Palaeozoic arachnids and their significance for arachnid phylogeny

Jason A. DUNLOP

Department of Earth Sciences, University of Manchester, Manchester, M13 9PL, UK.

ABSTRACT

Chelicerata originated from among the Arachnomorpha, though their relationships to other arachnomorph taxa remain uncertain. Chelicerata can be defined on the presence of a median eye tubercle and a postabdomen and comprise (*Lemoneites* (Xiphosura (Chasmataspida (Eurypterida + Arachnida)))). Arachnid origins are uncertain. Arachnida are currently recognized as monophyletic, though Scorpiones and Eurypterida may represent sister taxa and a number of arachnid characters, e.g. book-lungs, are convergent terrestrial adaptations. Some of the Gilboa trigonotarbids may, in fact, be early representatives of extant orders. Trigonotarbida show evidence of a vestigial third cheliceral segment, suggesting two-segmented chelicerae evolved through loss of the most basal segment, and a new cheliceral orientation, palaeognathy, of paraxial, downwards-hanging chelicerae. Of the extinct orders, Trigonotarbida may be sister group of Ricinulei, Phalangiotarbida resemble Opilioacari and Haptopoda resemble Uropygi. A possible sister group of Schizomida has been identified among fossil Uropygi.

INTRODUCTION

Palaeozoic arachnids have been known since Corda (1835) described a fossil scorpion from Bohemia, but their significance for understanding arachnid evolution has not always been fully appreciated. The Palaeozoic era is perhaps the most interesting time phylogenetically, since it saw the origin of the arachnids, their transition from sea to land and their radiation into the recognisable orders; three of which became extinct by the end of the Palaeozoic. There have been a number of significant monographs and reviews of Palaeozoic arachnids (Frič 1904; Pocock 1911; Petrunkevitch 1913, 1945, 1949, 1953, 1955; Waterlot 1949, 1953; Savory 1964). Based on these, some

authors incorporated extinct arachnid groups into their phylogenetic schemes (Petrunkevitch 1949; Zachvatkin 1952; Dubinin 1962; Savory 1971; Grasshoff 1978; Beall & Labanderia 1990). However, the most significant recent accounts of arachnid phylogeny (Weygoldt & Paulus 1979; Lindquist 1984; van der Hammen 1989; Shultz 1990) did not include extinct groups, primarily on account of their morphological characters being poorly known. Recent research has begun to re-examine fossil arachnids (Selden 1993), in particular the exceptionally preserved faunas from early terrestrial Lagerstätte (Shear 1991). Serious errors in previous studies of fossil arachnids are evident, particularly in Petrunkevitch's monographs (Selden 1993) and descriptions of both new and existing Palaeozoic arachnids are currently under way (e.g. Jeram 1994a, b; Dunlop 1994a-d, 1995a, b, 1996 a-d; Dunlop & Horrocks 1996 a, b; Selden 1996; Selden & Shear 1996). The arachnid fossil record was reviewed by Selden (1993a, b), arachnid terrestrialisation was reviewed by Selden and Jeram (1989) and Palaeozoic arachnid faunas were reviewed by Shear and Kukalová-Peck (1990), Shear (1991) and Selden and Dunlop (in press). This present paper identifies key areas in arachnid phylogeny where the fossil evidence is crucial to our understanding of the evolution of the group.

THE CHELICERATA

Current phylogenetic models recognise Arthropoda as monophyletic (e.g. Wheeler *et al.* 1993), in which broad clades of arthropods have been recognised: e.g. Crustacea, Arachnomorpha (chelicerates, trilobites and a number of problematic extinct forms), Marellomorpha (problematic extinct forms) and Atelocerata (insects and myriapods) (Wills *et al.* 1995). Chelicerates clearly belong in the Arachnomorpha Heider, 1913 (alternatively called Arachnata), though their position relative to the other arachnomorphs is still open to question. Extant chelicerates were traditionally diagnosed on the presence of chelicerae, though these structures are rarely preserved in fossils. Dunlop and Selden (in press) recognized the presence of a median eye tubercle and differentiation of the opisthosoma into a preabdomen and postabdomen (i.e. the arachnid pygidium; a similar structure being present in the primitive synziphosurans) as better diagnostic characters for Chelicerata; characters which can be recognized in fossil taxa. Based on this, Dunlop and Selden (in press) restricted Chelicerata to (*Lemoneites* (Xiphosura (Chasmataspida (Eurypterida + Arachnida)))) (Fig. 1). In our model the enigmatic Ordovician fossil *Lemoneites* Flower, 1968 is sister group to all other chelicerates and the closest thing we have to an ancestral chelicerate. In addition to the living chelicerate taxa, i.e. horseshoe crabs and arachnids, we recognise eurypterids (sea scorpions) and the chasmataspids as two distinct taxa within Chelicerata; chasmataspids were originally considered to be

xiphosurans (Størmer 1972). Our model excludes aglaspidids from Chelicerata, a group resembling xiphosurans, included in Chelicerata by Weygoldt and Paulus (1979), but removed from it by Briggs *et al.* (1979). It also excludes the supposed Cambrian chelicerate *Sanctacaris* Briggs *et* Collins, 1988, which has not emerged as sister group to Chelicerata in subsequent phylogenetic analyses (e.g. Wills *et al.* 1995). The position of the pycnogonids remains uncertain, but they have been placed as sister group of the Chelicerata by Wheeler *et al.* (1993).

