrial rocks of from Argentina (Pinto and Hünicken, 1980), Spain (Selden and Romano, 1983), Czechoslovakia (Opluštil, 1985), and Germany (Jux, 1982).

The exquisite preservation of the Rhynie Chert meant that Hirst (1923) could describe minute details of the trigonotarbids from that deposit. Trigonotarbids from Gilboa (Shear *et al.*, 1987) not only confirmed Hirst's observations but also uncovered further morphological features of these interesting animals. Later work has shown that some of the species described as trigonotarbids in 1987 were really spiders or other pulmonate arachnids (Selden *et al.*, 1991), but the systematic position of the Trigonotarbida, sister to all other pulmonates, was strengthened. A trigonotarbid and centipedes, found together with early land plants in Silurian (basal Pridoli) sediments at Ludford Lane, Ludlow, England (Jeram

et al., 1990), pushed back the earliest record of land animals by around 16 million years and indicated that trigonotarbid was among the earliest terrestrial animals.

ARANEAE

Great strides have been made recently in spider systematics (Coddington and Levi, 1991) and concomitantly, new finds of fossil spiders have added to the geological record. The oldest spider is *Attercopus fimbriunguis* Shear, Selden and Rolfe, 1987, from Gilboa; supposed spiders from Rhynie (Hirst, 1923) and Alken-an-der-Mosel (Stormer, 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 other spiders, lacking the 'compression zone Y' of Manton (1977). Autapomorphies of the *Attercopus* clade are: fimbriate paired claws, spinules on the palpal femur, and lack of trichobothria; the latter feature is puzzling.

In spite of descriptions of Devonian and Carboniferous araneomorph spiders (Archaeometidae Petrunkevitch, 1949; Pyritaraneidae Petrunkevitch, 1953), none of those seen by the author could be proved to be a spider at all. Petrunkevitch seemed to concur with Fritsch (1904) and Pocock (1911) in their placement of fossils in the Araneomorphae without question, even if he disagreed with their detailed descriptions. All of these authors seemed to place fossils in Araneomorphae on the basis of their general resemblance to particular groups of araneomorph spiders rather than real characters. For example, Petrunkevitch (1953:107) defined Pyritaraneidae and redefined Archaeometidae as araneomorph spiders with segmented opisthosomae, differing from each other by their laterigrade and prograde legs respectively. Nowhere is the identification as araneomorphs questioned. Eskov and Zonshtein (1990a) considered segmentation of the opisthosoma in the Pyritaraneidae to be an artifact, but agreed that this family belongs in Araneomorphae. Selden *et al.* (1991) studied *Archaeometia nephilina* Pocock, 1911 in the British Museum (Natural History) and a plaster cast of *A. devonica* Stormer, 1976 from the Senckenberg Museum, concluding that neither species was a spider and that *A. devonica* may not be an arachnid at all. Carboniferous Arthrolycosidae Fritsch, 1904 and Arthromygalidae Petrunkevitch, 1923 in the British Museum (Natural History) can be placed with the mesotheles because of the distinct tergites on their opisthosomae. Eskov and Zonshtein

(1990b) argued for a new group of Carboniferous 'labidognathous liphistiomorphs' on the evidence that the fossils lacked chelicerae yet any spider with orthognath chelicerae would have them preserved if the carapace and palps were. This argument presupposes that orthognath chelicerae are always correct, which they may not be. To argue morphology from preservation (or lack of it!) is a dangerous practice.

Until recently, no mygalomorph spider was known earlier than the Tertiary. Eskov and Zonshtein (1990a) described some mygalomorphs from Siberia and Mongolia, placing them in the modern Mecicobothriidae, Atypidae and Antrodiaetidae. They are exceptionally well preserved, but poorly illustrated and described; in contrast, the line drawings are of high quality. In 1992, with the description of a Triassic mygalomorph, *Rosamygale*, our knowledge of the antiquity of mygalomorphs was more than doubled (Selden and Gall, 1992). This was placed in the extant family Hexathelidae, and suggests a widespread distribution of the family across Pangaea before rifting of the supercontinent. Hexathelids show many plesiomorphic characters among mygalomorphs but nevertheless, mygalomorphs may yet be found in Palaeozoic rocks.

