

Review Article

Geological history and phylogeny of Chelicerata

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ARTICLE INFO

Article history:

Received 1 December 2009

Accepted 13 January 2010

Keywords:

Arachnida
Fossil record
Phylogeny
Evolutionary tree

ABSTRACT

Chelicerata probably appeared during the Cambrian period. Their precise origins remain unclear, but may lie among the so-called great appendage arthropods. By the late Cambrian there is evidence for both Pycnogonida and Euchelicerata. Relationships between the principal euchelicerate lineages are unresolved, but Xiphosura, Eurypterida and Chasmataspida (the last two extinct), are all known as body fossils from the Ordovician. The fourth group, Arachnida, was found monophyletic in most recent studies. Arachnids are known unequivocally from the Silurian (a putative Ordovician mite remains controversial), and the balance of evidence favours a common, terrestrial ancestor. Recent work recognises four principal arachnid clades: Stethostomata, Haplocnemata, Acaromorpha and Pantetrapulmonata, of which the pantetrapulmonates (spiders and their relatives) are probably the most robust grouping. Stethostomata includes Scorpiones (Silurian–Recent) and Opiliones (Devonian–Recent), while Haplocnemata includes Pseudoscorpiones (Devonian–Recent) and Solifugae (Carboniferous–Recent). Recent works increasingly favour diphyletic mite origins, whereby Acaromorpha comprises Actinotrichida (Devonian–Recent), Anactinotrichida (Cretaceous–Recent) and Ricinulei (Carboniferous–Recent). The positions of the Phalangiotarbida (Devonian–Permian) and Palpigradi (Neogene–Recent) are poorly resolved. Finally, Pantetrapulmonata includes the following groups (listed here in their most widely recovered phylogenetic sequence): Trigonotarbida (Silurian–Permian), Uraraneida (Devonian–Permian), Araneae (Carboniferous–Recent), Haptopoda (Carboniferous), Amblypygi (?Devonian–Recent), Thelyphonida (Carboniferous–Recent) and Schizomida (Paleogene–Recent).

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1. Introduction

Chelicerata *s.l.* includes Arachnida, Xiphosura, the extinct Eurypterida and Chasmataspida, and – more controversially – Pycnogonida. More than 100 000 recent species have been described, and in megadiverse groups like mites and spiders this number continues to increase substantially year on year. Arachnids and their relatives are thus the second most diverse group of modern arthropods after the hexapods. Most chelicerates are terrestrial and generally fill the role of predators, feeding on other arthropods or occasionally small vertebrates. As a group, mites exhibit a broader ecological spectrum which includes ectoparasitism, detritivory and plant-feeding. Although presumably derived from aquatic ancestors, marine and fresh-water chelicerates are less common today and restricted to the sea spiders, horseshoe crabs, and a few secondarily aquatic spiders and mites (especially Hydracarina). It should be added that the mid to late palaeozoic Eurypterida was a substantial aquatic group at that time and may

well have included the largest arthropods ever to have lived (Braddy et al., 2007).

Chelicerata has traditionally received only cursory treatment in palaeontological textbooks. Despite this neglect, fossils of arachnids and their relatives are actually more diverse and abundant than might be expected. Dunlop et al. (2008b) documented nearly 2000 currently valid fossil chelicerate species in the literature; ca. 1600 of them arachnids. Since this publication, Wunderlich (2008) has added about 100 more spider species. Much of this palaeodiversity is concentrated into localities yielding exceptional preservation (Table 1). There is also substantial bias in favour of particular groups – spiders especially – and it is not clear to what extent this reflects real diversity patterns from former eras or how much of this is collection bias or the result of intensive study by Wunderlich (1986, 1988, 2004, 2008) in particular, who created many taxa based on weak, non-cladistic evidence. The last comprehensive study documenting first and last geological occurrences of chelicerate taxa was Selden's (1993a) contribution to *Fossil Record 2*; together with the corresponding summary by Selden (1993b). Further reviews can be found in Selden and Dunlop (1998), Dunlop and Selden (2009), and references therein. Much of the basic pattern outlined in Selden (1993a,b) remains valid, although important discoveries

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Table 1

Significant localities yielding fossil Chelicerata referred to in the text together with their stratigraphical position. Approximate absolute ages in millions of years (Ma) derived from the literature and/or the timechart of the *British Geological Survey*.

Locality	Country	Stratigraphical age	Ma
<i>Cenozoic localities</i>			
Onyx marble	USA (AZ)	Neogene (?Pliocene)	?2–5
Dominican Republic amber	Dominican Republic	Neogene (Miocene)	ca. 16
Chiapas amber	Mexico	Neogene (Miocene)	ca. 16
Shanwang	China (Shandong)	Paleogene (Oligocene)	23–29
Bitterfeld amber	Germany	Paleogene (?Oligocene)	23–29
Baltic amber	Baltic region	Paleogene (Eocene)	45–50
<i>Mesozoic localities</i>			
New Jersey amber	USA (NJ)	Late Cretaceous (Turorian)	89–94
Myanmar (Burmese) amber	Myanmar	Early Cretaceous (?Albian)	110–112
Crato Formation	Brazil	Early Cretaceous (Aptian)	111–125
La Voulte-sur-Rhône	France	mid-Jurassic	161–165
<i>Palaeozoic localities</i>			
'Rotliegend'	Germany	Permian (Asselian)	281–290
Mazon Creek	USA (IL)	Carboniferous (Westphalian D)	306–308
Coseley	England	Carboniferous (Duckmantian)	310–312
Hagen-Vorhalle	Germany	Carboniferous (Marsdenian)	318–319
Gilboa	USA (NY)	Mid-Devonian (Givetian)	ca. 392
Hünsrück Slate	Germany	Early Devonian (Emsian)	398–406
Rhynie Chert	Scotland	Early Devonian (Pragian)	407–411
Herefordshire Lagerstätte	England	Silurian (Wenlock)	ca. 425
Pentland Hills	Scotland	Silurian (Wenlock)	423–428
'Orsten'	Sweden	Cambrian (Furongian)	488–501

in the last few years have pushed back the oldest limits of some lineages quite substantially.

1.1. What do fossils tell us?

The principal value of the fossil record is in documenting minimum ages for cladogenesis (Table 2). For example scorpions go back nearly 430 Ma and further finds could potentially push the oldest dates back even further. Assuming that a given lineage must be at least as old as its sister-group, stratigraphical occurrences can be superimposed onto cladograms (Fig. 1) to predict the presence of groups whose fossil record is either sparse or absent. Among arachnids, this extrapolation through so-called range extension and ghost lineages has been applied most successfully to spiders (Penney et al., 2003).

The resulting evolutionary trees – combining cladograms with the fossil record – can be used to help calibrate (or even falsify) molecular clocks (Dunlop and Selden, 2009), and/or to constrain estimates of divergence times inferred from molecular markers (Giribet et al., 2009, Fig. 10 for opilionids). They also reveal how well the fossil record fits a given estimate of phylogeny. An extreme view would actually be to sacrifice parsimony in favour of a better stratigraphic fit; as advocated in stratocladistics (cf. Fisher, 2008; and references therein). Shultz (1994) critically discussed this controversial methodology as specifically applied to arachnids. Nevertheless, conflicts between a taxon's best supported position in a cladogram and its oldest stratigraphic record can and do exist. Scorpions are, at ca. 428 Ma, the oldest unequivocal arachnids. They resolve as basal arachnids in some hypotheses (Weygoldt and Paulus, 1979), but as more derived in others (Shultz, 1990, 2007; Giribet et al., 2002). Discrepancies between geological history and phylogeny present us with specific challenges for our future understanding of arachnid evolution.

In general, the role of individual fossils in phylogenetic reconstruction has always been controversial. The situation for Chelicerata is no exception (see e.g. 4.8). Even the best preserved fossils can never reveal the full suite of morphological (and of course molecular) characters available from living specimens. That said,

recent advances in imaging techniques are dramatically improving both the quantity and quality of information that can be retrieved. Chelicerate examples include virtual fossils reconstructed by grinding through the matrix (Orr et al., 2000; Siveter et al., 2004), X-ray computer tomography (micro-CT) (Henderickx et al., 2006; Penney et al., 2007; Garwood et al., 2009; Heetoff et al., 2009) and combining images at different focal planes within translucent material (Kamenz et al., 2008). It is to be hoped that such improvements in methodology will reduce the number of equivocal characters which make comparisons between fossils and living forms so challenging.

Most fossil chelicerates can be assigned to existing crown-group taxa or clearly-definable extinct (Palaeozoic) orders. There are, however, exceptions. Amongst sea spiders (Pycnogonida), horse-shoe crabs (Xiphosura), scorpions (Scorpiones) and whip scorpions (Theyphonida) there are some very old fossils, noticeably different from living forms, which offer the potential to reconstruct stem-lineages and ground pattern character states for these groups. Furthermore, a handful of enigmatic taxa have proved difficult to place within the traditional orders, usually because they are incomplete. It should also be stressed that there are no clear examples of missing links in the arachnid fossil record – although the recently proposed Uraraneida of Selden et al. (2008a) probably comes closest – revealing transitions from one major clade to another, or that unequivocally resolve between competing higher-level phylogenetic hypotheses. Perhaps for this reason, historical attempts to reconstruct arachnid phylogeny usually paid scant attention to fossil groups, or simply excluded them entirely (Wheeler and Hayashi, 1998). More integrative studies (Shear et al., 1987; Selden et al., 1991; Giribet et al., 2002; Shultz, 2007) include extinct taxa among the terminals and our present understanding of arachnid geological history is summarized here in the hope of encouraging further work of this nature.

2. Methods

Fossil Chelicerata and their relatives were reviewed from the literature, together with hypotheses about their probable stem-

Table 2
Summary of the geological history for each of the major clades discussed in the text – see also Fig. 1. Traditional 'orders' in bold, the four major arachnid clades *sensu* Shultz (2007) numbered. Maximum ranges of absolute ages given in millions of years (Ma).

Taxon	Author	Oldest	Youngest	Ma
Chelicerata <i>s.l.</i>	Heymons, 1901	Cambrian (Furongian)	Recent	501–0
Pycnogonida	Latreille, 1810	Cambrian (Furongian)	Recent	501–0
Euchelicerata	Weygoldt and Paulus, 1979	?Cambrian (Furongian)	Recent	7501–0
Xiphosura	Latreille, 1802	Ordovician (Ashgill)	Recent	445–0
Chasmataspida ^a	Caster and Brooks, 1956	?Cambrian (Furongian)	Devonian (Eifelian)	7501–391
Eurypterida ^a	Burmeister, 1843	Ordovician (Sandbian)	Permian (?Lopingian)	460–251
Arachnida	Lamarck, 1801	Silurian (Wenlock)	Recent	428–0
1. Stomothecata	Shultz, 2007	Silurian (Wenlock)	Recent	428–0
Scorpiones	C.L. Koch, 1851	Silurian (Wenlock)	Recent	428–0
Opiliones	Sundevall, 1833	Devonian (Pragian)	Recent	411–0
2. Haplocnemata	Börner, 1904	Devonian (Givetian)	Recent	392–0
Pseudoscorpiones	De Geer, 1778	Devonian (Givetian)	Recent	392–0
Solifugae	Sundevall, 1833	Carboniferous (Westph. D)	Recent	308–0
3. Acaromorpha	Dubinin, 1957	Devonian (Pragian)	Recent	411–0
Actinotrichida	Grandjean in van der Hammen, 1961	Devonian (Pragian)	Recent	411–0
Anactinotrichida	Grandjean in van der Hammen, 1961	Cretaceous (Turonian)	Recent	94–0
Ricinulei	Thorell, 1876	Carboniferous (Marsden.)	Recent	319–0
Phalangiotarbida ^a	Haase, 1890	Devonian (Pragian/Ems.)	Permian (Asselian)	411–281
Palpigradi	Thorell, 1888	Neogene (?Pliocene)	Recent	75–0
4. Pantetrapulmonata	Shultz, 2007	Silurian (Přídolí)	Recent	419–0
Trigonotarbida ^a	Petrunkovitch, 1949	Silurian (Přídolí)	Permian (Asselian)	419–281
Tetrapulmonata	Shultz, 1990	Devonian (Givetian)	Recent	392–0
Uraraneida ^a	Selden et al., 2008a	Devonian (Givetian)	Permian (Kungur.)	392–271
Araneae	Clerck, 1757	Carboniferous (Duckmant.)	Recent	312–0
Schizotarsata	Shultz, 2007	?Devonian (Givetian)	Recent	7392–0
Haptopoda ^a	Pocock, 1911	Carboniferous (Duckmant.)	–	312–310
Pedipalpi	Latreille, 1810	?Devonian (Givetian)	Recent	7392–0
Amblypygi	Thorell, 1882	?Devonian (Givetian)	Recent	7392–0
Uropygi	Thorell, 1882	Carboniferous (Marsden.)	Recent	319–0
Thelyphonida	Latreille, 1804	Carboniferous (Marsden.)	Recent	319–0
Schizomida	Petrunkovitch, 1945	Paleogene (Oligocene)	Recent	34–0