ARACHNID ORIGINS

It has been suggested that arachnids evolved from aglaspidids (Bristowe 1971; Starobogatov 1990), an animal similar to the Devonian chasmataspid *Diploaspis* (Bergström 1979) or a primitive xiphosuran (Beall & Labanderia 1990). Arachnids cannot be derived directly from xiphosurans, chasmataspids or eurypterids, each of which has its own autapomorphies (i.e. ophthalmic ridges (Xiphosura), a 9-segmented postabdomen (Chasmataspida) and a metastoma and genital appendage (Eurypterida). Arachnida and Eurypterida are currently regarded as sister groups (Weygoldt & Paulus 1979; Shultz 1990) (but see below). Eurypterids are known from the Lower Ordovician, but arachnids are not recorded until the Silurian (Selden 1993), leaving a gap of some 60 million years between the supposed origin of the arachnids and their appearance in the fossil record. We have no idea what the earliest arachnids were like, though the primitive stylonurid eurypterids with a carapace bearing multifaceted lateral eyes, a twelve-segmented opisthosoma with a telson, and legs with a double femur ending in trifurcate claws, might give the closest picture of a.hypothetical common ancestor (Fig. 2) (see also Shultz 1990, fig. 3). Savory's (1971) 'archaearachnid', heavily influenced by considering palpigrades to be the most primitive arachnids, with its divided carapace and sternum, and protruding leg coxae is a poor model, since many of its features are not seen in arachnid outgroups such as eurypterids and xiphosurans.

ARACHNID MONOPHYLY

Chelicerata traditionally comprised Merostomata (Xiphosura and Eurypterida), which were aquatic, and Arachnida, which were terrestrial. Kraus (1976) and Selden and Siveter (1987) argued that Merostomata was merely an aquatic grade of chelicerate, rather than a natural group, and cladistic analyses have supported this interpretation (Weygoldt & Paulus 1979; Shultz 1990) (Fig. 1). Bergström (1979) and Selden and Jeram (1989) further suggested that Arachnida might similarly be a terrestrial grade of chelicerate. Van der Hammen (1989) supported arachnid polyphyly, arguing that opilionids, scorpions and xiphosurans formed a taxon, Myliosomata, separate from the remaining arachnids, the taxon Rostrosomata; the

two groups distinguished by their mouthparts and method of feeding. Both Weygoldt and Paulus (1979) and Shultz (1990) supported arachnid monophyly and presented synapomorphies of Arachnida, e.g. slit sensilla, reduced carapace plueral margin, anteroventrally directed mouth, no appendages on the first opisthosomal segment and spermatozoa with coiled axonemes.

From a palaeontological perspective the most significant question for arachnid phylogeny concerns the position of the scorpions and eurypterids. Lankester (1881) first proposed that scorpions were closer to eurypterids than the other arachnids, a view which would render Arachnida as it is currently recognized polyphyletic. Scorpion–eurypterid relationships have been supported by Versluys and Demoll (1920), Raw (1957), Sharov (1966), Bristowe (1971), Grasshoff (1978), Kjellesvig-Waering (1986) and Starobogatov (1990). However, these authors were not always explicit about whether they considered scorpions to be closer to eurypterids than to other arachnids or whether scorpions were primitive arachnids derived from a common ancestor with eurypterids. Shultz (1990) criticized supporters of scorpion–eurypterid similarities for basing their conclusions on overall similarities (possibly due to convergence or mimicry?) and symplesiomorphies rather than specific synapomorphies.

The strongest potential synapomorphy of Scorpiones + Eurypterida is the 5-segmented postabdomen; a 3-segmented postabdomen is primitively present in other arachnids and also in xiphosurans, but this in itself must be weighed against the arachnid synapomorphies proposed above. Scorpions are the oldest arachnids and the earliest forms were almost certainly aquatic (Selden & Jeram 1989; Jeram 1994a). Neontologists have relied on extant scorpion morphology and, often dated, accounts of eurypterid morphology, in phylogenetic analyses. Stockwell (1989) and Jeram (1994a) recognized three orders of scorpions, Protoscorpiones, Palaeoscorpiones and Scorpiones, the first two of which were aquatic. Current evidence supports arachnid monophyly (Shultz 1990), but this hypothesis remains to be tested against the inclusion of fossil scorpions as distinct taxa and a reappraisal of eurypterid morphological characters. Dunlop and Braddy (in press) described isolated, notch-like structures on the podomeres of a eurypterid which show similarities to arachnid slit sensilla, though are an order of magnitude wider than typical arachnid sensilla.