Mesozoic spiders have only recently been discovered. The oldest fossil araneomorph is *Juraraneus rasnitsyni* Eskov, 1984, placed in a new family, Juraraneidae, in the Araneoidea. *Juraraneus*, like the mygalomorphs described by Eskov and Zonshtein (1990a), is well preserved but rather poorly documented for such an important find, so it is difficult to be sure whether the placement is justified. Eskov (1987) has also described Archaeidae from the Jurassic of Kazakhstan from where Filistatidae are currently being described (Eskov, 1990).

Recent finds of Cretaceous araneomorphs have emphasized the diversity of a spider fauna of modern aspect during this period. Unfortunately, some show little morphological detail (Jell and Duncan, 1986), but Selden (1990a) described specimens from the Lower Cretaceous of north-east Spain, beautifully preserved in lithographic limestone. The specimens included a deinopoid and a tetragnathid, so both cribellate and cribellate orb-web 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 3 families are known to have become extinct since the Palaeogene (Eskov, 1990).

UROPYGI

Well preserved uropygids are found in Coal Measure rocks in Europe (e.g. Brauckmann and Koch, 1983) and North America. All are placed in the modern Thelyphonidae.

SCHIZOMIDA

Three species of schizomids are known from the Pliocene 'Onyx Marble' quarries of Arizona and one from the Oligocene of China (Lin *et al.*, 1988).

AMBLYPYGI

Fossil amblypygi are known from the Coal Measures of Europe and North America and from 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).

ARACHNID PHYLOGENY

Selden (1990b) discussed three recent phylogenetic hypotheses with the evidence of the fossil record (Fig. 3). A cladogram which accurately reflects evolutionary events predicts that successive dichotomies should occur in ascending chronological order, and a complete fossil record should show this. Weygoldt and Paulus's (1979) analysis (Fig. 3c) predicts that palpigrades should occur in strata at least as old as Devonian because the more derived mites and pseudoscorpions occur in beds of that age. In their scheme, Opiliones occupy a derived position. Van der Hammen (1989; fig. 3b) suggested that Opiliones should occur the Cambrian since they are tentatively shown as sister group to Xiphosura + Scorpiones. Shultz (1989, 1990; Fig. 3a) also placed Opiliones in a position which predicts their presence in Silurian times. Since scorpions were aquatic then, so would opilionids have been.

None of the phylogenetic analyses (Fig. 3) incorporated extinct groups. Whilst it is impossible to include ancestors in cladistic analyses, there is no reason why well known extinct groups should not be included, say at the Carboniferous level. Apart from the enigmatic palpigrades and the highly derived Schizomida, for which fossil evidence is lacking, all arachnid orders were in existence by that time.