^a Extinct groups.

lineage and evolutionary relationships. The sequence of taxa and clade names adopted here essentially follows the most recent and comprehensive estimate of phylogeny by Shultz (2007). As a caveat, some of these clades are better supported than others and specific areas of conflict and alternative hypotheses are noted where appropriate. A distinction is made between the traditional and familiar orders – groups like Araneae (spiders), Scorpiones (scorpions) and Opiliones (harvestmen), the limits of which are usually clearly defined and which are historically very stable – and the more fluid supraordinal taxa. Significant localities yielding fossil chelicerates are listed in Table 1 with their relevant ages; other localities are mentioned in the text. Details of the actual number of fossil species (as of August 2008) in each traditional order can be found in Dunlop et al. (2008b, Table 1).

3. Chelicerate origins and possible stem-group forms

3.1. Arthropods resembling horseshoe crabs

Chelicerata *s.l.*, or even Euchelicerata, does not have a clearly defined stem-lineage. There is no fossil which can unequivocally be accepted as a common ancestor of the group. Historically, chelicerates were often assumed to be related to – perhaps even derived from – the extinct trilobites (Raw, 1957; Lauterbach, 1983; Weygoldt, 1998). This concept was largely based on similarities between trilobites and (larval) horseshoe crabs, and has been formalised under clade names like Arachnata or Arachnomorpha. Caution is needed here, since there is a diversity of early Palaeozoic, non-trilobite arthropods and different authors have applied names like

Arachnomorpha to different sets of taxa. Trilobite affinities for chelicerates were critically examined by Scholtz and Edgecombe (2005, 2006), who stressed that many of the supposed synapomorphies for trilobites and horseshoe crabs are absent in pycnogonids and arachnids. Based on head segmentation and the shared presence of homologous antennae, Scholtz and Edgecombe preferred to group the trilobites with mandibulate arthropods.

Other popular candidates for basal chelicerates include members of the extinct Aglaspidida. These early Palaeozoic arthropods were originally included within Merostomata and were explicitly placed by Weygoldt and Paulus (1979) as the sister-group of Euchelicerata (see 4.3). Aglaspidids were by now something of a bucket taxon for problematic fossils resembling horseshoe crabs and Briggs et al. (1979) demonstrated that at least the core genus *Aglaspis* lacks chelicerae and does not have a true prosoma bearing six pairs of appendages. The limitations, diagnostic characters and affinities of Aglaspidida were reviewed in some detail by Van Roy (2006), who concluded that they are probably closer to trilobites than to chelicerates.

3.2. Great appendage arthropods (Cambrian)

Recent work has highlighted one assemblage of early to mid Cambrian fossils which could be part of the group which eventually gave rise to arachnids (Chen et al., 2004; Cotton and Braddy, 2004). These animals have been variously named great appendage arthropods, megacheirans or even protochelicerates; see also Dunlop (2006) and Edgecombe (2010) for an overview. They express a head region bearing four pairs of limbs (i.e. they lack the

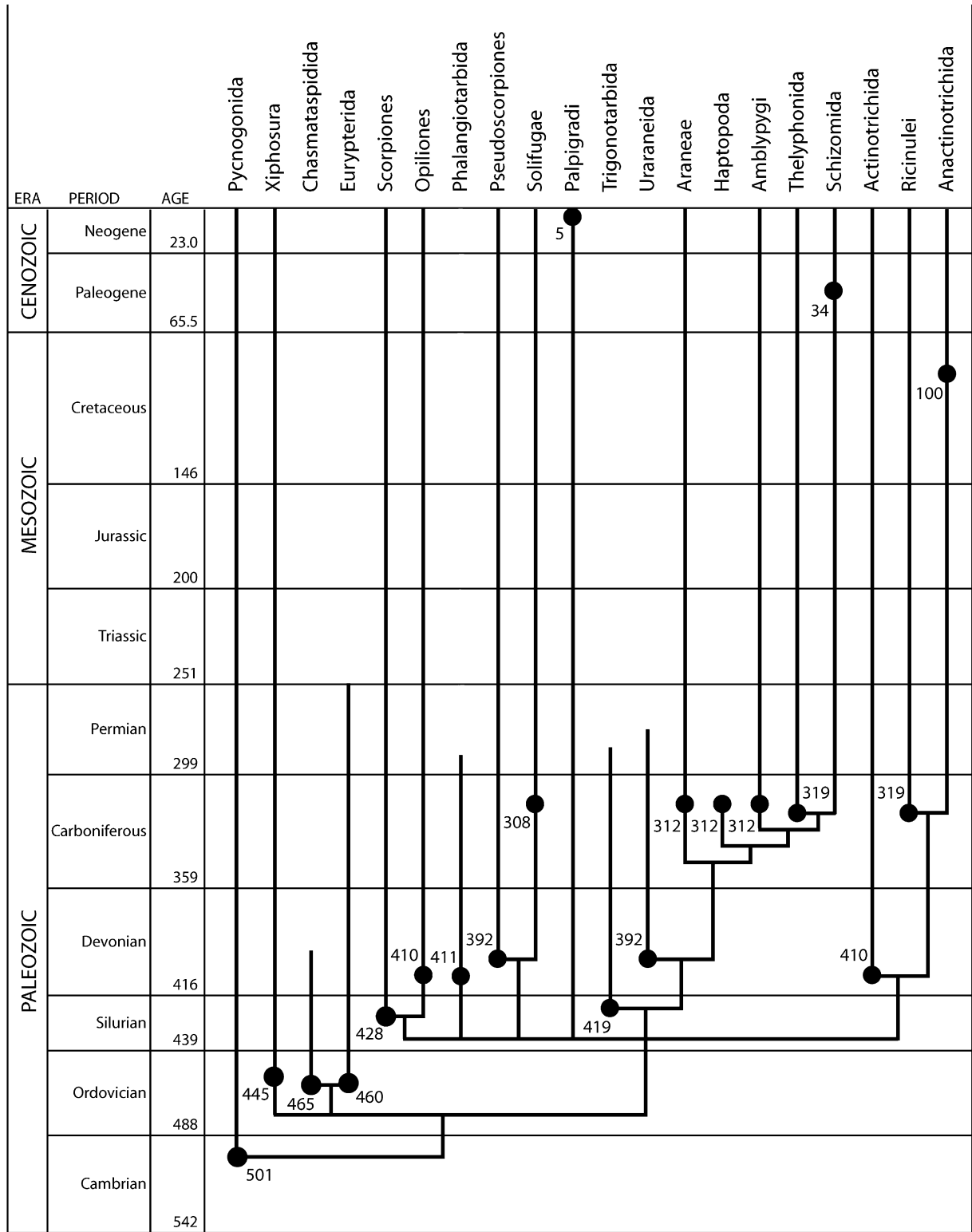


Fig. 1. Arachnid phylogeny *sensu* Shultz (2007) superimposed on the currently known stratigraphic record. Adapted from Dunlop and Selden (2009).

prosoma) followed by a longer trunk region, also bearing appendages. What they do share in common is a pair of large, raptorial, in some cases subchelate appendages at the anterior end of the animal, which could conceivably be homologous with the raptorial (a1) chelicerae of arachnids and their relatives. This hypothesis remains preliminary. Anterior grasping limbs are obviously

adaptive and could have arisen in different arthropod lineages through homoplasy. There are also differing opinions about what constitutes a great appendage arthropod *sensu stricto*, whether the raptorial appendage is equivalent to chelicerae/antennae or a more anterior element lost in modern arthropods, and whether these fossils belong in the euarthropod stem- or crown-group. Further

details of these debates and alternative evolutionary scenarios can be found in, e.g. Budd (2002), Chen et al. (2004), Scholtz and Edgecombe (2006) and Kühl et al. (2009).

4. Geological history of individual clades

4.1. *Chelicerata s.l. (Cambrian–Recent)*

The textbook concept of Chelicerata groups together Pycnogonida and Euchelicerata, a clade supported primarily by the chelate chelifores of sea spiders and the chelicerae of euchelicerates; see Dunlop and Arango (2005) for a review. Recent debate has focused on whether sea spiders are indeed the sister-group of Euchelicerata, or of a clade named Cormogonida comprising all non-pycnogonid euarthropods. Edgecombe (2010) reviews these alternative scenarios in further detail. Significantly, chelifore/chelicera homology was challenged on neuroanatomical grounds by Maxman et al. (2005), although subsequent studies using both Hox gene data (Manuel et al., 2006) and morphology (Brenneis et al., 2008) continue to support the traditional usage of chelate (a1) head appendages as the most convincing diagnostic character for Chelicerata. Further details of arthropod head appendages, and their homology between lineages, can be found in Scholtz and Edgecombe (2006), and references therein.

Sea spiders can potentially be traced back to the late Cambrian (Furongian epoch: Tables 1 and 2). If sea spiders are chelicerates and if they do have a Cambrian record (see 4.2), they jointly represent the oldest occurrence of Chelicerata *s.l.* They are roughly coeval with fossil resting traces which appear to have been made by a chasmataspid-like animal (see 4.5) assignable to the euchelicerate branch, and which again date from the end of the Cambrian. None of the early or mid Cambrian arachnomorphs can be explicitly referred to Chelicerata, thus on current evidence the chelicerate fossil record probably dates back at least 500 million years.

4.2. *Pycnogonida (Cambrian–Recent)*

Sea spiders are entirely marine and are defined by a suite of autapomorphies (Dunlop and Arango, 2005) such as the proboscis, unique oviger appendages, general reduction of the body and the displacement of organ systems into the legs. Their unusual appearance has led to difficulties in placing them phylogenetically (see 4.1). The oldest putative sea spiders are a series of phosphatised larval instars (Fig. 2A) from the late Cambrian Orsten of Sweden (Waloszek and Dunlop, 2002). Probably at a post-protonymphal stage, these fossils are notable for preserving vestiges of what look like pre-chelicerate appendages and gnathobase-like elements on the two postcheliceral larval limbs. In a holistic approach to sea spider evolution, Bamber (2007) excluded the Orsten fossils from Pycnogonida. This was based partly on the pre-chelicerate elements alluded to above. These could, however, just be a plesiomorphic remnant of the euarthropod ground plan; see e.g. Scholtz and Edgecombe (2006: 406). Bamber's other non-pycnogonid feature is a misinterpretation: he claimed (p. 301) that the larval limbs were biramous, but this is not the case in the original description.

The second oldest sea spiders come from the Silurian Herefordshire Konservat-Lagerstätte in England (Siveter et al., 2004) and are followed by a suite of taxa from the Early Devonian Hunsrück Slate of Germany (Bergström et al., 1980; Poschmann and Dunlop, 2006). These assemblages are interesting in that some of the early sea spiders retain the presumably plesiomorphic feature of a longer, segmented trunk behind the walking legs, and in two cases retain either a lanceolate or a flagelliform telson. The name Pycnogonida is now conventionally used to refer to all sea spiders,

living and extinct. The hypothesis of Bergström et al. (1980) envisaged the Hunsrück fossils forming a succession of extinct stem-group taxa which first lose the telson and then successively reduce the trunk leading up to a crown-group Pantopoda – defined here by the reduction of the body behind the last pair of limbs to a small tail end. Thus one Hunsrück fossil, and all living sea spiders, were traditionally assigned to Pantopoda.