CONVERGENCES DUE TO TERRESTRIALISATION

The position of scorpions aside, the recognition that the oldest scorpions were aquatic and that none of the other arachnid orders can be derived from scorpions implies that arachnids terrestrialized independently at least twice (Selden & Jeram 1989). What this means is that many of the textbook characteristics of arachnids, e.g. book-lungs (derived from book-gills to

breath in air), trichobothria (modified hairs detecting air vibrations) and perhaps Malphigian tubules (producing the terrestrial excretory product guanine), are convergent terrestrial adaptations. As such these characters are not recognized as synapomorphies of Arachnida, nor should they be ((see Shultz (1990) for a discussion of Malphigian tubules)). The comparative physiology of these convergent terrestrial adaptations within arachnids may prove an interesting line of future research.

Relating to the question of arachnid monophyly above, if other arachnid synapomorphies could be argued as terrestrial adaptations then the case for arachnid polyphyly would be strengthened. For example slit sensilla could be argued as convergent adaptations aiding proprioception during terrestrial locomotion (see also above), with greater stresses on the leg cuticle on land without the buoyancy of water. Similarly, the anteroventrally directed mouth might be relate to a move away from gnathobasic feeding, which is less practical on land. The posteriorly directed mouth of gnathobasic feeders (xiphosurans, eurypterids) could be interpreted as being orientated to receive food coming anteriorly from the gnathobases, while the anteroventrally directed arachnid mouth receives food primarily masticated by the preoral chelicerae. Interestingly, among the Tetrapulmonata (Trigonotarbida, Araneae, Amblypygi, Uropygi, Schizomida) the Lower Devonian Rhynie chert trigonotarbids retain remnants of gnathobases on their coxae (Dunlop 1994a) and their mouth is significantly less anteroventrally orientated than in other tetrapulmonate groups (Dunlop 1994b, figs. 1–4).