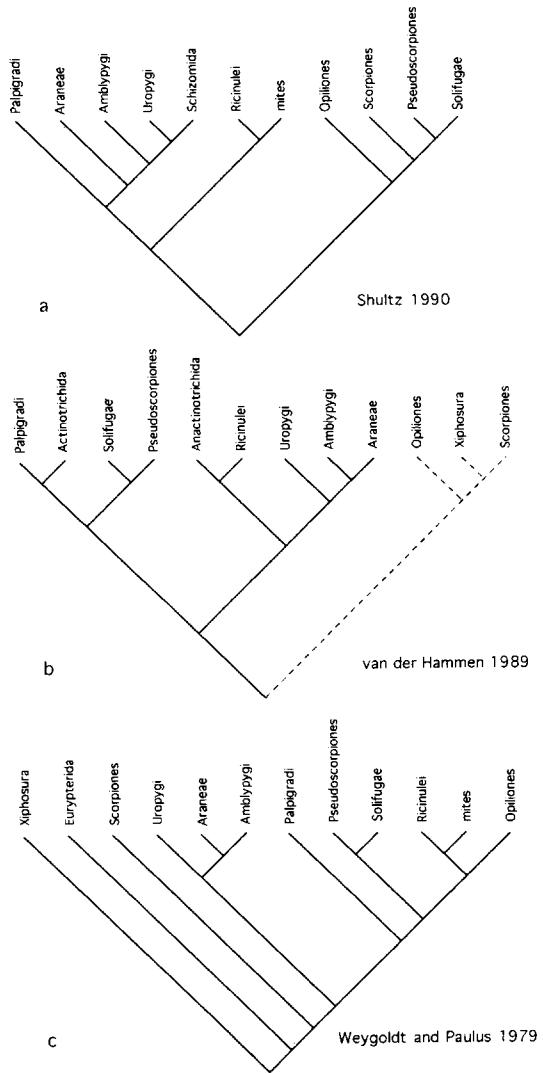


FIG. 3. Cladograms of relationships among the arachnid groups as viewed by a, Shultz (1990); b, van der Hammen (1989); and c, Weygoldt and Paulus (1979). Interrupted lines indicate uncertainty.

FUTURE PROSPECTS

Work in progress includes: palaeophysiology of early terrestrial chelicerates—aquatic and terrestrial adaptations in eurypterids, scorpions, and other Siluro-Devonian arachnids; palaeobiology of the Trigonotarbiidae; and Cretaceous spiders from Canadian amber and the Santana Formation of Brazil.

Much of Petrunkevitch's work needs revision. A new phalangiotarbid fauna has been collected in recent years from a coal mine tip in Somerset, England (Beall, 1991). Carboniferous Anthracomartida and Haptopoda need to be restudied, particularly in relation to the now extremely well known and possibly related trigonotarbids. The identity of described Amblypygi is in little doubt, but modern descriptions would be helpful. In need of critical examination are: the single fossil solifuge *Protosolpuga* from Mazon Creek, the supposed palpigrae *Sternarthron* from the Jurassic of Germany, and the amber spiders described by Petrunkevitch (e.g. 1942, 1950, 1958). The problem with these spiders is that over the years some of the supposed 'amber' in collections has discoloured, which suggests it may not be truly Palaeogene but rather more recent copal or other resins.

Successful palaeoarachnology requires knowledge of both Recent arachnids and understanding of styles of fossil preservation. Much previous work suffered from erroneous interpretations of one sort or another. Goals for future work are: to understand the origin of the present-day diversity of arachnids and the relationships among the various groups, and the reconstruction of ancient terrestrial ecosystems.

LITERATURE CITED

- BEALL, B.S. 1986. Reinterpretation of the Kustarachnida. (Abstract). *American Arachnology* 34: 4.
1991. The Writhlington phalangiotarbids: their palaeobiological significance. *Proceedings of the Geologists Association* 102: 161-168.
- BERGSTROM, J. 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. Pp. 3-56. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).
1981. Morphology and systematics of early arthropods. *Abhandlungen des Naturwissenschaftlichen Verein in Hamburg* 23: 7-42.
- BERGSTROM, J., STÜRMER, W. & WINTER, G. 1980. *Palaeoisopus*, *Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. *Paläontologische Zeitschrift* 54: 7-54.
- BOUDREAUX, H.B. 1979. Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. Pp. 551-86. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).
- BRAUCKMANN, C. & KOCH, L. 1983. *Prothelyphonus naufragus* n. sp., ein neuer Geißelscorpion [Arachnida: Telyphonida: Telyphonidae] aus dem Namurium (unteres Ober-Karbon) von West-Deutschland. *Entomologia Generalis* 9: 63-73.
- BRIGGS, D.E.G., BRUTON, D.L. & WHITTINGTON, H.B. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. *Palaentology* 22: 167-180.
- BRIGGS, D.E.G. & COLLINS, D. 1988. A Middle Cambrian chelicerate from Mount Stephen, British Columbia. *Palaentology* 31: 779-98.
- BRIGGS, D.E.G. & CROWTHER, P.R. (eds). 1990. 'Palaeobiology: a synthesis'. (Blackwell Scientific Publications: Oxford, London, Edinburgh, Boston, Melbourne).
- 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'. 2nd Edn. (William Pickering: London).
- BULANOVA-ZACHVATINA, E.M. 1974. New genera of oribatid mites from the Upper Cretaceous of Taimyr. *Paleontologicheskii Zhurnal* 2: 141-144.
- CAMPOS, D.R.B. 1986. Primeiro registro fóssil de Scorpionoidea na Chapado do Araripe (Cretáceo Inferior), Brasil. *Anais da Academia Brasileira de Ciências* 58: 135-137.
- CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* 22: 565-592.
- 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.
1987. A new archaetid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called "Gondwanan" ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175: 81-106.
1990. Spider paleontology: present trends and future expectations. *Acta Zoologica Fennica* 190: 123-127.
- ESKOV, K. & ZONSHEIN, S. 1990a. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata: Araneae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 178: 325-368.
- 1990b. A new classification for the order Araneida (Arachnida: Chelicerata). *Acta Zoologica Fennica* 190: 129-137.
- FRITSCH, A. 1901. 'Fauna der Gaskohle. IV. Permische Arachniden'. p.56, pls.153-154, text-figs. 359-363.
1904. 'Palaeozoische Arachniden'. (A. Fritsch: Prague). 86pp., 15 pl.