Subsequent studies suggest that the base of the pycnogonid tree is rather more complicated – compare e.g. Siveter et al. (2004), Poschmann and Dunlop (2006), Bamber (2007) and Arango and Wheeler (2007: Fig. 1) – whereby Palaeozoic and extant genera often resolve mixed amongst each other without a clear sequence of character transformations. This raises the question of whether Pantopoda is still as a useful concept and even if it is retained it would either be Silurian–Recent or Devonian–Recent, depending on which fossils are eventually included. The post-Palaeozoic record of Pycnogonida is very poor. Published reports of Jurassic sea spiders from Solnhofen in Germany are misidentified crustacean larvae, but genuine Mesozoic Pycnogonida have been described from the Jurassic of La Voulte-sur-Rhône in France by Charbonnier et al. (2007). These fossils were tentatively assigned to the extant families Ammotheidae, Colossendeidae and Endeidae.

4.3. *Euchelicerata (Cambrian–Recent)*

Euchelicerata was established by Weygoldt and Paulus (1979) to encompass xiphosurans, eurypterids and arachnids. It seems to be one of the most stable clades in arthropod phylogeny. Like Chelicerata *s.l.*, the oldest record of Euchelicerata is the late Cambrian sequence of chasmataspid resting traces (see 4.5). These impressions explicitly preserve one of Weygoldt and Paulus' defining characters of Euchelicerata, namely the presence of plate-like opercula on the ventral surface of the opisthosoma (Dunlop et al., 2004a: Figs. 9 and 10). Traditionally, euchelicerates were divided into a largely terrestrial Arachnida and an aquatic Merostomata (i.e. horseshoe crabs and the extinct eurypterids); although this approach has been criticised by, e.g., Kraus (1976) for being ecological rather than explicitly phylogenetic in nature.

Weygoldt and Paulus (1979) introduced an alternative clade, Metastomata, for (Eurypterida + Arachnida). This hypothesis implies a questionable homology between the plate-like and perhaps appendage-derived metastoma of eurypterids – a feature also seen in chasmataspidids – and the sternum of arachnids. Nevertheless, eurypterids and arachnids were also recovered together by Shultz (1990) and Giribet et al. (2002: Fig. 6), but the name Metastomata has not become established in the literature. In his latest analysis, Shultz (2007: Fig. 1) was not able to offer any resolution between Xiphosura, his Eurypterida *s.l.* (see 4.6) and Arachnida, thus these basal divisions within Euchelicerata merit further investigation.

A further fossil arthropod worth mentioning is the enigmatic *Offacolus* from the Herefordshire Lagerstätte (Orr et al., 2000). Reconstructed from serial sections, it also has plate-like opisthosomal opercula which would support its referral to Euchelicerata. Interestingly, *Offacolus* appears to retain biramous postcheliceral limbs throughout the prosoma – a feature restricted today to the flabellum on the last walking leg of horseshoe crabs. Dunlop (2006: Fig. 13) suggested that this Silurian fossil could resolve at the very base of Euchelicerata.

4.4. *Order Xiphosura (Ordovician–Recent)*

Horseshoe crabs are widely cited as classic examples of living fossils and their body form and development via a trilobite larva are largely responsible for the idea that chelicerates and trilobites

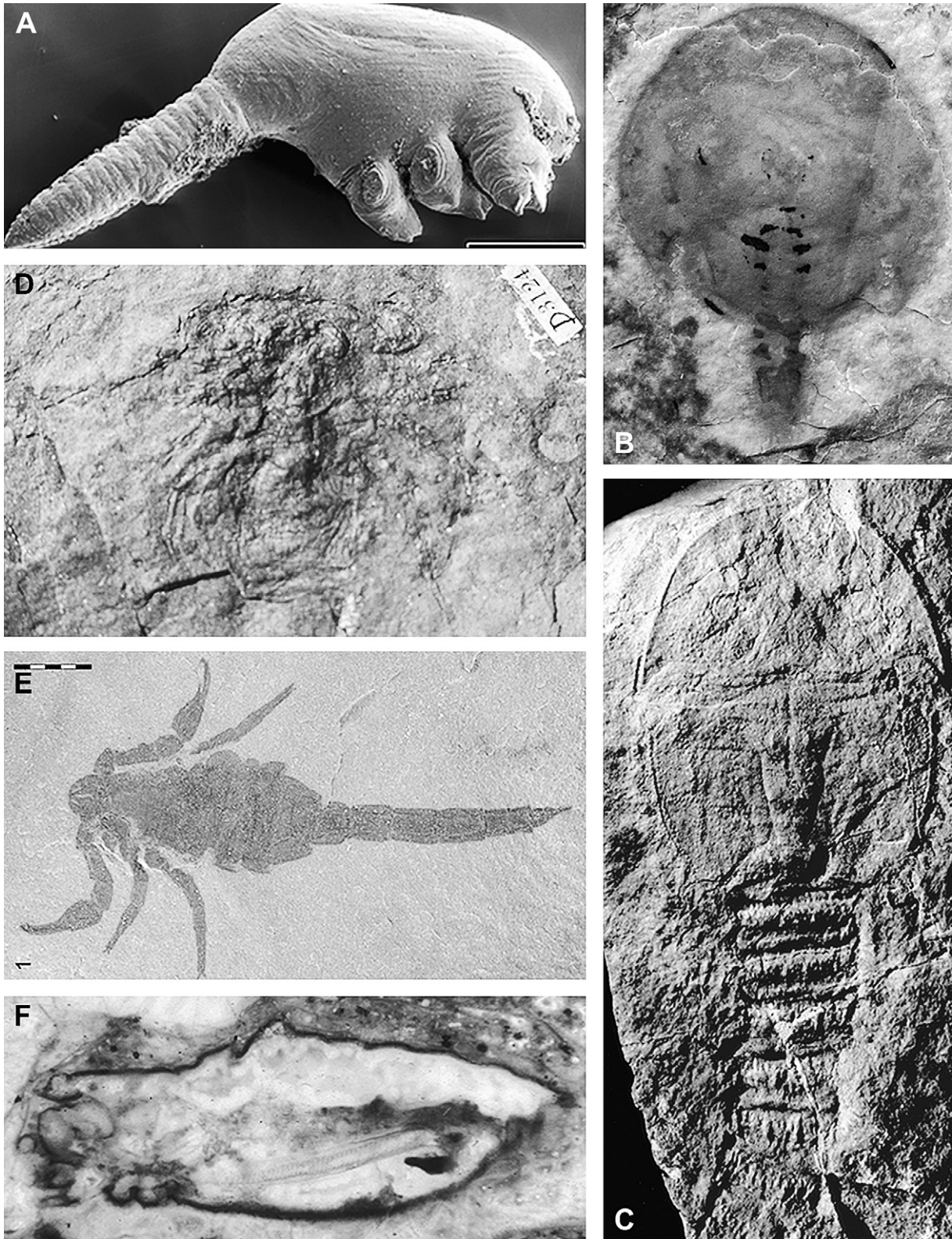


Fig. 2. Oldest examples of fossil Pycnogonida, the ‘merostome’ orders and Stethostomata. (A) Scanning electron micrograph of *Cambropycnogon klausmuelleri* Waloszek and Dunlop, 2002 (Pycnogonida) from the late Cambrian (Fungorian) Orsten of Sweden; image courtesy of Dieter Waloszek, Ulm. (B) *Lunataspis aurora* Rudkin et al., 2008 (Xiphosura: Xiphosurida) from the Ordovician of Manitoba, Canada; image courtesy of David Rudkin and Graham Young. (C) *Chasmataspis laurencii* Caster and Brooks, 1956 (Chasmataspidida) from the mid Ordovician of Tennessee, USA. Older resting impressions of a similar looking animal are known from the Late Cambrian. (D) *Brachyopterus stubblefieldi* Störmer, 1951 (Eurypterida) from the Ordovician of Wales; image courtesy of James Lamsdell. The photo shows the original condition of the specimen which is now encased in resin rendering further study very difficult. (E) *Proscorpio osborni* (Whitfield, 1885) (Scorpones) from the late Silurian of New York, USA. A slightly older mid Silurian species is known from Scotland, but is not well preserved. (F) Longitudinal section through the body of *Eophalangium sheari* Dunlop et al., 2004a,b,c (Opiliones: Eupnoi) from the early Devonian Rhynie chert of Scotland showing internal features like the ovipositor; image courtesy of Hagen Haas, Münster. Specimen size in A 0.25 mm, B 20 mm, C 60 mm, D 80 mm (in life), E 22 mm, F 5.7 mm.

might be related (see 3.1). Only four living species are known, but they occur sporadically throughout geological time. Historically, a number of problematic fossils were assigned to Xiphosura, including aglaspids (see 3.2), chasmataspids (see 4.5) and specimens known only from isolated head shields. Xiphosura was traditionally divided into two suborders: Synziphosura and Xiphosurida. The (largely Cambrian) problematic fossils were excluded from Xiphosura by Anderson and Selden (1997) who further demonstrated that the synziphosurines are not a clade, but rather a paraphyletic grade or stem-group of basal horseshoe crabs leading up to the crown-group Xiphosurida. This crown-group was redefined as horseshoe crabs in which the previously articulated opisthosomal segments have fused together into a single dorsal plate: the thoracetrone, or tergum *sensu* Shultz (2001). In Anderson and Selden's (1997: Fig. 4) scheme horseshoe crabs first appear properly in the Silurian, with a late Devonian genus forming the sister group of Xiphosurida – the crown-group itself dating back to the early Carboniferous.

This neat stratigraphic sequence of phylogeny was recently overturned by the surprising discovery of an Ordovician (Ashgill, ca. 445 Ma) xiphosurid (Rudkin et al., 2008). Clearly closer to modern Xiphosura rather than synziphosurines in morphology (Fig. 2B), it is both the oldest member of the crown-group and at the same time the oldest known horseshoe crab. By contrast the oldest synziphosurine currently comes from the Silurian (Llandovery, Telychian, ca. 428–433 Ma) of Wisconsin (Moore et al., 2005b) and this stem-group assemblage can now be traced up into the Early Carboniferous (Moore et al., 2007).

Detailed studies of the extant genus *Limulus* show that the first opisthosomal and part of the second opisthosomal segments have actually become incorporated into the prosoma (Shultz, 2001) to form a cephalothorax (not to be confused by the more general use of this term for the prosoma of spiders). Synziphosurines seem to retain this first opisthosomal segment as a separate tergite, albeit often reduced to a microtergite (Anderson and Selden, 1997). As noted by Moore et al. (2005b), this has implications for homologising segment counts between taxa. It is not entirely clear at which node in the tree encephalization of the first opisthosomal segment occurred, but Rudkin et al. (2008) suggested that it may already have happened in their Ordovician fossil. In well preserved synziphosurines (Moore et al., 2005a) the seventh pair of appendages (i.e. opisthosomal segment 1) is retained as fully developed walking legs; and is thus functionally part of the prosoma. These legs are reduced to the chilaria of modern horseshoe crabs. Many synziphosurines also express a short postabdomen of three segments – a character also seen in the Ordovician xiphosurid – which implies that such a postabdomen is part of ground pattern in horseshoe crabs.

Within the crown-group, xiphosurids are found quite commonly in the late Carboniferous Coal Measures. Most of these forms show segmentation on the fused thoracetrone. The path to fully modern horseshoe crabs begins in the Carboniferous with the oldest members of the superfamily Limuloidea (e.g. Racheboeuf et al., 2002). Fossils assignable to the extant family Limulidae are known from the Triassic onwards, the best known being the often beautifully preserved *Mesolimulus* from Solnhofen in Germany. Mesozoic Xiphosura were reviewed by Hauschke and Wilde (1991) and there is a handful of fully modern-looking Cenozoic examples.