RADIATION OF THE EARLY ARACHNIDS

The oldest arachnid fossils come from early terrestrial Lagerstätte (e.g. Hirst 1923; Størmer 1970; Shear et al. 1987; Jeram et al. 1990; Selden et al. 1991; Dunlop 1996b). The earliest faunas (Upper Silurian–Lower Devonian) contain scorpions, mites and the extinct order Trigonotarbida. By the Middle Devonian at Gilboa, New York, there are the first occurrences of spiders (Selden et al. 1991) and pseudoscorpions (Shear et al. 1989). At least two arachnid taxa (scorpions and non-scorpion arachnids) may have terrestrialised independently, but it is interesting to speculate whether the non-scorpion arachnids differentiated into recognisable orders prior to terrestrialisation, or whether there were one or more 'pioneer' taxa which terrestrialised and underwent adaptive radiation into vacant terrestrial niches. I favour the latter hypothesis, but the fossil record is currently too poor to test these ideas. Selden et al. (1991) speculated that in the Devonian there were a number of early arachnids that did not fit into arachnid orders as they are currently recognised. For example Gelasinotarbus bonamoae from Gilboa, described as a trigonotarbid by Shear et al. (1987), but lacking the diagnostic divided tergites of this extinct order, may be part of this early radiation.
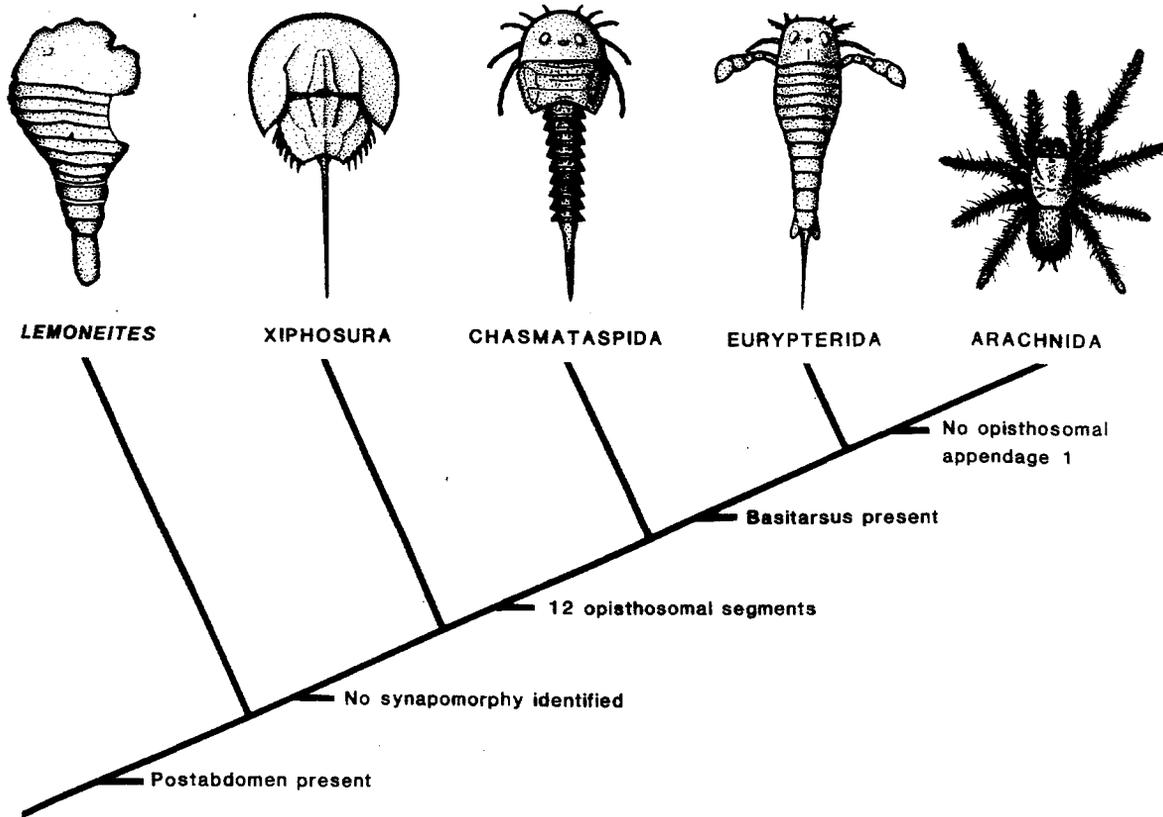
Fig. 1. Phylogeny of the Chelicerata, modified from Dunlop and Selden (in press). In this model Chelicerata comprises four major taxa, Xiphosura, Chasmataspida, Eurypterida and Arachnida with the enigmatic and poorly preserved fossil, *Lemoneites*, as the sister group to all other chelicerates.
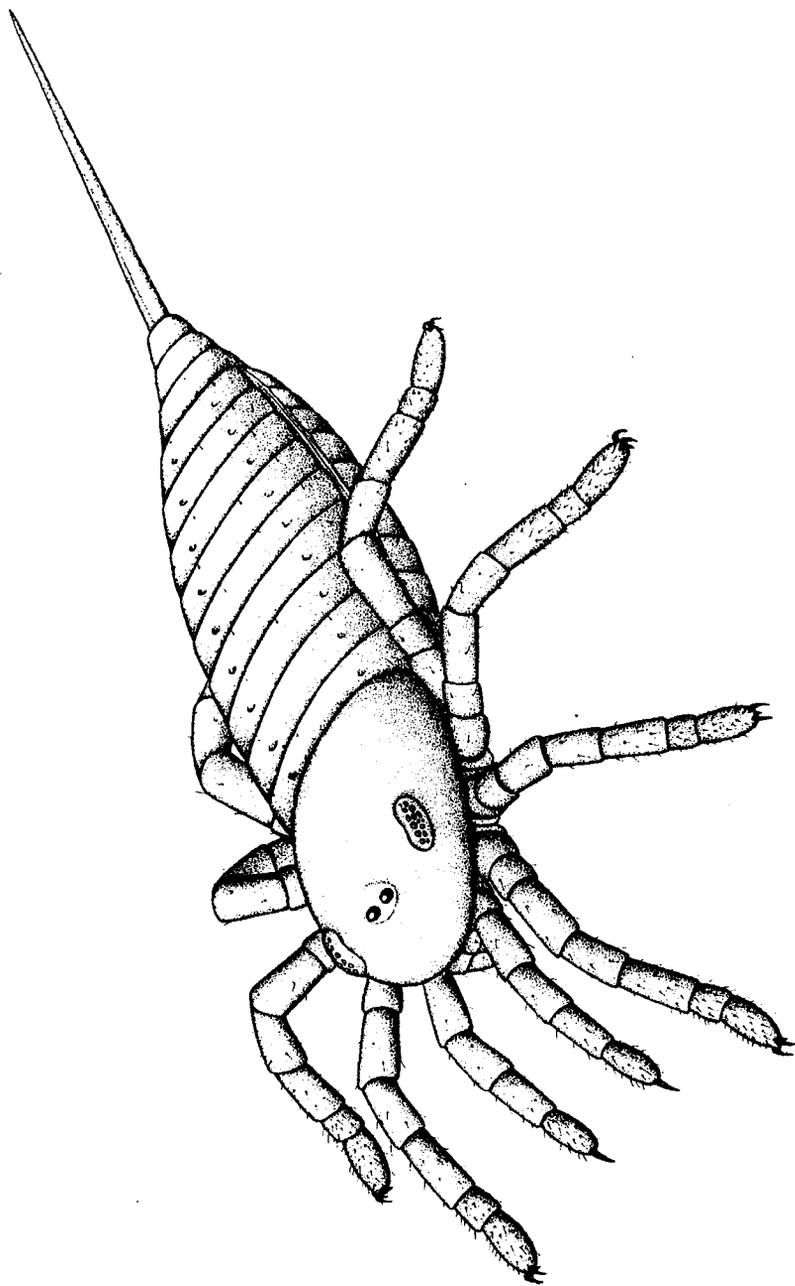
Fig. 2. Reconstruction of a hypothetical common ancestor of the (nonscorpion?) arachnids. The model shows the plesiomorphic character states of a twelve-segmented opisthosoma, an undivided telson, double femora and multifaceted lateral eyes. See text for details.
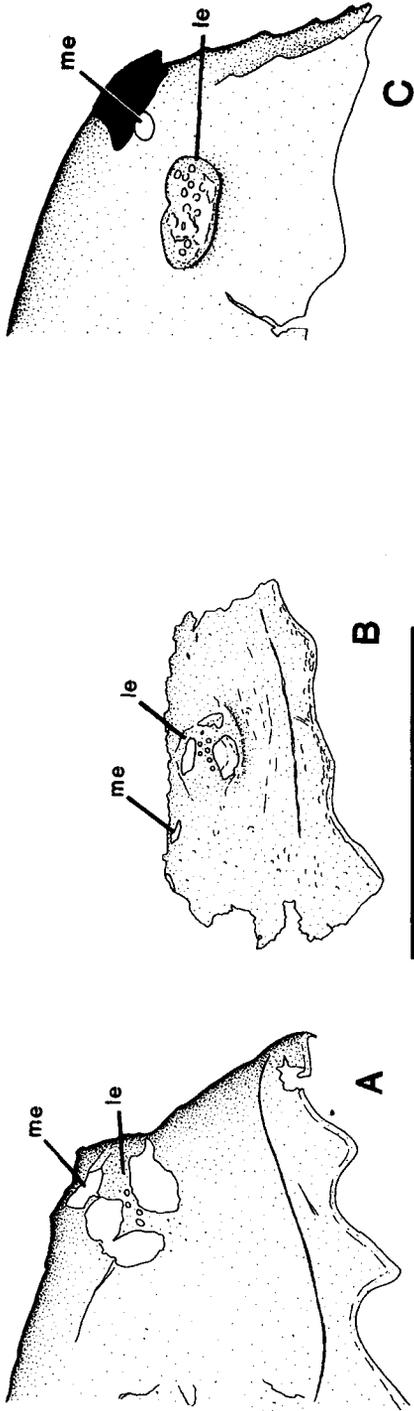
Fig. 3. *Camera lucida* drawings of eye arrangement in Devonian arachnids. A - *Gelasinotarbus reticularis* (American Museum of Natural History No. 329-31a-M3) in lateral view. B - *Gelasinotarbus heptops* (American Museum of Natural History No. 411-7-AR25) in frontal view. Both from the Middle Devonian of Gilboa, NY, described as trigonotarbids, but showing a pattern of three lateral eye lenses (a triad) more consistent with extant tetrapulmonate orders (Araneae, Amblypygi, Uropygi) than other trigonotarbids. C - *Palaeocharinus* sp. (British