- GALL, J.-C. 1971. Faunes et paysages du Grès à Voltzia du nord des Vosges. Essai paléocécologique 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.
- HAASE, E. 1890. Beiträge zur Kenntnis der fossilen Arachniden. Zeitschrift der Deutschen Geologischen Gesellschaft 42: 629-657.
- 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.
1986. Comparative studies in Chelicerata IV. Apatellata, Arachnida, Scorpionida, Xiphosura. Zoologische Verhandlungen, Leiden 226: 1-52.
1989. 'An introduction to comparative arachnology'. (SPB Academic Publishing: The Hague). x + 576pp.
- HIRSCHMANN, W. 1971. A fossil mite of the genus *Dendrolaelaps* (Acarina, Mesostigmata, Digamasellidae) found in amber from Chiapas, Mexico. 69-70. In Petrunkevitch, A. (ed.) Studies of fossiliferous amber arthropods of Chiapas, Mexico. University of California Publications in Entomology: 63, vi + 106pp., 3 pls.
- HIRST, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). Annals and Magazine of Natural History (9) 12: 455-474.
- JELL, P.A. & DUNCAN, P.M. 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., SELDEN, P.A. & EDWARDS, D. 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.
- KETHLEY, J.B., NORTON, R.A., BONAMO, P.M. & SHEAR, W.A. 1989. A terrestrial alicorhagiid mite (Acari: Acariformes) from the Devonian of New York. Micropaleontology 35: 367-373.
- KJELLESVIG-WAERING, E.N. 1978. The Phalangiotarvida (Arachnida) of Mazon Creek. Geological Society of America, Abstracts with Programs 10: 258-259.
1986. A restudy of the fossil Scorpionida of the world. Palaeontographica Americana 55: 1-287.
- KOCH, C.L. & BERENDT, G.C. 1854. 'Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt'. (Berlin). 124pp. [Published posthumously with footnotes by A. Menge].
- KRIVOLUTSKY, D.A. & RYABININ, N.A. 1976. Oribatid mites in Siberian and Far East amber. Reports of the Academy of Sciences, USSR 230: 945-948. [In Russian].
- 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 QI-BIN, YAO YI-MIN, XIANG WEI-DA & XIA YU-RONG. 1988. An Oligocene micropalaeontomofauna from Gubei District of Shandong and its ecological environment. Acta Micropalaeontologica Sinica 5: 331-345.
- MANTON, S. M. 1977. 'The Arthropoda. Habits, functional morphology, and evolution'. (Clarendon Press, Oxford). xxii + 527 pp.
- 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.
- NORTON, R.A., BONAMO, P.M., GRIERSON, J.D. & SHEAR, W.A. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. Journal of Paleontology 62: 259-269.
1989. Fossil mites from the Devonian of New York State. 271-277. In Channabasavanna, G.P. and Viraktamath, C.A. (eds.) 'Progress in Acarology. Vol. 1. Systematics and Taxonomy of Acari'. (Oxford and IBH Publishing Co. Pvt. Ltd: New Delhi, Bombay, Calcutta).
- OPLUŠTIL, S. 1985. New findings of Arachnida from the Bohemian Upper Carboniferous. Vestn. Ustred. ust. geol. 60: 35-42.
- PAULUS, H.F. 1979. Eye structure and the monophyly of Arthropoda. 299-383. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).
- PETRUNKEVITCH, A. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Transactions of the Connecticut Academy of Arts and Sciences 18: 1-137.
1923. On families of spiders. Annals of the New York Academy of Sciences 29: 145-180.
1942. A study of amber spiders. Transactions of the Connecticut Academy of Arts and Sciences 34: 119-464.
1945. Palaeozoic Arachnida of Illinois. An inquiry into their evolutionary trends. Illinois State Museum, Scientific Papers 3(2): 1-72.
1949. A study of Palaeozoic Arachnida. Transactions of the Connecticut Academy of Arts and Sciences 37: 69-315.
1950. Baltic amber spiders in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, Harvard University 103: 259-337.
1952. Macroevolution and the fossil record of Arachnida. American Scientist 40: 99-122.
1953. Palaeozoic and Mesozoic Arachnida of