4.5. Order Chasmataspidida (?Cambrian–Devonian)

Chasmataspids are an extinct order of presumably aquatic euechelicerates which were originally interpreted as unusual horseshoe crabs (see 4.4). The group can be characterised by the unique character of an elongate, nine-segmented postabdomen. Nevertheless, there are some doubts about its monophyly given

that the oldest body fossil is more xiphosuran-like in habitus, while the younger taxa share obvious synapomorphies with eurypterids like the metastoma plate covering the posterior leg coxae and an opisthosoma with a median abdominal appendage. As a consequence of this, phylogenetic analyses have recovered chasmataspids as paraphyletic with respect to eurypterids (Tetlie and Braddy, 2004; Shultz, 2007) – although these two studies differed in the details of their placement. The oldest potential record of Chasmataspidida is the series of ventral resting impressions with the characteristic body tagmosis found in the late Cambrian Hickory Sandstone of Texas. The oldest body fossils (Fig. 2C) come from the Ordovician of Tennessee (Caster and Brooks, 1956; Dunlop et al., 2004a) and there are further records from the Silurian (Tetlie and Braddy, 2004) and Devonian of Europe and Russia. The youngest chasmataspid comes from the mid-Devonian of Scotland (Anderson et al., 2000).

4.6. Order Eurypterida (Ordovician–Permian)

Eurypterids (or sea scorpions) are extinct chelicerates which formed a significant group during the mid Palaeozoic. Morphologically diverse, sometimes reaching huge size (Braddy et al., 2007) and with more than a passing resemblance to scorpions, they were traditionally diagnosed by the possession of a median abdominal appendage and a metastoma plate. The discovery of both these characters in at least some Chasmataspidida (see 4.5) contributes to the current uncertainty about whether eurypterids and chasmataspids should be treated as a single clade. Shultz (2007), for example, combined them as Eurypterida *s.l.*, albeit based on analysing only a limited sample of eurypterids. Tollerton (1989), following Størmer and Waterston (1968), attempted to establish one of the more unusual-looking eurypterid lineages – the large, truncated, sweep-feeding Cryotoctenida – as a separate order. However, this involved simply accumulating apomorphies without demonstrating that retaining cryotoctenids within the traditional Eurypterida would render the group paraphyletic. Eurypterid phylogeny, distribution and diversity over geological time were reviewed in some detail by Tetlie (2007).

Reports of late Cambrian eurypterids (e.g. Chlupáč, 1995) are probably misidentifications of other early Palaeozoic groups like Aglaspida; see also comments in Van Roy (2006). The oldest unequivocal eurypterid (Fig. 2D) comes from the Ordovician (Sandbian, ca. 455–460 Ma) of Wales (Størmer, 1951). In fact Ordovician eurypterids are actually quite rare and many supposed taxa of this age have now been shown to be pseudofossils (Tollerton, 2004) – sedimentary structures which fortuitously resemble arthropod material. As a group, eurypterids appear to have peaked in the Silurian, before declining over the Devonian and Carboniferous, while at the same time shifting from full marine to more brackish, estuarine environments. However, as elaborated by Lamsdell and Braddy (2009), eurypterids can be broadly divided into the basal stylonurines and the more derived eurypterines; the latter being swimming forms in which the last pair of legs is modified into a paddle. Both clades evolved gigantism, but differ markedly in their overall geological histories, with the eurypterines peaking earlier and then possibly outcompeted by fish. The youngest records are stylonurines from the Late Permian (ca. 248–256 Ma) of Russia (Ponomarenko, 1985).

Some eurypterids, particularly the families Mixopteridae and Carcinomatidae, are remarkably scorpion-like in their gross morphology and a number of studies have suggested that scorpions and eurypterids could be sister-taxa (Kjellesvig-Waering, 1986; Dunlop and Webster, 1999), which would render Arachnida paraphyletic. A putative eurypterid–scorpion clade would extend back to the Ordovician (Sandbian, ca. 460 Ma), but this hypothesis has

not been recovered under parsimony (Giribet et al., 2002; Shultz, 1990, 2007). The most scorpion-like eurypterids – complete with a narrow tail and a curved, sting-like telson – are actually quite derived within Eurypterida (Tetlie, 2007). Although Shultz (2007) criticised previous proponents of the scorpion–eurypterid hypothesis, some effort seems to have been made *a priori* in his own study to avoid scoring similarities between scorpions and eurypterids as homologous character states. For example, a thirteen-segmented opisthosoma in which the last five form a narrow postabdomen occurs in scorpions, but the same tagmosis pattern was not scored for eurypterids on the grounds that Raw's (1957) arguments for thirteen segments were unconvincing, which is true. Twelve segments were thus assumed for eurypterids, but explicit figured evidence for a reduced thirteenth segment in eurypterids in a more recent study (Dunlop and Webster, 1999: Figs. 2 and 3) was simply omitted from Shultz's character discussion.

4.7. *Arachnida* (Silurian–Recent)

Most cladistic studies have recovered arachnids as a natural group (Weygoldt and Paulus, 1979; Shultz, 1990, 2007) and characters supporting a monophyletic Arachnida were detailed by Shultz (1990, 2001). These include a reduced head shield and loss of the cardiac lobe, an anteroventrally directed mouth and loss of the proventricular crop, absence of appendages (at least in adults) on the first opisthosomal segment, presence of slit sensilla and various details of the musculature. It should be added that under some parameters of analysis horseshoe crabs or sea spiders were dragged up tree into Arachnida (Giribet et al., 2002: Figs. 5 and 6), and the scorpion/eurypterid situation has been noted above (see 4.6). The balance of evidence currently favours arachnid monophyly and Shultz (2007) recognised four major divisions – Stomothecata, Haplocnemata, Acaromorpha and Pantetrapulmonata – but with little resolution between these clades. Thus, like the base of Euchelicerata, early radiations among Arachnida appear obscure. Given that a putative Ordovician mite (see 4.15) remains controversial, the oldest unequivocal arachnid is a Silurian scorpion (see 4.9).

4.8. *Stomothecata* (Silurian–Recent)

Stomothecata was introduced by Shultz (2007) to encompass (Scorpiones + Opiliones). The clade was defined primarily on the presence of a stomotheca, a preoral cavity formed from the coxapophyses (or endites) projecting from the coxae of the pedipalps and the first walking leg – as well as some details of mouthpart musculature. The inclusion of scorpions dates this clade to at least the Silurian (see 4.9). Scorpions and harvestmen do not particularly resemble one another, and this has caused some resistance in accepting that they might be closely related (Weygoldt, 1998; Dunlop and Webster, 1999). Fossil data are not supportive of Stomothecata and is an example of the conflict which can occur when stem-group fossils differ from the crown-group. Specifically, many Palaeozoic scorpions show a much simpler arrangement of the coxo-sternal region with no evidence for coxapophyses (Kjellesvig-Waering, 1986; Dunlop et al., 2008a). This implies that the stomotheca could be homoplastic, evolving independently within the scorpion and harvestmen lines. Shultz's (2007) speculation that early scorpions may have borne a stomotheca in the form of soft cuticular lips on their coxae – which have simply not been preserved – cannot be tested against the currently known fossils.

4.9. *Order Scorpiones* (Silurian–Recent)

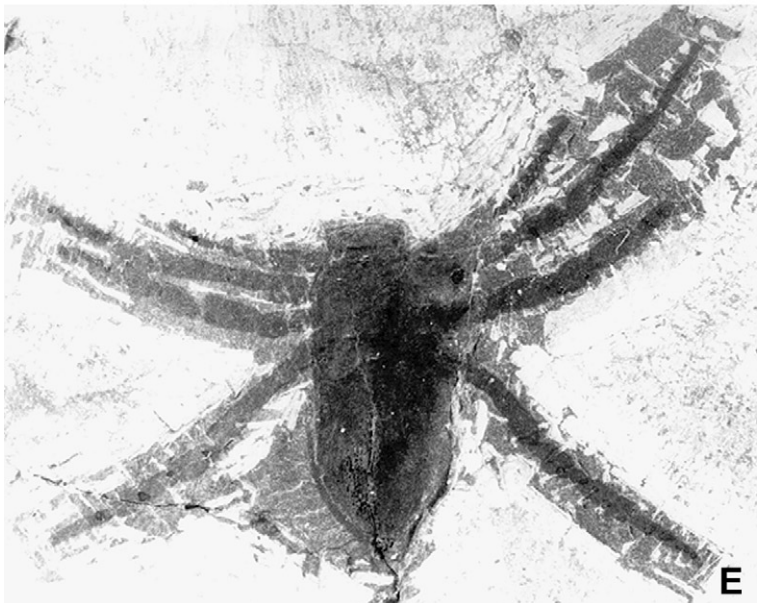
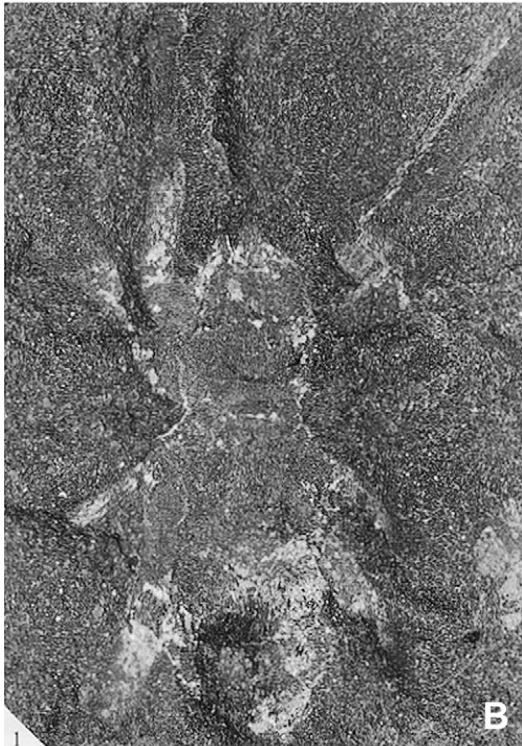
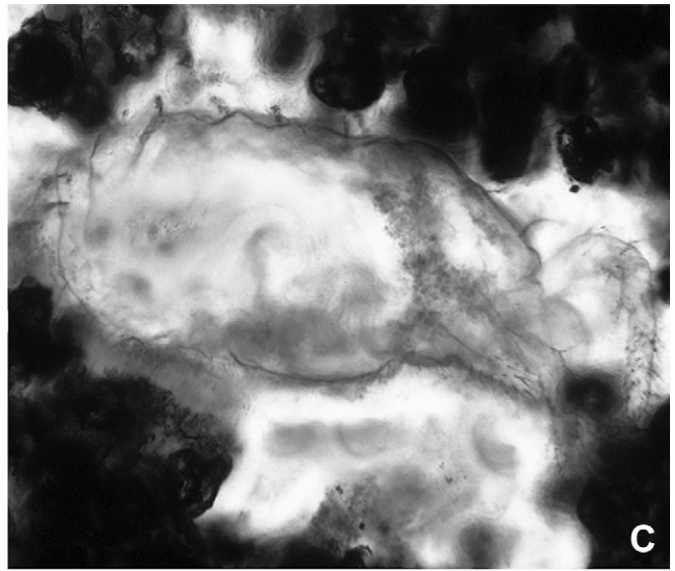
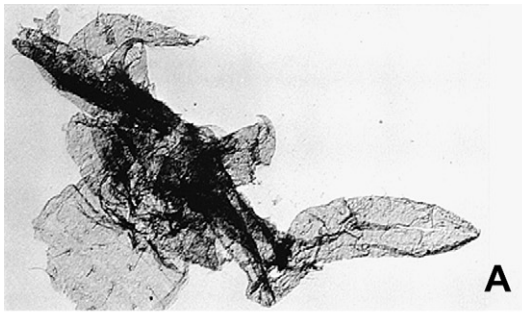
Scorpions are easily recognised by their combination of pedipalpal claws, a metasoma (tail) terminating in a stinger and

comb-like pectines on the underside of the body. There are currently more Palaeozoic species known than Mesozoic or Cenozoic ones. Our understanding of early scorpion evolution suffers from the typological scheme proposed by Kjellesvig-Waering (1986) in the most comprehensive monograph of the group to date. This posthumous work has proved problematic, with his principal division into a presumed aquatic lineage (Branchioscorpionina) – including the majority of the Palaeozoic species – and the terrestrial Neoscorpionina, first appearing in the late Carboniferous. Kjellesvig-Waering also raised numerous, often monotypic, higher taxa rendering his whole classification cumbersome and top-heavy. He also had a habit of applying questionable morphological observations (e.g. putative gills or gill opercula) from a few fossils to all animals thought to belong to a particular group. Whether early scorpions really were aquatic has been critically discussed by Scholtz and Kamenz (2006). They argued that detailed homologies in lung morphology between scorpions and other arachnids favour a single (terrestrial) common ancestor. This hypothesis still has to contend with, for example, fully articulated fossil scorpions found in the marine Devonian Hunsrück Slate environment. Poschmann et al. (2008) restudied putative (and possibly secondarily derived?) structures in the Devonian scorpion genus *Waeringoscorpio* which closely resemble the external gills of modern aquatic insects.