Museum of Natural History In 24673) in lateral view. From the Lower Devonian of the Rhynie chert, Scotland, a trigonotarbid showing the tetrapulmonate groundplan of multiple, small lateral eye lenses. me = median eye, le = lateral eye lenses, scale bar = 1 mm.
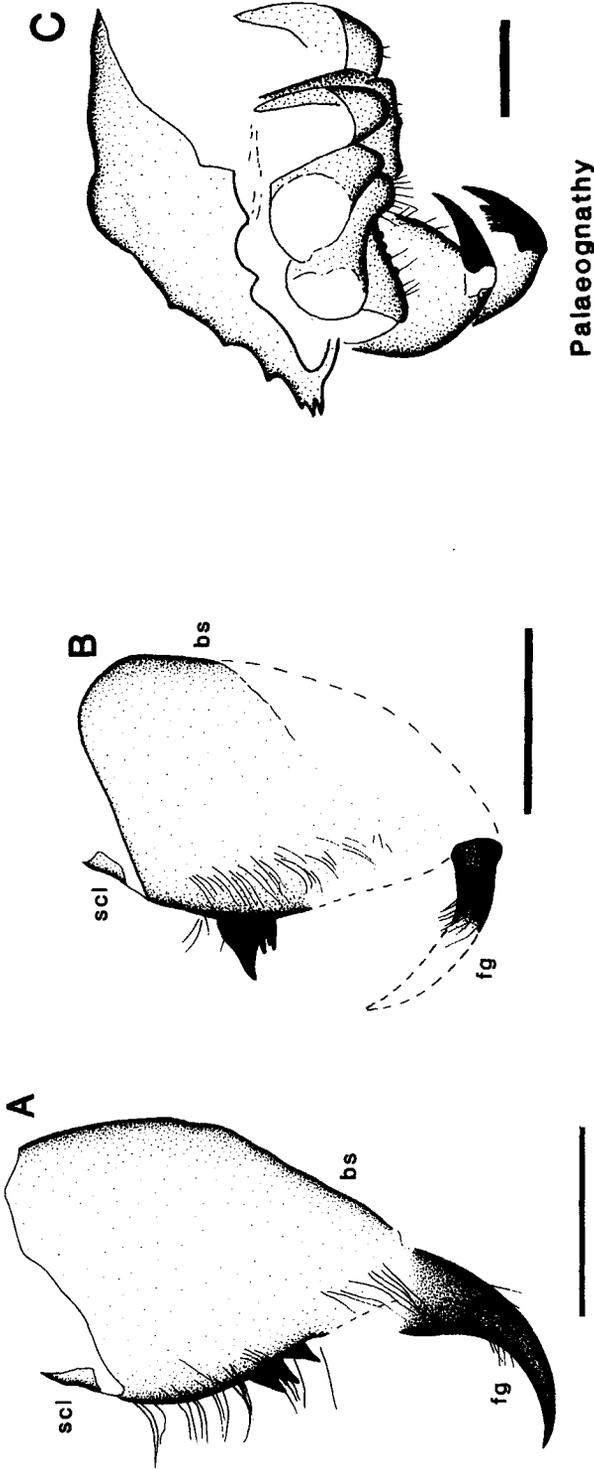
Fig. 4. *Camera lucida* drawings of the chelicerae of trigonotarbid arachnids from the Lower Devonian of the Rhynie chert, Scotland. A - British Museum of Natural History In 24701 and B - In 24675 showing the small sclerite (scl) in the basal membrane of the chelicera interpreted as a vestigial remnant of the most proximal segment in a three-segmented chelicera. bs = basal segment of chelicera, fg = fang. C - British Museum of Natural History 24673 (reverse side of Fig. 3C) showing paraxial, downwards-hanging chelicerae, a condition termed palaeognathy, possibly representing the groundplan of tetrapulmonate arachnids. Scale bars = 0.25 mm.
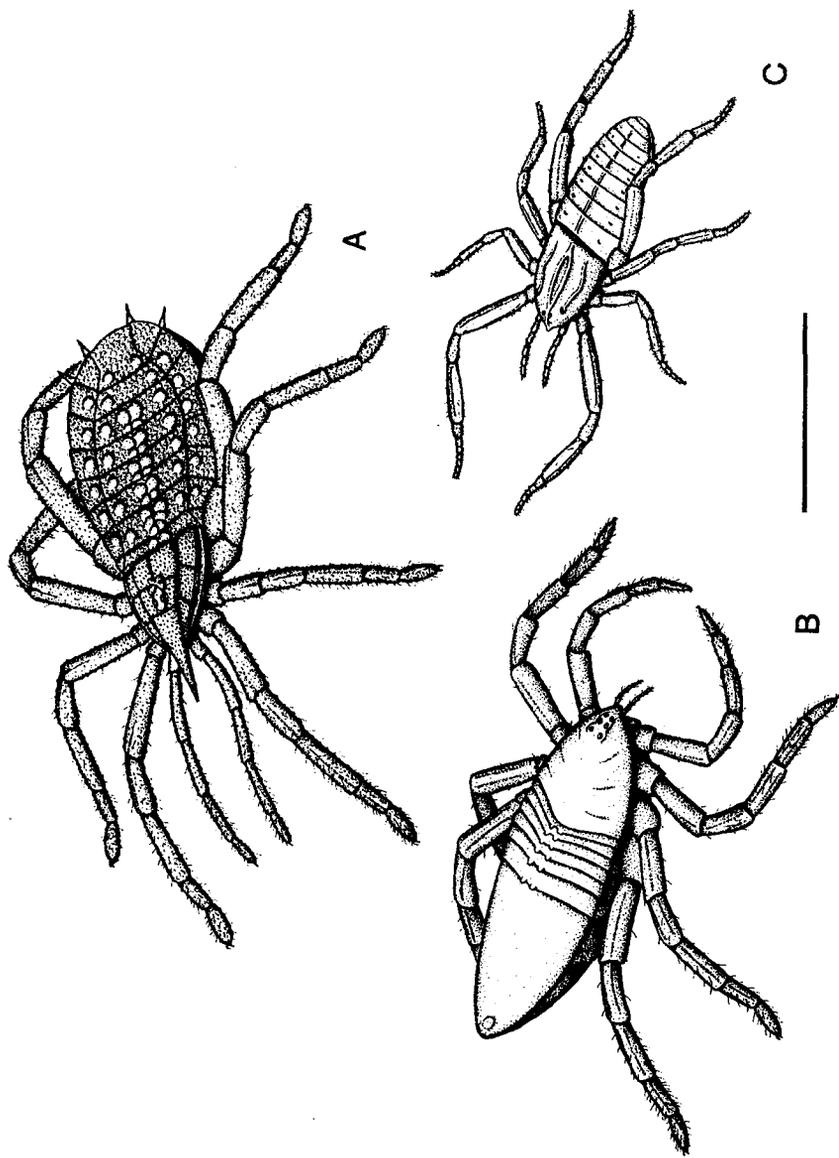
Fig. 5. Reconstructions of representatives of the three extinct arachnid orders. A - *Eophrynus prestvicii* (Trigonotarbida). B - *Goniotarbus tuberculatus* (Phalangiotarbida). C - *Plesiosiro madeleyi* (Haptopoda). All examples from the Upper Carboniferous of the UK. Scale bar = 1 cm.