- Europe. Geological Society of America, Memoir: 53, xi + 1-128 pp.
1955. Arachnida. p.42-162. In Moore, R.C. (ed.) 'Treatise on invertebrate paleontology. Part P. Arthropoda 2'. (Geological Society of America and University of Kansas Press: Boulder, Colorado and Lawrence, Kansas). xvii + 181pp.
1958. Amber spiders in European collections. Transactions of the Connecticut Academy of Arts and Sciences 41: 97-400.
- PINTO, I.D. & HÜNICKEN, M.A. 1980. *Gondwanarachne* a new genus of the order Trigonotarbitida (Arachnida) from Argentina. Boletín de la Academia Nacional de Ciencias, Córdoba, Argentina 53: 307-315.
- POCOCK, R.I. 1902. *Eophrynus* and allied Carboniferous Arachnida. Part 1. Geological Magazine, decade 4 9: 439-448.
1903. A new Carboniferous arachnid. Geological Magazine, decade 4 10: 247-251.
1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. Monograph of the Palaeontographical Society 64: 1-84.
- POINAR, G.O. & SANTIAGO-BLAY, J.A. 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.
- PRUVOST, P. 1919. Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La faune continentale du terrain houiller du Nord de la France. Mémoires pour servir à l'explication de la carte géologique détaillée de la France. (Ministère des Travaux Publics, Paris). 584 pp.
- ROLFE, W.D.I. & BECKETT, C.M. 1984. Autecology of Silurian Xiphosurida, Scorpionida, and Phyllocarida. In Bassett, M.G. and Lawson, J.D. (eds) 'Autecology of Silurian Organisms'. Special Papers in Palaeontology 32: 27-37.
- ROWLAND J.M. & SISSOM, W.D. 1980. Report on a fossil palpigrade from the Tertiary of Arizona, and a review of the morphology and systematics of the order (Arachnida: Palpigradida). Journal of Arachnology 8: 69-86.
- SCHAWALLER, W. 1979. Erstnachweis der Ordnung Geißelspinnen in Dominicanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Amblypygi). Stuttgarter Beiträge zur Naturkunde, Serie B 50: 1-12.
1982. Spinnen der Familien Tetragnathidae, Uloboridae und Dipluridae in Dominicanischem Bernstein und allgemeine Gesichtspunkte (Arachnida, Araneae). Stuttgarter Beiträge zur Naturkunde, Serie B 89: 1-19.
1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber. Palaeontology 34: 971-976.
- SCHAWALLER, W., SHEAR, W.A. & BONAMO, P.M. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). American Museum Novitates 3009: 1-17.
- SCUDDER, S.H. 1890. Illustrations of the Carboniferous Arachnida of North America, of the orders Anthracomarti and Pedipalpi. Memoirs of the Boston Society of Natural History 4: 443-456, pls 39, 40.
- SELDEN, P.A. 1990a. Lower Cretaceous spiders from the Sierra de Montsech, north-east Spain. Palaeontology 33: 257-285.
- 1990b. The arachnid fossil record. Newsletter of the British Arachnological Society 58: 4-6.
1992. The fossil ricinuleids. Transactions of the Royal Society of Edinburgh: Earth Sciences 83: 595-634.
1993. Aglaspidida, Pycnogonida and Chelicerata. In Benton, M.J. and Whyte, M.A. (eds) 'The fossil record 2'. (Chapman and Hall: London, New York, Tokyo, Melbourne, Madras). (in press).
- SELDEN, P.A. & GALL, J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France. Palaeontology 35: 211-235.
- SELDEN, P.A. & JERAM, A.J. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. Transactions of the Royal Society of Edinburgh; Earth Sciences 80: 303-310.
- SELDEN, P.A. & ROMANO, M. 1983. First Palaeozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock (Stephanian; Prov. Leon, N.W. Spain), with remarks on aphantomartid taxonomy. Boletino del Instituto Geologia e Mineralogia d'España 94: 106-112.
- SELDEN, P.A. & SHEAR, W.A. 1992. A myriapod identity for the Devonian 'scorpion' *Tiphoscorpio hueberi*. Bericht des naturwissenschaftlich-Medizinischen Vereins in Innsbruck, Supplement 10: 35-36.
- SELDEN, P.A., SHEAR, W.A. & BONAMO, P.M. 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.
1931. Milben im Bernstein. Bernsteinforschungen 2: 148-180.
- SHEAR, W.A., BONAMO, P.M., GRIERSON, J.D., ROLFE, W.D.I., SMITH, E.L. & NORTON, R.A. 1984. Early land animals in North America. Science 224: 492-494.
- SHEAR, W.A. & SELDEN, P.A. 1986. Phylogenetic relationships of the Trigonotarbitida, an extinct order of arachnids. Actas X Congressos Internacional de Aracnologia, Jaca, España, 1986 1: 393-397.
- SHEAR, W.A., SELDEN, P.A., ROLFE, W.D.I., BONAMO, P.M. & GRIERSON, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbitida). American Museum Novitates 2901: 1-74.
- SHEAR, W.A., SCHAWALLER, W. & BONAMO,