Kjellesvig-Waering's classification has not generally been recovered by subsequent cladistic analyses (Stockwell, 1989; Jeram, 1994a,b, 1998). Unfortunately, these author's results have not been fully translated into formal systematic nomenclature, although Dunlop et al. (2008a) did begin to synonymize some apparently superfluous family names. Drawing on published cladograms, a developing broad pattern (see e.g. Dunlop et al., 2007: Fig. 3) recognises a basal group Palaeoscorpionina, a more derived lineage Mesoscorpionina and their sister group, Neoscorpiones including the scorpion crown-group Orthosterni. Further work is needed to test the monophyly and exact composition of these assemblages, but an outline history of the main events in early scorpion evolution can be suggested follows.

A supposed Ordovician scorpion from Colorado mentioned by Fisher (1978: Fig. 7) is wholly unreliable, being based on an isolated head shield only. The oldest unequivocal scorpion comes from the mid Silurian Pentland Hills of Scotland (Laurie, 1899) and is closely followed by further examples from the late Silurian of Europe and North America (see e.g. Dunlop et al., 2008a) (Fig. 2E). These palaeoscorpions are characterised by a simple coxo-sternal region and persist into the Carboniferous (Leary, 1980). Mesoscorpions show the clear development of coxapophyses (and thus the stomotheca; see 4.8). They first appear in the Devonian (Jeram, 1998) and make up most of the finds from the Carboniferous (Jeram, 1994a). From the mesoscorpions comes first unequivocal record of book lungs. The lineage persists into the Triassic, where a rich vein of material is known from the English West Midlands (Wills, 1947), and may even extend into the Jurassic (Dunlop et al., 2007). Their sister-group is the Neoscorpiones, characterised by features like reduced lateral eyes, with two lineages: the extinct Palaeosterni and the crown-group Orthosterni.

The oldest Orthosterni – defined as scorpions bearing spiracles within the sternite, as opposed to at its margins – comes from the late Carboniferous and this final transition to fully modern lineages was documented by Jeram (1994b). The oldest fossils potentially assignable to a living superfamily (Buthoidea) were reported from the Early Triassic (ca. 245–251 Ma) Bundsandstein of France (Lourenço and Gall, 2004); although this placement is in dispute. The oldest unequivocal members of living families (Hemiscorpiidae, Chactidae) come from the Early Cretaceous Crato Formation (Menon, 2007). An increasing number of Cenozoic records have been published in recent years, largely from Baltic



amber and almost always comprising extinct genera within the basal family Buthidae (e.g. Lourenço et al., 2005).

4.10. Order Opiliones (Devonian–Recent)

Harvestmen are defined by a number of autapomorphies, such as repugnatorial glands in the prosoma and tracheae opening on the genital segment, and can be divided into four quite distinct suborders (see e.g. Giribet et al., 2002, 2009). The oldest harvestman comes from the Early Devonian Rhynie Chert of Scotland (Dunlop et al., 2004c). This material is remarkably well preserved (Fig. 2F) and includes details like the tracheal tubes as well as two further typical harvestman features: the penis of the male and the ovipositor of the female. The Rhynie fossils were assigned to the Eupnoi clade which includes the common ‘daddy long-legs’ type of harvestmen today. A handful of Carboniferous fossils are known and include what is probably oldest member of the Dyspnoi clade. Other late Carboniferous Coal Measures harvestmen have been assigned to extinct (dypsnooid?) families (Petrunkevitch, 1955), although the validity and placement of these families are questionable since they are defined, in part, on patterns of coxo-sternal morphology radically different from the morphology seen in all other harvestman. The extinct Carboniferous order Kustarachnida was based on misidentified harvestman fossils.

Only four Mesozoic harvestmen have been formally named, the oldest being two eupnoids from the Jurassic of Daohugou in China (Huang et al., 2009); one of which is assignable to Sclerosomatidae as the oldest example of an extant family. A dypsnooid (Giribet and Dunlop, 2005) and a cyphophthalmid (Poinar, 2008) are known from Late Cretaceous Myanmar amber. Most records of fossil harvestmen come from Cenozoic ambers and all four suborders have been recorded. The oldest example of Laniatores comes from Baltic amber and was redescribed by Ubick and Dunlop (2005). Further laniatorids can be found in Dominican Republic amber (e.g. Cokendolpher and Poinar, 1998; summary in Kury, 2003) and all belong to modern New World genera. A further example of Cyphthophthalmi comes from the German Bitterfeld amber (Dunlop and Giribet, 2003). The age of this amber is in dispute, with the latest proposal being late Oligocene. Modern-looking eupnoids and dypsnooids are also present in both Baltic and Bitterfeld amber and most can be assigned to living genera. A detailed review of the harvestman fossil record – including taxa erroneously assigned to Opiliones – can be found in Dunlop (2007).

4.11. Haplocnemata (Devonian–Recent)

Haplocnemata is the second major division of the arachnids and embraces pseudoscorpions and solifuges. The name was introduced by Börner (1904). This group was also supported by van der Hammen (1989) and references therein who used an alternative name Apatellata. This is less appropriate as studies of limb musculature showed that these arachnids do possess a patella in the legs; see e.g. Shultz (1990). Haplocnemata has been recovered in most cladistic studies (Weygoldt and Paulus, 1979; Shultz, 1990, 2007; Wheeler and Hayashi, 1998). It is supported by characters like two-articled chelicerae with a ventral insertion of the movable

finger, a projecting beak (or epistomal–labral plate) bearing the mouth, elongate patellae in the legs, tarsi ending in an adhesive pad or pulvillus and tracheal openings on the third and fourth opisthosomal segments. The inclusion of pseudoscorpions (see 4.12) dates this clade to at least the mid-Devonian. Note that at least the projecting beak and cheliceral fang orientation are potentially also present in mites. Alberti and Peretti (2002) discussed the fact that male genitalia and sperm morphology do not support Haplocnemata, yielding instead characters shared by solifuges and actinotrichid mites.

4.12. Order Pseudoscorpiones (Devonian–Recent)

Pseudoscorpions resemble scorpions without a tail and can be explicitly defined by characters like cheliceral silk glands. The oldest pseudoscorpion (Fig. 3A) is a remarkable find from the mid-Devonian of Gilboa near New York, USA (Schawaller et al., 1991), which even preserves the characteristic cheliceral spinning apparatus. It was assigned to its own extinct family within the Devonian–Recent suborder Epiocheirata; which encompasses those families with more plesiomorphic traits. Further epiocheirate pseudoscorpions are found in Baltic (e.g. Henderickx et al., 2006) and Dominican Republic amber. The second suborder, Iocheirata, goes back to at least the Early Cretaceous based on records from Myanmar amber (Cockerell, 1917). Again, there are further examples of iocheirates from Baltic and Dominican amber. All can be assigned to extant families and to a mixture of both modern and exclusively fossil genera. At least one Dominican amber pseudoscorpion has been treated as indistinguishable from a living Caribbean species (Judson, 1998). Phoretic behaviour, in which pseudoscorpions attach themselves to the limbs of flies or other arthropods, is well known from various representatives of modern families. It has also been observed in amber pseudoscorpions (e.g. Judson, 2004). All fossil taxa are included in the online catalogue of Harvey (2009).

4.13. Order Solifugae (Carboniferous–Recent)

Solifuges, or camel spiders, have numerous distinctive characters. These include maleolli – ventral sensory organs at the base of the last two pairs of legs – an adhesive organ at the tip of the pedipalp and a male flagellum on the dorsal surface of the chelicera. The oldest unequivocal solifuge (Fig. 3B) comes from the late Carboniferous of Mazon Creek, Illinois, USA (Petrunkevitch, 1913), but is preserved in little more than outline and cannot be assigned to any particular modern group (Selden and Shear, 1996). It is interesting in that it comes from a presumably humid coal forest environment, whereas modern solifuges tend to be associated primarily with arid habitats today. The next youngest example, which is also the first solifuge assignable to an extant family (Ceromidae), comes from the Early Cretaceous Crato Formation of northeastern Brazil (Selden and Shear, 1996). These Crato solifuges are well preserved and show that ceromids were originally a Gondwanan family, but one which must have since died out in South America and is restricted today to southern Africa. Fossil Solifugae are also known from Baltic (Dunlop et al., 2004b) and Dominican Republic amber (Poinar and Santiago-Blay, 1989). These

Fig. 3. Oldest examples of fossil Haplocnemata, Acaromorpha and the enigmatic order Phalangiotarbita. (A) *Dracochela deprehendor* Schawaller et al., 1991 (Pseudoscorpiones) from Gilboa, New York, USA; reproduced from Schawaller et al. (1991). (B) *Protosolpuga carbonaria* Petrunkevitch, 1913 (Solifugae) from the Late Carboniferous Coal Measures of Mazon Creek, USA; reproduced from Selden and Shear (1996). (C) Mite, probably assignable to *Protospeleorchestes pseudoprotacarus* Dubinin, 1962 (Acari: Actinotrichida: Endeostigmata), from the early Devonian Rhynie cherts of Scotland; image courtesy of Hagen Haas, Münster. (D) *Cornupalpatum burmanicum* Poinar and Brown, 2003 (Acari: Anactinotrichida: Ixodida) from late Cretaceous Burmese amber; image courtesy of George Poinar jr, Oregon. (E) *Curculioides adompha* Brauckmann, 1987 (Ricinulei) from the Late Carboniferous Coal Measures of Hagen-Vorhalle, Germany; image courtesy of Carsten Brauckmann, Clausthal and Lutz Koch, Ennepetal. (F) *Devonotarbus hombachensis* Poschmann et al., 2005 (Phalangiotarbita) from the Early Devonian of the Rhenish Massif, Germany; image courtesy of Markus Poschmann, Mainz. Specimen size in A 0.2 mm (body incomplete), B 13 mm, C 0.5 mm, D 3.3 mm, E 12 mm, F 6.5 mm.

were assigned to the extant families Daesiidae and Ammotrechidae respectively. This is biogeographically consistent with the modern distribution of these families. Daesiids are quite widely distributed, including southern Europe, while ammotrechids are restricted to the Americas.

4.14. *Acaromorpha* (Devonian–Recent)

Acaromorpha is the third major division and encompasses ricinuleids and both lineages of mites (see 4.15, 4.16). It has been recovered in most phylogenies (Weygoldt and Paulus, 1979; Shultz, 1990, 2007; Wheeler and Hayashi, 1999) and is principally supported by the presence of hexapodal larvae. In both groups the hatching instar has only six legs and acquires the full complement of eight later in its postembryonic development. A more problematic character – or character complex – is the gnathosoma; see comments in Dunlop and Alberti (2008). This distinct, movable, anterior region of the body bears the chelicerae, mouth lips and pedipalps. Some authors have scored this as present in mites and ricinuleids; others treat it as unique for mites only (Weygoldt and Paulus, 1979). Acaromorpha can potentially be dated to the Ordovician, and unequivocally to the Early Devonian, through the inclusion of Actinotrichida (see 4.15).