EARLY OCCURRENCES OF EXTANT ORDERS?

A number of isolated carapaces from Gilboa, described as trigonotarbids by Shear *et al.* (1987), have lateral eyes with three large lenses plus a number of tiny lenses, for example *Gelasinotarbus reticulatus* (Fig. 3A), *Gelasinotarbus heptops* (Fig. 3B) and *Aculeatarbus depressus* (Shear *et al.* 1987, Figs. 141–148). Kraus and Kraus (1993) regarded the arrangement of lateral eye lenses into 'triads' as the ground plan of the tetrapulmonate arachnids with the loss of the minor lenses as a synapomorphy of Araneae, Amblypygi, Uropygi. The Lower Devonian trigonotarbid arachnids from the Rhynie chert have lateral eyes consisting of multiple small lenses (Hirst 1923; Dunlop 1994a) (Fig. 3C). By outgroup comparison with the compound lateral eyes of xiphosurans and eurypterids, this pattern of lateral eyes with numerous small lenses is probably close to the groundplan for arachnids (see also Fig. 1), as opposed to the triads of Kraus and Kraus (1993), and would be the plesiomorphic state within trigonotarbids. Since trigonotarbids are not ancestral to any other tetrapulmonate (Dunlop 1994a), if *Gelasinotarbus* and *Aculeatarbus* are trigonotarbids then their traids of three large lateral eye lenses must be convergent with those of the extant tetrapulmonates. An intriguing alternative, which does not require convergence, is that the *Gelasinotarbus* and *Aculeatarbus* fossils represent the carapaces of early forms of extant tetrapulmonates. Specifically, *Gelasinotarbus heptops*, with its lateral eye lenses on a discrete tubercle, resembles an amblypygid or uropygid while *Gelasinotarbus reticulatus* and especially *Aculeatarbus depressus*, with the lateral eye triads coalescing on a single tubercle with the median eyes, resemble spiders. Unfortunately it is difficult to refer much of this fragmentary Gilboa material to particular orders, and the current referral of much of it to Trigonotarbida is questionable. The ocular arrangement in the earliest unequivocal spider, *Attercopus*, from Gilboa is not known (Selden *et al.* 1991).

CHELICERAL ORIENTATION AND EVOLUTION

The Palaeozoic fossils from the Rhynie chert also have a significant bearing on our understanding of cheliceral evolution. Three-segmented, chelate chelicerae are regarded as the plesiomorphic state in arachnids (Shultz 1990), as seen in outgroups such as xiphosurans and eurypterids. Two-segmented, so called 'clasp-knife' chelicerae were interpreted as synapomorphic for the tetrapulmonate arachnids (Shear *et al.* 1987; Selden *et al.* 1991). The Rhynie chert trigonotarbid fossils have chelicerae with a typical tetrapulmonate clasp-knife morphology, but with a small sclerite located in a membrane proximal to the basal segment of the chelicera (Fig. 4A). This sclerite could be some sort of plagula, i.e. a derived muscle

attachment site to aid cheliceral mobility (J. Shultz pers. comm.). An analogous sclerite, the Chilum, occurs between the clypeus and chelicerae of many spiders (Joqué 1991), though this structure is in the membrane opposite the cheliseral tooth row, while trigonotarbid sclerite is adjacent to the tooth row. Alternatively I favour its interpretation as a vestigial remnant of the most proximal cheliceral segment relative to a three-segmented ancestor. What this implies is that the two-segmented tetrapulmonate condition arose from the three-segmented condition by the successive reduction and eventual loss of the most proximal cheliceral segment and not, for example, by fusion of cheliceral segments.

Additionally, the Rhynie chert trigonotarbids have chelicerae which were paraxial, as in a mygalomorph (orthognathous) spider, but hung beneath the carapace as in an araneomorph (labidognathous) spider (Fig. 4B). Traditionally, orthognathy and labidognathy were seen as alternative states, with orthognathy the more primitive of the two (Kaestner 1952). Kraus and Kraus (1993) introduced a new state, plagiognathy, intermediate between orthognathy and labidognathy, present in mesothele and hypochilid spiders, and which they proposed as the plesiomorphic state for spiders. The cheliceral orientation of the Rhynie chert trigonotarbids (paraxial, downwards-hanging), which appears also to be present in other less well preserved trigonotarbids, differs from the three orientations noted above and deserves a new term, palaeognathy. Downward-hanging chelicerae are seen in eurypterids and xiphosurans and so it is possible that palaeognathy represents the groundplan cheliceral orientation within the Arachnida (or at least the Tetrapulmonata) (see also Fig. 1). It is worth noting that cheliceral orientation is highly varied within spiders, but that all three cheliceral orientations described for spiders (Kraus & Kraus 1993) can be derived from the trigonotarbid condition by simple torsions of the basal segment. To achieve orthognathy and/or labidognathy from palaeognathy via plagiognathy requires reversals in the basal segment position. Tracing the evolution of the chelicerae in tetrapulmonate arachnids remains an interesting line of future research.