- P.M. 1989. Record of Palaeozoic pseudoscorpions. *Nature* 341: 527-529.
- SHULTZ, J.W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* 97: 1-56.
1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6: 1-38.
- SIVHED, U. & WALLWORK, J.A. 1978. An early Jurassic oribatid mite from southern Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 100: 65-70.
- STOCKWELL, S.A. 1989. 'Revision of the phylogeny and higher classification of scorpions (Chelicerata)'. Unpublished Ph.D. thesis, University of California, Berkeley.
- STØRMER, L. 1955. Merostomata. P4-P41. In Moore, R.C. (ed.) 'Treatise on invertebrate paleontology. Part P. Arthropoda 2'. (Geological Society of America and University of Kansas Press: Boulder, Colorado and Lawrence, Kansas). xvii + 181pp.
1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 1. Arachnida. *Senckenbergiana Lethaea* 51: 335-69.
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.
- WEYGOLDT, P. 1980. Towards a cladistic classification of the Chelicerata. 8th International Congress of Arachnology, Wien, 1980: 331-334.
- WEYGOLDT, P. & PAULUS, H.F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 17: 85-200.
- 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. *Palaeontographical Society Monographs* 437, 441: 1-137.
- WOOD, S.P., PANCHEN, A.L. & SMITHSON, T.R. 1985. A terrestrial fauna from the Scottish Lower Carboniferous. *Nature* 314: 355-356.