As an alternative to Acaromorpha, ricinuleids also share characters with the extinct trigonotarbid (see 4.21) such as divided opisthosomal tergites and a locking mechanism between the prosoma and opisthosoma. Scoring these, Giribet et al. (2002) recovered (Ricinulei + Trigonotarbid), although this was not the most parsimonious result in Shultz (2007). A further potential synapomorphy shared by ricinuleids and trigonotarbids has recently come to light (Dunlop et al., 2009): a tiny claw at the distal end of the pedipalp. Whether this is enough to invalidate Acaromorpha is a moot point, but it is an example of how considering fossil data might help to place a difficult modern group. A putative ricinuleid–trigonotarbid clade would date back to the late Silurian.

4.15. *Order Actinotrichida* (Devonian–Recent)

It has now become commonplace to treat mites (Acari) as two distinct clades (cf. Alberti and Michalik, 2004; Dunlop and Alberti, 2008; and references therein). These are usually named Actinotrichida (=Acariformes) and Anactinotrichida (=Parasitiformes s.l.). Historically, there has been considerable debate about whether Acari is monophyletic; van der Hammen (1989) and references therein was probably the most active proponent of diphyly, drawing on earlier work by François Grandjean in particular. However van der Hammen's rejection of cladistic methodology limited the wider impact of his views. Nevertheless, the most recent analysis (Shultz, 2007) recovered the two main mite clades as paraphyletic with respect to ricinuleids. The two lineages are thus treated separately here. They also have quite different fossil records, an older overview of which can be found in Bernini (1986). Mites are the most diverse living arachnids, but in general they seem to be rather under-represented in the fossil record, at least in terms of formally named species. This is largely due to a lack of qualified workers in this field. Fossil mites are reported quite frequently from amber for example, but are usually only identified down to the major taxa.

Actinotrichids are extremely diverse both in their morphology and ecology, but can be broadly divided into two main groups (e.g. Dunlop and Alberti, 2008: Fig. 2), namely Trombidiformes and Sarcoptiformes. Given the uncertainty about the Ordovician record (see below), the oldest unequivocal actinotrichid mites come from the Early Devonian Rhynie Chert of Scotland (Hirst, 1923). Originally treated as single species, they were subsequently recognised (Dubinin, 1962) as multiple taxa belonging to the basal sarcoptiform

lineage Endeostigmata (Fig. 3C) and to a further trombidiform lineage, Eupodina. A mid-Devonian record from Gilboa (Kethley et al., 1989) is also an endeostigmatid. There then follows a considerable hiatus until members of other trombidiform taxa begin to appear with some regularity in the Cretaceous. A detailed review is beyond the scope of this study, but the oldest occurrence of all mite families with a fossil record is tabulated in Dunlop and Selden (2009). Some of the more important trombidiform lineages dating back to the Cretaceous include Prostigmata (e.g. Zacharda and Krivoluckij, 1985) and its constituent Parasitengona and Trombidia clades. Water mites (Hydracarina) also belong to the parasitengonids, but have a very poor record with only one convincing (Miocene) record (Cook in Palmer, 1957). Among the Eupodina there are Cretaceous bdellid (snout) mites (Ewing, 1937) and even Miocene leaf galls potentially assignable to the tiny and otherwise difficult to fossilise eriophryid (gall) mites (Ambrus and Hably, 1979). Baltic amber yields the most diverse assemblage of Cenozoic trombidiform mites.

Sarcoptiformes mostly comprises oribatids and astigmatids; although oribatids may be paraphyletic with respect to these astigmatids. Oribatida (=Cryptostigmata) are diverse and widespread. Many taxa live in soil and organic humus, although a wide spectrum of habitats has been recorded for this group. The oldest putative actinotrichid mite – indeed the oldest putative arachnid – is an oribatid (Bernini et al., 2002) from the Early Ordovician (Arenig ca. 475 Ma) of Sweden. Its sheer age, together with its tentative assignment to the fairly derived Brachypylina lineage, renders this find highly controversial. For this reason it is not formally adopted as the oldest actinotrichid record in Table 2. Bernini et al. argued that it is not a modern contaminant and suggested that it could have lived in organic debris washed up on the shoreline. The oldest unequivocal oribatids are members of extinct (basal) families known from the mid-Devonian of Gilboa (Norton et al., 1988). Subsequent finds from the Late Devonian and early Carboniferous have been referred to various basal living families (Subías and Arillo, 2002). Thanks to their typically highly sclerotised bodies, oribatids have the richest fossil record of any mite group. There are significant records from both Mesozoic amber and non-amber sediments, as well as numerous Cenozoic species (e.g. Heetoff et al., 2009), mostly from Baltic amber; see Krivolutsky and Druck (1986) for an overview. Some Baltic amber finds seem almost indistinguishable from modern oribatids, being distinguished from them only as subspecies bearing the name 'fossilis' (cf. Sellnick, 1919). Many oribatids have been found as subfossils in Quaternary peat samples or archeological deposits. All can be assigned convincingly to recent species and are useful in palaeoenvironmental reconstruction.

Finally, Astigmata includes groups like food and storage mites, house dust mites, fur and feather mites – specifically those causing mange and scabies. Widespread, but typically tiny and poorly sclerotised, they have an extremely poor fossil record with only two convincing representatives from Mexican Chiapas amber (Türk, 1963) and from Sicily (Pampaloni, 1902). Both are Neogene in age.

4.16. *Order Anactinotrichida* (Cretaceous–Recent)

Compared to actinotrichids, the anactinotrichid mites have a surprisingly poor fossil record. Taking each of the four major groups individually, Opilioacarida are known from Eocene Baltic amber (Dunlop et al., 2004b), as are Gamasida (=Mesostigmata) (e.g. Witaliński, 2000). Compared to the abundance of gamasids in soil and similar habitats today, the fact that only a handful of fossils have been found is surprising. It seems likely that more gamasids remain unrecognised and undescribed in various ambers. Holothyrid mites do not have a fossil record, but a number of fossil ticks

(Ixodida) are known and were reviewed by [de la Fuente \(2003\)](#). Both hard (Ixodidae) and soft ticks (Argasidae) are known, but the monotypic recent family Nutallellidae lacks a fossil record. The oldest hard ticks (Ixodidae) come from Myanmar amber (e.g. [Poinar and Brown, 2003](#)) (Fig. 3D) and there are younger records from Baltic amber ([Weidner, 1964](#)). The oldest soft tick (Argasidae) comes from Late Cretaceous New Jersey amber ([Klompen and Grimaldi, 2001](#)). All fossil anactinotrichid mites discovered thus far have been assigned to extant genera.

4.17. Order Ricinulei (Carboniferous–Recent)

Fossil ricinuleids have only been found in the late Carboniferous Coal Measures of Europe and North America (e.g. [Pocock, 1911](#); [Petrunkevitch, 1913](#)). They were fully revised by [Selden \(1992\)](#), who divided them into two suborders. The fossil Palaeoricinulei retains visible eyes. In one family the opisthosoma does not have the usual pattern of tergites, but instead is divided by a median sulcus. The first such fossils to be discovered – which predated the discovery of living ricinuleids – were misinterpreted as beetles. The recent suborder Neoricinulei has reduced eyes, visible as photoreceptive patches. The oldest ricinuleid comes from the late Carboniferous of Hagen-Vorhalle in Germany ([Brauckmann, 1987](#)) (Fig. 3E) and fossil taxa were also listed in the catalogue of [Harvey \(2003\)](#).

4.18. Order Phalangiotarbida (Devonian–Permian)

Phalangiotarbitids are an extinct and rather enigmatic arachnid order, sometimes referred to as Architarbitida in the older literature. They have an oval to torpedo-shaped body in which the carapace bears six eyes on an anterior tubercle. Their anterior opisthosomal segments are very short and crowded together, while at the terminal end of the opisthosoma there is, uniquely among arachnids, an apparently dorsal anal operculum. The legs are quite robust, but the pedipalps and mouthparts seem to be tiny and are thus poorly known from the available material. Phylogenetically, they have been compared both to harvestmen (Opiliones) and opilioacarid mites, with the most recent attempt to resolve their relationships ([Pollitt et al., 2004](#)) finding weak support for placing them close to the tetrapulmonate arachnids (see 4.22). [Shultz \(2007\)](#) did not include phalangiotarbitids in his analysis and until their mouthparts can be clearly seen, their affinities are likely to remain obscure. The oldest example is from the Early Devonian of Germany ([Poschmann et al., 2005](#)) (Fig. 3F). In this publication it was assigned to a Siegenian (ca. 407–411 Ma) age, although this term is no longer seen as standard and overlaps with the now more established Pragian–Emsian. Phalangiotarbitids can be quite common at some late Carboniferous Coal Measures sites ([Pocock, 1911](#); [Petrunkevitch, 1913, 1949](#); [Pollitt et al., 2004](#)). The youngest record comes from an early Permian Rotliegend locality in Germany ([Rössler et al., 2003](#)).

4.19. Order Palpigradi (Neogene–Recent)

Palpigrades are tiny, weakly sclerotised arachnids whose phylogenetic position has proved difficult to resolve. [Weygoldt and Paulus \(1979\)](#) placed them at the base of their lungless Apulmonata group and [Shultz \(1990\)](#) resolved them basal to his tetrapulmonate arachnids. In the latest scheme ([Shultz, 2007](#)) they do not fall clearly within any of his four major divisions. Despite palpigrades popular perception as primitive arachnids – thanks in part to their retention of a suite of probably plesiomorphic characters – they actually have the worst fossil record of any arachnid group. Reports of Jurassic palpigrades from Solnhofen in Germany are based on misidentified insects ([Delclòs et al., 2008](#)). The only genuine fossil

palpigrades come from the Neogene Onyx Marble of Arizona ([Rowland and Sissom, 1980](#)). The single species is also listed by [Harvey \(2003\)](#). Although recognisable as a palpigrade, it cannot be assigned convincingly to either of the two extant families based on the characters preserved.