POSITION OF THE EXTINCT ORDERS

By the Carboniferous period all extant arachnid orders have been recorded except for Schizomida and Palpigradi, both of which are small and weakly sclerotized with poor preservation potential. Additionally three extinct arachnid orders have been recognized (Dunlop in press c): Trigonotarbida, Phalangiotarbida and the monotypic Haptopoda (Fig. 5). Trigonotarbida (Fig. 5A) have two pairs of book-lungs (Claridge & Lyon 1961) and so can be placed in Tetrapulmonata (Shear et al. 1987; Selden et al. 1991). However, both Trigonotarbida and Ricinulei have divided tergites and a locking ridge between the prosoma and opisthosoma, formed from opisthosomal tergite 1

and ventral depressions to accommodate the leg 4 coxae. Based on these synapomorphies Dunlop (in press b) proposed that Trigonotarbida and Ricinulei are sister groups, though still within Tetrapulmonata. This proposal raises questions over the position of Acari, the traditional sister group of Ricinulei (Weygoldt & Paulus 1979; Shultz 1990) and assumes that opilionid and ricinuleid similarities (elongate leg 2, anteriorly placed gonopore) are convergent.

The position of the other two extinct orders is less clear. Phalangiotarbids show similarities to opilioacarid mites (Dunlop 1995c), specifically carapace shape and an opisthosoma with anteriorly abbreviated tergites (Fig. 5B). However, phalangiotarbids lack the dorsal spiracles characteristic of opilioacarids (van der Hammen 1989), phalangiotarbids having three pairs of, presumably tracheal, spiracles opening ventrally on the abbreviated sternites (unpublished observations). Phalangiotarbid mouthparts are highly reduced, but poorly known. Some evolutionary models regard cyphophthalmid opilionids and opilioacarid mites as being closely related (e.g. Savory 1971) and this such models merit further consideration, with the inclusion of the phalangiotarbids as a possible key group for understanding mite evolution.

Haptopoda superficially resemble uropygids (Fig. 5C) and could be sister group of Amblypygi + Uropygi (Dunlop in prep.) on the synapomorphies of sub-divided tarsi and an elongate leg pair 1. Haptopoda also appear to have lateral eye tubercles resembling those of uropygids and amblypygids. The greatest difficulty with this hypothesis is that Haptopoda have a broad prosoma–opisthosoma junction; this junction is reduced in all other tetrapulmonates. Shear and Kukalová-Peck (1990) speculated that Haptopoda were opilionids, though they lack an elongate leg pair 2 and it is difficult to demonstrate other opilionid autapomorphies (e.g. penis, prosomal repugnatorial glands) in the Haptopoda fossils.

FOSSILS AND EXTANT ORDERS

The Palaeozoic examples of some extant arachnid orders are very similar to extant forms, e.g. Amblypygi (Dunlop 1994c) or so rare and poorly preserved that they are barely recognisable as that order, e.g. Solifugae (Selden & Shear 1996). Palaeozoic Opiliones require revision before their significance can be assessed while Palaeozoic Ricinulei were revised by Selden (1992). Among the Uropygi many of the Palaeozoic forms are almost indistinguishable from extant taxa and can be placed in the living family, Thelyphonidae (Petrunkevitch 1955). However re-examination of this material by Dunlop and Horrocks (1996a) identified two Carboniferous uropygids with an anteriorly pointed carapace lacking median eyes. This morphology is reminiscent of the carapaces of the micro-whip scorpions (Schizomida) and Dunlop and Horrocks (1996a) proposed that these fossil

taxa represent a sister group of Schizomida. The implication of this is that schizomids evolved from a group of uropygids lacking median eyes some time in the Palaeozoic.

Recently, Selden (1996) recognized the first mesothelid spider, *Eothele*, from the late Carboniferous of France. The other Palaeozoic spiders, though having segmented opisthosomas, cannot be referred to Mesothelae (Selden 1996) and some of the fossils described as spiders probably belong to other orders (e.g. the supposed Carboniferous araneomorphs (Pocock 1911) appear to be bizarre opilionids (unpublished observations)). To date *Eothele* is the only Palaeozoic spider which can be reliably referred to a modern group. The oldest mygalomorph is Triassic (Selden & Gall 1992) and an undescribed Triassic spider may be the oldest araneomorph. Though the Mesozoic arachnid fossil record is very poor (Selden 1993a, b), primarily due to a lack of productive localities, on current evidence there seems to have been a shift from the Palaeozoic arachnid faunas, to some extent dominated by the extinct orders, to a more modern arachnid fauna by the Mesozoic. This model remains to be tested against further discoveries of fossil arachnids.

Acknowledgements

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