4.20. Pantetrapulmonata (Silurian–Recent)

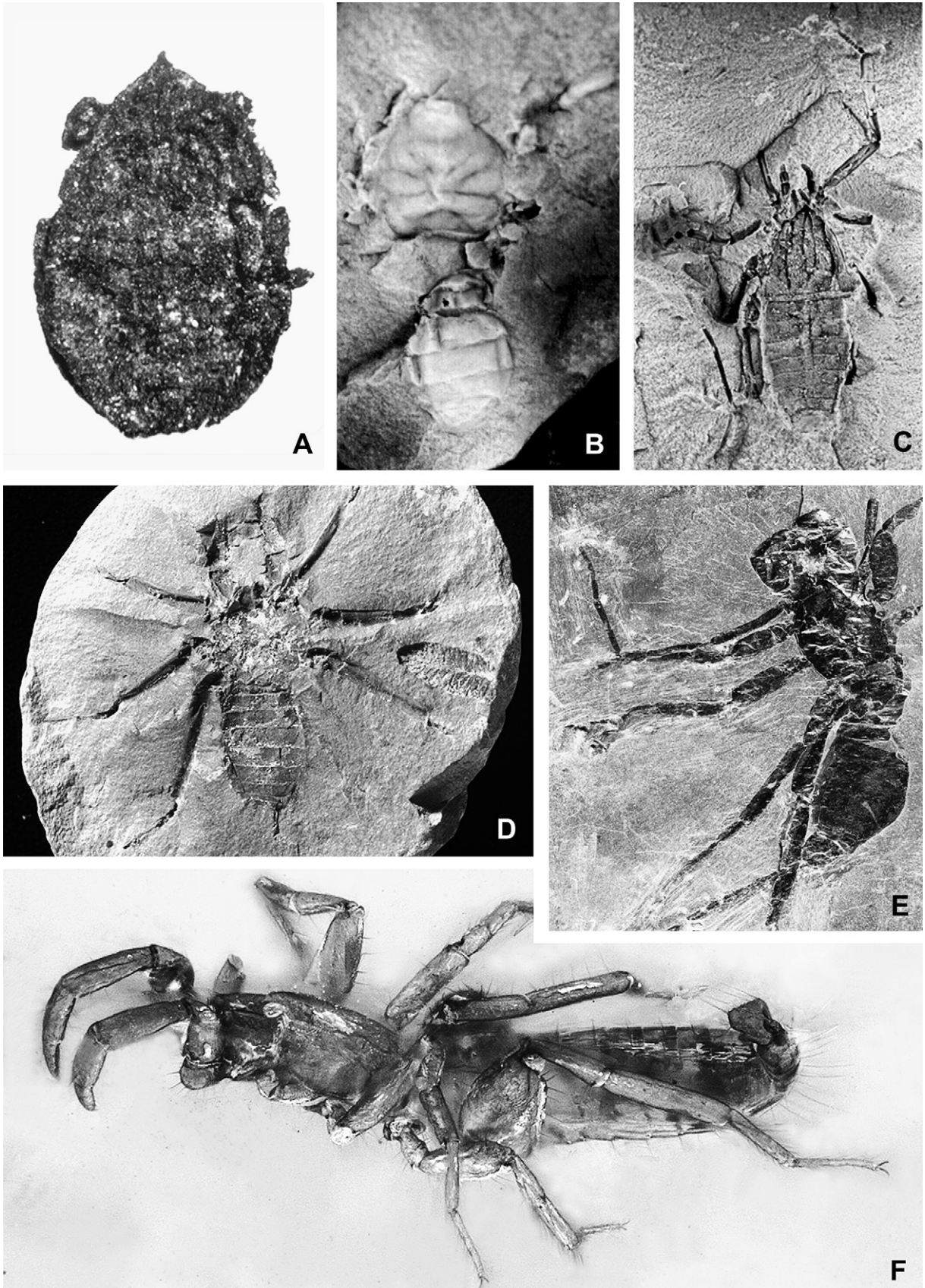
This clade name was introduced by [Shultz \(2007\)](#) as the fourth major arachnid division to formalise a convincing previous result ([Shear et al., 1987](#); [Selden et al., 1991](#)) that the extinct order Trigonotarbitida is basal to the Tetrapulmonata (see 4.22). Pantetrapulmonates share characters such as two pairs of book lungs in the ground pattern and clasp-knife chelicerae in which a fang articulates against the basal article. The inclusion of trigonotarbitids (see 4.21) dates Pantetrapulmonata to at least the late Silurian.

4.21. Order Trigonotarbitida (Silurian–Permian)

Trigonotarbitids are an extinct order of arachnids which at one stage were artificially split into two supposedly unrelated groups: Trigonotarbitida and Anthracomartida. Their most noticeable feature is a division of the opisthosomal tergites into median and lateral plates; a character they share with ricinuleids (see 4.14). Exceptionally preserved Devonian fossils from the Rhynie Chert ([Hirst, 1923](#)) and Gilboa ([Shear et al., 1987](#)) mean that their external morphology is quite well known and even the microstructure of their book lungs can be resolved ([Claridge and Lyon, 1961](#); [Kamenz et al., 2008](#)). Micro-CT has added further morphological details from Carboniferous species ([Garwood et al., 2009](#)). A claim – in a conference abstract – by [Easterday \(2003\)](#) that trigonotarbitids might have used silk based on the putative presence of tubercles resembling the silk-combing calamistrum of modern cribellate spiders is unsubstantiated. Better preserved trigonotarbitids, like those from the Rhynie Chert, show no evidence for either spinnerets or silk gland spigots. The oldest trigonotarbitid (Fig. 4A) comes from the late Silurian (Přídolí, ca. 417–419 Ma) of the Welsh Borderlands ([Dunlop, 1996](#)) and is closely followed by several Early Devonian species from Germany and the UK. Trigonotarbitids have been recorded most frequently from the Late Carboniferous Coal Measures of Europe and North America ([Pocock, 1911](#); [Petrunkevitch, 1913, 1949](#)). By this time they had they radiated into a number of families, with an apparent trend in some lineages to evolve a more robust, tuberculate and spiny body. Fossils of trigonotarbitids are more abundant than fossils of spiders at this time, but whether this reflects real patterns of diversity in life is not clear. The youngest trigonotarbitids come from early Permian ‘Rotliegend’ localities in Germany ([Rössler et al., 2003](#)).

4.22. Tetrapulmonata (Devonian–Recent)

Tetrapulmonata is probably the least contentious part of the arachnid tree, and was recognised as early as the late 19th century ([Pocock, 1893](#); [Börner, 1904](#)). Various historical names in the literature such as Caulogastra, Arachnidea or Megoperculata *sensu* [Weygoldt and Paulus \(1979\)](#) are its equivalent. All recent, comprehensive studies group spiders, whip spiders (Amblypygi), whip scorpions and schizomids together ([Weygoldt and Paulus, 1979](#); [Shear et al., 1987](#); [Selden et al., 1991](#); [Wheeler and Hayashi, 1998](#); [Giribet et al., 2002](#); [Shultz, 1990, 2007](#)). Tetrapulmonata refers to the presence of two pairs of book lungs; the second pair is modified to trachea in many spiders and lost in schizomids. However, the latest scheme ([Shultz, 2007](#)) placing trigonotarbitids – which also have four lungs – outside this clade means that Tetrapulmonata s.s. has to be rediagnosed. This requires further clarification. The



synapomorphies listed by, e.g. Shear et al. (1987: pp. 11–14) for tetrapulmonates excluding trigonotarbids are either non-fossilizable (sperm morphology, secretions protecting eggs), have since been recognised in Rhynie Chert trigonotarbids too (a labium, perhaps the rocking patella–tibia articulation; JAD pers. obs.) or refer to lateral eyes without multiple lenses which overlooks the fact that whip scorpions retain very tiny supplementary lenses here too (Weygoldt and Paulus, 1979: p. 106). Tetrapulmonata can tentatively be traced back to the mid-Devonian assuming it includes Uraraneida (see 4.23), as well as on the presence of possible whip spiders (see 4.27).

4.23. Order Uraraneida (Devonian–Permian)

This recently established order (Selden et al., 2008a) was created for two fossils, previously interpreted as spiders, from the mid-Devonian of Gilboa (Selden et al., 1991) and the Permian of the Ural Mountains in Russia (Eskov and Selden, 2005). Uraraneids were spider-like animals with a segmented opisthosoma, but which also retained a flagelliform telson. Significantly, they could produce silk from spigots, but these were arranged along the ventral sternites of the opisthosoma and not coalesced into spinnerets as in true spiders (see 4.24). Further details about Uraraneida, and its significance for understanding spider and/or tetrapulmonate origins, can be found in Selden et al. (2008a).

4.24. Order Araneae (Carboniferous–Recent)

With over a thousand fossil species described, spiders are the best represented arachnid group by a considerable margin. The previous oldest spider (cf. Selden et al., 1991) has now been reassigned to Uraraneida (see 4.23) and thus opisthosomal silk glands are no longer a unique spider character. Araneae must now be redefined on the presence of discrete spinnerets, as well as further autapomorphies like a male pedipalp modified for sperm transfer and, in both sexes, a naked (i.e. hairless) cheliceral fang. What remains to be clarified is whether spinnerets are retained opisthosomal appendages, or whether these limbs were lost in the spider stem-lineage (they are absent in uraraneids) and somehow genetically reactivated in spiders (Selden et al., 2008a). An older review of the possible origins of spinnerets and of silk use can be found in Shultz (1987). A frequently perpetuated myth is the assumption that cheliceral venom glands are also autapomorphic for spiders. These glands – and the associated duct opening through the fang – are absent in Uloboridae (a derived family), but also in the basal suborder Mesothelae (cf. Haupt, 2003: Fig. 6). This implies that venom use first appeared in the more derived suborder Opisthothelae, which on current evidence must have split from the mesotheles by the late Palaeozoic. The spider fossil record has been considered by Penney et al. (2003), Selden and Penney (2007), and particularly in the recent substantial review by Selden and Penney (2010). Strictly fossil families were assessed by Penney and Selden (2006). A complete list of all fossil spiders (Dunlop et al., 2010), including synonyms and incorrectly assigned taxa, can be found online as a regularly updated appendix to Norman Platnick's World Spider Catalogue.

The recognition of Uraraneida renders the oldest record of Araneae a series of fossils from the Late Carboniferous British Middle Coal Measures of England (Pocock, 1911) (Fig. 4B). These are part of

a handful of putative fossil spiders with segmented opisthosomas – probably mesotheles or something very much like them – recorded throughout the Carboniferous Coal Measures of Europe and North America (Petrunkevitch, 1913, 1955). The supposed giant fossil spider *Megarachne* from the Coal Measures of Argentina is a misidentified eurypterid (Selden et al., 2005). The first unequivocal mesothele comes from the late Carboniferous of France (Selden, 1996). As the name implies, in Mesothelae the spinnerets emerge more or less centrally on the ventral surface of the opisthosoma. The French fossils provide a minimum date for the split between the mesotheles and Opisthothelae. This more derived suborder encompasses the vast majority of the living (and fossil) spiders and is defined by spinnerets which have migrated backwards into a more terminal position on the opisthosoma. A modern consensus phylogeny for spiders can be found in, e.g. Coddington (2005: Fig. 2.2) and major clades discussed below are based on this work.

Opisthothelae is further subdivided into Mygalomorphae, i.e. tarantulas and trap-door spiders and their relatives, and Araneomorphae which encompasses all the rest. The Triassic period yields examples of both infraorders. The oldest mygalomorph (Selden and Gall, 1992) dates to ca. 240 Ma and this French fossil was assigned to Hexathelidae; a family which includes today the notorious Sydney funnel web. The oldest araneomorphs go back ca. 225 Ma (Selden et al., 1999) and come from South Africa and Virginia, USA. They cannot be referred to an existing family with confidence, but may belong to the Araneoidea superfamily (i.e. orb-weavers, cobweb spiders and their relatives). Jurassic spiders are extremely rare, but araneomorph records from Central Asia include putative members of both the araneoid (Eskov, 1984) and palpimanoid (Eskov, 1987) superfamilies. The composition of Palpimanoidea is controversial, but further examples of this group have been described from the mid Jurassic (ca. 165 Ma) of Daohugou in China (Selden et al., 2008b) – a locality which is likely to play a major role in our future understanding of spider evolution.

The Cretaceous record of spiders is rather better, and includes further examples of extant mygalomorph families from Central Asia (Eskov and Zonstein, 1990). Based on somewhat limited data, these authors proposed a Mesozoic 'age of mygalomorphs' during which Mygalomorphae were supposed to be predominant. Subsequent finds of numerous Cretaceous araneomorph spiders do not support this hypothesis (Selden and Penney, 2010). A more pertinent suggestion is the idea that the rise of the flowering plants led to an increase in flying (i.e. pollinating) insects and a consequent radiation of (web-building?) spider families able to catch them; see Penney (2004) for a comparison of the insect and spider fossil record. For example specimens from Sierra de Monstech in Spain reveal the characteristic tarsal claws of orb-weaving spiders (Selden, 1989) and even the webs themselves can also be preserved; as in early Cretaceous (110 Ma) Spanish amber (Peñalver et al., 2006).

In recent years discoveries from various Cretaceous ambers have transformed our understanding of the spider fossil record, including even older evidence for orb-weavers (Penney and Ortuño, 2006) in Álava amber (ca. 115–120 Ma); also from Spain. Cretaceous ambers have yielded the oldest putative records of numerous modern spider families (Penney et al., 2003: Figs. 1 and 2; Dunlop et al., 2010); including members of the more primitive Haplogynae lineage, such as Oonopidae and Segestriidae, as well as various orb-

Fig. 4. Oldest examples of fossil Pantetrapulmonata. (A) *Palaeotarbus jerami* (Dunlop, 1996) (Trigonotarbida) from the late Silurian of Ludford Lane, UK; image courtesy of Andy Jeram, Belfast. (B) *Eoecteniza silvicola* Pocock, 1911 (Araneae) from the late Carboniferous Coal Measures of the West Midlands, UK; reproduced from Dunlop (1999). (C) *Plesiosiro madeleyi* Pocock, 1911 (Haptopoda) from the late Carboniferous Coal Measures of the West Midlands, UK; image courtesy of Mark Bell, Bristol. (D) *Graeophonus anglicus* Pocock, 1911 (Amblypygi) from the late Carboniferous Coal Measures of Hagen-Vorhalle, Germany; image courtesy of Carsten Brauckmann, Clausthal and Lutz Koch, Ennepetal. (E) *Parageralinura naufraga* (Brauckmann and Koch, 1983) (Thelyphonida) from the Late Carboniferous Coal Measures of Hagen-Vorhalle, Germany; image courtesy of Carsten Brauckmann, Clausthal and Lutz Koch, Ennepetal. (F) Unpublished schizomid (Schizomida) from Neogene (Miocene) Dominican amber; a slightly older but poorly illustrated example is also known from the Oligocene of China. Specimen size in A 1.4 mm, B 11 mm, C 13 mm, D 14 mm, E 16 mm, F 2.5 mm.

weavers (Araneidae, Tetragnathidae, Uloboridae), money spiders (Linyphiidae) and members of the so-called RTA (retrotibial apophysis) clade which, as the name suggests, have a distinctive projection from the tibia of the male pedipalp. The last includes both sheet- or tangle web-builders, but also many spiders – particularly in the ‘two-clawed’ *Dionycha* clade – which have abandoned webs in favour of a free-running or a sit-and-wait hunting strategy. Cretaceous RTA-clade spiders include Dictynidae and Pisauridae. This overall distribution of Cretaceous taxa led Penney et al. (2003) to suggest that, as a group, spiders were little affected by the K–T mass extinction event. Yet some extinct families are only known from Cretaceous amber and numerous taxa of this age, including further new families, were raised by Wunderlich (2008); but see Selden and Penney (2010) for a critique of the practice of raising apparent stem-taxa automatically to family status.

In general, Wunderlich preferred to emphasise differences between Cretaceous and Cenozoic spider faunas. For him the Cretaceous shows an abundance of haplogyne spiders, with the major radiations of araneoids and RTA-clade spiders occurring in the Cenozoic; although it should be added that Wunderlich’s analysis lacks the statistical rigour of Penney et al. (2003). A further problem is the recent appearance of (largely non-amber) Mesozoic fossils assigned to extant taxa (Chang, 2004; Kim and Nam, 2008; Cheng et al., 2009), whose description as the oldest example of their respective family or genus is not always reflected in the quality of the illustrations. Erroneous identifications can obviously skew the overall pattern of taxon distribution over time; putative Jurassic Theridiidae (cobweb spiders) and Gnaphosidae (flat-bellied spiders) are a case in point here, since all other records are restricted to the Cenozoic.

The majority of fossil spiders come from Cenozoic ambers, particularly from the Baltic region, the Dominican Republic and Chiapas State in Mexico, as well as a number of non-amber Cenozoic localities. Most belong unequivocally in modern families; although the fundamentally different modes of preservation mean that it is difficult to compare non-amber spiders directly with both amber fossils and living species. The all-important palpal organ of mature males is rarely recovered from flattened specimens. Even among amber taxa, older names based on somatic characters, or for female or juvenile specimens, will probably have to be abandoned. Key studies of amber spiders include Koch and Berendt (1854), Petrunkevitch (1942, 1946, 1950, 1958, 1963, 1971), Wunderlich (1986, 1988, 2004, 2008), and references therein and Penney (2008). Quaternary copals have also yielded a number of generally rather modern-looking species. Jörg Wunderlich has been particularly active in creating (extinct) genera and species; although initial revisions suggest that amber palaeodiversity has been somewhat exaggerated (cf. Harms and Dunlop, 2009). Tomographic methods of study are only just beginning (Penney et al., 2007), but should be encouraged as they allow fossils to be integrated even further into character systems available for living spiders.

Most extant spider families have a Cenozoic fossil record (Dunlop et al., 2010), although there is an obvious bias against purely southern-hemisphere taxa, since there are comparatively few productive fossil localities in the southern-hemisphere compared to the Holarctic and Neotropical regions. Interestingly, there are numerous examples of Cenozoic fossils from the northern-hemisphere (e.g. Micropholcommatidae: Penney et al., 2007) belonging to groups now restricted to the southern-hemisphere. This implies a more cosmopolitan distribution of these families in the past. It is also interesting to note that, on current data, some of the most species-rich and abundant living families – such as wolf spiders (Lycosidae), sac spiders (Clubionidae and Corrinidae), huntsman spiders (Sparassidae), crab spiders (Thomisidae) and jumping spiders (Salticidae) – are restricted to the Cenozoic. These groups

often first appear in Baltic amber (ca. 50 Ma), although wolf spiders may be an even younger radiation. Furthermore, many of these ‘late-comers’ are also those families that have largely abandoned web-building as the means of catching prey and this may give some ecological support to Wunderlich’s (2008) hypothesis of derived clades of spiders undergoing largely Cenozoic radiations.

4.25. *Schizotarsata* (?Devonian –recent)

Shultz (2007) proposed a tentative *Schizotarsata* clade to encompass the extinct order Haptopoda (see 4.25) plus the Pedipalpi (see 4.26); a relationship previously suggested by Dunlop (1999). As its name implies, *Schizotarsata* can be principally defined by the subdivision of the leg tarsi into a series of short articles. However, the equivocal nature of many characters in Haptopoda renders this relationship uncertain. Possible whip spider fragments from the mid-Devonian provide a questionable maximum age for this assemblage, but it can only be dated with confidence to the late Carboniferous.

4.26. Order Haptopoda (Carboniferous)

The monotypic, extinct order Haptopoda (Fig. 4C) was established by Pocock (1911) and was restudied by Petrunkevitch (1949) and Dunlop (1999), who confirmed its status as a distinct type of arachnid. These animals have an oval body with a distinctive pattern of ridges on the carapace. The first legs are quite long, have an inflated tibia, and look as though they may have been used in a tactile way. A possible relationship with harvestmen (Opiliones) has been mooted in the literature, although the latest analysis resolved Haptopoda closest to Pedipalpi (see 4.24). Fossils of Haptopoda are restricted to the late Carboniferous locality of Coseley in England.

4.27. Pedipalpi (?Devonian–Recent)

Historically, Pedipalpi was treated as an order in its own right. It is currently used as the clade name for (Amblypygi + Uropygi). These orders are principally united by the elongate and tactile first pair of legs and raptorial, subchelate pedipalps which lend the clade its name. Most of the comprehensive cladistic analyses have recovered this group (Giribet et al., 2002; Shultz, 1990, 2007). Possible whip spider fragments from the mid-Devonian of Gilboa provide a tentative maximum age for this assemblage of taxa. Pedipalpi can be dated with confidence to at least the late Carboniferous through the inclusion of whip scorpions.

Other studies have highlighted synapomorphies between whip spiders and spiders such as the narrow pedicel between the prosoma and opisthosoma, a prosomal sucking-stomach and details of the genital system and sperm structure (Weygoldt and Paulus, 1979; Wheeler and Hayashi, 1998; Alberti and Michalik, 2004; Fig. 51). These authors grouped (Araneae + Amblypygi) together under the name Labellata. If this hypothesis was to prove correct – and Shultz (1999) presented a suite of largely skeletomuscular characters which contradict it – Labellata would potentially extend back to the mid-Devonian based on the presence of uraraneids (as spider progenitors), and perhaps also whip spiders.

4.28. Order Amblypygi (?Devonian–Recent)

Limb and cuticle fragments from the mid-Devonian (Givetian, ca. 385–392 Ma) of Gilboa include a patella bearing a trichobothrium, a character found today only in legs 2–4 of Amblypygi. The oldest unequivocal whip spider comes from Coseley (Pocock, 1911), part of the late Carboniferous British Middle Coal Measures

(Fig. 4D), and they also occur at the slightly younger Mazon Creek locality in the USA (Petrunkevitch, 1913). These Carboniferous fossils resemble the most basal extant family Paracharontidae and share with them the (?plesiomorphic) character of fairly short pedipalps which articulate up and down rather than from side to side as in the majority of living species. There is a considerable hiatus until whip scorpions appear again in the Early Cretaceous Crato Formation of Brazil (Dunlop and Martill, 2002). They have also been found in Dominican Republic amber (Schawaller, 1979) and the probably contemporary Chiapas (Mexican) amber. All these Mesozoic–Cenozoic fossil whip spiders have been assigned to the extant family Phrynidae and two to the living genus *Phrynus*.

4.29. *Uropygi* (Carboniferous–Recent)

Uropygi is used in this sense for (Thelyphonida + Schizomida), although other authors prefer to use *Uropygi* as the ordinal name for whip scorpions only (e.g. Harvey, 2003). An alternative clade name for these two orders, Petrunkevitch's (1949) *Camarostomata*, has not been widely adopted. *Uropygi* is a strongly supported clade. Schizomids look very much like miniature whip scorpions and share with them details such as the fusion of the pedipalpal coxae to form the so-called camarostome. The presence of Coal Measures whip scorpions (see 4.29) dates *Uropygi* back to at least the late Carboniferous.

4.30. Order *Thelyphonida* (Carboniferous–Recent)

Whip scorpions are an easily recognisable group and their apomorphies include pygidial defense glands which can spray a vinegar-like substance and result in another of their common names: vinegaroons. The oldest examples come from the late Carboniferous Coal Measures of Europe and North America (Pocock, 1911; Petrunkevitch, 1913). The fossil species were catalogued by Harvey (2003) and this assemblage was revised by Tetlie and Dunlop (2008). These authors recognised the Coal Measures fossils as a series of plesion genera outside the crown-group family Thelyphonidae. This crown-group can now be defined as having a more explicitly subchelate pedipalp, with spine-like apophyses from the palpal patella and tibia not seen in the earlier, Palaeozoic species. One Carboniferous genus is potentially a stem-group schizomid, sharing with this order the lack of median eyes and pedipalps which primarily moved up and down rather than from side to side as in modern Thelyphonida. The oldest whip scorpion is from the late Carboniferous of Hagen-Vorhalle in Germany (Brauckmann and Koch, 1983) (Fig. 4E). The first fossils assignable to the single living family, Thelyphonidae, come from the Crato Formation of Brazil (Dunlop and Martill, 2002). They are the only Mesozoic record of this group. A putative Neogene whip scorpion from California is a misidentification.

4.31. Order *Schizomida* (Paleogene–Recent)

Schizomid autapomorphies include a modified male flagellum at the end of the opisthosoma and loss of the second pair of book lungs. Their fossil record is poor. The oldest schizomid comes from the Oligocene of Shanwang in China (Lin et al., 1988). Three more described species have been found in the much younger Onyx marble of Arizona (e.g. Petrunkevitch, 1945). Intervening material from Miocene Dominican Republic amber (Fig. 4F) has been figured, and will shortly be formally described (Krüger and Dunlop in press). Fossil taxa were included in the catalogues of both Reddell and Cokendolpher (1995) and Harvey (2003). One Onyx Marble species – as well as the Shanwang form – are currently placed in an extinct family, Calcitronidae. However, Reddell and Cokendolpher (1995)

cautioned that Petrunkevitch's fossil family is not defined on characters allowing meaningful comparison with the two living groups: Hubbardiidae and Protoschizomidae. The other two Onyx Marble schizomid species are currently assigned to extinct genera within the Hubbardiidae.

Acknowledgements

I thank Paul Selden and Greg Edgecombe for helpful comments, and those colleagues who provided images as detailed under the figure legends.

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